



Review Article

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What Indicators Could be Useful to Understand the Development of Digestive Tract, During the Early Ontogeny of Teleost Fish?



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Abstract

Nowadays, the most of studies about the digestive physiology and structure changes during the initial ontogeny of cultured fish, have been focused to describe the indicators (associated with those changes), punctual and reclusively. Moreover, there are not enough indicators, when the digestive morphological and functional changes, are described in certain fish in particular. The present review, try to describe and compile the indicators of digestive morpho functional development, attending the feed habits, as well as the kind of ontogeny that undergo the teleost fish, which, it almost not be considered. The review tries to explain, the importance of show possible synergy between biochemistry (enzymology), histological, histochemical, molecular, mainly genomic aspects (among others); towards an integral and reliable description of the morpho functional changes in the digestive tract of fish. In this sense, the present work, try to elucidate a particular case of *Mayaheros urophthalmus* (a native species from the Southeast of Mexico), where it has described a pool of indicators associated to the morpho functional changes of its digestive tract. The indicators of digestive morpho functional development can be therefore, complementary mutually. Finally, it has compiled and summarized some indicators of digestive morpho functional changes, towards a better knowledge of the digestive physiology, during the initial ontogeny of teleost fish.

Keywords: Ontogeny; Indicators; Development; Morpho functional; Teleosts; Nutrition

Introduction

At present, the optimization of the nutritional quality of live feed in teleost fish larviculture has directed research to the use of live feed with a view to strengthen the larviculture phase, the most critical in fish culture. Despite this leading to unquestionable progress in the culture of freshwater and marine fish, the high cost of establishing infrastructure for secondary cultures has seriously decreased the profitability of aquaculture. The nutritional quality of live feed does not always satisfy the nutritional requirements of larvae during culture. The production of live feed may thus face difficulties such as a variable nutritional quality and supply [1,2]. Since some decades ago, studies have tried to determine the physiological capacity of organisms to hydrolyze the ingredients present in the diet, from the point of view of their enzymatic machinery, and have progressively obtained more encouraging results, though not completely successful. Rosenlund et al. [3]

established that inert diets make it possible to introduce nutrients that are not available in live feed, and to determine the capacity of organisms to digest particular ingredients. Such studies, which have revolutionized the point of view about the processes of ingestion, digestion, and assimilation of nutrients of fish farmer, during their early ontogeny.

It has increased the knowledge about the most important morphological events, in the digestive tract that take place, throughout this critical stage, as well as on the functional events (considering laboratory and field records have shown that morphology and function are closely related). The sequence of events that characterizes the most important changes, that take place, throughout the morphological and functional development of the incipient alimentary canal in fish larvae; is a clear indicator of the process that starts with fertilization and embryo development,

will finally end in the morphological-structural maturation of the digestive tract, and attached glands, and their proper functioning. Such indicators, which may reflect the capacity of the fish to experiment changes, from larva to juvenile, in a relatively short time; towards a better understand the maturation process of the digestive function. It has been possible to determine the precise instant of the beginning of the change from larva to juvenile and, thus, of a change in feeding regime (from live feed to inert food).

The indicators may also represent tools for the diagnosis of the nutritional condition of cultured fish, as Gisbert et al. [4] stated. The indicators used up to now in studies on the early ontogeny of commercially important fish have been mainly morpho functional, biochemical, histochemical, immunological, and molecular. They are important because they provide a greater number of elements that will progressively make it possible to do without live feed through the design of inert food that agrees with the physiology and digestive capacity of the cultured fish and will result in a significantly more profitable fish farming activity. This review describes the morpho functional changes that take place and analyses the indicators have been already validated, as tools (and potential indicators), in order to determine the degree of development of the digestive morphology and function during the early ontogeny of teleost fish.

Types of Ontogeny and Indicators

Ontogeny is defined as the morphological and functional changes that fishes undergo, during their early biological life. A successful development of the digestive system is essential for the survival and growth of fish larvae as it allows them to capture, ingest, digest, and absorb food [5], as do the adults of their species. Although fish larvae are morphologically capable of capturing food items in their first exogenous feeding [6,7], the digestive system requires a series of structural changes before becoming fully functional [8]. The general sequence of events during the ontogeny of teleost fish, were described by Govoni et al., [9]; who proposed that a primitive intestine is segmented into three regions: the foregut, midgut, and hindgut. The foregut forms the esophagus and stomach, the midgut forms the small and big intestines, and the hindgut forms the rectum and anus. Balon [10] described three types of ontogenies in teleost fish: indirect, transition and direct, and proposed that ontogeny is a hierarchical model of fish life history. Thus, the ontogeny had split, into the sequential periods of embryo, larva, juvenile, adult and mature (senescence) in the case of indirect ontogeny; and embryo, juvenile, adult and mature in the case of direct ontogeny (note the absence of the larval period).

In the case of transition ontogeny, the model proposed the periods of embryo, fry, juvenile, adult and mature. The fry step is a type of larval vestige according to Balon [10]. Each period, divided by natural borders and comprises a sequence of organization intervals in "jumps". The intervals or "homeoretic" states called

steps, separated by stable thresholds. The steps considered the basic units in the ontogenetic scale. Thus, the period is the longest interval and separated from the others by thresholds. The phase is the next interval by which, a stage divided by morphological units of lower ontogenetic significance, mainly for identification purposes. The step is the shortest natural interval, separated by thresholds, and the concept of stage is an instant state in ontogeny. Aspects of the ontogeny types that has been mentioned above, are discussed as follow next.

Indirect Ontogeny

The first period, the embryo, is characterized by endogenous feeding, that is to say, by the acquisition of nutrients from parental sources [11]. The time between hatching and the moment when the eyes have reached the pigmentation, is the time during which larvae feed solely on their yolk reserves [12]. This time of endogenous feeding tends to be very short and followed by a long larval stage (that depends on exogenous feeding), that leaves the larvae vulnerable and prone to a high mortality. Numerous species produce eggs and small larvae with organs and tissues that are immature at the hatching [13]. However, many fish with an indirect ontogeny produce a great number of embryos and larvae to compensate for this vulnerability [14]. The larvae may also occupy many niches (plancton, in the case of teleosts) and thus avoid competing for food. Gisbert et al. [4] stated that fish larvae generally hatch more prematurely than other vertebrates, suggesting that the space-time sequences in teleost larvae are notably different from those of the higher vertebrates.

In consequence, fish larvae go through significant morpho-structural and physiological changes during the first weeks of life, such as has been observed in flounders [15]. Many studies have been carried out, during the last two decades, in order to determinate the digestive capacity and nutritional requirements of fish larvae and juveniles [16]. Organogenesis and the changes in digestive enzyme activity, as well as the characteristics of the development of the digestive tract, have been well documented for several species, including the European seabass *Dicentrarchus labrax* [17], the sole *Paralichthys californicus* [18], the red drum *Sciaenops ocellatus* [19]. Morpho functional, biochemical, and molecular indicators were considered, following the digestive ontogeny in Balon model (2002), as well as the feeding habits of the species and the studies carried out to date for each case.

Carnivorous fish

At hatching, the mouth and the anus are shut, in some species [20,21]. Such characteristics were observed by Gisbert et al., [22], in the sole *P. californicus*, including a closed and straight tube (non-differentiated oropharynx and anus). Between days 1 and 2 after hatching (dah), the oropharynx presents morpho histological features such as some layers of squamous cells and a few taste buds. During these days, the intestine is rudimentary and is made of simple ciliated columnar epithelium. While the yolk sac is

present, the hindgut presents a 90° curve and an intestinal valve is formed to divide the intestine in two regions, the pre-valvular intestine and the post-valvular intestine. Both regions present a basophilic cytoplasm and prominent eosinophilic microvilli [22]. The post-valvular intestine lacks Goblet cells [21], while the gastric glands appear (indicating digestive immaturity).

However, the activity of certain enzymes is required for larval digestion to take place immediately after hatching. Alliot et al. [23] recorded trypsin and chymotrypsin (pancreatic enzymes), using biochemical techniques, immediately after the hatching of *D. labrax*. García-Gasca et al. [24] detected trypsinogen gene expression in egg rRNA (75 hours after fertilization, haf) in *Spherooides annulatus*. Gisbert et al. [22] detected acidophilic zymogen grains (pancreatic enzyme precursors) in the exocrine pancreas at 1 dah, before the start of exogenous feeding, with an increase in their numbers when exogenous feeding started in *P. californicus*, and Yanes-Roca et al., [25], confirmed the importance of pancreatic secretions in larval development during the early ontogeny of the black snook *Centropomus nigrescens*. The pre-valvular intestine, has been described as the main site for extracellular digestion in the digestive tract during the larval stage, as result of its alkaline pH and the presence of trypsin secreted by the exocrine pancreas [26,27].

Shortly afterwards, and coinciding with the first exogenous feeding, the alimentary canal changes and forms the oropharynx, esophagus, pre and post-valvular intestines and rectum. Several authors have observed this in other carnivorous species like *Paralichthys senegalensis* [28] and the yellowtail flounder *Limanda ferruginea* [29]. A fold formed by ciliated columnar cells starts to differentiate at 4 dahs, in the terminal region of the esophagus, from the pre-valvular foregut in *P. californicus* [22]. The number of Goblet cells increases around 10 dahs. These cells secrete glycoproteins and mucin, the substances that make lubricating mucous membranes in the anterior oropharynx and esophagus, an organ in which no histological changes were observed, until metamorphosis, as occurs in *P. californicus*. At this age, one may also observe a canine tooth in the posterior region of this cavity, and the mucous membrane in the intestine is mostly rectilinear and presents several short folds. The first Goblet cells become visible in both regions of the intestine. *Spherooides annulatus* presents a marked change in the expression of trypsinogen intensity at 13 dahs [24].

The Goblet cells increase in number with the differentiation of the intestinal mucous membrane and are most abundant in the pre-valvular intestine. Histologically, these cells dye a dark blue, which have a relationship, with the presence of a mixture of carboxylate and sulfated glycoproteins and of neutral glycoproteins. Folding in the pre-valvular intestine increases between 19 and 23 dah and the folds occupy most of the intestinal lumen, whereas the post-valvular intestine presents few folds in a rectilinear mucous membrane [22]. The migration of the eye in *P. californicus*

(27-30 dah) coincides with the differentiation of the gastric glands and the decline of supranuclear bodies in the post-valvular intestine [22], indicating the presence of pinocytotic absorption and proteolytic digestion in the intracellular environment, that take place through a five-step process: pinocytosis, transport, accumulation, digestion, and extinction [30]. Larval digestion in fish with an indirect ontogeny is intracellular [9] and becomes extracellular when the transformation takes place.

The intracellular digestion compensates the incomplete digestion that occurs in the primitive midgut, which decreases its contribution to digestion as the alimentary canal matures, especially when a functional stomach appears, which may be the most important indicator of digestive maturation in carnivorous fish. It has been widely documented that a morpho functional indicator of the full maturity of the stomach is the presence of gastric glands in the fundal stomach, whereas a significant enzymatic indicator of stomach maturity is a high level of pepsin which, is secreted by the gastric glands. The occurrence of these three changes is an indicator of the threshold of a digestive tract in an advanced state of maturity. Govoni et al. [9] stated that the presence of vacuoles and supranuclear inclusions is an indicator of a functional alimentary canal. García-Gasca et al. [24] recorded a marked decrease in the levels of mRNA that codes for mRNA trypsinogen, starting at 28 dah in *S. annulatus*, which coincided with the change in diet from *Artemia* nauplii to a formulated micro diet. Darias et al. [31] detected a relatively constant trypsinogen expression during the first month of life of *Pagrus pagrus* that decreased towards the 50 dah, suggesting that trypsinogen plays a secondary role in protein digestion.

The same synchronic behaviour (a decrease in trypsin activity as an indicator of stomach differentiation) was recorded for the striped beakfish *Oplegnathus fasciatus* [32], although the decrease in trypsin activity was more premature (starting at a peak at 19 dah). However, the most notable change in the stomach, and the start of the juvenile stage as well, is the development of the gastric glands, as Pradhan et al. [33] pointed out. These changes may thus be useful indicators to pinpoint the process of digestive maturation.

Omnivorous fish

Few studies have been carried out on the ontogenetic dynamics of omnivorous fish. In their study on the development of digestive enzymes during the early ontogeny of *Mayaheros urophthalmus*, López-Ramírez et al. [34] recorded trypsin and chymotrypsin activity before hatching. This was also recorded for the rohu carp *Labeo rohita*, in which there is amylase, protease, lipase and alkaline phosphatase enzymatic activity at 4 dah [35]. Important digestive enzymes have been documented as present at the moment when the mouth opens [36,37]. The opening of the mouth and, thus, the beginning of exogenous feeding determine the regional differentiation of the intestine in many teleost species [38-40]. Continuing with *M. urophthalmus*, its larvae present a

marked activity of several digestive enzymes at 13 dah, as is also the case in species like *P. californicus* [41].

The biochemical characterization of *M. urophthalmus* larvae indicates that precisely at 13 dah is the best moment to substitute live feed with artificial food, and this coincides with a visible increase in the activity of enzymes such as trypsin, chymotrypsin, aminopeptidase, carboxypeptidase, and the acid and alkaline phosphatases [34]. Aminopeptidase and alkaline phosphatase are intestinal enzymes that play a part in the digestion of small peptides and the assimilation of nutrients, respectively [42]. Their sustained increase throughout early ontogeny indicates an improvement in the intestinal digestion capacity [43]. Trypsin has been reported as the enzyme that is most responsible for alkaline proteolysis in *Paralabrax maculofasciatus* larvae [44], whereas in *M. urophthalmus*, proteolytic activity is represented by chymotrypsin. This explains why chymotrypsin has been identified as part of the enzymatic machinery of omnivorous and herbivorous fish, while trypsin has been recorded for carnivorous fish [45].

These same authors recorded the presence of trypsin, chymotrypsin, aminopeptidase and cathepsin (an indicator of intracellular proteolysis and, thus, of a primitive or immature alimentary canal) before hatching (0 dah) and at 3 dahs, respectively. In the larvae of another omnivorous fish, *Pagellus erythrinus* (with a certain tendency towards carnivory, like *M. urophthalmus*), the differentiation of the digestive tract produces an oropharynx, an esophagus, a presumptive stomach and an intestine at 3 dah [46,47], morpho functional indicators that coincide with the first exogenous feeding. From these findings it follows that there is a certain functional capacity in the digestive tract at this age. The indicators that change at the beginning of exogenous feeding in omnivorous fish are an increase in trypsin activity and the start of chymotrypsin activity as an indicator of a possible beginning of mixed feeding (a mixture of endogenous and exogenous food items).

Enzymatic activity may thus be a true indicator of the digestive capacity of omnivorous fish like the common carp *Cyprinus carpio* Jian variety, as Yan and Qiu-Zhou [48] stated. Despite most of the studies on the early ontogeny of fish having focused on carnivorous species of the Mediterranean Sea and the Northern Atlantic, it is possible to summarize the relevant changes that may be used as indicators of the degree of maturation of a fish, on the ontogenetic scale. Yan and Qiu-Zhou [48] stated that the digestive function is correlated with the development of the intestine in fish without a stomach, such as *C. carpio* Jian variety. Micale et al. [46] reported on important indicators (time of mouth opening, absorption of yolk sac and formation of gastric glands, among others) for *P. erythrinus* larvae. Moreover, Cuenca et al., [47], revealed a relationship between the full differentiation of the stomach (histology), peaks of expression of α -amylase (molecular indicator) and peaks of acid proteases (biochemical indicator), in *M. urophthalmus*, at 13 dde; as synchronous events of maturation

of the digestive tract.

Herbivorous fish

Hatching of herbivorous cyprinids like *Ctenopharyngodon idellus* produces incomplete organisms in which the differentiation of the organs, particularly of the digestive tract [9,49], continues during the post-embryonic stage [50]. Also, when growth rates are as much as 30% d⁻¹ [51], the digestion presents an extremely pronounced enzymatic activity. Exogenous feeding starts even before the absorption of the yolk sac, and the alimentary canal is short and straight during this stage [52] and may measure 50% of the body length [50]. The short larval intestine is capable of breaking down and assimilating easily digestible elements, mainly zooplankton [53]. The intestine grows slowly during the larval stage and the time of intestinal passage is positively correlated with the relative length of the intestine [54].

The time available for the processes of digestion and absorption increases gradually, until the fish changes into an adult [52]. Thus, both the time of passage and the length of the intestine may be considered indicators of digestive maturity in cyprinids, particularly the herbivores. On another note, digestive enzyme activity is low during the first feeding stage and increases during larval development [38]. Also, the digestive enzymes in natural zooplanktonic prey survive in the digestive tract of the predators and minimally increase the enzymatic activity in the hosts [52]. Regarding trypsin activity in adults, it is significant in the foregut and midgut, though not in the hindgut where enzyme activity practically disappears [55]. In larvae, however, hydrolysis continues in the hindgut [52]. Guo-Liang et al. [56] studied the gene expression of trypsinogen and the specific activity of trypsin throughout the ontogeny of *C. idellus* and suggested that trypsin activity is important in larvae.

The decrease in the activity of this end protease enzyme in the hindgut throughout early ontogeny may be a good indicator of digestive development, at least for the larval stage. *C. idellus* does not have a stomach, which means that the whole digestive process takes place all along the intestine (mainly the foregut and midgut), which is designed to optimize the digestion and assimilation of nutrients. In agreement with this, the intestinal enzymatic machinery of *C. idellus*, which includes proteases, lipases, cellulases and amylases, has been analysed by Wu and Zhu [57]. Horn et al. [58] detected a marked amylase and maltase activity in *Atherinops affinis* (an estuarine herbivorous fish), enzymes that degrade the alpha polysaccharides present in the diet. In turn, adult herbivorous fish owe their high digestive efficiency to the great intestinal surface that is provided by a very long intestine and is available for assimilation and digestive processes.

In relation to this, Horn et al. [58] concluded that the intestine is longer and has a greater intestinal surface in *A. affinis* than in *Atherinopsis californiensis* and *Leuresthes tenuis*, an omnivore, and a carnivore, respectively. However, fish with no stomach and no mechanism of stomach digestion require intracellular

digestion, which commonly occurs during the early ontogeny of teleost fish (until the formation of the gastric glands, indicators of the developed differentiation of a functional stomach). Liu et al. [59] detected the presence of cathepsin D that plays a part in the digestion of proteins in *C. idellus*, an enzyme indicator of intracellular digestion like leucine alanine peptidase [27].

Transition Ontogeny

The yolk in fish with a transition ontogeny is abundant and dense during the embryo stage, providing ideal conditions for a rapid change to the juvenile stage (at least compared with fish that have an indirect ontogeny and a longer larval stage). The most representative species of this group are the fish of the Salmonidae family, which, produce big demersal eggs and well-developed fry [60]. Six hours after fertilization, salmonid eggs have small blastodiscs, narrow perivitelline spaces, and lipid globules located around the animal pole and connected to the cytoplasmic region, while the embryo and the oil droplet are located in the upper part of the yolk [60]. Dahl et al. [61] described a comparative study of the morphological characteristics of the progeny of *O. mykiss* obtained from the wild, from culture, and from hybrids obtained from breeding animals of both groups, in which they observed minimum differences with respect to growth.

Regarding the ontogenetic study of salmonids, Godorilov [62] described the early ontogeny of the Atlantic salmon *Salmo salar*, established a mathematical model to identify the stages of embryogenesis considering as the minimum unit the formation of a pair of somites, and suggested the model could be applied to other species. One of the most emblematic indicators in fish of this group is the presence of pepsin and trypsin during the hatching of *O. mykiss* [63]. Pavlov and Moksness [60] compared the early ontogeny of *S. salar* and *Anarhichas lupus* (a fish of direct ontogeny) and found greater technological advantages in the culture of *A. lupus* than in that of *S. salar*, considering the more complex life cycle of this last species. Rungruangsak-Torrissen et al. [64] studied the different expressions of trypsin and chymotrypsin and their effect on the growth of *S. salar*, and found that the first decreases in activity when growth is favoured by external (fasting, temperature and diet composition) and internal (life stage) factors, while the second increases in activity under conditions that limit growth (fasting). Thus, enzymatic activity, at least in the salmonid group, is an indicator of the way in which the internal and external factors in fish culture act and interact.

Furthermore, histological, and histochemical techniques have shown an accumulation of protein inclusion bodies, in the epithelial cells of the midgut of salmonid larvae which, results in the intracellular digestion. This event is less important in fish with a direct transition ontogeny, as they already have a functional stomach (before the absorption of the yolk sac and at the first exogenous feeding), similar to those of adult fish [9]. Thus, fry (a stage exclusive of fish with a transition ontogeny) present

most of the characteristics of juveniles shortly after hatching (as they hatch also as eleuthero embryos), which makes them very developed larval vestiges. In this sense, Sarieyyüpoğlu et al. [65] recorded the start of the formation of the stomach from the mucous membrane of the esophagus in the freshwater trout *O. mykiss* at 2 dah. This offers advantages to fry as, at this stage in the ontogenetic scale, they present a structurally and functionally more advanced digestive tract at the time of hatching, compared with fish with an indirect ontogeny.

Direct Ontogeny

Studies on morpho functional changes in fish with a direct ontogeny are few (particularly in the case of species that are cultured). The embryonic development of this group follows the general pattern of teleost fish, though with marked differences. An internal fertilization has been showed in the Atlantic wolffish *Anarhichas lupus* [66]. Some species like *Xenomelaniris brasiliensis* (a brackish atherinid fish with an embryonic stage that lasts approximately 143 h, the moment when hatching takes place) have well pigmented eyes and the first outlines of pectoral fins even before hatching [67], these being typical indicators of fish with a direct ontogeny. On the other hand, most marine fish larvae do not have the capacity to feed immediately after hatching and depend on the yolk sac (not dense) until their eyes and mouth become functional. In contrast, at the hatching, *A. lupus* is an eleuthero embryo with characteristics of a premature juvenile that allow it to adapt immediately to the pelagic environment [60]. At the start of the first exogenous feeding, *A. lupus* has a developed morphology, especially regarding the digestive system [60], that provides it with a greater probability of survival and a reduced vulnerability during early ontogeny. Hellberg and Bjerås [68], suggested that an increase in the amount of lipids in *A. lupus* was associated with the maturation of epithelium cells in the intestine. Thus, the capacity to absorb lipids in the intestine of fish with a direct ontogeny may constitute a clear indicator of intestinal differentiation during ontogeny, especially during the larval stage.

Morpho functional Indicators of Maturation

According to Ma et al. [69], there are two stages of capital importance in the process of maturation of the digestive function in fish larvae: first the functionality of pancreatic secretions and second the formation of the epithelium with the brush border membranes of the intestine. These events have described in *D. labrax* [70], *Solea senegalensis* [18] and *S. ocellatus* [19,71]. Notwithstanding these changes are complete in most species, physiological changes take place from the moment of the first exogenous feeding until the transformation into juveniles. Such changes include the reorganization of the muscular trunk, the differentiation of the gills, and of bone tissue; as well as the development of a functional stomach and the establishment of acid digestion [6,13,18,40,72-74].

These last changes indicate that the individual is in a condition of digestive maturation that allows it to carry out the ingestion, digestion, and assimilation of nutrients efficiently. Gisbert et al. [4] pointed out that histological indicators are a useful and precise tool that helps understand the transcendental changes that take place during the early ontogeny of teleost fish, even considering their limitations in the study of wild populations. The profile of the digestive enzymes is also an indicator of the digestibility and use of nutrients [35]. For example, it has revealed that pepsin, trypsin, and amylase activity is high in omnivore and herbivore larvae. In contrast, carnivore larvae have a high activity of pepsin, trypsin, chymotrypsin and aminopeptidase, and a very low activity of amylase, with a few exceptions like *O. mykiss*. The presence or absence of amylase activity is a useful indicator of the feeding habits of a species, but also of digestive maturation, as activity is high in the early larval stages of several species and decreases when morpho functional maturity is established [75]. A high amylase activity in larvae could be associated with the activity of lactase in the postnatal stages of mammals, which decreases when digestion becomes similar to that of the adults of the species.

Another important indicator of structural and functional changes during the development stages of many species is the relationship between extracellular digestion represented by enzymes of the brush border (aminopeptidase N, alkaline phosphatase, and maltase) and intracellular digestion measured by cytosolic enzymes (leucine alanine peptidase). While cytosolic activity predominates during the first days after hatching, it decreases at the same time that the enzymes of the brush border increase in activity, together with the development and establishment of the intestinal mucous membrane. According to a functional point of view, digestive activity depends on several factors, among which the hormones stand out. An important indicator is cholecystokinin (CCK), a hormone produced in the foregut and is responsible for pancreatic enzymatic secretion, the secretion of bile, and the contraction, filling and emptying of the intestine [76]. Despite there being few studies on this aspect, CCK has been detected at 1 dah in the Japanese sole *Paralichthys olivaceus* [77], the bluefin tuna *Thunnus thynnus* [78] and the sweet fish *Plecoglossus altivelis* [79]. However, no CCK has been detected in the intestinal tract of the Atlantic sole *Hippoglossus hippoglossus* [80,81], indicating that the presence of this hormone may depend on changes in the levels of expression determined by genetic and/or nutritional factors.

Molecular Indicators of Fish Maturation

Functional genomics studies were initiated in model species, and then in those marine and freshwater which, economic importance with the goal to understand the ontogenetic changes occurring in first stages of development in order to improve the feeding schemes in these critical days. Fish physiology studies include the zebrafish *Danio rerio* [82], medaka *Orzias latipes* [83], pufferfish *Fugu rubripes* [84], channel catfish *Ictalurus punctatus*

[85], Atlantic salmon *Salmo salar* [86], turbot *S. maximus* [87], European seabass *D. labrax* [88], between others. These studies summarize the dramatic changes, which, fish undergoes along the first days of development until reaching a definitive phenotype.

The ontogenetic changes are represented by morphological modifications, including cell differentiation and proliferation, growth, and functional maturation until reaching juvenile or adult way of life. Those process, require a high degradation degree at every modification step, which, are genetically programmed. One of main external factors influencing gene regulation is the maturation, is the nutrition, which, play a determinant role, during the first steps phases of grown and development in fish larvae [89]. In this sense, it has been the relationship between the expression of CCK, neuropeptide Y (NPY) and grown hormone (GH) versus the nutrition regime (mainly live prey) in cod larvae *G. morhua* [90]. The former author found that the transcription of level of CCK, as well as the digestive enzymes trypsin and amylase were transcribed, according to the feeding composition, suggesting the use of these indicators of nutrition in the early phase of fish development.

More recently, the functional modifications associated to the GI-tract organogenesis were described during the metamorphosis of Atlantic halibut (*Hippoglossus hippoglossus*) since an anatomical, biochemical, and molecular perspectives [91]. It was observed that the multiple functions of the teleost stomach develop synchronously during metamorphosis, and it was established a correlation between the transcript abundance of ghrelin and the stomach development, as well as the establishment of the proteolytic activity. In recent years, the majority of fish ontogeny related-studies were carried out by using a small number of target genes by semi-quantitative or qPCR, and/or some studies by *in situ* hybridization (FISH). Subtractive hybridization and construction of cDNA libraries (SSH), where also utilized to elucidate gene that are differentially expressed and allows the comparison of two DNA population of a fraction enriched in differential distributed molecules, involved in the regulation of ontogeny and related processes. cDNA libraries construction permitted the analysis of thousands of genes or whole genome by microarrays, and to know the mechanisms related to the morphologic, structural, and functional changes in fish larvae, describing the metabolic pathways and gene individual interaction involved in the metabolism, grown, differentiation, digestion, transport, absorption, among other biological process.

The study of Sarrapoulou et al., [92] permits the insight into the molecular basis of development and stress, in aquaculture species by mean of creation of gene expression profiles for sea bream by microarray hybridization and contributes to a better understanding of the genetic background of fish physiology, which, may help to improve aquaculture practices. Functional genomics studies are also possible by the use of microarrays generated in non-model species, such as that performed by Darias et al.,

[88], where they used cross-species hybridization among fish of different taxonomic families. They used more than 9000 cDNA trout *O. mykiss*, clones originated from two pooled-tissues libraries [93] to elucidate the changes in gene expression, occurring over sea bass *D. labrax* larval development. They observed an overexpression of 485 genes related to organogenesis, 29 to the energetics pathways, 67 to the biosynthesis and 5 to digestion. Through this transcriptomic analysis and its validation by qPCR, has been identified several molecular markers which, indicate GI-tract maturation.

During the past several years, the information concerning fish transcriptomic are increasing because the establishment of high-through put sequencing technologies, termed next-generation sequencing (NGS) technologies which, have been exploited to analyze the dynamic transcriptome, and the resulting technology is termed RNA sequencing (RNA-seq), Qian et al., [94]. As consequence of low cost and rapid development of these technologies, the transcriptomes have been studied, in both model and non-model fish, not only for the quantification of change of in expression level, but also mapping and annotating the transcriptome with the aim to understand the biological process, such as development, adaptive evolution, host immune response, and stress response. Thus, in order to summarize, the table 1 shows some relevant indicators, that accompany the main changes of the morpho functional development in teleost fish, principally of cultured species.

Discussion

Knowledge of the ontogenetic dynamics in teleost fish is fundamental in order to select indicators for the important events that take place in the process of digestive maturation, which may establish a reference for the design of inert food, particularly for the early life stages of commercially important species and of those with a potential for culture. It is necessary to understand the morpho functional changes, as very few studies to date have focused on relating the indicators considered in the present review to the morpho functional development of fish. Even more, little it has been done, to establish the possible synergies among the indicators that have been mentioned, which may describe more fully the relevant and particular changes that take place during the early ontogeny of teleost fish. The prevalence of one type of enzyme in the enzymatic machinery of a fish, may be a prominent indicator of digestive maturation, and thus of the composition of the feed to be provided, and of the approximate times, throughout the early ontogeny of the species under study.

Histological, biochemical, and molecular tools are widely used at present, being extremely useful and allowing a deeper and more precise knowledge of the times at which the relevant events occur throughout the early ontogeny of teleost fish. Samples taken throughout the ontogenetic series may record such changes through the determination of morphological and structural changes, enzymatic activity dynamics, the detection of the genes responsible for the molecular expression of digestive enzymes in

time and, in this way, complete the information generated by other techniques. Recording the more or less exact times of enzymatic expression may turn out to be an indicator of important events throughout the histogenesis and organogenesis of the alimentary canal. Despite the high relevance of the biochemical and molecular indicators, it is necessary to first consider the structure (inherent to the morphological indicators), and then the functional aspects of fish development.

Actually, there is not enough information about the role, of abiotic and biotic factors, on the enzymatic mechanisms in teleost fish. Temperature could play a crucial role on the intestinal tract hydrogen strength (pH), of freshwater fish [95]. Furthermore, it has been studied the pH and its effect, on the activity enzymatic in teleost fish, mainly their optimal values, that differ depending on different group of digestive enzymes [96]. Moreover, the knowledge about the role of abiotic and abiotic factors, during the development of digestive tract, in the early ontogeny fish is poor. Finally, it is important to consider more biochemical, genetic, immunological, endocrinological and hematological events (among others), involving complementary disciplines like functional genomics, in order to obtain a greater number of indicators that may lead to a greater understanding of the process of digestive maturation in teleost fish, particularly of commercially valuable species and those with a potential for culture.

Finally, it is necessary to notice that not only is important to have in mind a list of molecular markers or those events involved in organogenesis to describe the changes that occur in initial ontogeny, but also the correlation with those external factors responsible for the phenotype. One of these external factors is the nutrition, because is determinant in enzyme and hormone regulation related to fundamental changes to obtain high quality juveniles. Studies on the digestive larval physiology are of the capital importance, to know their enzymatic adaptations to dietary changes [95]. The combination of physiological studies and the ecological knowledge on teleost fish, could contribute to promote the growth and survival during the larvae fish period [97].

According to the indicators of the morpho functional development above described, it has been analyzed a particular case of *M. urophthalmus*, a native fish from Southeast of Mexico, which is an excellent candidate for freshwater aquaculture [98]. Finally, it is recommendable, to use at least three tools of study, to interpret different kind of indicators of digestive morpho functional development, simultaneously. In this sense, several indicators could be complementary on the study of biological process, as the morpho functional development, of the digestive tract in teleost fishes.

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