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Understanding fish muscle growth regulation to optimize aquaculture production

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ABSTRACT

Aquaculture has become an agronomic activity with noticeable development around the world to respond to the simultaneous decrease of fish captures and the increasing demand of aquatic products for human consumption. However, different problems limit the development of this industry and one of those is the time required for most of the cultured fish species to achieve economically viable the commercial size. The knowledge up to date of the regulatory systems involved in controlling growth has improved very much but, it is still necessary to devote efforts to transform the basic information in application to fish culture production. The aim of the present review is to summarize the knowledge acquired with the studies about the GH/IGF axis and other hormones regarding their function on the regulation of fish muscle development and growth. To this end, GH and IGFs effects in muscle cells on metabolism and development are examined, as well as the contribution of IGF-I binding proteins, IGF-I receptors and their downstream regulated molecules like TOR and its relation with cell proliferation and differentiation and the myogenic regulatory factors. The effect of regulatory molecules on cultured myocytes are reviewed as well as in vivo responses, including the model of sustained and maintained swimming. Key aspects we consider should be further investigated to complete the scenario of the regulation of fish muscle are also proposed.

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1. Introduction

The double role of muscle, mechanic and metabolic, requires specific regulatory systems that furthermore will change as a function of age, reproductive stage and during annual cycles. It should be also considered that under the name of muscle there is a big variety of tissues performing different functions including, for instance, the slow and fast skeletal muscles; although most of the information available refers to fast skeletal muscle that is also the most interesting part of body fish in terms of aquaculture product (Mommsen, 2001).

Among the regulatory systems, hormones play an essential role through a systemic action that will affect all target tissues. But there are also the local actions that in the case of the growth hormone (GH) and insulin-like growth factors (IGFs) modulate effects in specific tissues such as the muscle. In fact, the GH/IGF axis is considered the most important endocrine system regulating skeletal growth, although modulation of other hormones like insulin, thyroid hormones, steroids, etc. allows the fine control of muscle growth and development as well

as the adaptation to endogenous and external changes (Moomsen and Moon, 2001).

The myogenic regulatory factors (MRFs) represent another important group of molecules that exert a significant role specially for muscle development but also during the period of compensatory growth after fasting or reproductive stage, as well as for tissue regeneration after an injury. MRFs, myocyte enhancer factors (MEFs) and myostatin are the best known molecules involved but, there are other factors less specific for muscle that also have important roles during myogenesis (e.g. FGF, HGF, PAX, Sox, etc.) (Fuentes et al., 2013). Moreover, in recent years, the target of rapamycin (TOR) complex has appeared as an important level of integration between nutritional and endocrine inputs to improve growth (Vélez et al., 2014, 2016), which is of significant interest for fish culture.

Due to the dynamic role of muscle from a metabolic point of view, the endogenous proteolytic systems, which include the calpains, the cathepsins and the ubiquitin-proteasome system, are considered also key regulatory factors controlling growth potential. They are very important systems in a tissue that often changes its metabolic role from an anabolic and synthetic side to a proteolytic mode to provide the organism with a supplementary load of amino acids and energy.

Muscle growth in fish has also a differential trait from other vertebrates seen in many species, that of continuous growth. This fact

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determines that after sexual maturation fish continue to grow still with important rates of muscle hyperplasia in comparison with most mammals, which can change muscle mass only by hypertrophy (Stickland, 1983). Furthermore, this also occurs in a reduced group of fish species (e.g. zebrafish, *Danio rerio*) that has been dubbed as a determined growth species (Biga and Goetz, 2006). Continuous growth in fish offers an interesting model of research on the role of stem cells, and also gives valuable possibilities for application to aquaculture.

In the last years, different publications have claimed the interest of exercise as a mechanism to improve fish aquaculture production, providing good results in growth and flesh quality. In mammals, it is well known that exercise stimulates a GH response that consequently provokes skeletal growth. Thus, it is interesting to consider the possibility of applying exercise during fish growth, which furthermore, due to the high level of muscle plasticity, can respond with hyperplasia, which has been demonstrated to be very important for flesh quality (Blasco et al., 2015).

Our group has a long history in the research of fish metabolism and endocrinology and in the last years has focused its attention in the regulation and improvement of fish growth by means of in vitro and in vivo approaches. The aim of this review is to summarize the current information in fish muscle growth regulation, focusing primarily in GH/IGF axis and its systemic and local actions on myocytes, and to propose new molecules and approaches that can be interesting for basic research and its application for fish aquaculture.

2. Endocrine regulation of fish muscle growth

2.1. Growth hormone effects

The GH/IGF axis is the main regulator of growth in vertebrates; its role in fish has been demonstrated in many species and previously reviewed (Company et al., 2001; Reinecke et al., 2005; Reinecke, 2010; Reindl and Sheridan, 2012; Fuentes et al., 2013). GH exerts significant metabolic effects, as the regulation of muscle protein synthesis, determining an increase on growth by both hyperplasia and hypertrophy. There are many references describing the effects of GH treatment on muscle protein synthesis, muscle growth acceleration, hyperplasia, muscle accretion, etc. (reviewed in: Moomsen and Moon, 2001). Furthermore, it should be taken into account that the indirect effects of GH in fish growth can increase appetite or the intestinal nutrient uptake. An interesting aspect to consider is what part of the GH effect corresponds to its direct action on muscle and what is mediated through IGFs secreted by the liver under GH stimulation.

In this sense, several studies in salmonids have demonstrated that a GH chronic treatment causes an increase in plasma IGF-I levels (Biga et al., 2005; Raven et al., 2012; Kling et al., 2012). Moreover, such a treatment provoked an increase in IGF-I gene expression in the liver in coho salmon (*Oncorhynchus kisutch*) (Raven et al., 2012) as well as also in muscle and other tissues in rainbow trout (*Oncorhynchus mykiss*) (Biga et al., 2004b), thus supporting both systemic and local paracrine/autocrine actions for GH and IGFs.

The studies on GH receptors and their signal transduction are rather recent, and have demonstrated the existence of two main receptors (GHR-I and GHR-II) with complementary functions (Fuentes et al., 2013). Truncated variants of GHR-I (tGHR-I) have been characterized in turbot (*Scophthalmus maximus*) (Calduch-Giner et al., 2001), and in other related species as Japanese flounder (*Paralichthys olivaceus*) (Nakao et al., 2004) or fine flounder (*Paralichthys adspersus*) (Fuentes et al., 2012). In the last case, tGHR-I has been postulated as responsible for the slow growth of this species. Two different GH receptors were also described in several other fish species (Tse et al., 2003; Benedet et al., 2005; Saera-Vila et al., 2005; Jiao et al., 2006; Walock et al., 2014) and in gilthead sea bream muscle (*Sparus aurata*), different responses to fasting and re-feeding were described (Saera-Vila et al., 2005). We have recently observed that both muscle GH receptors play different

roles in gilthead sea bream adapted to exercise (Vélez et al., 2016). These results agree with the fact that, in gilthead sea bream, GHR-I seems to be more involved in anabolic signals, while GHR-II is directed towards energy depot mobilization, although more studies are required in different species and conditions to generalize these results. Fish GH receptor signaling is even a younger discipline and Fuentes et al. (2013) have reviewed the state of the art. Although the main pathways are well conserved among vertebrates, it seems that both isoforms use slightly different transduction molecules (Jiao et al., 2006; Kittilson et al., 2011; Fuentes et al., 2012) with GHR-I working more through STAT5 and GHR-II through ERK (Kittilson et al., 2011). Fuentes et al. (2012) pointed out that in fine flounder, the JAK2/STAT5 pathway is inactivated during fasting but reactivated with nutritionally favorable conditions, which is in agreement with the GH receptor division of function observed in gilthead sea bream.

There are not many studies on the direct effect of GH on muscle but Rius-Francino et al. (2011) demonstrated the stimulatory effect of gilthead sea bream GH on proliferation of cultured gilthead sea bream myocytes (Fig. 1 insert). Interestingly stronger stimulatory effects on myocytes proliferation were obtained when GH was administrated together with IGF-I or IGF-II (Fig. 1). The GH transgenic coho salmon (Devlin et al., 1994) has represented a valuable model to study the biology of growth, metabolism and behavior (Abernathy et al., 2015; de la García et al., 2015; Chen et al., 2015; Kim et al., 2015a, 2015b) showing that GH overexpression produces both muscle hyperplasia and hypertrophy. Levesque et al. (2008) summarized the main facts that explain the higher growth in GH transgenic Atlantic salmon (*Salmo salar*), comprising the higher numbers of myogenic precursor cells, their proliferation rates and their direct proliferative response to GH treatment. GH transgenic fish have been obtained for other species like rainbow trout, carp (*Cyprinus carpio*), tilapia (*Oreochromis niloticus*), channel catfish (*Ictalurus punctatus*) or zebrafish (Devlin et al., 2001; Rasmussen and Morrissey, 2007; Figueiredo et al., 2007).

The different experiments of GH treatments (Raven et al., 2012; Kling et al., 2012; Biga et al., 2004a, 2004b, 2005; Gahr et al., 2008) demonstrated the effects of this hormone on metabolism and muscle growth. Biga et al. (2004a) found that GH treatment in rainbow trout increases myosin protein levels, thus regulating the expression of the most abundant muscle protein. Gahr et al. (2008) reported that even after short-term treatment, GH augmentation alters the expression of genes involved in metabolism and growth regulation in rainbow trout.

Nevertheless, Biga and Mayer (2009), showed a differential regulation of the growth-related genes as effect of GH treatment, in a comparative experiment with an indetermined and a determined growth fish species (i.e. giant danio, *Danio aequipinnatus* and zebrafish, respectively). In this work, the IGF-I and GHR-I expression was higher in giant danio muscle than in zebrafish. However, the same treatment increased the myostatin expression in zebrafish, whereas it was down-regulated in the case of giant danio. These results suggest that myostatin could be responsible for limiting the growth stimulation caused by GH treatment in this determinate-growth species (zebrafish).

Interestingly, GH transgenic fish were unable to respond to GH treatment, indicating that transgenic fish show certain level of saturation on stimulatory growth pathways (Raven et al., 2012). Recently, we have treated gilthead sea bream fingerlings and juveniles with GH (Vélez et al., unpublished data) and results demonstrated also in this species a growth increase and diminution of fat depots.

On the other hand, GH immunoneutralization in rainbow trout (Fauconneau et al., 1996) decreased mainly muscle protein synthesis, together with a decrease in body weight. In zebrafish, Silva et al. (2015) achieved a double mutant for GH and GHR that resulted in lower weight and a strong decrease of the somatotrophic axis intracellular signaling by diminishing its signal transducer (STAT5.1). McMenamin et al. (2013) identified a zebrafish GH1 mutant, vizzini, which exhibited abnormal small body size and increased accumulation of adipose tissue. All these results support the direct action of GH on

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