Fish Physiol Biochem (2020) 46:177–186
https://doi.org/10.1007/s10695-019-00707-5

Insulin-like growth factor I of Yellow catfish (*Pelteobagrus fulvidraco*): cDNA characterization, tissue distribution, and expressions in response to starvation and refeeding

Qin Qin · Xiaohui Chen · Xiaochen Zhu · Xiangfei Li · Yingying Zhao · Zhiqiang Xu · Wenbin Liu

Received: 27 May 2019 / Accepted: 4 September 2019 / Published online: 11 November 2019

Abstract The full-length cDNA coding IGF-I was cloned from the liver of Yellow catfish *Pelteobagrus fulvidraco*. The tissue distributions of IGF-I in adults were then analyzed by using real-time PCR. The effects of starvation (3 weeks) and subsequent refeeding (3 weeks) on the compensatory growth performance in juvenile fish weighing 3.80 ± 0.78 g and hepatic IGF-I mRNA expressions were also investigated. The cDNA obtained covered 884 bp with an open reading frame of 480 bp encoding 159 amino acids. It is composed of a signal peptide with 41 amino acids (AAs), a mature peptide comprising the B, C, A, and D domains (71 AAs) and E domain of 47 AAs. Sequence alignment and phylogenetic analysis revealed a high degree of conservation (71–87%) among the species of Siluriformes and some closely related species. In adults, the highest IGF-I expression was observed in the liver, followed by the brain, whereas relatively low expressions were detected in muscle and stomach. Both body weight and length increased significantly in fish fed to satiation continuously. Body weight, body length, condition factor, and hepatic IGF-I expressions were all decreased remarkably with increasing starvation times, but increased significantly after refeeding. The results showed that the expression of IGF-I was positively correlated with feed intakes and IGF-I may play a key regulatory role for somatic growth induced by compensatory growth in Yellow catfish.

Keywords Compensatory growth · Insulin-like growth factor I · Molecular cloning · *Pelteobagrus fulvidraco* · Tissue distribution and expressions

Q. Qin
Surgery of Traditional Chinese Medicine Research Institute, Longhua Hospital Affiliated to Shanghai University of Traditional Chinese Medicine, Shanghai 200032, China

Q. Qin · X. Chen · Z. Xu
Freshwater Fisheries Research Institute of Jiangsu Province, Nanjing 210017, China

X. Zhu · Y. Zhao
Liaoning Provincial key Laboratory of Zoonosis, College of Animal Science & Veterinary Medicine, Shenyang Agricultural University, Shenyang 110866, China

X. Li · W. Liu (✉)
Laboratory of Aquatic Nutrition and Ecology, College of Animal Science and Technology, Nanjing Agricultural University, Nanjing 210095, China
e-mail: wbliu@njau.edu.cn

Introduction

Insulin-like growth factor I (IGF-I) is a mitogenic polypeptide with similar molecular structure to insulin. The structure and elementary endocrine function of IGF-I are highly conserved among vertebrates (Moriyama et al. 2000). In fish, apart from being involved in metabolism (Castillo et al. 2004), reproduction (Weber and Sullivan 2000), development (Pozios et al. 2001), and osmoregulation (McCormick 2001), IGF-I is a primary mediator of the effects of growth hormone (GH) (commonly known as the GH-IGF-I axis). It plays a key part in the regulation of systemic growth and hastens growth

on almost every cell in the organism (Yakar et al. 2002). Considering its critical biological functions, since the first fish IGF-I was isolated from coho salmon (Cao et al. 1989), many studies have reported the characterizations of IGF-I from different fish species (Clay et al. 2005; Sciara et al. 2008; Xu et al. 2014).

Compensatory growth (CG), also known as catch-up growth, is a phase of accelerated growth when favorable conditions are reinstated after a period of growth restraint mainly induced by complete or partial food deprivation (Ali et al. 2003). Because CG results in enhanced food efficiency and growth rate, the studies for CG in cultivated fish have been carried out in last decades (Won and Borski 2013). Although the underlying mechanisms are still poorly understood, the relevant suites of physiological responses are largely governed by the GH-IGF-I axis during the episodes of food deprivation (Cameron et al. 2007; Imsland et al. 2008). Taking this into account, it is of great significance to examine the time-course responses of the IGF-I to food deprivation and refeeding.

Yellow catfish (*Pelteobagrus fulvidraco*) distributes in lakes and river channels in eastern Asia from Laos and Vietnam to southeastern Siberia. Due to its great economic value, tolerance for long distance transportation, and widespread availability of fry, it has now become one of the most important freshwater finfish species in Chinese aquaculture (Wu et al. 2010; Dong et al. 2011; Jia et al. 2016). In 2016, its production was 355,700 tons in China according to the data of Ministry of Agriculture of the People's Republic of China (CFSY, 2016). Therefore, this study was conducted to characterize the full-length cDNAs of the IGF-I of Yellow catfish. The relationship between IGF-I expressions and growth indexes of this species, body weight (BW), body length (BL), and condition factor (CF), was also investigated during starvation and refeeding periods. The data obtained here might illustrate the effects of IGF-I in the compensatory growth of the *P. fulvidraco*. It might also benefit the designation of appropriate feeding strategies to promote compensatory growth in future studies.

Materials and methods

Fish and tissue collection

Juvenile and adult of *P. fulvidraco* were collected from the Freshwater Fisheries Research Institute of Jiangsu Province (Jiangsu, China). Prior to experiments, fish were maintained in a recirculating aquaculture system in the laboratory under the following conditions: water temperature, 25–27 °C; dissolved oxygen (DO), 5.0–6.0 mg/L; pH, 7.2–7.6; photoperiod, 12:12 h (dark:light). Fish were fed with concentrated feed (Ningbo Tech-bank, China), which contains 38% protein and 7% lipid for fortnight.

The samples were anesthetized by diluted MS-222 (tricaine methanesulfonate, Sigma, USA) at the concentration of 100 mg/L. After euthanization, certain tissues from each sample (weight of 101.09 ± 20.2 g) were immediately collected and stored in liquid nitrogen for further study.

Feeding regimes experiment

The juvenile fish (initial weight3.80 ± 0.78 g) were randomly divided into two groups (experimental group and control group). Each group had three replicates, including 30 individuals per subgroup. Whole experiment lasted for 6 weeks, and it included two stages, the starvation stage (weeks 1 to 3) and refeeding stage (weeks 4 to 6). The fish in the control group(C) were fed three times a day (6:30, 12:00, and 17:30) with the commercial diet (Ningbo Tech-bank, China) until satiation throughout the experiment. After the starvation stage, fish in the experimental group were fed to satiety three times a day (6:30, 12:00, and 17:30) in the refeeding stage. Fish were sampled at 0, 7, 14, and 21 days during fasting and at 7, 14, and 21 days during refeeding, respectively. At each sampling time point, three individuals were collected randomly from each subgroup of experiment group (totally nine individuals). After the weight and total length of sampled fish were measured individually, liver tissues were subsequently frozen in liquid nitrogen. Growth indices including final weight and CF were calculated according to the formula $CF = 100 \times (\text{weight}/\text{total length}^3)$.

Isolation of full-length IGF-I cDNA

Total RNA was extracted from the liver tissue of an adult *P. fulvidraco* using Trizol Reagent (Invitrogen, USA), and the remaining DNA was removed by DNase digestion. Primer IGF-I-F and IGF-I-R were designed based on the highly conserved region s of IGF-I from some closely related teleost species to obtain an IGF-I cDNA fragment of the *P. fulvidraco* (Table 1). First-strand

cDNA was synthesized by reverse transcription according to the instructions of Clontech SMARTer™ RACE cDNA Amplification kit (Takara, China).The specific primer was designed based on the obtained IGF-I fragment to perform the 3′/5′-cDNA end amplification (RACE), using SMARTer™ RACE cDNA Amplification Kit (Invitrogen, USA).The obtained PCR products were cloned into a pGEM T-Easy vector (Promega) and sequenced from both directions, which were used to assemble the full-length IGF-I cDNA for the *P. fulvidraco*.

Phylogenetic analysis with homologous genes

Homology search was carried out from NCBI database by the BLASTN and BLASTP (Altschul et al. 1997), and multiple alignments were performed by CLUSTAL X (Thompson et al. 1997). The putative amino acid sequences of the identified IGF-I cDNA and other related sequences were used to build a topological tree via MEGA6.0 with the neighbor-joining (NJ) method (Tamura et al. 2013) with 1000 times bootstrap test.

QPCR analysis

The spleen, anterior intestine, posterior intestine, liver, head kidney, skin, gill, brain, ovary, stomach, testis, muscle, and adipose tissues were collected from six adult *P. fulvidraco* (3 males and 3 females). Total RNA was extracted by Trizol Reagent (Invitrogen, USA), and the quality and quantity of RNA were detected by Nanodrop (Nanodrop Technology, USA). The residual DNA was digested through DNase digestion. QPCR primers for *P. fulvidraco* were designed by the Primer 3. As an internal reference gene, β-actin was used to calibrate the cDNA template. First-strand cDNA was synthesized using SYBR® PrimeScript™ RT-PCR Kit. The amplification program contained 40 cycles of 95 °C for 15 s, 60 °C for 30 s, and 72 °C for 30 s. The $2^{-\Delta\Delta Ct}$ method was used for the analysis of the relative gene expressions of the IGF-I in *P. fulvidraco* (Livak and Schmittgen 2001).

Statistical analysis

Data about IGF-I mRNA expression and the growth performance were recorded, and the normality of distribution and homogeneity of variances was estimated utilizing Kolmogorov-Smirnov test and Levene's test, respectively. One-way ANOVA followed by Duncan's test was employed to estimate the starvation/refeeding effects on growth indices when variances were homogenous. Kruskall-Wallis test was employed if variances were not uniform. Dunnett's T3 test was utilized to analyze the post hoc multiple comparisons of mean values. *t* test or Mann-Whitney *U* test was used to compare the two means depending on homogeneity of variances between treatments, whenever appropriate. IBM SPSS Statistics version 19 was used to perform all the above-mentioned statistical analyses, and significant difference was considered between different treatments if *P* was smaller than 0.05.

Results

IGF-I cDNA sequence features and protein sequence homology with other species

The cDNA of *P. fulvidraco*, with 879 bp in length, containing the open reading frame, the sequence encoding IGF-I and a poly (A) tail, was identified (KX434878). The coding region of 480 bp, which encodes a polypeptide comprising 597 amino acids, was preceded by a 270 bp 5′-UTR and followed by a 134 nt 3′-UTR (Fig. 1). It is composed of a signal peptide (41 aa), domain B (29 aa), domain C (12aa), domain A (21 aa), domain D (9 aa), and domain E (47 aa) (Fig. 2). The predicted mature IGF-I protein has 71 amino acid residues with a calculated molecular mass of 17.58 kD. We compared the protein sequences encoded by IGF-I of *P. fulvidraco* with some closely related species in GenBank. The percent identity between deduced amino acids of IGF-I in *P. fulvidraco* and those of other species was as follows: *Ictalurus punctatus* (87%, NP_001187224.1), *Ctenopharyngodon idella* (85%, ABU40947.1), *Cyprinus carpio* (78%, ABQ08938. 1), *Danio rerio* (77%, NP_571900.1), *Elopichthys bambusa* (77%, AEA72297.1), *Carassius auratus* (76%, ABG75920.1), *Esox lucius* (73%, XP_010902153.1), *Pimephales promelas* (73%, AAT02176.1), and *Salmo salar* (*Atlantic salmon*) (71%, ABO36526.1). IGF-I domains starting locations are indicated at the top of the graphic (B, C, A, D, E). The domain of the IGF genes was underlined. Asterisks indicate the residues of the conserved feature of the IGFBP binding surface on conserved domain IGF.

Table 1 Nucleotide sequences and positions of primers used in the experiment

Primer name	Primer sequence(5′-3′)	Usage
IGF-I-F	GTCTCGCGGCCGCGCGCTC	IGF-I partial fragment amplification
IGF-I-R	TTGCTGAAATAAAAGCCCC	IGF-I partial fragment amplification
HSY-1F	AAACGCTGGGATGTCTAAAGGA	3′RACE
HSY-2Fi	GAGTCGAAGGCGGGTCC	3′RACE
RC36-R2	TCCGCCCCGCACAGGGTCTCAG	5′RACE
RC36-R4	GACCCGCCTTCGACTCCACCG	5′RACE
RC36-Fi	TAATGTAGATAAATGTGAGGGA	IGF-I DNA amplification
HSY-4Ri	CCTCGGCTTGAGTTCTTCTGA	IGF-I DNA amplification
qPCR-F	AACGACTCGAGATGTACTGCG	Primers for qPCR
qPCR-R	GTTTCTTTGGTGTTTTGGACG	Primers for qPCR
β-actin-F	TCCGTGACATCAAGGAGAAGC	Housekeeping gene primers
β-actin-R	AGAGGAGGAAGAGGCAGCAGT	Housekeeping gene primers

Phylogenetic trees for IGF-I

To determine the evolutionary relationships between *P. fulvidraco* and other species, a phylogenetic tree was built based on the results of multiple alignments (Fig. 3).The results present two distinct clades. Amphibians, reptiles, birds, and mammals were in one clade, while Siluriformes, Cypriniformes, Perciformes, Acipenseriforms, and other teleost fish were in the other clade. Among them, *P. fulvidraco* first clustered with *I. punctatus* which was also belonging to order Siluriformes with a high bootstrap value of 100%.

Expression of IGF-I mRNA in *P. fulvidraco* tissues

The expression of IGF-I mRNA was detectable in all tissues involved (Fig. 4). The expression in the liver presents the highest level, while lower expression was found in the brain, spleen, head kidney, and adipose than that of the liver. Detectable amounts of IGF-I mRNA were also found in the posterior intestine, ovary, muscle, skin, gill, anterior intestine, testis, and stomach, with lower expression level.

The growth indexes of fish subjected to different feeding regimes

During the experiment, fish in the control group grew gradually, and starvation of experimental group had significant impact to fish growth and CF (Fig. 5a, b, and c). By the end of the 3-week starvation period, the BL, BW, and CF of the test group were dramatically lower than those of the control group ($P < 0.01$). Specifically, the BL and BW of the starved group were 6.16 cm and 3.01 g in comparison with 7.16 cm and 6.20 g of the control group. The CF values were 1.28 and 1.67 in the experimental group and control group, respectively. After 2 weeks refeeding, the BL and BW of test group increased highly significantly ($P < 0.01$), while CF increased significantly ($P < 0.05$). By the end of the 3-week refeeding, no statistically significant difference was found between the test group and control group ($P > 0.05$).

mRNA expressions of IGF-I in the liver of *P. fulvidraco* subjected to different feeding regimes

Initially, hepatic IGF-I expressions showed slight difference within control treatment ($P > 0.05$). After 1 week, the IGF-I mRNA expressions in the experimental group were significantly lower than those of the control group ($P < 0.05$). After 2 weeks starving, the hepatic IGF-I expressions were decreasing further ($P < 0.01$).

Refeeding of the starving fish increased the hepatic IGF-I expressions significantly ($P < 0.05$). By the end of the 3-week refeeding, the difference between the two groups was not statistically significant anymore.

```
     taatgtagataaatgtgagggatttctccactaaatccgtctcc
     tgtccgctaaatctcacgtctccgaatcgagcctgcgcaatggaa
     caaagtcggaatatcgagacgtgacaccggcaccgcgtttcttcc
     tcgcagcttcttttattgcagctttaaaaaatatatatatatata
     tacatatacatatatatattttaatttacttatattatttta
     ttttaatgactttgggacaagcgtttctccggacaaacgctggg
271  ATGTCTAAAGGACATTTGGGTAATGTCCTAAAGTGGACCATGCGC
       M  S  K  G  H  L  G  N  V  L  K  W  T  M  R
316  TGTGTGTCTCGGGGCCGCGCGCTCTCCCGGCTGCTGCTGCTGTGC
       C  V  S  R  G  R  A  L  S  R  L  L  L  L  C
361  GCGCTCGCGCTGACGCCGGTGGAGTCGAAGGCGGGTCCTGAGACC
       A  L  A  L  T  P  V  E  S  K  A  G  P  E  T
406  CTGTGCGGGGCGGAGCTGGTGGACACGCTGCAGTTTGTGTGCGGA
       L  C  G  A  E  L  V  D  T  L  Q  F  V  C  G
451  GACCGGGGCTTTTATTTCAGCAAGCCAACAGGCTACGGCCCCAAC
       D  R  G  F  Y  F  S  K  P  T  G  Y  G  P  N
496  TCACGGCGCTTGCACAACCGTGGCATTGTAGATGAATGCTGTTTC
       S  R  R  L  H  N  R  G  I  V  D  E  C  C  F
541  CAGAGCTGTGAGCTAAAACGACTCGAGATGTACTGCGCATCAGCC
       Q  S  C  E  L  K  R  L  E  M  Y  C  A  S  A
586  AAGTCTGGTGGTAAAGCTCCAAGATCCGTACGAGAGCAACGGCAC
       K  S  G  G  K  A  P  R  S  V  R  E  Q  R  H
631  ACAGACACGTCCAAAACACCAAAGAAACCTATATCTGGCCACAGC
       T  D  T  S  K  T  P  K  K  P  I  S  G  H  S
676  CAAACACCCTGTAAGGAAGTCCATCAGAAGAACTCAAGCCGAGGA
       Q  T  P  C  K  E  V  H  Q  K  N  S  S  R  G
721  AACACCGGGGGGAGGAACTATCGGATGTAG 750
       N  T  G  G  R  N  Y  R  M  *
     ttaagtgaaggatcggagtggaaatatcggacagtgccgaacgcg
     acggaagagaaagtagaaccttacctggtcttcaagaggaaaaca
     aaacaaacaaacaaacaaacaaaaaaagcaaaacaaaacaaaaa
```

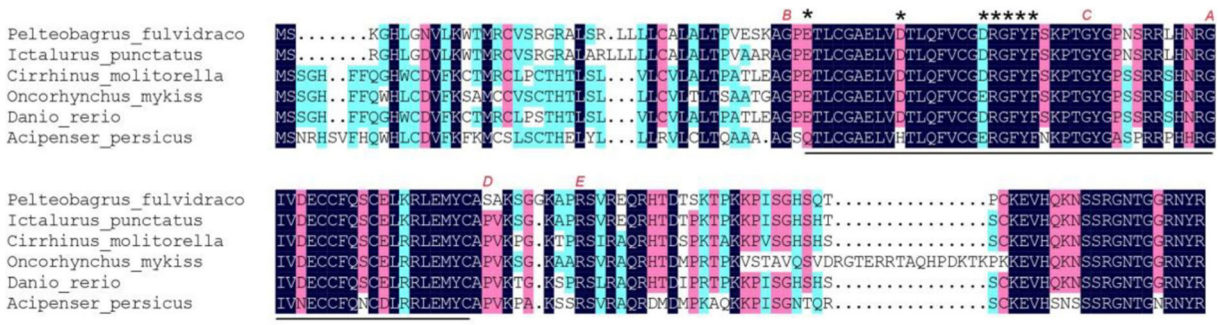

Fig. 1 The complete nucleotide sequence of the pre-pro IGF-I cDNA of *P. fulvidraco*. The lowercase letters are the 3′ untranslated region and 5′ untranslated region. The predicted pre-pro IGF-I peptide contains the signal peptide (residues 1–41, is underlined), the mature peptide (residue 42–112), and the E domain (residues 113–159). Initiation codon (ATG) is boxed and stop codons are shown in italics. IGF domain is in bold letters

Fig. 2 Comparison of the primary amino acid sequence of mature IGF-I of *P. fulvidraco* with some closely related species. IGF-I domains starting locations are indicated at the top of the graphic (B, C, A, D, E). The domain of the IGF genes was underlined. Asterisks indicate the residues of the conserved feature of the IGFBP binding surface on conserved domain IGF

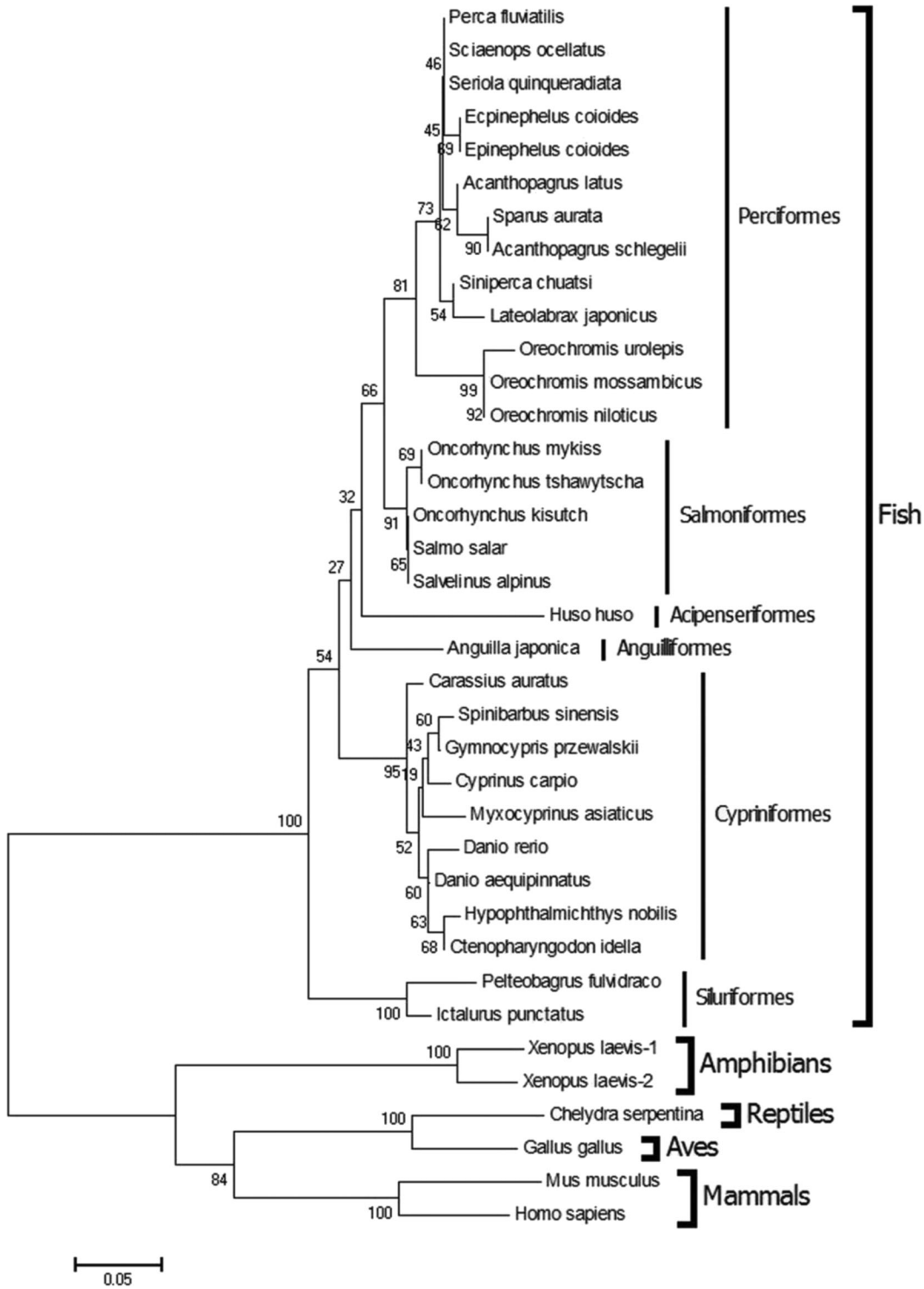

Fig. 3 Neighbor-joining phylogenetic tree IGF-I from *P. fulvidraco* and other species. The IGF-I sequences included in this analysis other than *P. fulvidraco* are *Ictalurus punctatus* (NP_001187224) and *Homo sapiens* (nm_000612)

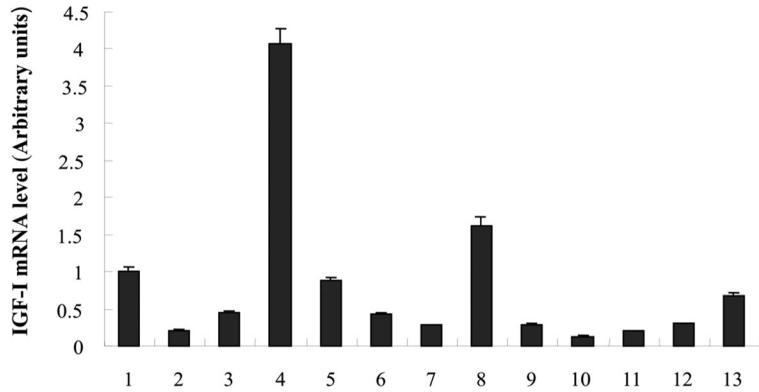

Fig. 4 Reverse transcriptase polymerase chain reaction (RT-PCR) expression analysis on IGF-I gene. For tissue expression, data are referred to the values obtained in the spleen. Each column represents the mean ($n = 3$) and the vertical bars indicate S.E.M. Lanes correspond to (1) spleen, (2) anterior intestine, (3) posterior intestine, (4) liver, (5) head kidney, (6) skin, (7) gill, (8) brain, (9) ovary, (10) stomach, (11) testis, (12) muscle, and (13) adipose

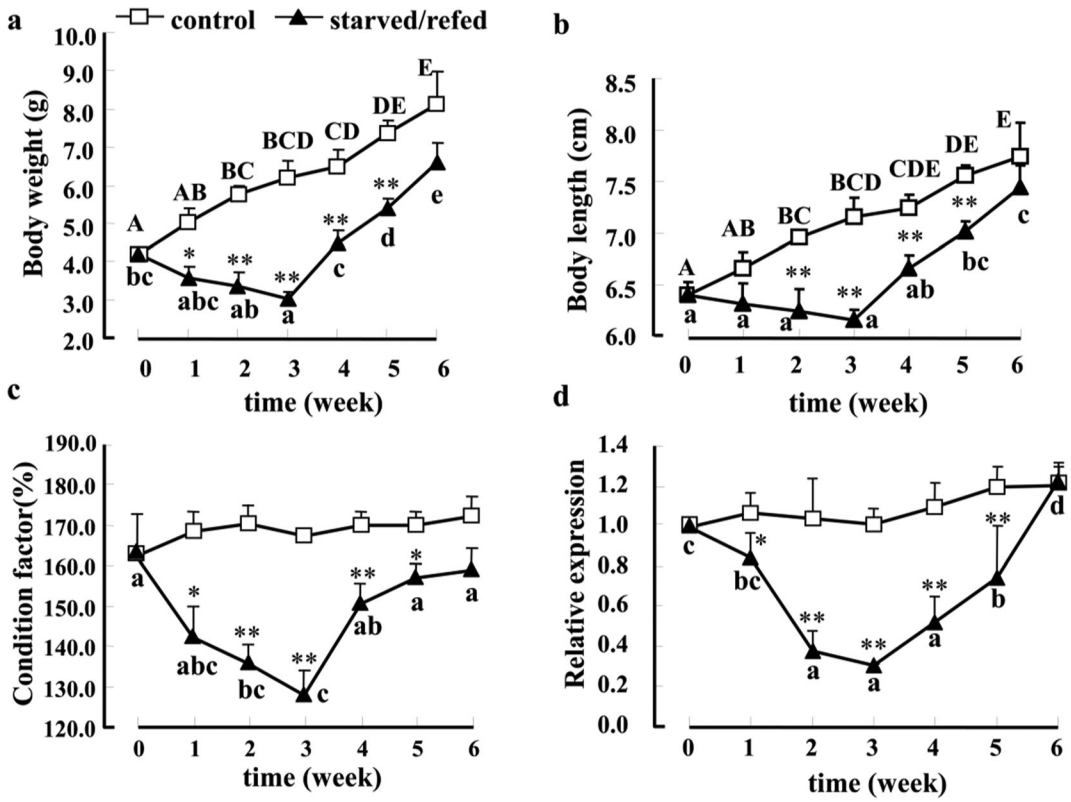

Fig. 5 Changes of body weight (**a**), body length (**b**), condition factor (**c**), and hepatic IGF-I mRNA expression (**d**) of juvenile *P. fulvidraco* subjected to different feeding regimes. Fish in the control group (□) were fed three times a day throughout the experiment. Fish in the test group (▲) were starved for 3 weeks and then refed three times a day for the next 3 weeks. Each point represents the means ± S.E.M. ($n = 9$). Significant differences ($P < 0.05$) among sampling times within each treatment are indicated by different letters (upper case for control, lower case for starved, and refed group). * indicates a significant difference ($P < 0.05$) between the two treatments at each sampling time. **$P < 0.01$

Discussion

In this study, the cloning and characterization of *P. fulvidraco* IGF-I mRNA were described. The deduced amino acid sequence revealed high identity with other teleost fish and other vertebrates. The homology between *P. fulvidraco* and *I. punctatus* is 87%. Because only the two Siluriformes species IGF-I sequences were obtained so far, it seems to be not enough to conclude the homology of IGF-I among all Siluriformes. More IGF-I of Siluriformes and other species needed in-depth study.

The IGF-I mRNA was detected in all tissues we analyzed in *P. fulvidraco* in the present study. Similarly, in other teleosts, birds, and even mammals, the highest IGF-I mRNA expressions were also found in hepatic tissue, while the expressions were detectable but relatively lower in those non-hepatic tissues (Duan et al. 1993; Duguay et al. 1994; Inoue et al. 2003; Vong et al. 2003; Biga et al. 2004; Caelers et al. 2004). These results indicated that extrahepatic IGF-I had tissue-specific paracrine/autocrine functions, which was also common in mammals (Sara and Hall 1990; Jones and Clemmons 1995). In this study, the predominant expression was observed in the liver. The transcript levels in the intestine, spleen, head kidney, and mesenteric adipose tissue were also remarkable. The abundant presence of IGF-I mRNA in liver was not surprising in fish (Moriyama et al. 2000) because the liver was commonly accepted as the most important tissue to synthesize and secrete IGF-I (Shamblott et al. 1995; Moriyama et al. 2000). The relatively high expression found in brain was also justifiable since IGF-I play a critical role in the regulation of cell growth and development, especially in nerve cells (Yakar et al. 2002). However, the aforementioned studies mainly focused on mammals; the functions of IGF-I in neurogenes in fish have still not been well understood and should be studied further. As for the gastrointestinal tract, the moderate abundance could indicate the differential physiology of intestine regions and the response to GH (Sciara et al. 2008). However, after the chronic stimulation of GH, analysis of difference in absorption capacity between the anterior and the posterior intestine may provide an answer to this question. Because this tissue is a complex, essential, and highly active metabolic and endocrine organ, the relatively high expression of IGF-I in adipose was also rational (Kershaw and Flier 2004). It responds to afferent signals from traditional hormone systems and the central nervous system, as well as expresses and secretes factors with important endocrine functions (Kershaw and Flier 2004). Due to the fact that little literature is available concerning the potential roles of the spleen and head kidney in endocrine regulations, the moderate IGF-I expressions in both organs are hard to explain, as warrants further in-depth studies.

The comparison of IGF-I expression between starving and refeeding group in juvenile *P. fulvidraco* was carried out to investigate its potential effects in the systemic growth of fish. Deprivation of food for 1–2 weeks resulted in a remarkable decrease in BW, BL, and CF than those of the fed group ($P < 0.05$). However, all parameters increased significantly after a refeeding period of 3 weeks, and finally there was no statistical difference between the experimental group and the control group ($P > 0.05$). This was the consequence of compensatory growth, which was a common phenomenon that organisms grow rapidly after a period of slow development (Ali et al. 2003; Jobling 2010). Similar findings have also been observed in Atlantic cod (*Gadus morhua*), that complete compensation was observed after 3 weeks fasting (Jobling et al. 1994).

Long-term nutrition deprivation prolonged starvation lead to a remarkable reduction of hepatic IGF-I mRNA expression in *P. fulvidraco* ($P < 0.05$), and refeeding restored the expression to normal level ($P > 0.05$). These results suggested that nutritional condition played a vital role in hepatic IGF-I expressions in teleost fish. Together with the results in growth performance, it suggested that (1) starvation reduced IGF-I mRNA expression in the hepatic tissue as well as systemic tissues, and finally results in growth retardation of *P. fulvidraco*; and (2) refeeding induced an enhanced expression of IGF-I, thus may accelerate the growth rate of this species. However, further investigation concerning the effects of feeding regimes on the entire GH-IGF-I axis is needed to achieve further understanding of functions of this axis, particularly how to regulate the growth of skeleton and the partition of nutrient (Navarro and Gutiérrez 1995; Pérez-Sánchez and Bail 1999).

Funding information This study was funded by the Major Project for New Cultivar Breeding of Jiangsu Province (PZCZ201742) and the China Agriculture Research System (CARS-46). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable Institutional Animal Care and Use Committee (IACUC) of Nanjing Agricultural University were followed by the authors. All efforts were made to minimize the suffering of the animals.

References

Ali M, Nicieza A, Wootton RJ (2003) Compensatory growth in fishes: a response to growth depression. Fish Fish 4:147–190. https://doi.org/10.1046/j.1467-2979.2003.00120.x

Altschul SF, Madden TL, Schäffer AA, Zhang J, Zhang Z, Miller W, Lipman DJ (1997) Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. Nucleic Acids Res 25:3389–3402

Biga PR, Schelling GT, Hardy RW, Cain KD, Overturf K, Ott TL (2004) The effects of recombinant bovine somatotropin (rbST) on tissue IGF-I, IGF-I receptor, and GH mRNA levels in rainbow trout, *Oncorhynchus mykis*. Gen Comp Endocrinol 135: 324–333. https://doi.org/10.1016/j.ygcen.2003.10.014

Caelers A, Berishvili G, Meli ML, Eppler E, Reinecke M (2004) Establishment of a real-time RT-PCR for the determination of absolute amounts of IGF-I and IGF-II gene expression in liver and extrahepatic sites of the tilapia. Gen Comp Endocrinol 137: 196–204. https://doi.org/10.1016/j.ygcen.2004.03.006

Cameron C, Moccia R, Azevedo PA, Leatherland JF (2007) Effect of diet and ration on the relationship between plasma GH and IGF-1 concentrations in Arctic charr, *Salvelinus alpinus* (L.). Aquac Res 38:877–886

Cao QP, Duguay SJ, Plisetskaya E, Steiner DF, Chan SJ (1989) Nucleotide sequence and growth hormone-regulated expression of salmon insulin-like growth factor I mRNA. Mol Endocrinol 3(12):2005–2010

Castillo J, Codina M, Martínez ML, Navarro I, Gutiérrez J (2004) Metabolic and mitogenic effects of IGF-I and insulin on muscle cells of rainbow trout. Am J Phys Regul Integr Comp Phys 283:R647–R652

Clay LA, Wang SY, Wolters WR, Peterson BC, Waldbieser GC (2005) Molecular characterization of the insulin-like growth factor-I (IGF-I) gene in channel catfish (*Ictalurus punctatus*). Biochim Biophys Acta 1731:139–148. https://doi.org/10.1016/j.bbaexp.2005.10.001

Dong Z, Ge J, Li K, Xu Z, Liang D, Li J, Li J, Jia W, Li Y, Dong X, Cao S, Wang X, Pan J, Zhao Q (2011) Heritable targeted inactivation of myostatin gene in yellow catfish (*Pelteobagrus fulvidraco*) using engineered zinc finger nucleases. PLoS One 6(12):e28897

Duan C, Duguay SJ, Plisetskaya EM (1993) Insulin-like growth factor I (IGF-I) mRNA expression in coho salmon, *Oncorhynchus kisutch*: tissue distribution and effects of growth hormone/prolactin family proteins. Fish Physiol Biochem 11:371–379. https://doi.org/10.1007/BF00004587

Duguay SJ, Swanson P, Dickhoff WW (1994) Differential expression and hormonal regulation of alternatively spliced IGF-I mRNA transcripts in salmon. J Mol Endocrinol 12:25–37. https://doi.org/10.1677/jme.0.0120025

Imsland AK, Foss A, Roth B, Stefansson SO, Vikingstad E, Pedersen S, Sandvik T, Norberg B (2008) Plasma insulin-like growth factor-I concentrations and growth in juvenile halibut (*Hippoglossus hippoglossus*): effects of photoperiods and feeding regimes. Comp Biochem Physiol A Mol Integr Physiol 151:66–70. https://doi.org/10.1016/j.cbpa.2008.05.179

Inoue K, Iwatani H, Takei Y (2003) Growth hormone and insulin-like growth factor I of a Euryhaline fish *Cottus kazika*: cDNA cloning and expression after seawater acclimation. Gen Comp Endocrinol 131:77–84. https://doi.org/10.1016/S0016-6480(02)00650-0

Jia B, St-Hilaire S, Singh K, Gardner IA (2016) Farm-level returns and costs of yellow catfish (*pelteobagrus fulvidraco*) aquaculture in Guangdong and Zhejiang provinces, China. Aquaculture Reports 4(C):48–56

Jobling M (2010) Are compensatory growth and catch-up growth two sides of the same coin? Aquac Int 18:501–510. https://doi.org/10.1007/s10499-009-9260-8

Jobling M, Meløy OH, Santos JD, Christiansen B (1994) The compensatory growth response of the Atlantic cod: effects of nutritional history. Aquac Int 2:75–90. https://doi.org/10.1007/BF00128802

Jones JI, Clemmons DR (1995) Insulin-like growth factors and their binding proteins: biological actions. Endocr Rev 16:3–34. https://doi.org/10.1210/edrv-16-1-3

Kershaw EE, Flier JS (2004) Adipose tissue as an endocrine organ. J Clin Endocrinol Metab 89:2548–2556. https://doi.org/10.1210/jc.2004-0395

Livak KJ, Schmittgen TD (2001) Analysis of relative gene expression data using real-time quantitative PCR and the $2^{-\Delta\Delta CT}$ method. METHODS 25:402–408. https://doi.org/10.1006/meth.2001.1262

McCormick SD (2001) Endocrine control of osmoregulation in teleost fish. Am Zool 41:781–794

Ministry of Agriculture of the People's Republic of China (2016) China fishery statistical yearbook. Chinese Agricultural Press, Beijing, p 31

Moriyama S, Ayson FG, Kawauchi H (2000) Growth regulation by insulin-like growth factor-I in fish. Biosci Biotechnol Biochem 64:1553–1562. https://doi.org/10.1271/bbb.64.1553

Navarro I, Gutiérrez J (1995) Fasting and starvation. In: Hochachka PW, Mommsen TP (eds) Biochemistry and molecular biology of fishes, vol 4. Elsevier, Amsterdam, pp 393–434

Pérez-Sánchez J, Bail PYL (1999) Growth hormone axis as marker of nutritional status and growth performance in fish. Aquaculture 177:117–128. https://doi.org/10.1016/S0044-8486(99)00073-3

Pozios KC, Ding J, Degger B, Upton Z, Duan C (2001) IGFs stimulate zebrafish cell proliferation by activating MAP kinase and PI3-kinase-signaling pathways. Am J Phys Regul Integr Comp Phys 280:R1230–R1239

Sara VR, Hall K (1990) Insulin-like growth factors and their binding proteins. Phys Rev 70:591–614. https://doi.org/10.1152/physrev.1990.70.3.591

Sciara AA, Somoza GM, Arranz SE (2008) Insulin-like growth factor-I of pejerrey, *Odontesthes bonariensis*: cDNA characterization, tissue distribution and expression profiles after growth hormone administration. J Exp Zool 309:407–418. https://doi.org/10.1002/jez.466

Shamblott MJ, Cheng CM, Bolt D, Chen TT (1995) Appearance of insulin-like growth factor mRNA in the liver and pyloric ceca of a teleost in response to exogenous growth hormone. P NATL ACAD SCI USA 92:6943–6946. https://doi.org/10.1073/pnas.92.15.6943

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. Mol Biol Evol 30:2725–2729. https://doi.org/10.1093/molbev/mst197

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 25:4876–4882. https://doi.org/10.1093/nar/25.24.4876

Vong QP, Chan KM, Cheng CH (2003) Quantification of common carp (*Cyprinus carpio*) IGF-I and IGF-II mRNA by real-time PCR: differential regulation of expression by GH. J Endocrinol 178:513–521

Wang Y, Cui Y, Yang Y, Cai F (2000) Compensatory growth in hybrid tilapia, *Oreochromis mossambicus* × *O. niloticus*, reared in seawater. AQUACULTURE 189:101–108. https://doi.org/10.1016/S0044-8486(00)00353-7

Weber G, Sullivan CV (2000) Effects of insulin-like growth factor-I on in vitro final oocyte maturation and ovarian steroidogenesis in striped bass, *Morone saxatilis*. Biol Reprod 63:1049–1057

Won ET, Borski RJ (2013) Endocrine regulation of compensatory growth in fish. Front Endocrinol 4:1–13

Wu S, Gao T, Zheng Y, Wang W, Cheng Y, Wang G (2010) Microbial diversityof intestinal contents and mucus in yellow catfish (*Pelteobagrus fulvidraco*). Aquaculture 303(1):1–7

Xu Y, Zang K, Liu X, Shi B, Li C, Shi X (2014) Insulin-like growth factors I and II in starry flounder (*Platichthys stellatus*): molecular cloning and differential expression during embryonic development. Fish Physiol Biochem 41:139–152. https://doi.org/10.1007/s10695-014-0012-y

Yakar S, Rosen CJ, Beamer WG, Ackert-Bicknell CL, Wu Y, Liu JL, Ooi GT, Setser J, Frystyk J, Boisclair YR, LeRoith D (2002) Circulating levels of IGF-I directly regulate bone growth and density. J Clin Invest 110:771–781. https://doi.org/10.1172/JCI15463