Comparative Biochemistry and Physiology, Part A 151 (2008) 66–70

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

Plasma insulin-like growth factor-I concentrations and growth in juvenile halibut (*Hippoglossus hippoglossus*): Effects of photoperiods and feeding regimes

Albert K. Imsland [a,c,*], Atle Foss [b], Bjørn Roth [c,d], Sigurd O. Stefansson [c], Erik Vikingstad [b], Skjalg Pedersen [e], Trond Sandvik [e], Birgitta Norberg [f]

[a] *Akvaplan-niva Iceland Office, Akralind 4, 201 Kópavogur, Iceland*
[b] *Akvaplan-niva Bergen, P.O. Box 2026 Nordnes, N-5817 Bergen, Norway*
[c] *Department of Biology, University of Bergen, P.O. Box 7800, 5020 Bergen, Norway*
[d] *Norconserv Processing Research-Nofima, Box 327, 4001 Stavanger, Norway*
[e] *Marine Harvest Norway Ltd. Grev Wedels Plass 5, P.O. Box 370, N-0102 Oslo, Norway*
[f] *Institute of Marine Research, Institute of Marine Research, Austevoll Research Station, N-5392 Storebø, Norway*

ARTICLE INFO

Article history:
Received 21 February 2008
Received in revised form 22 May 2008
Accepted 29 May 2008
Available online 4 June 2008

Keywords:
IGF-I
Growth
Feeding regimes
Photoperiod
Hippoglossus hippoglossus
Halibut

ABSTRACT

The effects of photoperiod and feeding regimes on plasma IGF-I levels and their relationship with growth rate of juvenile halibut (initial mean weight 364 g) were investigated by rearing fish under five different photoperiod regimes and two feeding regimes for 14 months. The entire photoperiod experiment was divided into 3 phases where the fish in each phase were exposed to either natural photoperiod (N), stimulated photoperiod with long day and short night (S) or continuous light (L). Thus, the following five photoperiod combinations were tested: a) Control group (NNN) b) Group 2A (NLN) c) Group 2B (NNL) d) Long day-natural group (SNN) e) Production group (LNN). In addition, the Control group was split into two parts and fed according to two different feeding regimes: a) Continuous fed group: Fish fed every day. b) Starvation/re-fed group: Fish were starved for 5 weeks and then re-fed for 10 weeks, and the treatment repeated during the whole experimental period. The analyses of IGF-I were performed from individually tagged fish in all groups in September 2005 and March 2006. In order to test how rapidly starvation affects circulating IGF-I levels samples were taken from the Starvation/re-fed group after a 10 days starvation (September) and immediately after 10 weeks of feeding (March). A significant relationship between IGF-I levels and individual growth in the preceding period and photoperiod and starvation treatment was found on both occasions. In conclusion, the present study indicates that plasma IGF-I levels are correlated to growth in Atlantic halibut, and affected by photoperiod treatment or compensatory growth during re-feeding. Correlation between individual growth rate and IGF-I levels was low, but significant, highlighting the complexity of how environmental factors affect the endocrine and physiological regulation of growth in fish.

1. Introduction

Energy metabolism and growth in teleost fish are under complex endocrine control that directly or indirectly involves several hormones (e.g. Pérez-Sánchez, 2000; Björnsson et al., 2002). Growth hormone (GH), insulin-like growth factor-I (IGF-I), and insulin are of prime importance, as all three have both metabolic (e.g. Björnsson, 1997; Planas et al., 2000) and growth-promoting (e.g. Le Bail et al., 1998; Björnsson et al., 2002; Imsland et al., 2007) functions. Plasma levels of IGF-I increase during the growing season in temperate fishes (Mingarro et al., 2002), and are stimulated by increased temperature (Beckman et al., 1998; Imsland et al., 2007) and day-length (McCormick et al., 2000). Furthermore, treatment of fish with IGF-I implants stimulates growth (McCormick et al., 1992). IGF-I in fish has been associated not only with growth, but also with feeding rates (Beckman et al., 2004), metabolism (Castillo et al., 2004), development (Pozios et al., 2001), reproduction (Weber and Sullivan, 2000), and osmoregulation in seawater (McCormick, 2001).

McCormick et al. (2000) provided the first evidence that photoperiod regulates circulating levels of IGF-I in fish. They found that plasma IGF-I levels increased in Atlantic salmon, *Salmo salar* L. in line with increasing day-length between March and May. Weltzien et al. (2003) investigated endocrine regulation of growth and maturation in male Atlantic halibut, *Hippoglossus hippoglossus* L., from juvenile to adult stage (2–6 years of age). Although no clear seasonal pattern in plasma IGF-I levels could be discerned, they were correlated to body weight during the periods of slow growth in winter/spring. How long day and continuous light modulate IGF-I levels in Atlantic halibut is currently unknown.

Compensatory growth (GC) is described as a phase of accelerated growth, commonly seen when favourable conditions are restored after a period of growth depression (Ali et al., 2003). In most studies GC has

* Corresponding author. Akvaplan-niva Iceland Office, Akralind 4, 201 Kópavogur, Iceland. Tel.: +354 562 58 00; fax: +354 564 58 01.
E-mail address: ai@akvaplan.niva.no (A.K. Imsland).

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doi:10.1016/j.cbpa.2008.05.179

been investigated as a response after a period of total or partial feed deprivation and does not seem to be related to body size (Skalski et al., 2005). GC has been reported in several pleuronectids (Bejda et al., 1992; Paul et al., 1995; Sæther and Jobling, 1999; Heide et al., 2006). During fasting, fish sequentially mobilize carbohydrate, lipid and protein reserves, and exhibit a rapid recovery of these reserves following episodes of enforced hypophagia (Ali et al., 2003). Although the physiological regulation of the partitioning of metabolites in fish is still poorly understood, it is clear that the endocrine system is involved; thyroid hormones, glucocorticoids, GH, IGF-I, pancreatic hormones and gastrointestinal tract hormones all play essential roles (Mommsen, 2001; Power et al., 2001). Of these, GH and IGF-I have been implicated in the regulation of metabolic events during episodes of dietary limitation or deprivation (Cameron et al., 2007).

The present experiment was carried out to investigate the interrelationship between plasma IGF-I levels, growth rate, feeding regimes and photoperiod in juvenile Atlantic halibut.

2. Materials and methods

2.1. Pre-experimental protocol

Atlantic halibut (*H. hippoglossus* L, Pleuronectidae) used in the present experiment originated from the broodstock of Fiskeldi Eyjafjarðar Ltd. (Iceland). The eggs were stripped, fertilised and incubated on 7 January, 2003. They were then transferred to the facilities of Risør fisk Ltd. (Norway) where they hatched on 3 February. The larvae were fed enriched Artemia from 17 February, and the weaning period commenced on 15 May. On 19 August 2003 the fish were transported to the commercial halibut facilities of Stolt Sea Farm Ltd. at Eggesbøneset (Møre and Romsdal), Norway and reared under continuous light. On 25 August, a total of 1200 juvenile halibut were moved to the Bergen High Technology Centre (BHTC). Out of a group of 1200 experimental fish, 236 tagged fish were used in the current study. Two weeks before the start of the laboratory trial at BHTC the fish were tagged intraperitoneally with Trovan® Passive Integrate Transponder tags (N=236). A detailed description of methodology and results during the laboratory trial (13 September–21 December 2004) has been published and can be found in Heide et al. (2006) and Imsland et al. (2006), whereas here we only report final mean weights of the experimental groups in the laboratory trial (21 December 2004) as part of the growth trial from December 2004 to March 2006.

2.2. Experimental study—photoperiods

After the termination of the laboratory trial at BHTC, all fish were reared at 10 °C and LDN, and transported by truck on 10 January 2005 back to the production site of Marine Harvest at Eggesbønes. Here the individually tagged fish were held in four land-based tanks with 8 m^2 bottom area and reared at ambient temperatures (annual mean temperature, 9.2 °C; range mean temperatures, max. 11.7 °C in September, min. 6.7 °C in March) together with an additional 300 other (untagged) halibut. Initial mean mass (SD) was 368.5 g (±108.2 g). The fish were hand-fed five times a week using a commercial formulated feed from Dana Feed (9 mm, Dan-Ex 1562, containing 18% fat and 54% protein). Light was supplied by 33 W luminous tubes kept above the tanks. One tank was surrounded by light proof walls, stretching from the tank surface to the ceiling in the hall, and was used for those fish that at any given time were exposed to continuous light.

In the period from 13 September 2004 to 2 March 2006, the fish were reared at five different photoperiod regimes (Table 1):

1. Control group (NNN): Simulated natural photoperiod (N) throughout the experiment, N_{total}=31.
2. Production group (LNN): Continuous light (L) in laboratory trial—N in long-term trial at Eggesbønes, (this was the current production regime applied by Marine Harvest), N_{total}=41.
3. Long day-natural group (SNN). Long day (20 h): short night (4 h) in laboratory trial (S)—N in long-term trial, (SNN), N_{total}=31.
4. Group 2A (NLN): N in laboratory trial – LD24:0 between Feb. and Nov. 2005 – N from Nov. 2005 to March 2006, N_{total}=26.
5. Group 2B (NNL): N in laboratory trial and until Nov. 2005 at Eggesbønes – LD24:0 between Nov. 2005 and March 2006, N_{total}=26.

2.3. Experimental study—feeding regimes

On 13 September 2004, two experimental groups were established, with one starvation/re-fed group (N_{total}=54) and one continuously fed group as control (N_{total}=27). The starvation/re-fed group was reared as follows: Cycles of 5 weeks starvation followed by 10 weeks re-feeding repeated during the whole experimental period. The continuously fed control group was fed 1–2 times each day during the whole trial. Both groups were reared at simulated natural photoperiod (N) during the entire experimental period. At sampling in September 2005 the starvation/re-fed group had been starved for 10 days, whereas in March 2006 the fish were sampled immediately after 10 weeks of feeding. This sampling scheme was used to test how rapidly starvation affects circulating IGF-I levels.

2.4. Growth

Specific growth rate (SGR) was calculated according to the formula: $SGR=(e^g-1)\ 100$ 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.

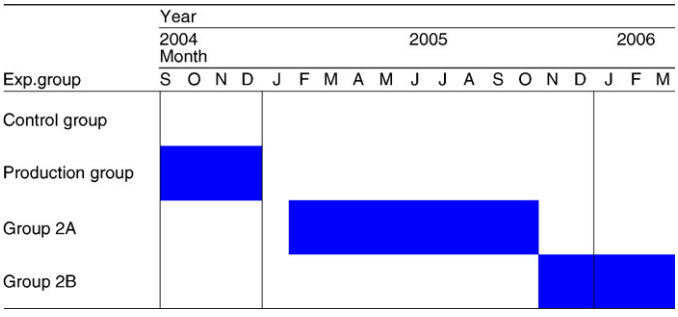
2.5. IGF-I levels

Blood was sampled from 17–20 individually tagged fish from each experimental group in September 2005 and March 2006. The fish were anaesthetised using 1 mg L^{-1} metomidate hydrochloride. Blood was drawn from the caudal vein and plasma separated by centrifugation, placed directly on ice and stored at −80 °C. Plasma levels of IGF-I were analyzed by a heterologous radioimmunoassay (RIA; Shimizu et al., 2000), validated for halibut. Anti-barramundi (*Lates calcarifer*) IGF-1, ^{125}I-labelled barramundi IGF-I tracer and recombinant barramundi IGF-I standard were purchased from GroPep Ltd (Adelaide, Australia). Serial dilutions of halibut plasma were parallel to the standard curve. The detection limit was 5 pg and the standard curve was linear between 10 and 150 pg. Intra-assay variation was 8.3% (N=12) and inter-assay variation was 6.2% (N=6).

2.6. Statistical methods

All statistical analyses were conducted using Statistica™ 8.0. To assess normality of distributions a Kolmogorov–Smirnov test was

Table 1
Schematic overview of the photoperiod regimes applied in the current study



Simulated natural photoperiod (LDN) is indicated by light grey bars, and continuous light (LD24:0) is indicated by dark bars.

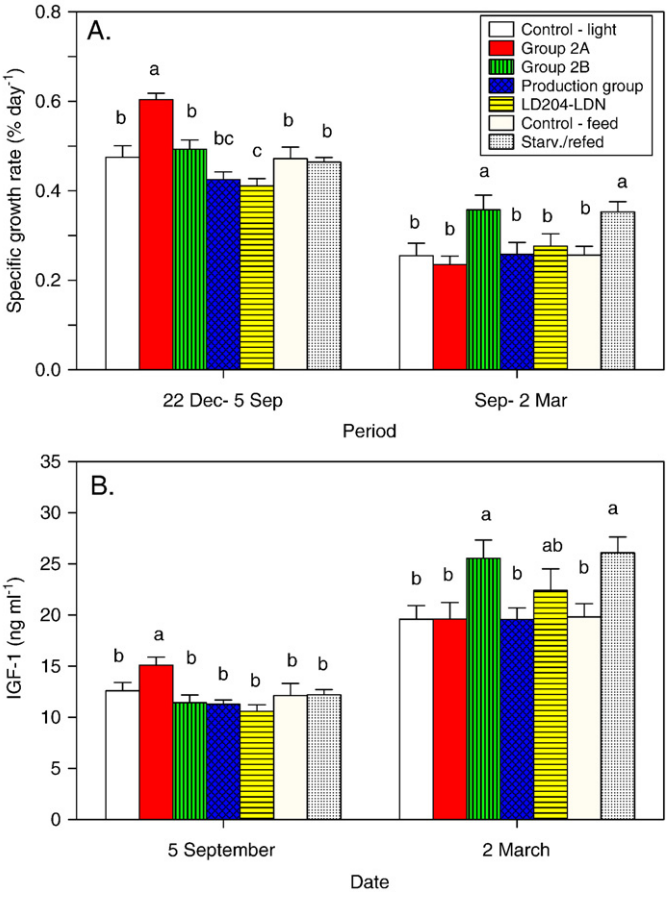


Fig. 1. Specific growth rates (A), and plasma IGF-I levels (B) of juvenile halibut reared at five photoperiod regimes and two feeding regimes for 14 months. Vertical whiskers indicate standard error of mean (SE). Different letters denote significant differences (Student–Newman–Keuls test, $P<0.05$) between experimental groups. Note that at sampling in September 2005 the Starv./re-fed group had been starved for 10 days, whereas in March 2006 the fish were sampled immediately after 10 weeks of feeding. This sampling scheme was used to test how rapidly starvation affects circulating IGF-I levels.

used and homogeneity of variances was tested using the Levene's F test. One way ANOVA was applied to calculate the effect of different photoperiods and feeding regimes on mean specific growth rates. Possible differences between photoperiod and feeding regimes on IGF-I levels were tested with a two way analysis of covariance (ANCOVA) with individual weight as a covariate. Significant differences revealed in ANOVA and ANCOVA were followed by a Student–Newman–Keuls multiple comparison test to determine differences among experimental groups. Correlations between IGF-I levels and specific growth rates in all treatment groups were tested by Persons product-moment correlations. Before combing all the data and testing for overall correlation, the homogeneity of slopes (or parallelism) hypothesis at each date was tested with an ANCOVA with IGF-I levels as the dependent variable, experimental groups as the independent effect, and growth as covariate. A significance level (α) of 0.05 was used if not stated otherwise.

3. Results

3.1. Growth and IGF-I in relation to photoperiod and feeding regimes

Growth rates varied between the experimental groups in both experimental periods (Fig. 1A), as the starvation/re-feeding regime and exposure to continuous light significantly, but transiently, increased growth (one way ANOVA, $P<0.05$). Between December 2004 and September 2005 Group 2A (reared at continuous light during that period) had the highest growth (one way ANOVA, $P<0.05$, Fig. 1A) and these differences were mirrored in the IGF-I levels on 5 September (two way ANCOVA, Fig. 1B). Between September 2005 and March 2006, the starvation/re-fed group exhibited compensatory growth and Group 2B (reared at continuous light during this period) had the highest growth of the photoperiod groups (one way ANOVA, $P<0.05$, Fig. 1A). Again these growth differences are to a large extent mirrored in measured IGF-I levels in March 2006 (two way ANCOVA $P<0.05$, Fig. 1B).

3.2. The interrelation between IGF-I levels and growth

The IGF-1 vs. growth relations were parallel in the different experimental groups on both dates (two way ANCOVA, $P=0.66$ and $P=0.43$ in Sept. 2005 and March 2006, respectively). However the intercepts are different ($P<0.05$) and near different ($P=0.08$) in Sept. 2005 and March 2006, respectively, which is not surprising given the IGF-I levels differed in the different experimental groups (see Fig. 1B). Overall, the IGF-I levels ranged between 5 and 40 ng mL^{-1} and, although there was a high variation in IGF-I levels within all groups, there was a significant relationship between IGF-I levels and specific growth rate during the previous period at both sampling dates (September 2005, Fig. 2A, $r=0.19$, $P<0.01$; March 2006, Fig. 2B, $r=0.35$, $P<0.001$).

4. Discussion

In the present study the IGF-I plasma levels in halibut were correlated to the growth rate, as observed in several salmonids (Duan,

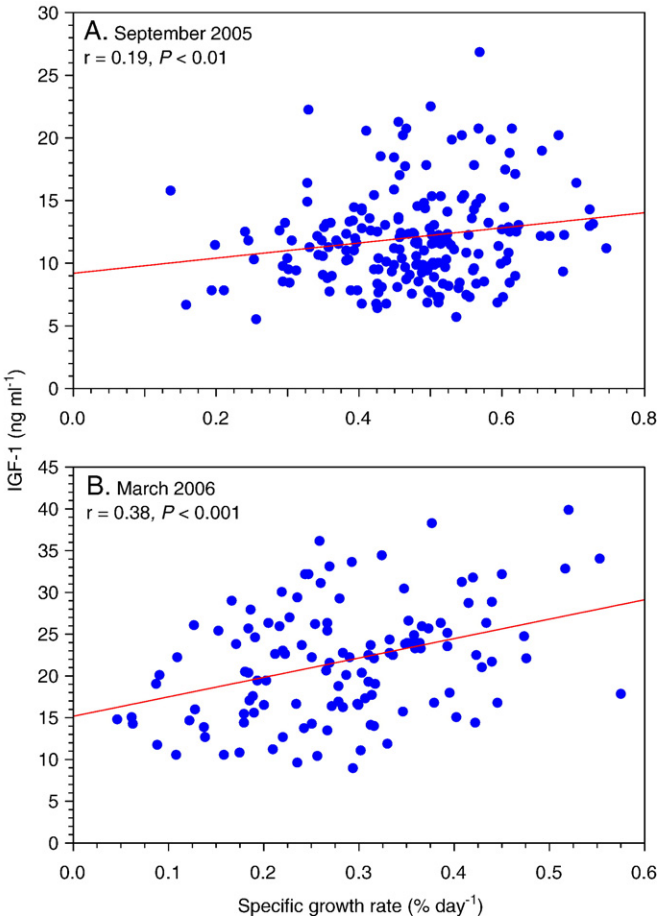


Fig. 2. Correlations between growth rates and IGF-I levels of juvenile halibut reared at five photoperiod regimes and two feeding regimes for 14 months.

1998; Pierce et al., 2001; Gabillard et al., 2005) and marine species (Matthews et al., 1997; Imsland et al., 2007), supporting the direct role of IGF-I in overall growth regulation. Weltzien et al. (2003) investigated endocrine regulation of growth and maturation in male Atlantic halibut from juvenile to adult stages (2–6 years of age). They found no clear seasonal pattern in plasma IGF-I levels, whereas a correlation to body weight during the periods of slow growth in winter/spring was seen.

A correlation between IGF-I levels and feeding regimes was observed in the present study. Plasma IGF-I levels in fish have previously been found to be associated with feed regimes in salmonids (Duan, 1998; Pierce et al., 2001), and marine species (Pérez-Sánches, 2000). As a characteristic feature, fasting and malnourished fish show a decrease in hepatic growth hormone (GH)-binding and circulating IGF-I levels, which increases pituitary GH release due to a lack of negative feedback inhibition by IGF-I on the pituitary somatotrophs. GH levels were not measured in the present study, but GH has been identified as a strong regulator of IGF-I levels in fish, by stimulating hepatic IGF-I secretion (see Björnsson et al., 2002). However, there is increasing evidence that regulation of IGF-I levels is more complex and often *apparently* GH-independent (Beckman et al., 1998, 2004; Pierce et al., 2001). While other regulators of IGF-I secretion have not been identified, evidence suggests nutritional and metabolic factors (Dickhoff et al., 1997; Duan, 1998). IGF-I function is also strongly affected by expression of IGF-I receptors in tissues as well as a number of IGF-I binding proteins in the circulation (see Reinecke et al., 2005). This complex regulation of IGF-I secretion and function may help to explain the relatively weak correlation between IGF-I levels and growth rate in the present trial.

Exposure to continuous light (LD24:0) improved growth during the present trial. Positive effects of extended photoperiod on growth have been recorded in several marine species (see Boeuf and Le Bail, 1999) including turbot (Imsland et al., 1997; Imsland and Jonassen, 2003) and halibut (Norberg et al. 2001; Imsland and Jonassen, 2003; Imsland et al., 2006). Reports on the effects of photoperiod on long-term growth and maturity in flatfish species are, however, limited. Holm (1995) reported higher growth in female halibut reared under constant light from September until May the year before maturation as compared with females reared under LDN. This indicates that extended photoperiod may have a growth-promoting effect on Atlantic halibut by altering age of 1st maturation in line with previous studies on salmonids (see Boeuf and Le Bail, 1999 for a review on effect of photoperiod on growth of salmonids species). In male Atlantic halibut, exposure to continuous light 15 and 5 months prior to spawning stimulated growth and accelerated the occurrence of first maturation by approximately 3 months (Norberg et al., 2001). In the present study exposure to continuous light 2 years (Group 2A) or 14 months (Group 2B) before expected age at first maturation lead to greatly improved growth, in line with these earlier findings.

Starvation and re-feeding had significant effects on IGF-I levels in Atlantic halibut. IGF-I levels were significantly higher in fish displaying compensatory growth (CG) compared to controls. It seems that elevated IGF-I levels in CG groups drop rapidly to control levels as the CG group in this study had similar IGF-I levels as control fish after 10 days of fasting. The decrease in plasma IGF-I concentrations after 10 days of food deprivation is consistent with observations in several other fish species during fasting or starvation (Uchida et al., 2003; Frantzen et al., 2004; Pierce et al., 2005; Cameron et al., 2007). In coho salmon, *Oncorhynchus kisutch* Walbaum, the decline in plasma IGF-I concentration in food-deprived fish was significantly lowered within 4 days and continued to decline until 15 days of food deprivation (Pierce et al., 2005), whereas other studies indicate that a much longer period of food deprivation is needed in order to detect a reduction in IGF-I levels (Cameron et al., 2007). The differences in these observations, and those of the current study, may suggest that body size, temperature or/and nutritional history of the fish before the onset of the deprivation period may influence the timing of the decline in plasma IGF-I levels. In Atlantic halibut it has been demonstrated that the proximal composition in groups undergoing starvation is not different compared to control (Heide et al., 2006), and hence suggested that the energy reserves stored in the liver are used to satisfy the energy demands during starvation in Atlantic halibut. Further, Grisdale-Helland and Helland (1998) suggested that halibut do not use the gastrointestinal region for deposition of excess energy in the form of fat, in contrast to the pattern seen in salmonids. Lower fat stores (Grisdale-Helland and Helland, 1998; Nortvedt and Tuene, 1998) in Atlantic halibut compared to many other species could help to explain the relative fast decrease in plasma IGF-I concentrations during starvation seen in the present study.

In conclusion, the present study show that plasma IGF-I levels are correlated to recent growth rate in Atlantic halibut. Plasma IGF-I levels increase in line with growth differences caused by photoperiod treatment or compensatory growth. Correlations between individual growth and IGF-I levels were low, but significant, highlighting the complexity of how environmental factors affect the endocrine and physiological regulation of growth.

Acknowledgements

This study was financed by the Norwegian Research Council (No. 158166/120) and the Icelandic AVS fund (AVS R 031 05).

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