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Bovine growth hormone treatment of channel catfish: strain and temperature effects on growth, plasma IGF-I levels, feed intake and efficiency and body composition

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Abstract

Channel catfish from two strains, USDA-103 and Norris, were reared in circular 800-l tanks and injected once weekly with 2.5 μg recombinant bovine growth hormone (rbGH) per gram body weight, or the saline vehicle. In addition to the rbGH, and strain treatments, half the tanks were supplied with well water of 26.0°C and the other half received water of 21.7°C. Growth rate, plasma insulin-like growth factor I (IGF-I) levels, feed consumption and body fatness of the fish injected with rbGH were higher than in saline-injected controls. Strain and temperature effects were also significant. Feed consumption was significantly greater with growth hormone treatment, higher temperature, and in the USDA-103 strain of catfish. Feed efficiency was significantly better in rbGH-injected fish. The effect of temperature on feed efficiency was also significant, higher temperature treatments performed better. Growth hormone enabled channel catfish to grow better at lower and higher temperatures than saline-treated counterparts.

Keywords: Recombinant growth hormone; Genetic effects; Temperature effects

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1. Introduction

Administration of growth hormone to a wide variety of fish generally results in a dose-dependent increase in growth (reviewed by Donaldson et al., 1979; McLean and Donaldson, 1993). It has been suggested that exogenous growth hormone causes improved growth through increased feed intake, and improved feed efficiency (Markert et al., 1977). Wilson et al. (1988) injected channel catfish, *Ictalurus punctatus*, with recombinant bovine growth hormone (rbGH), which resulted in increased weight gains, and increased fat deposition. Because of the consistent demonstration of growth promotion with GH treatment, there has been great interest in growth potential of fish transgenic for growth hormone constructs (see Devlin 1998; Dunham and Devlin, 1999). Growth hormone transgenic Pacific salmon, *Oncorhynchus* sp. have 1-year weight gains as much as 11 times greater than their non-transgenic counterparts (Devlin, 1998). Work done on growth hormone transgenic channel catfish showed that transgenic catfish grew as much as 26% faster than their non-transgenic counterparts (Dunham et al., 1992). The growth of GH transgenic fish may be especially enhanced during winter months when control animals have slow growth rates (Dunham and Devlin, 1999).

The annual growing season for channel catfish is typically 6–7 months in duration, between April and October. Low water temperatures, and possibly short daylength, from November through March, are thought to suppress feed intake and slow growth over winter (Tucker and Robinson, 1990). We are interested in improving the growth characteristics of channel catfish and investigating the potential for growth enhancement at cooler water temperatures with growth hormone treated animals. Studies on fish held at temperatures below growth optima, for example, carp (*Cyprinus carpio*) treated with porcine growth hormone (Teskeredzic et al., 1991) and coho salmon (*Oncorhynchus kisutch*) treated with rbGH (Down et al., 1988), showed that growth hormone treatment can at least partially overcome the negative effects of low temperature on feeding and growth.

Individual studies on the physiological effects of GH treatment in a variety of fishes have been mainly restricted to single strains. Growth and feed intake of the USDA-103 and Norris strains of channel catfish, were previously compared under various conditions (Silverstein et al., 1999b). The USDA-103 strain was found to have superior growth under conditions of full and restricted feeding, and superior feed intake with and without a short period of feed deprivation (Silverstein et al., 1999b). By examining the effects of GH treatment on growth and feeding in fish from these two strains with distinct phenotypes, GH treatment $\times$ strain interaction could be evaluated. The objectives of this study were to evaluate the effects of recombinant bovine growth hormone injection on growth, feed intake and feed efficiency when applied at 22°C and 26°C in two distinct strains of catfish.

2. Materials and methods

Fish used in this study came from two distinct genetic strains, the Norris strain and the USDA-103 strain. The Norris strain fish originate from the Norris fish farm in

Arkansas (Dunham and Smitherman, 1984). The USDA-103 strain has been under selective breeding at the USDA/ARS catfish genetics research unit in Stoneville, MS for two generations and the origin of this strain is described by Li et al. (1998). Both strains were represented by fish from multiple families. Mean initial sizes of Norris and USDA-103 fish were 17.1 ± 0.4 and 41.8 ± 1.4 g, respectively. Prior to distribution into treatment tanks, the fish were reared on 26.0°C flow through well water and fed daily to satiation. Fish were placed into 800-l indoor tanks, 34 fish in each tank on 16 November 1998, 1 week before injection treatments began, to acclimate to the tanks and temperature treatments. In addition to strain differences, temperature and hormonal treatments were applied. Water from wells with different temperatures, one well averaging 21.7°C (range from 21.4°C to 21.9°C) and the other 26.0°C (range from 25.7°C to 26.3°C), provided the temperature treatments. Water quality (pH ~ 8.6, dissolved oxygen levels > 5.0 mg l^{-1}) was similar between treatments. The hormonal treatment was a weekly intraperitoneal injection of sterile saline or recombinant bovine somatotropin (rbGH) dissolved in sterile saline. The rbGH, provided by Monsanto, was injected at the dose of 2.5 μg g^{-1} body weight. This dosage was selected based on the data provided in the 1993 review by McLean and Donaldson, and the observation that in some cases at higher doses, the positive effects of rbGH on growth are attenuated. These eight treatment combinations were reared in triplicate tanks. Feeding was done 6 days each week. A commercial floating catfish feed (32% protein, SF Services, Greenville, MS) was presented to fish in each tank until they reached apparent satiation, when feeding activity ceased. The amount of feed consumed by the fish in each tank was recorded daily. Treatments were initiated on 23 November 1998, after a 1-week acclimation period, and continued until 4 January 1999.

Total weights of all fish in each tank were measured weekly. Blood samples were collected from four fish from each tank during the fourth week of the study. These sampled fish were injected with rbGH or saline on Monday, 14 December 1998 and then sampled without replacement on Thursday, 17 December 1998. The blood was drawn into syringes treated with K_2EDTA as an anticoagulant, and centrifuged. The resulting plasma was separated and frozen at −80°C. These plasma samples were analyzed for insulin-like growth factor-I (IGF-I) content. The amount of fillet protein, fillet fat, and fillet moisture were compared among treatment groups at the end of the study. After the final total weights were taken, five fish from each tank were killed with an overdose of MS-222 and individually weighed to the nearest 0.1 g. The fish were filleted and the fillets from five individuals were pooled for proximate analysis. This provided one pooled sample for proximate analysis of fillets from each tank. Fillet samples were homogenized and crude protein, fat and moisture were determined in duplicate (Association of Official Analytical Chemists International 1995).

An index of growth a, based on the equation $\log_e G_w = a - 0.37 \log_e W$ (Silverstein et al., 1999b), was used to compare growth between strains. Briefly, G_w or specific growth rate was calculated as $G_w = 100 \times (\log_e W_2 - \log_e W_1) \times t^{-1}$. W_1 and W_2 are the weights at the beginning and end of the experiment t (days). W is mean fish weight during the growth interval, the intercept a represents the $\log_e G_w$ of a fish of unit size (i.e. 1 g). Higher a values indicate faster growth. Feed efficiency was calculated as grams of weight gain × grams of feed consumed^{-1} × day^{-1}. Weight adjusted daily feed

consumption was evaluated. This was calculated as the total weight of feed consumed over the 6-week study (g) × average weight of the fish during the course of the study (g) × (start weight + end weight/2)$^{-1}$ × no. of days^{-1}.

Total IGF-I was measured by radioimmunoassay (RIA) as described in Shimizu et al. (1999) using recombinant coho salmon (*O. kisutch*) IGF-I as the standard and rabbit polyclonal antibodies directed against barramundi (*Lates calcarifer*) IGF-I. A dilution/displacement curve of channel catfish plasma was compared to a coho salmon IGF-I standard (see Fig. 2). To make the dilution/displacement curve of catfish plasma in the IGF-1 RIA, plasma samples (0.5 ml) were first lyophilized to concentrate. After lyophilization, samples were reconstituted in 0.1 ml of 0.02 M sodium phosphate, 0.15 M NaCl, pH 7.4 (PBS) and subjected to acid–ethanol (AE, 87.5% ethanol and 12.5% 2 N HCl, v/v) extraction followed by cryoprecipitation (Breier et al., 1991). The extracted samples were serially diluted by the RIA buffer (PBS containing 1% BSA and 0.05% Triton X-100). The IGF-I standard was diluted by the RIA buffer and 0.025 ml of AE neutralized with Tris was added to each tube.

Weight differences were examined by two-way ANOVA with the fixed factors being temperature and injection. All other statistical analyses were conducted as a three-way ANOVA, the three fixed factors were strain, temperature and injection, with the full model including all interactions. The response variables examined with this model were the growth index *a*, feed intake, feed efficiency, and IGF-I content in plasma. The data from one of the Norris strain, 26°C, saline-injected replicate tanks were dropped from analyses of feed intake and feed efficiency. Other analyses included data from that tank. Although the growth of fish in this tank was similar to the other replicates in the same treatment, the amount of feed put in this tank was approximately 2.5 times greater than the other replicates. The coefficient of variation (CV) for feed consumption between tanks within this treatment went from 60% when including the outlying tank to 11% when excluding this replicate. No such deviations occurred in other treatments, the within-treatment CVs ranged from 2% to 14%, giving confidence to the rest of the feed consumption data. Plasma was collected from four fish in each tank. Plasma IGF-I content was analyzed in 10–12 individual plasma samples from each of eight treatment combinations. The variables fillet protein, fillet fat and dry matter were analyzed separately for each strain because the difference in size of the fish from the two strains was too great to correct for size effects. Fish size is known to have a significant effect on proximate composition (Robinson and Robinette, 1993). Main effect differences were considered significant when $P < 0.05$, interactions were handled more conservatively and considered significant when $P < 0.10$. ANOVAs were conducted using SAS GLM procedure (SAS, 1988).

3. Results

Growth hormone treatment, temperature and strain all had significant effects on the rate of weight gain, expressed by the growth index *a* (Table 1). The interactions of strain by temperature treatments ($P < 0.10$) and injection by temperature treatment ($P < 0.02$) were significant. The interaction of strain and temperature was due to the

Table 1
Means ± SD for growth index (a), feed consumption (g/100 g body weight, feed efficiency (g gain/g feed), plasma IGF-I level [*], percent moisture, percent fat, and percent protein. Body composition was measured on fillets, and data presented on wet weight basis. Sample size was $n = 3$, except where otherwise noted

Strain	Temperature	Injection	Growth index (a)	Feed consumption	Feed efficiency	IGF-I (ng/ml)	Percent moisture	Percent fat	Percent protein
Norris	21.7°C	Saline	$1.17 \pm 0.15^{a\#}$	1.51 ± 0.22^{a}	0.45 ± 0.02^{a}	4.19 ± 0.36^{a}	76.5 ± 1.4^{a}	3.3 ± 0.8^{ab}	18.7 ± 0.6^{ab}
		GH	1.77 ± 0.10^{bc}	1.79 ± 0.09^{b}	0.76 ± 0.05^{c}	8.09 ± 0.72^{b}	76.7 ± 0.8^{a}	4.6 ± 0.2^{b}	17.4 ± 0.6^{a}
	26.0°C	Saline[†]	1.98 ± 0.12^{bc}	1.68 ± 0.18^{ab}	0.99 ± 0.05^{d}	5.39 ± 0.28^{a}	76.7 ± 0.3^{a}	3.1 ± 0.2^{a}	19.0 ± 0.2^{b}
		GH	2.19 ± 0.20^{bd}	2.05 ± 0.21^{cd}	0.99 ± 0.08^{d}	8.81 ± 0.70^{b}	75.3 ± 0.3^{a}	5.0 ± 0.5^{ab}	18.4 ± 0.8^{ab}
USDA-103	21.7°C	Saline	1.95 ± 0.08^{bc}	1.86 ± 0.03^{bc}	0.63 ± 0.04^{b}	5.12 ± 0.24^{a}	75.3 ± 0.6^{a}	5.2 ± 0.5^{a}	18.2 ± 0.5^{b}
		GH	2.32 ± 0.05^{de}	2.21 ± 0.08^{de}	0.78 ± 0.05^{c}	12.07 ± 0.92^{c}	74.4 ± 1.4^{a}	7.3 ± 0.9^{b}	16.9 ± 0.3^{a}
	26.0°C	Saline	2.46 ± 0.06^{e}	2.06 ± 0.10^{cd}	0.94 ± 0.02^{d}	7.76 ± 0.45^{b}	74.7 ± 1.1^{a}	6.4 ± 1.1^{ab}	17.6 ± 0.5^{ab}
		GH	2.68 ± 0.11^{f}	2.38 ± 0.03^{e}	0.98 ± 0.06^{d}	12.03 ± 1.15^{c}	74.8 ± 1.6^{a}	6.9 ± 0.6^{ab}	17.1 ± 0.8^{ab}

[*] IGF-I values only are given as means ± SE ($n \geq 10$).
[#] Within columns, values with different superscripts are significantly different. For body composition data, comparisons were only made within strains.
[†] The mean ± SD for feed consumption and feed efficiency of the Norris, 26°C, saline treatment were calculated from two replicate tanks.

relatively larger improvement of Norris strain fish at the warmer temperature over the cooler temperature compared to the improvement shown by the USDA-103 strain. Nevertheless, the USDA-103 strain grew faster than Norris strain at both temperatures. An interaction between injection treatment and temperature was indicated because higher temperature caused a greater increase in growth performance of saline-injected fish than of rbGH-injected fish compared to the improvement seen at lower temperature. Weight gains over the 6-week experiment are shown by treatment in Fig. 1. Temperature effects on weight were significant by week 2 for the Norris strain and the Norris fish reared at 26°C were heavier through the end of the experiment. Additionally, the effect of GH treatment was also significant for the Norris strain by week 4. The USDA-103 strain fish reared at 26°C were heavier than their saline-treated counterparts at week 4 and through the end of the experiment, however, the main effect of injection treatment was not significant by itself.

Feed consumption (% consumption) was significantly affected by injection treatment, temperature and strain (Table 1). Injection of rbGH caused a 16% increase in consumption compared to saline-injected fish ($P < 0.001$). Warmer temperatures made a difference of 12% in consumption compared to fish raised at 21.7°C. The effect of strain was the largest, with USDA-103 strain fish eating 17% more than Norris strain fish. There were no interactive effects.

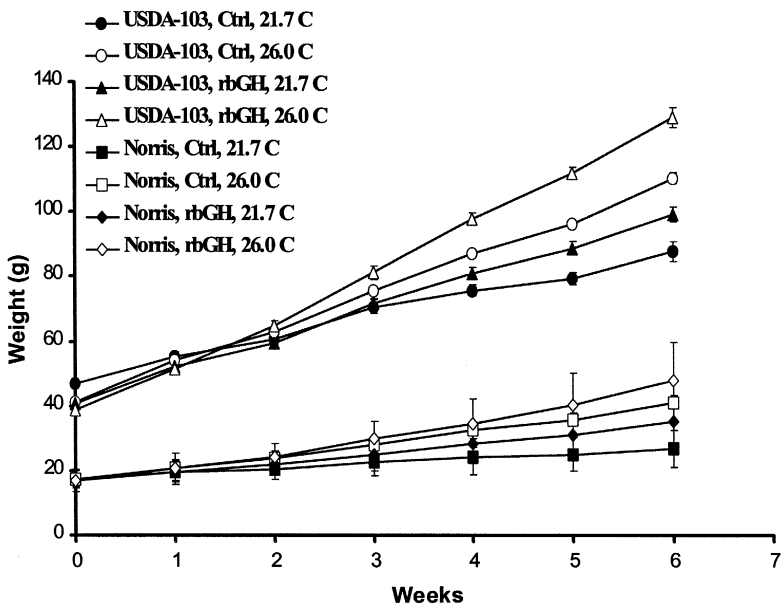

Fig. 1. Growth over time. Weekly injection of 2.5 μg/g body weight of recombinant bovine growth hormone (rbGH) or saline (Ctrl) was begun at week 0. Each point shows the average weight of individual fish in the treatment (mean ± SE) calculated from three replicate tanks. There were within strain differences in weight due to temperature in the Norris strain from week 2 through week 6, and in the USDA-103 strain from week 4 through week 6. The main effect of injection treatment was significant for the Norris strain from weeks 4 through 6.

Feed efficiency (Table 1) was significantly improved by growth hormone treatment and by warmer temperature. The effect of strain was not significant ($P > 0.05$). The performance of the USDA-103 strain was similar to the Norris strain, in terms of feed efficiency. Interactions between strain and temperature were significant, due to the greater improvement in feed efficiency of Norris fish over the USDA-103 fish at 26°C compared to 21.7°C. As with growth rate, the interaction of injection treatment and temperature with regard to feed efficiency was significant because higher temperature enhanced feed efficiency of saline injected fish more than of fish injected with rbGH compared to the improvement at lower temperature.

The dilution/displacement curve of catfish plasma in the IGF-I RIA showed parallelism with the coho salmon standard (Fig. 2.) The binding of some diluted samples was above 100% (Bo). This is due to the effect of AE in the assay. AE decreases the specific binding (but does not change the slope of the curve) and some of diluted samples contained less AE with Tris than the standard. IGF-I levels (Table 1) were significantly

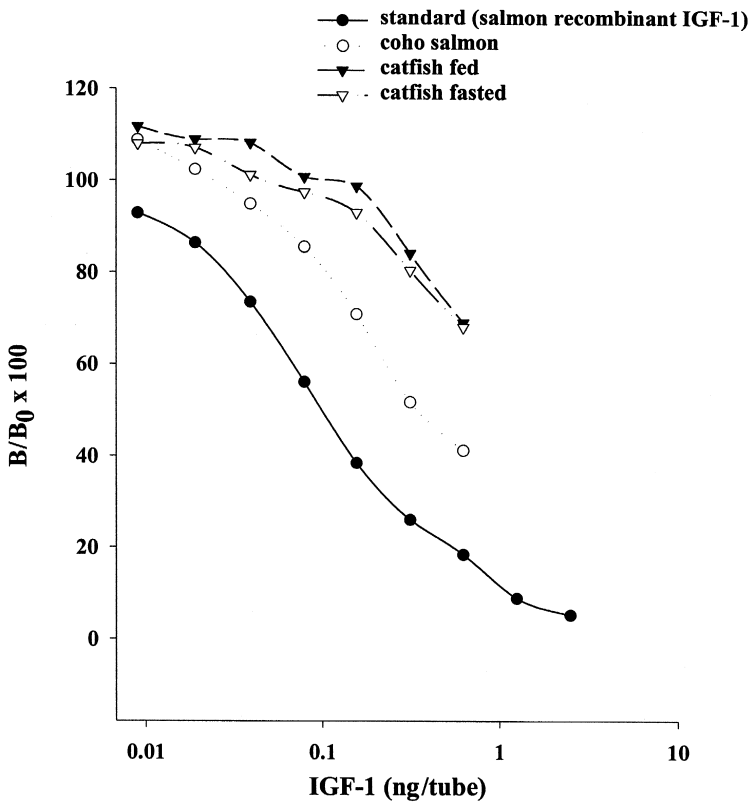

Fig. 2. RIA of IGF-1: dilution/displacement curve of acid ethanol-extracted plasma. The standard curve is made with recombinant coho salmon IGF-I (GroPep), the antibodies were developed against barramundi IGF-I (GroPep). Channel catfish and coho salmon dilution curves were made using plasma samples that were lyophilized and reconstituted with PBS prior to acid ethanol extraction.

higher in the USDA-103 strain, in fish injected with rbGH, and in fish at warmer temperatures. The strain by injection treatment interaction was significant because the USDA-103 strain had greater IGF-I plasma levels in response to rbGH injection than the Norris strain.

Proximate composition was analyzed within strains because of the size differences between Norris and USDA-103 strains of fish. Percent dry matter was not affected by temperature, or by injection treatment. Treatment with rbGH did lead to fatter fillets in USDA-103 strain fish (Table 1), however, while the trend was in the same direction in Norris fish, percent fat was not significantly affected by injection treatment. Percent protein in fillets was inversely related to percent fat (Table 1), only in the USDA-103 strain was the protein significantly lower due to injection with rbGH. The percentage of total weight made up by visceral fat (mean $\pm$ SD, 0.11 ± 0.01) was not affected by rbGH or temperature in either strain.

4. Discussion

Treatment with rbGH caused an increase in growth of channel catfish compared to controls. This was true for both USDA-103 and Norris strains of catfish and at both temperatures (21.7°C and 26°C) investigated. Treatment of teleosts with growth hormone has long been known to increase growth rate (reviewed by Donaldson et al., 1979; McLean and Donaldson, 1993). The growth-enhancing property of growth hormone has been attributed to increased feed consumption and improved feed efficiency in salmonids (Markert et al., 1977). In this study as well, increased growth rate was accompanied by increased feed consumption. Feed efficiency was improved with growth hormone treatment at 21.7°C, and was not significantly different at 26.0°C. Wilson et al. (1988) found increased feed consumption of channel catfish injected with rbGH bi-weekly. Although the feed efficiencies for fish reared at 26.7°C in that study were considerably lower than for the fish reared at 26.0°C in the present study (0.84 vs. 0.97) Wilson et al. (1988) also did not observe improved feed efficiency with rbGH treatment at temperatures in the optimum growth range.

There was a dramatic improvement in feed efficiency at the higher temperature although the temperature treatment varied by only 4°. This demonstrated that 26°C was near an optimal temperature for growth of channel catfish, whereas 21.7°C was clearly below the optimal temperature. Typical optimal temperatures for most strains of channel catfish are between 26°C and 32°C (Tucker and Robinson, 1990). Studies on carp at sub-optimal temperatures suggest that GH treatment can restore feeding and growth at temperatures clearly below growth optima (Teskeredzic et al., 1991), but as the temperature drops further, a limit is reached where growth hormone treatment cannot stimulate feeding and growth (Adelman, 1978). Clear growth acceleration with growth hormone treatment at temperatures between 6°C and 9°C was demonstrated by Down et al. (1988) working with coho salmon. These results all suggest that growth hormone treatment can extend the growing season in temperate fishes that experience variable temperature conditions during the annual growth cycle.

The mechanism by which growth hormone stimulates feed intake is not known. A direct effect of growth hormone on feeding through hypothalamic feeding centers has not been investigated in fish, but it is unlikely that the target of a pituitary hormone would be the hypothalamus. A more likely way for growth hormone to effect feed intake may be indirectly through metabolic changes such as increased nutrient utilization that feedback on hypothalamic centers regulating energy balance (Silverstein et al., 1999a) and feed intake (Peter, 1979; Bray, 1993).

Percent moisture and percent fat of the fillets were generally negatively associated, as has been seen in other studies of channel catfish proximate composition (e.g. Li and Robinson, 1998). Channel catfish injected with growth hormone were fatter than counterparts injected with saline. Wilson et al. (1988), working with the same species, measured whole body fat and found the same effect, GH treated fish were fatter. Conversely, the increased growth seen in salmonids treated with growth hormone is typically accompanied by reduced body fatness (Higgs et al., 1975; Gill et al., 1985; but see also Skyrud et al., 1989). In other teleosts investigated, an increase in weight was accompanied by body fatness increases as well (*C. carpio*, Adelman, 1977; *Ictalurus melas*, Kayes, 1977). It was suggested by Wilson et al. (1988) that rbGH may not interact fully with the catfish growth hormone receptor and thus stimulate feed intake without stimulating skeletal growth. This hypothesis seems unlikely because the elevation in plasma IGF-I levels seen in the present study suggests not only a functional ligand, but also a response to the GH/GH receptor interaction consistent with skeletal and muscle growth (Moriyama, 1995). We did not measure body length in this study, and so did not analyze skeletal growth, but fish treated with growth hormone had greater lean mass and greater fat mass than control fish. The lipolytic effect of growth hormone seen in salmonids was also seen in pigs (Campbell et al. 1989) and humans (Gertner, 1993), but not in birds (chickens, Cogburn et al., 1989; Moellers and Cogburn, 1995; and turkeys, Proudman et al., 1994). The reasons for the contrasting effects of growth hormone on body fatness in these diverse organisms remain to be elucidated. The potential for body fatness to increase with growth hormone treatment in channel catfish should be viewed with caution because increased body fat in juvenile fish may reduce feed intake over the long term (Shearer et al., 1997; Silverstein and Plisetskaya, 2000, in press). Furthermore, increased fat deposition is not desirable for commercially cultured catfish.

Faster growing fish had higher IGF-I levels. Elevation of IGF-I plasma levels by growth hormone treatment has been shown in a variety of vertebrates including teleosts (Humbel, 1990; Moriyama, 1995), and this effect was seen in channel catfish. The faster growing USDA-103 strain control fish had higher IGF-I plasma levels than the slower growing Norris strain control group. Plasma IGF-I levels in fish injected with rbGH were the same at both temperature treatments, but there was a trend for temperature to effect IGF-I levels in the control injected fish. This may be because warmer temperatures alone had a stimulatory effect on endogenous growth hormone secretion (reviewed by McLean and Donaldson, 1993) and, hence, plasma IGF-I levels, while rbGH caused maximal stimulation of plasma IGF-I levels at both temperatures. IGF-I levels were analyzed without correcting for size because there is no evidence that fish size effects plasma IGF-I level (Beckman et al. 1998; Silverstein et al., 1998). Nevertheless,

correlation between IGF-I plasma levels and growth rate has been shown in salmon (Beckman et al. 1998) and a relationship between IGF-I levels and growth rate of channel catfish is apparent here. These data suggest that the higher growth rate of the USDA-103 strain was related to the higher IGF-I levels. It should be kept in mind, however, that without information on IGF binding proteins and what fraction of the measured IGF-I is biologically active, the relationship between growth and IGF-I plasma content is not completely understood (Plisetskaya, 1998).

Strain effects were significant for many of the response variables evaluated. The USDA-103 strain performed better overall with faster growth rate, higher feed consumption, better feed efficiency at low temperature, and higher plasma IGF-I levels. These results support a genetic basis to variation in growth (Bondari, 1983) and possibly in response to growth hormone treatment. Furthermore, the overall better performance of the USDA-103 strain, and the responsiveness to growth hormone treatment, especially at lower temperature may be important for commercial culture of channel catfish. The potential for undesirable increases in body fatness and decreased fillet yield with GH treatment should be carefully watched.

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References

Adelman, I.R., 1977. Effects of bovine growth hormone on growth of carp (*Cyprinus carpio*) and the influences of temperature and photoperiod. J. Fish. Res. Board Can. 34, 509–515.

Adelman, I.R., 1978. Influence of temperature on growth promotion and body composition of carp (*Cyprinus carpio*) due to bovine growth hormone. Trans Am. Fish. Soc. 107, 747–750.

Association of Official Analytical Chemists International, 1995. Official Methods of Analysis. 16th edn. AOAC International, Arlington, VA, USA.

Beckman, B.R., Larsen, D.A., Moriyama, S., Lee-Pawlak, B., Dickhoff, W.W., 1998. Insulin-like growth factor-1 and environmental modulation of growth during smoltification of juvenile spring chinook (*Oncorhynchus tshawytscha*). Gen. Comp. Endocrinol. 109, 325–335.

Bondari, K., 1983. Response to bidirectional selection for body weight in channel catfish. Aquaculture 33, 73–81.

Bray, G.A., 1993. The nutrient balance hypothesis: peptides, sympathetic activity and food intake. Ann. N. Y. Acad. Sci. 676, 223–241.

Breier, B.H., Gallaher, B.W., Gluckman, P.D., 1991. Radioimmunoassay for insulin-like growth factor-I: solutions to some potential problems and pitfalls. J. Endocrinol. 128, 347–357.

Campbell, R.G., Steele, N.C., Capnera, T.J., McMurtry, J.P., Solomon, M.B., Mitchell, A.D., 1989. Interrelationships between sex and exogenous growth hormone administration on performance, body composition and protein and fat accretion of growing pigs. J. Anim. Sci. 67, 177–186.

Cogburn, L.A., Liou, S.S., Rand, A.L., McMurtry, J.P., 1989. Growth, metabolic and endocrine responses of broiler cockerels given a daily subcutaneous injection of natural or biosynthetic chicken growth hormone. J. Nutr. 119, 1213–1222.

Devlin, R.A., 1998. Transgenic salmonids. In: Houdebine, L.M. (Ed.), Transgenic Animals: Generation and Use. Harwood Academic Publishers, Canada, pp. 105–117.

Donaldson, E.M., Fagerlund, U.H.M., Higgs, D.A., McBride, J.R., 1979. Hormonal enhancement of growth. In: Hoar, W.S., Randall, D.J., Brett, J.R. (Eds.), Fish Physiology vol. 8 Academic Press, NewYork, pp. 456–598.

Down, N.E., Donaldson, E.M., Dye, H.M., Langley, K., Souza, L.M., 1988. Recombinant bovine somatotropin more than doubles the growth rate of coho salmon (*Oncorhynchus kisutch*) acclimated to seawater and ambient winter conditions. Aquaculture 68, 141–155.

Dunham, R.A., Devlin, R.H., 1999. Comparison of traditional breeding and transgenesis in farmed fish with implications for growth enhancement and fitness. Transgenic Animals in Agriculture. CAB International, pp. 209–229.

Dunham, R.A., Ramboux, A.C., Duncan, P.L., Hayat, M., Chen, T.T., Lin, C.M., Kight, K., Gonzalez-Villasenor, I., Powers, D.A., 1992. Transfer, expression, and inheritance of salmonid growth hormone genes in channel catfish, *Ictalurus punctatus*, and effects on performance traits. Mol. Mar. Biol. Biotech. 1, 380–389.

Dunham, R.A., Smitherman, R.O., 1984. Ancestry and breeding of catfish in the United States. Ala. Agric. Exp. Stn., Circ. 273 Auburn University, Auburn, AL, USA.

Gertner, J.M., 1993. Effects of growth hormone on body fat in adults. Horm. Res. 40, 10–15.

Gill, J.A., Sumpter, J.P., Donaldson, E.M., Dye, H.M., Souza, L., Berg, T., Wypych, J., Langley, K., 1985. Recombinant chicken and bovine growth hormones accelerate growth in aquacultured juvenile Pacific salmon *Oncorhynchus kisutch*. Biotechnology 3, 643–646.

Higgs, D.A., Donaldson, E.M., Dye, H.M., McBride, J.R., 1975. A preliminary investigation of the effect of bovine growth hormone on growth and muscle composition of coho salmon (*Oncorhynchus kisutch*). Gen. Comp. Endocrinol. 27, 240–253.

Humbel, R.E., 1990. Insulin-like growth factor I and II. Eur. J. Biochem. 190, 445–462.

Kayes, T., 1977. Effects of temperature on hypophyseal (growth hormone) regulation of length, weight, and allometric growth and total lipid and water concentrations in the black bullhead (*Ictalurus melas*). Gen. Comp. Endocrinol. 33, 382–393.

Li, M.H., Robinson, E.H., Wolters, W.R., 1998. Evaluation of three strains of channel catfish, *Ictalurus punctatus*, fed diets containing three concentrations of protein and digestible energy. J. World Aquacult. Soc. 29, 156–161.

Markert, J.R., Higgs, D.A., Dye, H.M., MacQuarrie, D.W., 1977. Influence of bovine growth hormone on growth rate, appetite, and food conversion of yearling coho salmon (*Oncorhynchus kisutch*) fed two diets of different composition. Can. J. Zool. 55, 74–83.

McLean, E., Donaldson, E.M., 1993. The role of growth hormone in the growth of poikilotherms. In: Shreibman, M.P., Scanes, C.G., Pang, P.K.T. (Eds.), The Endocrinology of Growth Development and Metabolism in Vertebrates Academic Press, New York, pp. 43–68.

Moellers, R.F., Cogburn, L.A., 1995. Chronic intravenous infusion of chicken growth hormone increases body fat content of young broiler chickens. Comp. Biochem. Physiol. 110A, 47–56.

Moriyama, S., 1995. Increased plasma insulin-like growth factor-1 (IGF-1) following oral and intraperitoneal administration of growth hormone to rainbow trout, *Oncorhynchus mykiss*. Growth Regul. 5, 164–167.

Peter, R.E., 1979. The brain and feeding behavior. In: Hoar, W.S., Randall, D.J., Brett, J.R. (Eds.), Fish Physiology vol. 8 Academic Press, New York, pp. 121–161.

Plisetskaya, E.M., 1998. Some of my not so favorite things about insulin and insulin-like growth factors in fish. Comp. Biochem. Physiol. 121B, 3–11.

Proudman, J.A., McGuinness, M.C., Krishnan, K.A., Cogburn, L.A., 1994. Endocrine and metabolic responses of intact and hypophysectomized turkey poults given a daily injection of chicken growth hormone. Comp. Biochem. Physiol. 109C, 47–56.

Robinson, E.H., Robinette, H.R., 1993. Effects of dietary protein level and feeding regimen on growth and on fatness of channel catfish, *Ictalurus punctatus*. J. Appl. Aquacult. 3, 67–89.

SAS Institute, 1988. SAS/STAT User's Guide. release 6.03 edn. SAS Institute, Cary, NC.

Shearer, K.D., Silverstein, J.T., Plisetskaya, E.M., 1997. The role of adiposity in food intake control of juvenile chinook salmon, (*Oncorhynchus tshawytscha*). Comp. Biochem. Physiol. 118A, 1209–1215.

Shimizu, M., Swanson, P., Dickhoff, W.W., 1999. Free and protein-bound insulin-like growth factor-I (IGF-I)

and IGF-binding proteins in plasma of coho salmon, *Oncorhynchus kisutch*. Gen. Comp. Endocrinol. 113, 398–405.

Silverstein, J.T., Plisetskaya, E.M., 2000. The effects of NPY and insulin on food intake regulation in fish. Am. Zool., in press.

Silverstein, J.T., Shearer, K.D., Dickhoff, W.W., Plisetskaya, E.M., 1998. The effects of growth and fatness on sexual development of chinook salmon (*Oncorhynchus tshawytscha*) parr. Can. J. Fish. Aquat. Sci. 55, 2376–2382.

Silverstein, J.T., Shearer, K.D., Dickhoff, W.W., Plisetskaya, E.M., 1999a. Regulation of nutrient intake and energy balance in salmon. Aquaculture 177, 161–169.

Silverstein, J.T., Wolters, W.R., Holland, M., 1999b. Evidence of genetic differences in food intake regulation in channel catfish, *Ictalurus punctatus*. J. Fish Biol. 54, 607–615.

Skyrud, T., Andersen, O., Alestrom, P., Gautvik, K.M., 1989. Effects of recombinant human growth hormone and insulin-like growth factor 1 on body growth and blood metabolites in brook trout (*Salvelinus fontinalis*). Gen. Comp. Endocrinol. 75, 247–255.

Teskeredzic, E., Tomec, M., Hacmanjek, M., McLean, E., Teskeredzic, Z., Donaldson, E.M., 1991. The effect of porcine somatotropin therapy upon growth and body composition of leather carp (*Cyprinus carpio* L.) maintained at sub-optimal temperatures. Riv. Ital. Acquacol. 26, 131–135.

Tucker, C.S., Robinson, E.H., 1990. Channel Catfish Farming Handbook. Van Nostrand-Reinhold, New York, 454 pp.

Wilson, R.P., Poe, W.E., Nemetz, T.G., MacMillan, J.R., 1988. Effect of recombinant bovine growth hormone administration on growth and body composition of channel catfish. Aquaculture 73, 229–236.