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Review On: Digestive System And Feeding Physiology Of Fish Presented To Instractor Of The Course: Advanced Animal Physiology (521)

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Abstract: Fish eat a wide variety of natural food, including plants and other organisms and commercially prepared diet. Fish ingest food through the mouth and break it down in the esophagus. In the stomach, food is further digested and, in many fish, processed in finger-shaped pouches called pyloric caeca, which secrete digestive enzymes and absorb nutrients. Organs such as the liver and pancreas add enzymes and various chemicals as the food moves through the digestive tract. The intestine completes the process of digestion and nutrient absorption. The small intestine is the part of the digestive tract following the stomach and followed by the large intestine, and is where much of the digestion and absorption of food takes place. In fish, the divisions of the small intestine are not clear, and the terms anterior or proximal intestine may be used instead of duodenum. The small intestine is found in all teleosts, although its form and length vary enormously between species. In teleosts, it is relatively short, typically around one and a half times the length of the fish's body. It commonly has a number of pyloric caeca, small pouchlike structures along its length that help to increase the overall surface area of the organ for digesting food. There is no ileocaecal valve in teleosts, with the boundary between the small intestine and the rectum being marked only by the end of the digestive epithelium. In fish, there is no true large intestine, but simply a short rectum connecting the end of the digestive part of the gut to the cloaca. In sharks, this includes a rectal gland that secretes salt to help the animal maintain osmotic balance with the seawater. The gland somewhat resembles a caecum in structure, but is not a homologous structure.

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1. Introduction

Feeding is a complex behavior consisting of food ingestion itself as well as foraging or appetitive behaviors which reflect motivation to consume food. Feeding is ultimately regulated by central feeding centers of the brain, which receive and process information from endocrine signals from both brain and periphery. These signals consist of hormones that increase or inhibit feeding. Feeding centers are also influenced by metabolic and neural peripheral signals providing information on meal ingestion and nutritional status (Cerdá-Reverter and Peter., 2003).

Detailed descriptions of the anatomy and physiology of GI tracts of numerous fish species have been covered in several reviews. Fish have the ability to rapidly and reversibly adapt GI tract characteristics to match the changes in functional demands that occur during their life history (e.g. metamorphosis, anadrome or catadrome migrations) or more frequently day to day or seasonal shifts in diet or environmental conditions; this ability is dependent on endocrine signaling pathways which are augmented by the enteric nervous system (Karila *et al.*, 1998). The wide diversity and levels of hormones and signaling molecules secreted by the numerous types of GI tract and endocrine pancreas cells allow fish to rapidly and reversibly alter characteristics of the GI tract and other organ systems to adapt to changes in the contents of the GI tract amounts and types of nutrients, pH, ionic composition etc. and environmental conditions (Holst et al., 1996). The key feature of the alimentary tract is its ability to digest foodstuffs to make them suitable for absorption by various transport mechanisms in the wall compartments of different GI sections (Bakke et al., 2011). Besides the hydrolytic reactions catalyzed by endogenous enzymes secreted by the pancreas and cells in the gut wall, which are considered to play the major roles in digestion, fermentation plays key roles in digestive processes in many monogastrics. The role of fermentation in fish is less clear due to a lack of knowledge, but it is considered to be of minor quantitative importance for nutrient supply in cold water species. However, qualitative importance may be significant regarding specific nutrients and immune stimulating processes.

The anatomy and physiology of the GI tract are important determinants for the establishment and for the quantitative as well as the qualitative aspects of its micro biota. The microbial communities may seem to be assembled in predictable ways (Rawls et al., 2006). The microbial communities transplanted from mice to gnotobiotic zebraish alter quantitatively in the direction of the normal biota of the zebraish species and vice versa. This indicates that environmental conditions of the intestine determined by speciesspecific parameters along the GI tract such as anatomy, endogenous inputs of digestive secretions, pH, osmolality, redox potential, compartment size and structure, passage rate and residence time, help to define and shape the GI tract micro biota. However, diet composition is also an important environmental condition for fish development. Diet composition is ideally species specific regarding available essential nutrients, but supplies variable amounts of unavailable material depending on the feedstuffs used in the diet formulations. The gut micro biota is also probably inevitably linked to digestion by the production of exogenous enzymes and vitamins produced which might aid host digestive function (Ray et al., 2012).

The large numbers of fish species, habitats, feeding habits and digestive tract anatomy and physiology, as well as the number of extrinsic and intrinsic factors affecting feeding behavior and physiology most probably result in complex species-specific feeding regulating mechanisms in fish, with a number of hormones and tissues involved (Elbaz *et al.*, 2012).

Diversity in morphology, anatomy and histology of the gastrointestinal tract in relation to phylogeny, feeding habits and environment; Feeding, digestion and absorption of nutrient, micronutrients and minerals; Barrier function and immunology; The role of the gastrointestinal tract in salt and water balance; The role of feeding in salt and water balance; Implications of GI function for gas exchange, acidbase balance and nitrogen metabolism; The GI tract as an endocrine/neuroendocrine/paracrine organ; The enteric nervous system; Mesenteric circulation and respiration of the GI tract; The GI tract in air breathing and nitrogen excretion.

The objective this review paper is:

> To understand the feeding biology of fish.

> To know the anatomy and physiology of digestive system of fish.

1.1. Study gap of the review

Al though our knowledge is limited for fish, it can be suggested that these fluids vary greatly in quantity as well as composition between intestinal segments and within species under different conditions. To our knowledge, no information has been reported in the scientific literature regarding quantities of water and material entering the GI tract of juvenile or adult fish. However, alterations in composition have been observed, and information is available that alterations are observed in activities of digestive enzymes within the gut contents of salmonids by incorporation of plant material in the diet as well as alterations in content of bile acids caused by dietary fiber. Various dietary components may serve as substrates for the gut microbes, and enzymes such as proteases and lipases, bile acid and antimicrobial components will also probably modulate the gut micro biota (Romarheim et al., 2006).

2. Review on digestion of fish and its feeding biology

2.1. General information about fish

Fish are the most diversified group of vertebrates, with 33,200 species identified to date in the world (Froese and Pauly, 2008). In Ethiopia, there are 175 fish species among these 40 species were endemic found only in Ethiopia. There are 27 fish species in Lake Tana and 20 of these are endemic (Vijverberg *et al.*, 2009). Based on the common species, the fish communities showed large differences in their species composition, except for Lake Abaya and Lake Chamo which were similar. The empirical model of Amarasinghe and Welcomme (2002) for African lakes was used to estimate fish species richness, which was compared with species presence reported in literature.

The principal Fish species and abundance of Ethiopia rift valley lakes are home for about 30 different native species of fish. However the distribution at fish diversity within the rift valley lake is extremely uneven. The Awash river bas in alone comprises eleven fish species which is about 37% of the fish found in Ethiopia rift valley and the southern Ethiopia rift valley lake such as lake Abaya and chemo comprises 20 fish species (Golubtsav *et al.*, 2002).

The different factors which affects aquatic organism living in the system an anthropogenic activities which are made in catchment of the reservoirs affect the water quality as well as quantity siltation of reservoirs is now becoming a well known phenomena in Ethiopia which are already experienced in almost all hydro electric power generation reservoirs, siltation also affect the fish community by reducing food organisms, depleting. The amount of oxygen for decomposing of organic materials increasing the turbidity of the water which reduces the euphoric or photo synthetic zone.

The number of endemics depends upon how taxonomic information is interpreted. We know that interpretations may vary from ours, so we do not represent our numbers as final. For instance, the African stony loach, Nemacheilus abyssinicus, is

seemingly endemic to Ethiopia. Taxonomic position of this species needs clarification since its affiliation with the genus Nemacheilus is doubtful. We should mention also one or two undescribed Garra species and possibly an un described species of the annual killifish, Nothobranchius found in the Gambela lowland (Golubtsov et al., 2002) as potential Ethiopian endemics inhabiting the White Nile system. We have no information about introduced fishes in these system. Taxonomic problems. Taxonomic position of fishes found in Ethiopian part of the White Nile basin, but not previously registered in the Nile system, remains to be clarified. Most of them seem to be conspecific or closely related to the species already known from the western parts of the Nilo-Sudan Ichthyofaunal Province (the Lake Chad and Niger basins, etc.).

No	Scientific Name	Common Name	Vernacular Name
1	Lates Niloticus	Nile Perch	Nech Asa
2	Oreochromis Niloticus	Nile Tilapia	Qoroso/Chogofe
3	Barbus Species	Barbus	Bilicha
4	Labeo Species	Labeo	Barbo/Lebi
5	Clarias Garipienus	Cat Fish	Ambaza
6	Bagrus Dockmac	Bagrus	Kerkero
7	Polypters Pichir	Nile Bihir	Eguwellia
8	Gymnarchus Niloticus	Gymnarchus	Wit
9	Malapterurus Species	Malapterurus	
10	Crussian Carp	Carp	Daba
11	Distichodus Niloticus	Distichodu	Piro
12	Hydrocynus Forskali	Hydrocynus	Weri
13	Heteroticus Niloticus	Heteroticus	Ediwela
14	Citharinus Citharinus	Citharinus	Ajaka
15	Synodontis Species	Synodontis	Akok

Table 1. Commercial available fish in Ethiopia (mulugeta wakijira, 2011)

2.2. Feeding biology of fish

Good nutrition in animal production systems is essential to economical production of a healthy, highquality product. In fish farming (aquaculture), nutrition is critical because feed typically represents approximately 50 percent of the variable production cost. Fish nutrition has advanced dramatically in recent years with the development of new, balanced commercial diets that promote optimal fish growth and health. The development of new species-specific diet formulations supports the aquaculture industry as it expands to satisfy increasing demand for affordable, safe, high-quality fish and seafood products.

2.2.1. Natural food

It is found naturally in the pond. It may include detritus, bacteria, plankton, worms, insects, snails, aquatic plants and fish. Their abundance greatly depends on water quality. Liming and fertilization, in particular organic fertilization, can help you to provide a good supply of natural food to your fish. (http://www.fao.org/fishery/static/FAO Training/FAO Training General X6709e x6709e10.htm)

2.2.2. Commercially Produced Feeds

Prepared or artificial feeds can be either complete or supplemental. Complete diets supply all the ingredients (protein, carbohydrates, fats, vitamins, and minerals) necessary for the optimal growth and health of the fish. Most fish farmers use complete diets, typically made up of the following components and percentage ranges: protein, 18-50 percent; lipids, 10-25 percent; carbohydrate, 15-20 percent; ash, <8.5percent; phosphorus, <1.5 percent; water, <10 percent; and trace amounts of vitamins and minerals. The nutritional content of the feed depends on what species of fish is being cultured and at what life stage. When fish are reared in high density indoor systems or confined in cages and cannot forage freely on natural food (e.g., algae, aquatic plants, aquatic invertebrates, etc.), they must be provided a complete diet. In contrast, supplemental (i.e., incomplete or partial) diets are intended only to help support the natural food normally available to fish in ponds or outdoor raceways. Supplemental diets do not contain a full complement of vitamins or minerals but are typically used to help fortify the naturally available diet with extra protein, carbohydrate, and/or lipids (Steven Craig, 2017).

2.2.2.1. Protein

Because protein is the most expensive component of fish feed, it is important to accurately determine the protein requirements for each species and life stage cultured. Proteins are formed by linkages of individual amino acids. Although more than 200 amino acids occur in nature, only about 20 amino acids are common. Of these, 10 are essential (indispensable) amino acids that cannot be synthesized by fish. The 10 essential amino acids that must be supplied by the diet are methionine, arginine, threonine, tryptophan, histidine, isoleucine, lysine, leucine, valine, and phenylalanine. Of these, lysine and methionine are often the first limiting amino acids.

Fish feeds prepared with plant protein (e.g., soybean meal) are typically low in methionine. Meanwhile, fish feeds manufactured with bacterial or yeast proteins are often deficient in both methionine and lysine. Therefore, these amino acids must be supplemented to diets when these sources of proteins are used to replace fishmeal. It is important to know and provide the dietary protein and specific amino acid requirements of each fish species to promote optimal growth and health. Protein levels in aquaculture feeds generally average 30 to 35 percent for shrimp, 28-32 percent for catfish, 35-40 percent for tilapia, 38-42 percent for hybrid striped bass, and 40-45 percent for trout and other marine finfish. In general, protein requirements are typically lower for herbivorous fish (plant-eating) and omnivorous fish (plant and animal eaters) than they are for carnivorous (flesh-eating) fish. Protein requirements are higher for fish reared in high-density systems compared to lowdensity culture (AVMA, 2017)

2.2.2.2. Carbohydrates

Carbohydrates (starches and sugars) are the least expensive sources of energy for fish diets. Although not essential, carbohydrates are included in aquaculture diets to reduce feed costs and for their binding activity during feed manufacturing. Dietary starches are useful in the extrusion manufacture of floating feeds. Cooking starch during the extrusion process makes it more biologically available to fish.

In fish, carbohydrates are stored as glycogen that can be mobilized to satisfy energy demands. They are a major energy source for mammals but are not used efficiently by fish. For example, mammals can extract about 4 calories of energy from 1 gram of carbohydrate, whereas fish can only extract about 1.6 calories from the same amount of carbohydrate. Fish can use up to about 20 percent of dietary carbohydrates (Michael and Schwarz, 2011).

2.2.2.3. Lipids

Lipids (fats) are high-energy nutrients that can be utilized to partially spare (substitute for) protein in aquaculture feeds. Lipids have about twice the energy density of proteins and carbohydrates. Lipids typically make up about 7-15 percent of fish diets, supply essential fatty acids, and serve as transporters for fat soluble vitamins.

Fish typically require fatty acids of the omega-3 and -6 (n-3 and n-6) families. Fatty acids can be (a) saturated fatty acids (no double bonds), (b) polyunsaturated fatty acids (>2 double bonds), or (c) highly unsaturated fatty acids (>4 double bonds). Marine fish and algal oils are naturally high in omega-3 highly unsaturated fatty acids (>30 percent) and are excellent sources of lipids for the manufacture of fish diets. Lipids from these sources can be deposited into fish muscle. People who then consume these fillets could enjoy the health benefits of consuming foods rich in omega-3 fatty acids, such as reduced symptoms of depression and improved cardiovascular health (Michael B, 1987).

2.2.2.4. Vitamins

Vitamins are organic compounds necessary in the diet to support normal fish growth and health. They are often not synthesized by fish and must be provided in the diet. The two groups of vitamins are watersoluble and fat-soluble.

Deficiency of each vitamin has specific symptoms, but reduced growth is the most common symptom of any vitamin deficiency. Scoliosis (bent backbone symptom) and dark coloration may result from deficiencies of ascorbic acid and folic acid, respectively (FDA., 2016)

2.2.2.5. Minerals

Minerals are inorganic elements necessary in the diet for normal body functions. They can be divided into two groups macro minerals and micro minerals based on the quantity required in the diet and the amount present in fish. Fish can absorb many minerals directly from the water through their gills and skin, allowing them to compensate to some extent for mineral deficiencies in their diet.

Common dietary macro minerals are calcium, sodium, chloride, potassium, chlorine, sculpture, phosphorous, and magnesium. These minerals regulate osmotic balance and aid in bone formation and integrity. Common micro minerals are iron, copper, chromium, iodine, manganese, zinc, and selenium. These trace minerals are required in small amounts as components in enzyme and hormone systems (Steven Craig, 2017).

2.3. Anatomy of GIT fish and its function

The structure and functional characteristics of the GI tract vary widely among species (Suyehiro 1942) and seem, to a great extent, to match the wide diversity of feeding habits and environmental conditions exploited by fish. The structure of the alimentary canal varies in different species of fish, and is generally adapted in relation to the food and feeding habits. Depending on feeding habits and diet, fish are generally classified as carnivorous (eating fish and larger invertebrates), herbivorous (consuming mainly plant material), omnivorous (consuming a mixed diet) and detritivorous (feeding largely on detritus) (Ringø et al., 2003), together with the genera Panaque and Chochliodon which are capable of digesting wood. However, such division may not always be correct since most species consume mixed diets or their feeding habits may change through the life cycle (Olsen and Ringø 1997). The variation becomes obvious by comparing the GI tract characteristics of carnivorous and herbivorous fish and those from freshwater and seawater.

The mucosal lining of the GI tract represents an interface between the external and internal environments, and in conjunction with the associated organs (e.g. pancreas, liver and gall bladder) provides the functions of digestion, osmoregulation, immunity, endocrine regulation of GI tract and systemic functions, and elimination of environmental contaminants and toxic metabolites. The GI tract is basically a tube that courses through the body. The GI tract in Atlantic cod is divided into the following characteristic regions: mouth, gill arch, oesophagus, stomach, mid intestine, distal intestine and fermentation chamber.

2.3.1. The anatomical structure on the mouth and its function

The digestive system, in a functional sense, starts at the mouth, with the teeth used to capture prey or collect plant foods. Mouth shape and tooth structure vary greatly in fishes, depending on the kind of food normally eaten. Most fishes are predacious, feeding on small invertebrates or other fishes and has simple conical teeth on the jaws, on at least some of the bones of the roof of the mouth, and on special gill arch structures just in front of the esophagus. The latter are throat teeth. Most predacious fishes swallow their prey whole, and the teeth are used for grasping and holding prey, for orienting prey to be swallowed (head first) and for working the prey toward the esophagus. There are a variety of tooth types in fishes. Some fishes, such as sharks and piranhas, have cutting teeth for biting chunks out of their victims. A shark's tooth, although superficially like that of a piranha, appears in many respects to be a modified scale, while that of the piranha is like that of other bony fishes, consisting of dentine and enamel. Parrot fishes have beaklike mouths with short incisor-like teeth for breaking off coral and have heavy pavement like throat teeth for crushing the coral. Some catfishes have small brush like teeth, arranged in rows on the jaws, for scraping plant and animal growth from rocks. Many fishes such as the Cyprinidae or minnows have no jaw teeth at all but have very strong throat teeth.

Some fishes gather plank tonic food by straining it from their gill cavities with numerous elongate stiff rods (gill rakers) anchored by one end to the gill bars. The food collected on these rods is passed to the throat, where it is swallowed. Most fishes have only short gill rakers that help keep food particles from escaping out the mouth cavity into the gill chamber.

Once reaching the throat, food enters a short, often greatly distensible esophagus, a simple tube with a muscular wall leading into a stomach. The stomach varies greatly in fishes, depending upon the diet. In most predacious fishes it is a simple straight or curved tube or pouch with a muscular wall and a glandular lining. Food is largely digested there and leaves the stomach in liquid form (https://www.britannica.com/animal/fish/Thedigestive-system).

2.3.2. Stomach and Intestinal Bulb

Two main groups of fish are commonly distinguished on the basis of presence or absence of stomach. The most remarkable feature of the digestive system of lampreys, haggish, chimaeras, and many herbivorous fishes belonging to Cyprinidae, Cyprinodontidae, Balistidae, Labridae. Scomberesocidae and Scaridae, is the lack of a true stomach. In cyprinids, for example marginal (Cirrhinus mrigala), the anterior part of the intestine becomes swollen to form a sac-like structure called the intestinal bulb or pseudogaster (Figure 1). In the absence of a stomach, the anterior intestine performs the function of temporary storage of ingested food (Sinha, 1983).

In stomach less fish the intestinal bulb apparently secretes mucus, and histological the mucosa resembles closely that of the intestine and is devoid of any digestive components (Manjakasy *et al.*, 2009). The mucosa of the intestinal bulb is thrown into prominent folds or villi (for lack of a better term; strictly speaking they are not true villi due to the absence of lacteals) that are lined with absorptive and mucussecreting cells. The absence of stomach in much stomach less fish is compensated by the presence of pharyngeal teeth or gizzards for grinding food (Fänge and Grove, 1979). Wood eating fishes have specifically adapted spoon shaped teeth for efficiently rasping wood (Nelson *et al.*, 1999).

The lack of a stomach in some species of fish raises questions regarding its significance. Several hypotheses have been put forward to explain the absence of a stomach which is often contradictory and speculative. The shape, size and structure of the stomach, when present, are related to the duration between meals and the nature of the diet (De Silva and Anderson, 1995). A stomach is denied as a portion of the digestive tract with distinctive cell lining, where acid is secreted, usually along with some digestive enzymes like pepsin (Olsen and Ringø, 1997).

In his early study, Suyehiro (1942) classified stomachs of fish into five categories according to their morphological appearance: (a) straight tube (Pleuronectidae, Esox), (b) U-shape (Salmonids), (c) V-shape (Plecoglossidae, Mugilidae, Salmonidae, Sparidae), (d) Y-shape (Mugilidae, Clupeidae), and (e) (Carangidae, Gadidae, Scombridae, I-shape Serranidae). The highest degree of modifications of the pyloric stomach have been reported in several members of Clupeoidei, Channidae, Mugili- dae, Acipenseridae, Coregoninae and Chanidae (milkish, Chanos chanos) where it acts as a 'gizzard' for trituration and mixing (Fänge De Silva and Anderson

1995). This development of a 'gizzard' has been attributed to microphage, and is thought to partly compensate for poor dentition (Pillay 1953). The anterior part of the stomach (cardiac or fundic region) is characterized by the presence of gastric glands (Figure 1.) and the musculature is also usually more prominent (De Silva and Ander- son 1995). The stomach mucosa is lined with columnar epithelium and studded with minute depressions, the gastric crypts or pits that lead into the tubular or alveolar gastric glands. Gastric glands are present in abundance throughout the cardiac stomach, so much so that they occupy the entire mucosal layer beneath the superficial epithelium. This part of the stomach is secretary in nature and is responsible for storage and initial physical and enzymatic breakdown of the diet; readers with special interest in this topic are referred to the comprehensive review of (Bakke et al., 2011). The mucosa of the posterior part of the stomach (pyloric stomach) contains many mucus-producing tubular mucus glands or pyloric glands. The number of these glands decreases considerably in the middle region and they are completely absent in the posterior region. The pyloric stomach is completely devoid of gastric glands. The pH of the stomach therefore varies and in salmonids it is between 3.0 and 4.5 (Gislason et al., 1996).



Figure 1. Alimentary tract of themrigal (Cirrhinusmrigala). IB, intestinal bulb; I, proximal intestine; MI, Midintestine; DI, distal intestine. Relative intestinal length (RIL) is14–15(Ray, 1982)

2.3.3. Pyloric Caeca

In a number of fish species, several finger-like outgrowths develop from the anterior part of the intestine in the region of pylorus. These are called pyloric caeca or intestinal caeca, and open into the lumen of the intestine. They are located proximal in the midgut region, and, when present, number from a few as in murrel Channa punctatus to several hundred as in Atlantic cod. The caeca of different species vary considerably in size, state of branching and connection to the gut (Ringø et al., 2003). Histological, they closely resemble the intestine and possibly serve to increase the absorptive surface of the gut (Bergot et al., 1975). The pyloric caeca are always absent in stomach less fish (Kapoor et al. 1975). Although the presence or absence of the pyloric caeca has no apparent correlation with the nature of the food or with feeding habits the caeca are typically absent or much reduced in omnivorous and herbivorous species (Rust, 2002). There is also no clear correlation between the number of caeca and the length of the gut, and feeding habits (Hossain and Dutta, 1996). Pyloric caeca have been reported to increase the surface area for digestion and absorption but do not have any role in fermentation or storage. In salmonids, the pH of caeca and caecal intestine is 7.0 and 7.5, respectively (Ringø et al. 2003).



Figure 2. Alimentary tract of murrel (Channapunctatus). ST, stomach; PC, pyloriccaeca; PI, proximal Intestine; DI, distal intestine. Relative intestinal length (RIL) is 0.5 (Ray, 1982)

2.3.4. Intestine

In fish, the intestine is the main organ for digestion/absorption. In addition to digesting and absorbing feedstuffs, the intestine is critical for water and electrolyte balance, endocrine regulation of digestion and metabolism, and immunity. The intestine shows considerable variation in its length and arrangement in different species of fish ((Ringø et al., 2003). Some fish have a relative intestinal length (RIL = length of intestine/length of body) less than 1, while some fish species have an RIL of 10 to 20 times their body length (Suyehiro, 1942). The highest RIL generally occurs in herbivorous and detritivorous species while the lowest is found in strictly carnivorous and predatory species. The intestine in Cyprinids and Loricariids exhibits wide range of looping and coiled arrangements (Figure 3),



Figure 3. Alimentary tract of detritivorous mrigal (Cirrhinusmrigala) showing extremely coiled intestine (Ray, 1982)

while omnivorous species show an intermediate condition. There are also differences in RIL within the same species. For example, in kalbasu (Labeo calbasu) the RIL of the detritivorous adult is higher (2.1 to 13.0) than that of fry feeding on zooplankton (0.5 to 1.0) (Sinha, 1976). It is assumed that the long intestinal length of herbivorous compared to carnivorous fish is due to the requirement for digesting and absorbing the portion of the plant food which they normally ingest in the adult stage (Sinha and Moitra 1975). The greater length and mass of the intestine in herbivores relative to carnivores have also been thought to allow for additional processing of relatively difficult to digest items. However, it is also possible that herbivorous and/or detritivorous fish consuming plant fibers and detritus depend on extended intestines in order to increase the utilization efficiency, which is not directly related to the surface area (Ringø et al., 2003).

Histological, the intestine in fish contains simple, columnar absorbing epithelium lined with brush border of microvilli, which is typical of absorptive tissue and goblet cells (mucus producing cells) (Anderson, 1995). The numbers of goblet cells are more numerous in the posterior region than in the anterior and middle regions (Ray and Moitra, 1982). The posterior part of the intestine is considered to be the main site for intestinal absorption of macromolecules in salmonids and some other fish species. The midgut starts immediately posterior to the pylorus and the hindgut is an extension of the midgut with gradually diminishing digestive and absorptive functions and increased level of mucus production (Ringø et al., 2003).

2.4. Endogenous Inputs of Digestive Secreta

Different enzymes, bile acids and pancreatic enzymes are constantly secreted or leaking into the GI tract from the wall tissue and from the liver and pancreas, respectively. These fluids contain a great range of compounds that may affect the growth and composition of the intestinal micro biota. Besides macromolecules such as a great number of proteins, for example digestive enzymes and mucopolysaccharides, these fluids contain phospholipids, bile acids, antioxidants such as glutathione, minerals, waste products eliminated from the body through the faeces (e.g. bilirubins giving colour to the faeces) and bicarbonate to stabilize the pH of the luminal contents.

2.5. Luminal PH

Information on the pH of digest along the GI tract of in fish is not well described in the scientific literature. In the stomach the pH values can be below 4, while in the pyloric region and the mid and distal intestine they are above 7 and mostly above 8. The pH

of the chyme seems to be regulated within fairly narrow ranges. In the stomach, pH seems to be higher in Atlantic salmon compared to mammals. This difference in pH may be of relevance for microbial survival and colonization in the stomach. No marked decrease in the distal intestine has been observed as might have been expected if the microbial activity was high (Gislason *et al.*, 1996).

2.6. Passage Rate and Residence Time

The passage rate and residence time in the various sections along the GI tract influence the microbial community and subsequently the host and the host-microbial interactions. Stomach evacuation rate and passage time through the intestine have been observed to vary with temperature, meal size, particle size, feed composition, previous nutritional history, fish size and stress (Fänge and Grove, 1979). Diet is also known to affect passage time and hence may affect microbial colonization in the gut. To our knowledge, no information is available on the relationship between gut microbiota colonization, gut passage rate and residence time, and this topic merits further investigations (Storebakken *et al.*, 1999).

Conclusion

The organization of the gastrointestinal (GI) tract of fish follows the basic features as in other vertebrate groups with a degree of variation in phylogeny and ontogeny, feeding habits, diet, nutrition, physiological conditions and the special functions the gut may perform. There are enormous variations in the morphology of the GI tract among various fish species. The variations in the organization of the GI tract ensure optimum utilization of dietary nutrients, which in many cases means efficient primary digestion and a large intestinal absorptive surface area. Different fish species have adapted different approaches to accommodate this objective. Of particular interest to fish nutritionists is the comparison of morphological features in relation to natural diets. In order to compare data obtained from one fish species with other species, it is essential to make divisions into a broad line of common morphological features.

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