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Short communication

Genotypic response to photoperiod treatment in Atlantic cod (*Gadus Morhua*)

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Abstract

Interactions between environment and genotype in individually tagged Atlantic cod juveniles (initial weight 9.1 g) were studied. Juvenile cod were reared for 3 months under simulated natural photoperiod (LDN) and continuous light (LD24:0) at 10 °C and 13 °C. At the end of the trial blood samples were taken from all fish and used to classify the fish according to their haemoglobin genotypes into three groups, *Hb-I*(1/1), *Hb-I*(1/2)and *Hb-I*(2/2). Individual growth trajectories and specific growth rate were studied in order to investigate whether these growth responses to extended photoperiods are genotype dependent.

Continuous light enhanced growth at both temperatures. However, a significant interaction between genotypes and photoperiods was found at both temperatures, demonstrated by the variation in genotype response towards photoperiod treatment. At both temperatures the highest growth rates were found for *Hb-I*(2/2) at LD24:0, whereas the lowest overall mean growth rates were found for the same genotype reared at LDN. Conversely, the *Hb-I*(1/1) genotype displayed the fastest specific growth rates in the LDN groups at both temperatures.

Keywords: Haemoglobin genotypes; Photoperiod; Genotypic response

1. Introduction

Information about the effect of photoperiod on growth in Atlantic cod, *Gadus morhua*(L.), is limited, although studies have shown that exposure to constant light throughout the juvenile stage has a growth promoting effect and may delay time at first sexual maturation (Hansen et al., 2001). Under altered photoperiods in commercial fish farming, fish are expected to adjust gradually to a new photoperiod regime by regulating, feeding activity, growth, and food utilization (Boehlert, 1981; Woi-

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wode and Adelman, 1991; Bromage et al., 2001). 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. Photoperiod manipulation has been shown to enhance growth in several species. In juvenile Atlantic salmon, *Salmo salar* L. (e.g. Stefansson et al., 1989; Solbakken et al., 1994), and Pacific salmonids, *Oncorhynchus* spp. (e.g. Clarke et al., 1981), a growth-promoting effect of extended photoperiods have been demonstrated. The same seems to be the case for splitnose rockfish, *Sebastes diploproa* L. (Boehlert, 1981), Atlantic cod (Folkvord and Otterå, 1993), turbot, *Scophthalmus maximus* Rafinesque (Imsland et al., 1995, 1997) and Atlantic halibut, *Hippoglossus hippoglossus* L. (Simensen et al., 2000) although the response does not appear as pronounced as that observed in salmonids.

The haemoglobin locus in Atlantic cod is characterised by at least three different genotypes called *Hb-I*(1/1), *Hb-I*(1/2) and *Hb-I*(2/2). Mork et al. (1984) and Nævdal et al. (1992) have reported growth differences related to genotypic haemoglobin polymorphism for juvenile cod at different temperatures. These genotype dependent growth rates are probably correlated with differences in functional properties of the haemoglobins as Karpov and Novikov (1980) reported specific temperature dependence of oxygen dissociation curves for cod haemoglobins. Whether the haemoglobin genotypes might respond differently to environmental variable other than temperature is at present unknown. In recent years, the genotype × photoperiod interactions have been extensively studied and documented in several plant species (e.g. Dwivedi et al., 2000; Giauffret et al., 2000; de la Vega et al., 2001; Przepiorkowski and St. Martin, 2003). These studies have indicated that the response to extended photoperiods may be genotype dependent. Such a dependency has, however, to the authors' knowledge not been demonstrated previously in fishes. In the current study, the growth properties of haemoglobin genotypes in Atlantic cod reared under simulated natural photoperiod (LDN) and continuous light (LD24:0) are investigated.

2. Materials and methods

2.1. Fish material and rearing conditions

The eggs were obtained from Sagafjord Seafarm AS, Stord, Norway and transported to the facilities of the University of Bergen where they were incubated. The broodfish were wild Norwegian Coastal Cod caught in the area around Bømlo (W-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 approx. 7 kg (max 18–min 5 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 at the Bergen High Technology Centre and reared at 10 °C and simulated natural photoperiod (LDN). This light regime was used throughout the acclimation period.

In beginning of September 2003 the fish ($N=181$) were distributed randomly into eight rearing tanks (see below). The fish used in the present study were reared together with 90–100 cod juveniles of the same size in each tank, as part of another study (not considered here). The growth study was carried out from 8 September 2004 until 12 December 2003. 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 integrated in the tank-cover provided light. Photon irradiance measured at the bottom of the tanks was ca. 5 μmol m^{-2} s^{-1}. Both, during the acclimation period and the experiment, the juveniles were fed a commercial formulated feed (Marin 10 and 20, Ewos A/S): 55% protein, 12% fat and 11% carbohydrate (gross

digestible energy 20.4 MJ kg^{-1}). Food 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 from 14 October.

2.2. Experimental design

On 25 August 2003 the fish (N=181) were tagged intraperitoneally with Trovan® Passive Transponder tags, and gradually acclimated over 1 day to 13 °C (four tanks) or kept on 10 °C (four tanks). At each temperature one group was exposed to simulated natural photoperiod for Bergen (60°25′N) generated by a computer program, including twilight periods, whereas the other group was exposed to continuous light (LD24:0). Each photoperiod/temperature regime consisted of two replicate tanks. We analyzed each temperature group separately so our set-up is a three way nested design where genotypes and photoperiods are crossed and replicates nested within genotypes and photoperiods. All fish were anaesthetised (metacain, 0.05 g l^{-1}), weighed individually (0.1 g) at 22 to 28 days interval during the experiment.

Specific growth rate (% day^{-1}, SGR) was calculated from $SGR=(e^g-1)100$ where $g=(\ln(W_2)-\ln(W_1))/(t_2-t_1)$ and W_2 and W_1 are individual weights at days t_2 and t_1, respectively. The experiment was terminated on 12 December 2003.

At the end of the experiment blood (0.2 ml) was sampled from the caudal vessels of each fish and kept on ice until analyzed. To classify the fish according to haemoglobin genotypes, the samples were analyzed by agar gel electrophoresis (AGE) using the method described by Sick (1961) with modifications (Jørstad, 1984). The AGE gels were stained in Brilliant Blue G Quick stain in perchloric acid and then destained by diffusion (14% acetic acid, 7% methanol) overnight. The haemoglobin components were identified manually using a transmitted light.

A three-way nested ANOVA (Zar, 1984) was applied to calculate the effect of different genotypes on mean weights and specific growth rates at the different photoperiod regimes, where genotypes and photoperiod are nested within the replicates. The model equation of the nested ANOVA had the form:

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

where μ is the general level; α_i is the treatment effect of genotype$_i$; β_j is the treatment effect of photoperiod$_j$; γ_{ij} is the effect of interactions between genotypes and photoperiod α_i and 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–

Table 1
Initial and final mean weights (g) and overall mean growth rates ($\overline{SGR}$, % day^{-1}) for cod of different haemoglobin genotypes reared at different photoperiods and temperatures

Temp.	Variable			Initial weights	Final weights	$\overline{SGR}$
	Genotype	Photoperiod	n			
10 °C	*Hb-I*(1/1)	LDN	21	8.8 (0.7)	51.8 (5.2)^{b}	1.80 (0.06)^{ab}
	Hb-I(1/2)	LDN	17	10.0 (0.7)	48.6 (4.7)^{b}	1.69 (0.07)^{b}
	Hb-I(2/2)	LDN	7	10.5 (1.1)	50.7 (5.2)^{b}	1.66 (0.11)^{b}
	Hb-I(1/1)	LD24:0	13	8.8 (0.8)	51.2 (4.8)^{b}	1.89 (0.07)^{a}
	Hb-I(1/2)	LD24:0	23	9.8 (0.6)	57.4 (4.5)^{ab}	1.89 (0.05)^{a}
	Hb-I(2/2)	LD24:0	12	9.4 (0.9)	59.2 (4.2)^{a}	1.99 (0.08)^{a}
13 °C	*Hb-I*(1/1)	LDN	20	8.6 (0.6)	60.2 (5.4)^{c}	2.04 (0.05)^{cd}
	Hb-I(1/2)	LDN	16	9.2 (0.7)	56.6 (6.0)^{cd}	1.87 (0.06)^{de}
	Hb-I(2/2)	LDN	6	8.3 (1.1)	43.6 (7.8)^{d}	1.80 (0.10)^{e}
	Hb-I(1/1)	LD24:0	15	9.8 (0.7)	70.2 (4.2)^{b}	2.09 (0.06)^{bc}
	Hb-I(1/2)	LD24:0	18	10.8 (0.7)	80.2 (5.7)^{ab}	2.16 (0.05)^{ab}
	Hb-I(2/2)	LD24:0	13	10.3 (0.8)	81.6 (4.7)^{a}	2.30 (0.07)^{a}

Results are given as mean (standard error of mean); n denotes number of fish of each genotype at each temperature. Different letters denote significant differences (Student–Newmans–Keuls multiple comparisons, P<0.05) between genotypes in relation to photoperiod regime within each temperature regime.

Keuls multiple comparison test to locate differences among treatments (Zar, 1984).

Individual growth trajectories were analyzed using a growth curve analysis MANOVA model (Timm, 1980). The model equation of the GCM had the form: $\mathbf{Y}(n \times p) = \mathbf{X}(n \times q)\mathbf{B}(q \times p) + E(n \times p)$ where $\mathbf{Y}(n \times \mathrm{p})$ are the growth at age vectors $\mathbf{y} = (y_1, y_2, \ldots, y_p)$ for each p (age) measurements 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., $q = \mathrm{age}_p + \mathrm{genotype}_i + \mathrm{genotype}_j + \mathrm{replicate}_k$; $i = Hb\text{-}I(1/1)$, $Hb\text{-}I(1/2)$, $Hb\text{-}I(2/2)$; $j = \mathrm{LDN}$, LD24:0; $k = $ replicate a, replicate b; $\mathbf{B}(q \times p)$ is the matrix of parameters estimated by the model; $E(n \times p)$

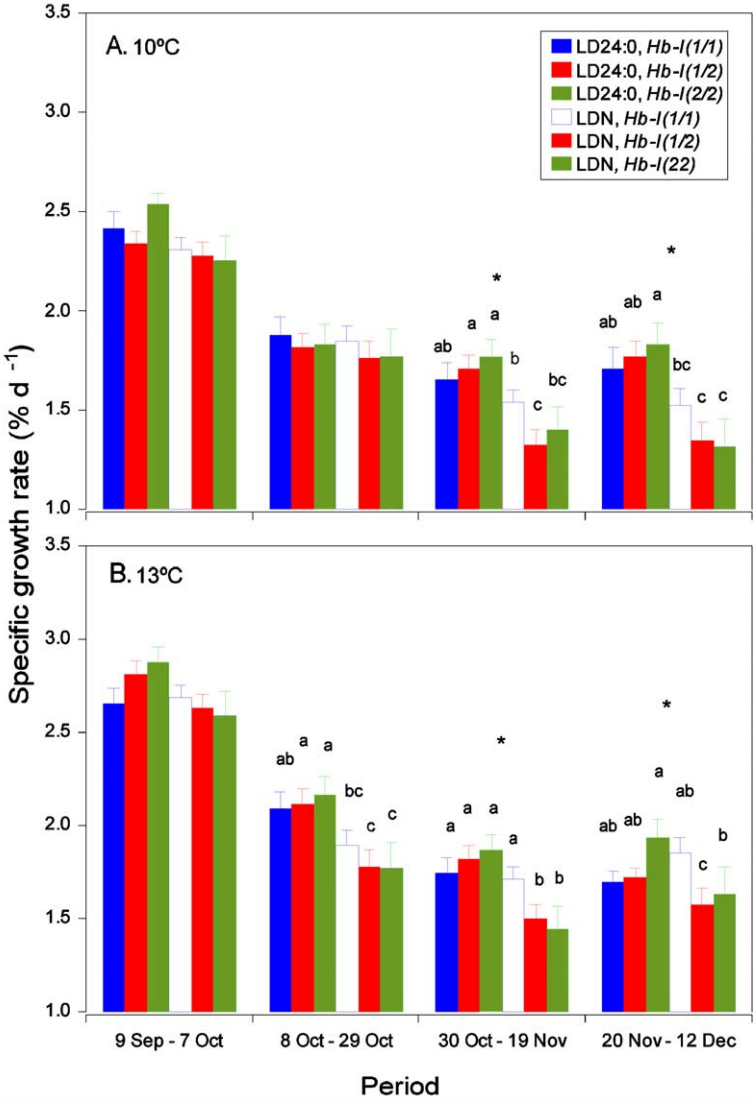

Fig. 1. Specific growth rates (mean ± S.E.M.) for individually tagged cod of different haemoglobin genotypes reared at different photoperiods and temperatures. (A) 10 °C, (B) 13 °C. Different letters denote significant differences (Student–Newman–Keuls test, $P < 0.05$) between genotypes at each sampling date within each temperature regime; * indicates a significant interaction between genotypes and photoperiod regime.

is the matrix of deviations for each individual from the expected value of $\mathbf{Y}=\mathbf{XB}$.

Separate analyses were made for each temperature.

3. Results

Juveniles with the *Hb-I*(2/2) genotype had the highest final mean weight in the LD24:0 groups at both temperatures and was significantly larger compared to juveniles of the *Hb-I*(1/1) genotype at this light regime (Table 1). Conversely, the *Hb-I*(1/1) juveniles had significantly higher final mean weight compared to *Hb-I*(2/2) juveniles in the LDN group at 13 °C, whereas no differences were found in the LDN group at 10 °C. Accordingly a significant interaction between genotypes and photoperiods (three way nested ANOVA, $P<0.05$) was found at both temperatures at the end of the experiment. In all groups except LDN at 10 °C *Hb-I*(1/2) juveniles had intermediate growth compared to the two other genotypes.

Mean individual growth trajectories varied significantly between photoperiods (GCM, $\text{MANOVA}_{\text{Photoperiod}}$, Wilk's lambda $(\Lambda)_{4,\ 165}=0.81$, $P<0.001$) as continuous light enhanced growth at both temperatures. However, the genotypes varied in their response towards photoperiod treatment (Table 1, Fig. 1). At both temperatures the highest overall growth rates were found in *Hb-I*(2/2) juveniles at LD24:0 (1.99 and 2.30% day^{-1}, for LD24:0 at 10 and 13 °C, respectively, Table 1), whereas the lowest overall mean growth rates were found for juveniles of the same genotype reared at LDN (1.66 and 1.80% day^{-1}, for LDN at 10 and 13 °C, respectively). Conversely, in the LDN groups at both temperatures (Table 1) the *Hb-I*(1/1) genotype had the highest growth rates. This interaction between genotypes and photoperiod tended towards significance ($\text{MANOVA}_{\text{Photoperiod}\times\text{Genotype}}$, Wilk's $\Lambda_{8,\ 330}=0.92$, $P=0.08$). The relative difference between the overall growth at LDN and LD24:0 varied between the temperatures and was greater at 13 °C (13% difference), and consequently an interaction between temperature and photoperiod was seen ($\text{MANOVA}_{\text{Photoperiod}\times\text{Temperature}}$, Wilk's $\Lambda_{4,\ 165}=0.91$, $P<0.01$).

When growth rates were analyzed separately for each temperature (Fig. 1) mean individual growth trajectories were found to vary between the genotypes at both temperatures. In general juveniles with the *Hb-I*(2/2) displayed significantly higher growth rates compared to the other genotypes at LD24:0, and juveniles with the *Hb-I*(1/1) genotype displayed best growth of the three genotypes at LDN (Student–Newman–Keuls test, $P<0.05$). At both temperatures the *Hb-I*(1/2) showed intermediate growth rates at both light regimes.

4. Discussion

Our results indicate an interaction between genotype and photoperiod in the growth of Atlantic cod. To the authors' knowledge this is the first published experimental study postulating this mechanism in fish. Photoperiod is known as one of the key regulators of the timing and intensity of smolt development in salmonids (Hoar, 1988) and there are indications that populations differ in their photoperiod perception. Accordingly, Stefansson et al. (1990) showed significant differences among families of Atlantic salmon in their response to photoperiods, ranging from LD8:16 to LD24:0. In their study, a significant photoperiod × family interaction suggests genetic differences in growth capacity of families and in the capacity to respond to the growth stimulating effect of continuous light. Further, as shown by Clarke et al. (1992) in chinook salmon, *Oncorhynchus tshawytscha* Walbaum, the life history pattern (i.e. occurrence of smolting) has a strong genetic basis, which probably operates by defining the way in which exogenous signals are transduced into physiological development. Nielsen et al. (2001) investigated whether variations in the progress and intensity of the smoltification process in Atlantic salmon may arise from local genetic adaptations. The authors found inter-strain differences in plasma growth hormone (GH) profiles suggesting differences among strains in the perception and processing of photoperiod cues into physiological response. The fact that genotypes may differ in their response towards extended and continuous light is now well documented for several plant species. This is apparent in species that experience a seasonal shift in light conditions (Dwivedi et al., 2000; Giauffret et al., 2000; de la Vega et al., 2001; Przepiorkowski and St. Martin, 2003). Our data indicate that a similar mechanism can

be found in teleost fishes and that the growth enhancing effect of photoperiod may differ not only between populations, but also at the genotype level.

The genotype by environment (G × E) interaction indicated in this study has been extensively studied in cod, but mostly with temperature as the environmental variable and population as the genotype variable (e.g. Svåsand et al., 1996; Otterlei et al., 1999). These studies have indicated population specific response towards temperature (i.e. a significant G × E interaction). Svåsand et al. (1996) and Otterlei et al. (1999) found differences in larval and juvenile growth between the Norwegian coastal cod (NC) and Arcto-Norwegian (AN) stocks with better growth seen in the NC larvae and juveniles. In two recent studies using cod from the northwest Atlantic (Purchase and Brown, 2000, 2001), differences in growth properties of different populations were found with higher maximum growth rates and better food conversion efficiencies in northern cod. Together, these studies suggest that adaptation to different environmental conditions may be widespread among populations of cod in the north Atlantic. It has been postulated that these population differences could present an evolutionary adaptation to different environments (Imsland and Jónsdóttir, 2002). Similarly, the interaction between genotypes and photoperiod found in this study could possibly present a genotypic adaptation to an environmental gradient, as Atlantic cod is distributed over a variety of photoperiod conditions in nature. It is notable that the *Hb-I*(2/2) genotype is the common genotype in northern Norway (Husebø et al., 2004) where midnight sun (i.e. continuous light) is experienced from May through July. It was suggested by Suthers and Sundby (1999) that the higher growth of juvenile cod under continuous light is a key factor for these fish to attain a critical size for over-winter survival. Our results indicate an association between the genotype displaying highest growth under continuous light (*Hb-I*(2/2)) and frequencies of that genotype (Husebø et al., 2004) in the northern range of its natural habitat.

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) by increasing the production of GH (Björnsson, 1997). 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, FCE) in both wild and selected strains, concurrent with an increase in GH, while the selected strains showed better food conversion than the wild strains at both LD24:0 and LDN. In contrast, Jonassen et al. (2000) reported improved FCE (but no difference in food consumption) in juvenile halibut subjected to continuous light at two temperatures. Accordingly, non-salmonids adjust to extended photoperiods by displaying higher feeding activity, growth and food utilization (Boehlert, 1981; Woiwode and Adelman, 1991). Boehlert (1981) found positive effects of photoperiod on growth in splitnose rockfish. Constant LD16:8 resulted in enhanced growth compared to LD12:12, and was probably related to a greater scope for growth due to a lower standard metabolic rate. Accordingly, it may be postulated that the apparent greater scope of growth seen for *Hb-I*(2/2) is due to a lower standard metabolic rate as studies have shown that this genotype has a higher capacity for utilizing oxygen. Brix et al. (1998) investigated the oxygen affinity of four of the Hb genotypes found in cod [*Hb-I*(1/1), *Hb-I*(1/2), *Hb-I*(2/2), and *Hb-I*(2/2b)]. They found that *Hb-I*(2/2b) (not part of this study) followed by *Hb-I*(2/2) had the highest oxygen affinity, suggesting that these types are more efficient in binding oxygen from the water. A better utilization of the oxygen supply (higher oxygen affinity) allows the animal to increase metabolism without increasing the cost of respiration, and hence increase growth (Fonds et al., 1992). According to Brett and Groves (1979), the physiologically useful food energy of young well-fed and growing carnivorous fish is divided into: 40% energy for growth + 60% energy for metabolism.

A more efficient utilization of the oxygen supply, i.e. higher oxygen affinity, can further reduce the metabolic expenditure so that even more energy can be channelled into growth, i.e. increased metabolic capacity (Brett and Groves, 1979; Fonds et al., 1992), which may help explain the growth differences seen between genotypes in the present study.

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 (Fig. 1). 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 for Atlantic halibut (Simensen et al., 2000), suggesting that the fish in seawater require some time to adapt to changes in photoperiod. Moreover, 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 approx. 12 h in September to 7 h in December.

In conclusion, a genotype dependent growth response on photoperiod was indicated among haemoglobin genotypes. Earlier studies have indicated that the *Hb-I*(2/2) genotype has better growth (Nævdal et al., 1992), highest competitive performance (Salvanes and Hart, 2000) and highest oxygen affinity (Brix et al., 1998) of the three genotypes. This is in line with the present data, which indicate that also photoperiod perception and its influence on growth varies between genotypes. In the culture of Atlantic cod continuous light has been found to increase growth and inhibit maturation in Atlantic cod (Hansen et al., 2001). Our data suggest that the genetic composition must be considered in order to increase the effect of photoperiod treatment in Atlantic cod.

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