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CANDIDATE GENES PROMISING FOR MARKER-ASSISTED SELECTION IN AQUACULTURE

(review)

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Abstract

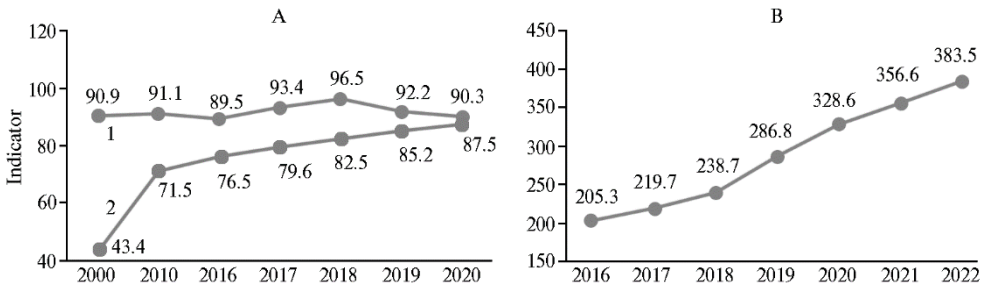
Modern aquaculture is a rapidly developing sector of food production that serves as a source of animal protein, essential amino acids, fats, vitamins, minerals, enzymes and is important for food security. In Russia, commercial fish farming is still significantly inferior in volume to industrial fish farming. A promising approach in the scientific support of commercial aquaculture is the search for polymorphic loci in candidate genes and the identification of reliable associations between various genotypes and productivity indicators for subsequent marker-assisted selection (MAS) of commercial aquaculture objects. The purpose of this review was to summarize and analyze publications concerning single nucleotide polymorphism (SNP) in genes affecting size and weight in fish. Body weight is one of the economically important characteristics for which selection is carried out in fish farms. It depends on the growth of skeletal muscle, so genes that influence the growth and development of muscle tissue are considered as potential candidate genes. The most important of them include the genes for myostatin (*MSTN*), insulin-like growth factors I and II (*IGF-I*, *IGF-II*), growth hormone (*GH*) and growth hormone receptor (*GHR*) (X.Y. Dai et al., 2015; D.L. Li et al., 2014). When assessing the effect of candidate genes on a particular trait, polymorphisms in those genes are first examined, and then the relationship between specific alleles/genotypes and phenotypic expression of the trait of interest is statistically assessed. If significant associations are found, this is considered evidence that the gene is either directly involved in the genetic control of the trait, or the functional polymorphism is located sufficiently close to the marker and the two loci are in linkage disequilibrium (M. Lynch and B. Walsh, 1997; D.L. Yowe and R. J. Epping, 1995). Myostatin plays an important role in inhibiting muscle growth and development. In most mammals, the loss or inactivation of myostatin (*MSTN*–/–) causes an increase in the size and number of myofibers, which leads to an increase in muscle mass (A. Clop et al., 2006; L. Grobet et al., 1997; D.S. Mosher et al. al., 2007; S. Rao et al., 2016). The genes for insulin-like growth factors I and II encode the corresponding polypeptide hormones which have a molecular structure similar to proinsulin and play an important role in regulation of growth, development and differentiation of cells and tissues in vertebrates (J.I. Jones et al., 1995; M Codina et al., 2008). Insulin-like growth factors I and II are the most important endocrine mediators of the action of growth hormone; they are synthesized in the liver, skeletal muscles and other tissues (W.J. Tao and E.G. Boulding, 2003; K.M. Reindl et al., 2011). Growth hormone, or somatotropin, is a polypeptide hormone that is synthesized in the somatotropic cells of the pituitary gland and participates in the regulation of somatic growth in fish (J.I. Johnsson and B.T. Bjцrnsson, 1994; B. Cavari et al., 1993). The growth hormone receptor is a transmembrane protein that belongs to the class 1 cytokine receptor superfamily and serves as an important regulator of growth and metabolism (T. Zhu et al., 2001). GHR as a receptor mediates the biological effects of growth hormone on target cells by transmitting a stimulatory signal across the cell membrane with subsequent induction of transcription of many genes, including *IGF-I* (Y. Kobayashi et al., 1999). SNPs in the genes *MSTN*, *IGF-I*, *IGF-II*, *GH*, *RGH* can affect the size and weight in various fish species and can be an auxiliary tool in breeding programs (D. Gencheva and S. Stoyanova, 2018; C. De-Santis and D.R. Jerry, 2007; Y. Sun et al., 2012). The functional characterization and associations of growth and development indicators with genetic polymorphisms in the genes of myostatin, insulin-like growth factors I and II, growth hormone and growth hormone receptor considered in the review allow us to recommend these genes as the most promising candidates for searching polymorphic loci with subsequent statistical assessment of the genotype—trait

relationship. The reliable associations can be used in marker selection to replace broodstocks and improve the efficiency of commercial aquaculture.

Keywords: candidate genes, aquaculture, body weight, polymorphic locus, marker-assisted selection, MSTN, myostatin, IGF-I, IGF-II, insulin-like growth factors I and II, GH, growth hormone, RGH, growth hormone receptor

Currently, aquaculture is one of the most promising and growing food industries. It has enormous potential to improve food security and meet consumer demand for fish products. According to FAO, over the past 20 years, from 2000 to 2020, global aquaculture production has increased from 43.4 to 87.5 million tons (Fig.) and in 2020 accounted for 49.2% of all fishery production. The growth trend continues and the aquaculture is expected to reach 52% by 2025, exceeding commercial fisheries [1].

Production of aquaculture in the Russian Federation (see Fig.) is constantly growing, from 205.3 thousand tons in 2016 to 383.5 thousand tons in 2022 [2, 3], that is, an average by 11% annually. In 2016, commercial fish farming made 4.3% of total fish production, in 2022, 7.8%, but this is significantly lower than global trends. Nevertheless, Russia has a significant fishing fund and a wide range of artificial breeding facilities that, together with growing demand, create significant potential for domestic aquaculture [4].



World fisheries products (1) **and aquaculture production** (2) (A, million tons**) [1] as compared fo commercial aquaculture** (thousand tons) **in Russia** (B) **[2, 3].**

Improving the efficiency of fish farming requires a thorough understanding of various aspects from breeding practices to molecular technologies. Global experience shows that fish breeding programs in countries with developed aquaculture (China, Korea, Norway, India, Indonesia, and Chile) involve DNA technologies to identify polymorphisms of genes for productivity traits. In Russia, it is also necessary to intensify genetic analysis of fish growth and productivity performance at the levels of genes or gene linkage groups. This will provide gene pool identification in breeding broodstocks and more precise and effective selection based on the polymorphisms of candidate genes that affect economically useful traits.

The purpose of the review is to summarize and analyze data on polymorphisms in genes affecting productivity traits in fish and to identify the most promising candidate genes for use in marker-assisted selection in domestic aquaculture.

Fish growth is economically significant and affects the efficiency of the industry. Body weight and growth rate are the indicators used for selection in fish farms. These indicators depend on the growth of skeletal muscles which account for up to 70% of the fish body weight [5]. Therefore, candidate genes may include genes for growth and development of muscle tissue [6, 7]. Skeletal muscle growth is controlled by a group of genes, the most important are myostatin (*MSTN*), insulin-like growth factors I and II (*IGF-I*, *IGF-II*), growth hormone (GH), and growth hormone receptor (*GHR*). There are reports about associations between polymorphisms of these genes and growth of some fish species in aquaculture, and

on the use of genomic data in marker-assisted selection [8-12].

To reveal the effect of candidate genes on a particular trait, polymorphisms in these genes are first examined, and the relationship between specific alleles/genotypes and phenotypic expression of the trait of interest is statistically assessed. Significant associations evidence that the gene is either directly involved in the genetic control of the trait, or the functional polymorphism is located sufficiently close to the marker and the two loci are in linkage disequilibrium [13, 14].

Let us consider some candidate genes and associations of their polymorphisms with growth and productive performce in fish.

Myostatin (*MSTN* gene). Myostatin, or growth differentiation factor 8 (*GDF-8*), is a member of the transforming growth factor-β (*TGF-β*) family which is critical for inhibiting muscle growth [15, 16]. In most mammals, loss or inactivation of myostatin (MSTN–/–) increases the size and number of myofibers, and, therefore, muscle mass [17-20].

In fish, the *MSTN* gene includes 3 exons and 2 introns; *MSTN* was revealed and characterized in *Salmo salar*, *Oreochromis mossambicus*, *Morone chrysops*, *Danio rerio*, *Lateolabrax japonicus* [21-24]. The *MSTN* gene has different expression profiles in vertebrates. In fish, unlike mammals, *MSTN* is expressed in different tissues and organs in addition to muscles. Thus, a number of studies carried out on various fish species reporte about the myostatin expression in brain, muscles, eyes, liver, ovaries, gills, kidneys, intestines, spleen, and skin [25-30].

Due to broader expression profile, it has been suggested that myostatin may also be involved in the regulation of other physiological processes unrelated to muscle growth [31]. Studies on *Danio rerio* and *Oryzias latipes* showed myostatin effects not only on growth, but also on the immune system [32, 33]. Myostatin is involved in osmoregulation and coordination of neuronal growth and development [34, 35].

Two myostatin isoforms were first identified by real-time PCR in Atlantic salmon (*Salmo salar*) as a non-mammalian species [21]. Four myostatin genes with the same genetic structure, the *MSTN1a*, *MSTN1b*, *MSTN2a*, and *MSTN2b* were foud in *Cyprinus carpio*. The *MSTN1a* and *MSTN1b* paralogs are 96% similar. *MSTN2a*, *MSTN2b* 94% similar. Differences were due to the length and sequence of introns. Two introns in the *MSTN2a* gene were longer than in the *MSTN2b* gene, 1384 bp and 1763 bp vs. 879 bp and 835 bp [36]. L. Liu et al. [37] cloned and characterized the *MSTN* gene of *Aristichthys nobilis* (abbreviated AnMSTN). The *MSTN* genomic sequence is 3769 bp long and consists of three exons and two introns, and the full length cDNA (2141 bp) of the gene had an open reading frame encoding a polypeptide of 375 amino acids. The resulting amino acid sequence of MSTN was 67.1-98.7% homologous to MSTN sequences of birds, mammals and teleosts. Sequence comparison and phylogenetic analysis showed that AnMSTN is the MSNT-1 isoform.

Phylogenetic analysis of the entire myostatin gene subfamily revealed the presence of several *MSTN* forms in teleosts. Genome duplication in the common ancestor of ray-finned fishes resulted in two distinct myostatin clades, *MSTN-1* and *MSTN-2* [38]. The second duplication event in salmonids occurred through tetraploidization and led to two subsequent divisions, one in each clade. This finding indicates that salmonids possess four different myostatin genes, two in the first clade (*MSTN-1a* and *MSTN-1b*) and two in the second clade (*MSTN-2a* and *MSTN-2b*) [39, 40]. Whole-genome duplication in ancient ray-finned fishes followed by tetraploidization in the ancestor of salmonids has complicated genomic studies of candidate genes in these fish because their genomes contain many genes with multiple copies [41].

MSTN is a candidate gene in selection for fish growth parameters that is

confirmed for different fish species (Table 1).

1. Associations of myostatin gene polymorphisms with indicators of fish growth performace

Species	Trait	Position	Authors
Cyprinus carpio	Feed conversion ratio, body weight	c.42A > G c.72C > T	Sun Y. et al., 2012 (44)
Cyprinus carpio	Feed conversion ratio, protein consumption efficiency	T2230C	Al-Khshali M.S. et al., 2020 (46)
Oreochromis niloticus	Body weight	Exon 2	Elkatatny N.A. et al., 2016 (43)
Aristichthys nobilis	Total length, body length, body weight	g.2770C > A	Liu L. et al., 2012 (50)
Salmo salar	Body weight, gutted carcass weight, headless carcass weight, fillet weight	g.1086C > T	Pecaloza C. et al., 2013 (48)
Oncorhynchus mykiss	Body weight, total length	g.1904T > C	Nazari S. et al., 2016 [49]
Verasper variegatus	Body weight, body length, body thickness	T355C	Li H. et al., 2012 [42]
Гибрид *Culter alburnus* (♀) × *Ancherythroculter nigrocauda* (♂)	Body weight, total length, body length, body height, head length	c.6T > C	Cheng L. et al., 2015 [47]
Cyprinus carpio	Average daily growth	C1031T	Yu J.H. et al., 2010 [45]
Ancherythroculter nigrocauda	Body weight, total length, body length, body height	g.1129T > C	Sun Y. et al., 2017 [51]
	Body weight, body height	g.1289G > A	

Single nucleotide polymorphisms (SNPs) in the *MSTN* gene can affect the body weight of fish. For example, SNP T355C in the promoter region of the myostatin gene is associated with growth traits in *Verasper variegatus*. Individuals with the CC genotype were superior in growth rates ($p < 0.01$) to the TC and TT genotypes. Mutations in the promoter may be involved in the control of *MSTN* gene expression, suggesting the possible existence of a regulatory mechanism to alter phenotypes [42].

Association analysis showed that SNPs c.42A > G and c.72C > T in the third exon were significantly associated with body weight ($p < 0.01$) and body condition coefficient ($p < 0.05$) in common carp (*Cyprinus carpio*), and haplotype analysis confirmed this relationship, showing an advantage ($p < 0.01$; $p < 0.05$) of the H7H8 haplotype in terms of growth [44]. In *Cyprinus carpio*, the average daily gains differed significant ($p < 0.05$) between fish with different genotypes for SNP at position C1031T of the *MSTN2a* gene. Correlation analysis showed that individuals with the TT genotype, on average, gain weight faster than carriers of the CT and CC genotypes, 112% vs. 67.3% [45]. For another SNP found in *Cyprinus carpio* at position T2230C, association analysis showed a significant effect ($p < 0.05$) of the polymorphism on feed conversion rate, protein intake, and protein efficiency ratio [46]. L. Cheng and Y.H. Sun [47] identified four new SNPs in the *MSTN* gene in the hybrid *C. alburnus* (♀) × *A. nigrocauda* (♂). One nonsynonymous SNP (c.6T > C) in exon 2 was significantly ($p < 0.01$) associated with body weight, total length, Smith body length, greatest body height, and head length. Fish with the H1H3TGGG/CAGG haplotype combination demonstrated the best growth performance ($p < 0.01$, $p < 0.05$) [47].

Three new SNPs were discovered in the *MSTN-1b* gene of *Salmo salar*. One of them (g.1086C > T) located within the 5′-flanking region had a significant relationship ($p < 0.05$) with body weight, eviscerated carcass weight, headless weight and fillet weight. Analysis of associations based on haplotypes confirmed this findings, since two haplotypes that had a significant association with body weight indicators, the hap4 and hap5 ($p < 0.05$ and $p < 0.01$, respectively) differed by a single substitution g.1086C > T. Alleles at this locus act additively thus providing a small percentage of the genetic variation in these phenotypes [48]. S. Nazari et al. [49] found an association between polymorphism at the g.1904T > C locus of the *MSTN-1* gene and growth performance (body weight and total length) in

domesticated *Oncorhynchus mykiss*. The results showed that rainbow trout with CC and TC genotypes had greater ($p < 0.05$) body weight and total length than those with the TT genotype.

The g.2770C > A polymorphism in the *MSTN-1* gene of *Aristichthys nobilis* is significantly associated ($p < 0.01$) with total length, Smith body length, and body weight [50]. Y. Sun et al. [51], in a sample of 300 *Ancherythroculter nigrocauda* individuals, revelaed a significant relationship ($p < 0.05$, $p < 0.01$) of SNP g.1129T > C with total length, Smith body length, body height and weight whereas SNP g.1289G > A was associated ($p < 0.05$) only with body weight and greatest body height. Fish with TC/TC or TC/GA genotype combinations showed better growth performance. Studies on *Danio rerio* compared the average length and body weight of individuals mutant for the *MSTNa* and *MSTNb* genes with the wild type fish during 1 to 6 months after fertilization. It was found that the body weight and length of fish with the *MSTNa–/–* genotype increased only slightly compared to the wild type, while males and females with *MSTNb–/–* genotypes at the age of 6 months had a significantly higher and wider body (by 62.36%) and greater body weight (by 51.97%).

Insulin-like growth factors I and II (*IGF-I*, *IGF-II* genes). In fish, the insulin-like growth factor (IGF) family includes three IGF peptides (IGF-I, IGF-II, IGF-III), two insulin-like growth factor receptors, and six IGF-binding proteins [52-54]. The genes for insulin-like growth factors I and II encode the corresponding polypeptide hormones which have a molecular structure similar to proinsulin and play a signifint role in regulating growth, development and differentiation of cells and tissues in vertebrates [55, 56]. Insulin-like growth factors I and II are the most important endocrine mediators of the growth hormone action; IGF-I and IGF-II are synthesized in liver, in skeletal muscles and in other tissues [57, 58].

In addition to growth, the *IGF-I* gene in fish is also associated with metabolism, regeneration [59], osmoregulation in seawater [60-62], and regulation of feed intake [63]. The distinct localization of *IGF-I* in the gonads of male and female fish indicates the role of the IGF system in differentiation of the gonads [64-67]. *IGF-I* is also involved in spermogonia proliferation and oocyte maturation [68, 69]. To study the effect of *IGF-I* on fish growth, a transgenic *Oryzias latipes* containing the promoter of the carp β-actin gene fused to the *rtIGF-I* cDNA was produced. The transgenic *Oryzias latipes* not only grew significantly faster than non-transgenic controls, but also hatched 2 days earlier than the control group. These results support the fact that *IGF-I* is involved in the regulation of fish growth and development [70]. Another study found that the expression of *IGF-I* and *IGF-II* in muscle increases dramatically in response to repeated feeding. As a reuslt, *IGF-I* and *FGF-II* are identified as promising candidate genes involved in the cellular signaling system that regulates myotomal muscle fiber growth in fish [71].

Many studies have identified *IGF-1* gene expression in a variety of salmonid tissues, including muscle, spleen, fat, intestine, liver, heart, testes, ovaries, kidneys, pituitary gland, and brain [72-74]. In juvenile carp and tilapia, the *IGF-I* and *IGF-II* genes are similarly widely expressed in different organs and tissues, with the highest levels of expression in the liver [75, 76]. Studies on sturgeon revealed an increase in the expression of the *IGF-II* gene in the spleen, stomach and kidneys compared to the *IGF-I* gene, the *IGF-I* mRNA level was higher in the intestines and muscles, and only in the liver the highest expression of two genes occurred simultaneously [77].

There are distinct differences between the gene structures that determine the synthesis of insulin-like growth factor I in mammals and fish. For example, in humans and rats, IGF-I is encoded by a single gene consisting of six exons spanning

more than 80 Kb of genomic DNA [78, 79], whereas the *IGF-I* genes of fish *Danio rerio*, *Salmo salar* and *Pleuronectes platessa* consist of five exons with the length of approximately 15, 22 and 17.5 thousand bp, respectively [80-82].

At an early stage of evolution of teleosts (approximately 320-350 million years ago), duplication of the entire genome occurred, so their IGF system is complicated by the presence of paralogous genes [83]. Additional forms of this gene arose in salmonids because the whole genome duplication of teleosts was followed by an additional duplication event in the salmon family 25-100 million years ago [84, 85] and also in the cyprinid subfamily [86]. It is estimated that 50% of duplicated genes have been further lost from the genome [87]. The remaining paralogs are undergoing subfunctionalization that modulates their expression [88].

Studies have shown the presence of multiple *IGF-I* mRNA transcripts encoding various IGF-I prohormones in salmonids. These mRNAs were designated Ea-1, Ea-2, Ea-3, and Ea-4 [89]. M.J. Shamblott et al. [90] in research with rainbow trout also detected all four types of *IGF-I* mRNA and four transcripts encoding the four proIGF-Is in salmonids [90, 70]. In *Epinephelus lanceolatus*, two *IGF-I* cDNA precursors were cloned, the *IGF-Ia* and *IGF-Ib* determining sequences of 159 and 186 amino acids, respectively, which are 98.4% and 98.7% identical to *IGF-I* found in *Epinephelus lanceolatus* [91]. M.H. Chen et al. [80] obtained data indicating the presence of two forms of the *IGF-I* gene, the *Ea-1* and *Ea-2* in *Danio rerio*; in another publication, paralogues were also found in the same fish species, the *IGF-1a* and *IGF-1b* for *IGF-I*, and the *IGF-2a* and *IGF-2b* for *IGF-II* [92].

Many studies have been carried out to search for polymorphisms in the *IGF-I*, *IGF-II* genes and assess their relationship with productivity performance of aquaculture objects. Table 2 shows the associations of polymorphisms of genes for insulin-like growth factors I and II with growth and development indicators of some fish species.

2. Associations of *IGF-I* and *IGF-II* gene polymorphisms with indicators of fish growth performace

Species	Trait	Position	Authors
Micropterus salmoides	Body weight, body thickness	5′ flanking region	Li X.H.et al., 2009 [94]
Cyprinus carpio	Body weight, body length	g.7627T > A	Feng X. et al., 2014 [97]
Pseudobagrus fulvidraco × *Pseudobagrus vachellii*	Body weight, fatness, body length, total length, head length, body height, caudal peduncle length, body thickness	97T > C	Chu M.X. et al., 2022 [54]
Oreochromis niloticus	Body weight	G161A	Yu J. et al., 2010 [99]
Salmo salar	Body weight, gutted carcass weight, headless carcass weight, fillet weight	g.5763G > T g.4671A > C	Tsai H.Y. et al., 2014 [93]
Dicentrarchus labrax	Body weight, total length	g.5127731G > T	Gokcek O.E. et al., 2020 [102]
Dicentrarchus labrax	Body weight, total length Total length	g.46749C > T g.46672A > G	Gokcek O.E. and Isık R., 2020 [103]
Sander lucioperca	Body weight	c.544+1111_544+1112 delAAinsTC	Teng T. et al.,2020 [98]
Lateolabrax maculatus	Head length, body thickness Total length Head length, body thickness Standard length	g2907C > T g3230A > C g3294C > T g5064C > T	Fan S. et al., 2023 [101]

In *Salmo salar*, three SNPs were identified in the *IGF-I* gene, namely, in the promoter (SNP1, g.5763G > T), in intron 1 (SNP2, g.7292C > T) and in intron 3 (SNP3, g.4671A > C). It was found that SNP1 and SNP3 were significantly associated with several weight traits ($p < 0.05$). Haplotype analysis confirmed the association ($p < 0.05$) between genetic variations in the *IGF-I* gene and total body weight, as well as fillet characteristics [93]. X.H. Li et al. [94] found that polymorphisms in the *IGF-I* gene promoter influence body weight and thickness

in a population of *Micropterus salmoides*. Fish with the AA genotype had significantly greater body weight and size than fish with the AB or BB genotypes. Polymorphisms in the promoter region and missense mutations in coding regions, unlike intronic polymorphisms or silent mutations in the coding regionare, seem to be related directly to the parameters affected by the candidate gene [95]. In another study [96], four SNPs (C127T, T1012G, C1836T, and C1861T) were found in the *IGF-II* gene in *Micropterus salmoides*. Association analysis showed that SNPs were not significantly associated with growth characteristics. However, significant associations ($p < 0.05$) were identified between diplotypes. Diplotypes H1H3 (CDCC/CDCC CDCC) and H1H5 (CTCC/TTTT) produced greater body weight than diplotypes H1H1 (CTCC/CTCCC), H1H2 (CTC/TGT) and H4H4 (TGC/TGC).

In the common carp (*Cyprinus carpio*), SNP g.7627T > A was identified in intron 2 of the *IGF-I* gene, which was significantly associated ($p < 0.05$) with body weight and length. The AA genotypes had a 5.9% higher average body weight than the TT genotypes [97]. In a cultivated population of *Sander lucioperca*, a SNP was found in intron 3 of the *IGF-II* gene, which has a significant correlation ($p < 0.05$) with body weight [98].

In a study on 264 *Pseudobagrus fulvidraco* × *Pseudobagrus vachellii* hybrids, one non-synonymous mutation (SNP 97T > C) was identified in the *IGF-II* gene, which was significantly associated ($p < 0.05$) with growth traits (Smith body length, total length, head length, maximum body height, caudal peduncle length, body thickness, body weight and fatness). This relationship was confirmed ($p < 0.05$) in the second population of 183 individuals [54]. In *Oreochromis niloticus* males of the GIFT breed, two G161A polymorphisms in exon 3 and a microsatellite locus in intron 3 identified in the *IGF-II* gene were significantly associated with growth. Different genotypes affected the growth rate in males ($p < 0.01$), the weight of males with the GG genotype (532 g) was 15.7% greater than that of carriers of the AG genotype (454 g). No differences were found in the growth rate of females [99]. These data are supported by another study which also found an association between a polymorphism in exon 3 of the *IGF-II* gene and body size in the GIFT population of *Oreochromis niloticus* [100].

Sequencing the *IGF-II* gene of *Lateolabrax maculatus* revealed four SNPs that significantly correlated with growth traits ($p < 0.05$). SNP g2907C > T was associated with head length and body thickness, SNP g3230A > C with total length, and SNP g3294C > T with body thickness and head length. Genotypes with SNP g5064C > T significantly differed in Smith body length [101]. Several single nucleotide polymorphisms in the *IGF-I* and *IGF-II* genes have been identified in the *Dicentrarchus labrax* population. In the 5′UTR region of the *IGF-I* gene, a relationship was found ($p < 0.05$) between SNP g.46749C > T and body weight, total length, as well as between SNP g.46672A > G and total length ($p < 0.05$). Fish with the GG genotype (*IGF-II-NdeI* locus) had greater body weight and total length ($p < 0.05$) than fish with the TG genotype [102, 103]. Overall, the research highlight the importance of the IGF system in indirectly affecting the growth and development of fish and show the possibility of using the *IGF-I* and *IGF-II* genes as genetic markers in aquaculture breeding.

Growth hormone (*GH* gene). Growth hormone, or somatotropin, is a polypeptide synthesized in the somatotropic cells of the pituitary gland. GH plays an important role in the regulation of fish somatic growth [104-107], osmoregulation [108-110], reproduction [111, 112], regulation of lipid and protein metabolism, carbohydrate metabolism through complex interactions with insulin and insulin-like growth factor 1 [113-115], in immunity responces [116, 117]. Moreover, investigations have shown that growth hormone also affects behavioral

responses such as appetite and foraging in rainbow trout and transgenic *Atlantic salmon* [118]. In salmonids, as in mammals, it is clearly evidenced that growth hormone is the major activator of the IGF system, since GH stimulates the expression of *IGF-I* and *IGF-II* genes in both the liver and other tissues [119-121].

Variability is a characteristic feature of the growth hormone gene in fish, distinguishes it from conservative growth hormone gene in mammals [122]. The growth hormone gene identified in *Ctenopharyngodon idellus*, *Hypophthalmichthys molitrix*, *Cyprinus carpio*, *Labeo rohita*, *Ictalurus punctatus*, and *Sarcocheilichthys sinensis* has five exons and four introns [123-128] that is similar to the *GH* structure in mammals [129]. However, among other teleost fish there are species in which the growth hormone gene consists of six exons and five introns, for example, *Salmo salar*, *Oncorhynch nerka*, *Oncorhynchus mykiss*, *Tilapia nilotica*, *Fugu rubripe*s, *Sparus aurata* [105, 130-134]. In many fish species, the growth hormone gene has a higher level of variation in non-coding regions than in other vertebrates, which is due to the presence of two functional copies of the gene, *GH1* and *GH2*. Two paralogues of the growth hormone gene were identified in *Oncorhynch nerka*, *Tilapia nilotica*, *Carassius auratus*, *Oncorhynchus tshawytscha*, *Cyprinus carpio*, *Salmo salar*, and *Oncorhynchus mykiss* [132, 135-140]. Expression of the hormone gene occurs in many tissues and organs, including the brain, liver, muscle, heart, spleen, kidneys, and ovaries, but the highest expression is found in the pituitary gland [91, 128, 141].

Complete or partial sequencing of the growth hormone gene in different fish species has revealed single-nucleotide polymorphisms and microsatellites which are proposed for marker-assissted selection. Table 3 presents associations of polymorphisms of the growth hormone gene with indicators of fish growth and development.

In the common carp (*Cyprinus carpio*), SNP A1132T was identified in intron 3 of the *GH* gene. Fish with the AA genotype had a significant superiority ($p < 0.05$) in body weight at the end of the growing period, average daily gain, relative growth rate, and specific growth rate over carriers of the AT and TT genotypes [142]. Correlation analysis (marker–trait) based on a general linear model (GLM) also showed a significant association between *GH-1* gene genotypes in *Cyprinus carpio* and body weight. The body weight of fish with genotype D was significantly ($p < 0.05$) greater compared to other genotypes [143].

3. Associations of the growth hormone gene polymorphisms with indicators of fish growth performace

Species	Trait	Position	Authors
Cyprinus carpio	Body weight, average daily gain, relative growth rate, specific growth rate	A1132T	Al-Azzawy M.A. et al., 2018 [142]
Cyprinus carpio	Body weight		Berenjkar N. et al., 2018 [143]
Sarcocheilichthys sinensis	Body length, total length, body weight, body height, body thickness, body condition factor	g.1541A > G	Zhu T. et al., 2020 [128]
	Body condition factor	g.242InDel	
Paralichthys olivaceus	Body weight, head length	1763(C > T)	Ni J. et al., 2006 [148]
Siniperca chuatsi	Body weight, total length, body length, body height	g.4940A > C	Tian C. et al., 2014 [144]
	Total length, body height	g.4948A > T	
	Body length	g.5045T > C	
Larimichthys crocea	Body weight, body length	(T > C) 692	Ni J. et al., 2012 [147]
Oreochromis niloticus	Body weight, gutted carcass weight, fillet weight, fillet length		Tanamati F. et al., 2015 [150]
Oreochromis niloticus	Total length, body length, body height, body thickness	Intron 1	Blanck D.V. et al., 2009 [151]
Oreochromis niloticus	Body weight	Promoter	Dias M.A. et al., 2019 [153]
Siniperca chuatsi	Body weight, body length, body thickness	g.5234T > G	Wang H. et al., 2016 [145]
	Body thickness	g.5045T > C	

Continued Table 3

Sparus aurata	Body weight	Promoter	Almuly R. et al., 2005 [149]
Siniperca chuatsi	Body weight, total length, body length, body height, head length	G1g.197C > A	Sun C.-F., et al., 2019 [146]
	Head length	G2g.2558C > G	
	Body weight, total length, body length, head length	G3 .2643C > G	

Four SNPs were identified in the *GH* gene of *Siniperca chuatsi* three of which have a significant correlation ($p < 0.05$) with growth parameters. Individuals with the CC genotype (g.4940A > C) had greater body weight, total length, Smith body length and body height than fish with the AA or AC genotypes. The carriers of the TT genotype (g.4948A > T) were superior to the genotypes AA or AT in height and the total body length, and fish with the genotype CC (g.5045T > C) had significant differences only in Smith body length [144]. In another study, two SNPs in exon 5 (g.5045T > C) and intron 5 (g.5234T > G) identified in *Siniperca chuatsi* were significantly associated with growth performance. Fish with the GG genotype (g.5234T > G) were significantly superior to carriers of the TT and TG genotypes in body weight ($p < 0.01$), Smith body length ($p < 0.05$) and body thickness ($p < 0.01$). The g.5045T > C locus significantly influenced ($p < 0.05$) only body thickness [145]. Analyzing the results of two previous studies, it should be noted that SNP g.5045T > C had a significant effect on productive indicators in two different populations of *Siniperca chuatsi*, which once again confirms the promise of this polymorphism in marker-assisted selection of this fish species. C. Sun et al. [146] identified four loci that significantly correlated with growth traits in *Siniperca chuatsi*. Loci G1 (g.197C > A), G3 (G3 g.2643C > G) and GH-AG are associated ($p < 0.01$) with body weight, total length, Smith body length, greatest body height and head length.

J. Ni et al. [147] in a *Larimichthys crocea* population from Zhejiang, identified a SNP (G→A) at position 196 of intron 1 of the *GH* gene associated with the highest body height ($p \leq 0.05$). In the population from Fujian, a SNP at position 692 (T→C) was identified in intron 2. The CD genotype had a positive correlation with body weight and total body length ($p \leq 0.01$). In P*aralichthys olivaceus*, in exon 4 of the growth hormone gene, one nonsynonymous mutation was identified at position 1763 (C > T), which positively correlates ($p < 0.05$) in the AB genotype with body weight and long head [148]. It was shown that in *Sarcocheilichthys sinensis* the polymorphic locus g.242InDel is associated ($p < 0.05$) with the fatness coefficient, and the polymorphism g.1541A > G ($p < 0.01$; $p < 0.05$) is associated with Smith body length, total length, greatest body height, body weight, body thickness and body condition index [128]. In the *Sparus aurata* population from the hatchery, a dinucleotide microsatellite polymorphism was detected in the promoter region of the growth hormone gene. Alleles 250 and 254 were found to be associated with the weight of the studied fish [149].

F. Tanamati et al. [150] identified polymorphisms in the *GH* promoter region in *Oreochromis niloticus*. Carriers of the *GH*db genotype had significantly heavier ($p < 0.05$) body weight, eviscerated carcass weight, as well as fillet weight and length, which indicates a correlation between *GH* variations and productivity traits in *Oreochromis niloticus*. D.V. Blanck et al. [151] described a polymorphism in intron 1 of the *GH1* gene in *Tilapia nilotica* that has a significant correlation with total length, standard length, and body height and thickness. It was found that the PstI+/– genotype is associated with better performance regardless of the fish breed. The authors believe that this association may be due to a direct effect of the *GH* gene's own regulation. S.K. Jaser et al. [152] and M.A. Dias et al. [153] also found SNPs in the promoter region of the growth hormone gene associated with fish growth performance in *Oreochromis niloticus*.

Growth hormone receptor (*GHR* gene). The growth hormone receptor, a transmembrane protein of the class 1 cytokine receptor superfamily [154] is a critical regulator of growth and metabolism. GHR, as a receptor, mediates the biological effects of growth hormone on target cells by transmitting a stimulatory signal across the cell membrane, followed by induction of transcription of many genes, including *IGF-I* [155].

In fish, the growth hormone receptor gene contains ten exons and is present as a double copy, the *GHR-I* and *GHR-II*, in *Paralichtys olivaceus*, *Salmo salar*, *Oncorhynchus mykiss*, *Sparus aurata*, and *Anguilla japonica* [156-159]. The *GHR-I* and *GHR-II* genes are highly transcribed, but their expression is unevenly localized showing some tissue specificity, i.e., the *GHR-I* expression in the liver and adipose tissue exceeds the *GHR-II* expression [158].

4. Associations of the growth hormone receptor gene *GHR* polymorphisms with indicators of fish growth performace

Species	Trait	Position	Authors
Pangasianodon hypophthalmus	Body length, body height, caudal peduncle length	SNP1 A > G	Jiang L.-S. et al., 2022 [160]
	Body length, body height	SNP2 T > G	
	Body weight, total length	SNP3 G > C	
	Body height	SNP4 A > G	
Oreochromis niloticus	Body weigh	2116C > A 2117A > G	Aboukila R.S. et al., 2021 [5]
Cynoglossus semilaevis	Body weight, gonad weight	c.G1357A	Zhao J.L, 2015 [163]
Oreochromis niloticus	Body weight, total length, head length, body height, body thickness, caudal peduncle length	Exon6_G121A Exon7_G72A Exon10_T66A Exon10_T129G Exon10_C153A	Chen B-L. et al., 2020 [162]
Culter alburnus	Body weight, body length, body height	Cal-GHR2-1	Liu Z.J. et al., 2020 [161]
	Body weight, body length	Cal-GHR2-3	
	Body mass	Cal-GHR2-4	

The growth hormone receptor is an important regulatory factor of the growth axis with great potential for use in fish marker-assisted selection. *GHR* genetic polymorphisms may interfere with normal GH function, thereby influencing growth traits. Therefore, an underlying mutation in the growth hormone receptor gene can affect its expression level [141, 160]. Table 4 presents associations of the *GHR* gene polymorphisms with indicators of fish growth performance.

L.-S. Jiang et al. [160] identified five SNPs in the 3′UTR of the growth hormone receptor gene in *Pangasianodon hypophthalmus*. It was found that fish with the GG genotype (SNP1 A > G) had greater Smith body length, the greatest body height and the length of the caudal peduncle ($p < 0.05$) compared to the AA genotype. In SNP2 T > G, the GG genotype was superior to the TT genotype in Smith body length, greatest body height and caudal peduncle length ($p < 0.05$). Fish with the GG genotype (SNP3 G > C) were significantly superior ($p < 0.05$) to carriers of the GC genotype in body weight and total length. The GG genotype (SNP4 A > G) had superiority in body height ($p < 0.05$). In another study, correlation analysis showed that four polymorphic microsatellite loci were significantly associated ($p < 0.05$) with growth traits in *Culter alburnus*. The Cal-GHR2-1 locus was associated with Smith body length and body weight, the Cal-GHR2-3 locus with body length and body weight, and the Cal-GHR2-4 locus with only body weight [161].

In *Oreochromis niloticus*, a significant relationship was revealed between polymorphisms of the Exon6_G121A, Exon7_G72A, Exon10_T66A, Ex-on10_T129G, Exon10_C153A, G214C loci of the *GHR1* gene and body weight, total length, head length, maximum body height, body thickness, and caudal peduncle length in Nile tilapia [162]. Two more weight-related SNPs at positions 2116C > A and

2117A > G of the growth hormone receptor gene were identified in *Oreochromis niloticus* [5]. In *Cynoglossus semilaevis*, an association ($p < 0.01$) of the c.G1357A locus of the *GHR* gene with body weight and gonad weight was detected [163].

Summarizing the review materials, we can conclude that in countries with developed aquaculture, genetic research is an integral part of programs to reduce long and labor-intensive periods of fish farming, and to increase the yield of marketable products. In the Russian Federation, genetic technologies has ensured identification of desirable genotypes in livestock, which has improved animal breeding programs [164-169].

Thus, many publications confirm functional parameters and associations of fish growth and productivity performance with genetic polymorphisms in the genes of myostatin, insulin-like growth factors I and II, growth hormone, and growth hormone receptor. Therefore, we can conclude that the *MSTN*, *IGF-I*, *IGF-II*, *GH*, and *GHR* are candidate genes the most promising for searching polymorphic loci and genotype–trait associations. The reliable associations can be involved in marker-assisted selection and replacement of broodstocks to improve the efficiency of commercial aquaculture.

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