MODERN APPROACH TO AQUAFEED FORMULATION AND ON-FARM FEED MANAGEMENT
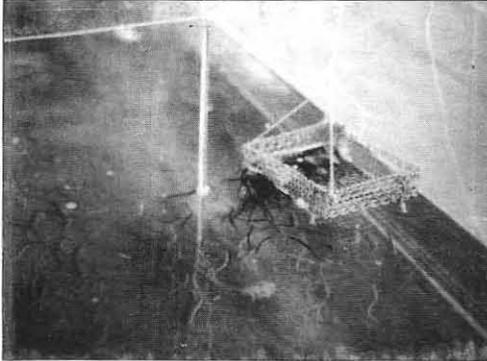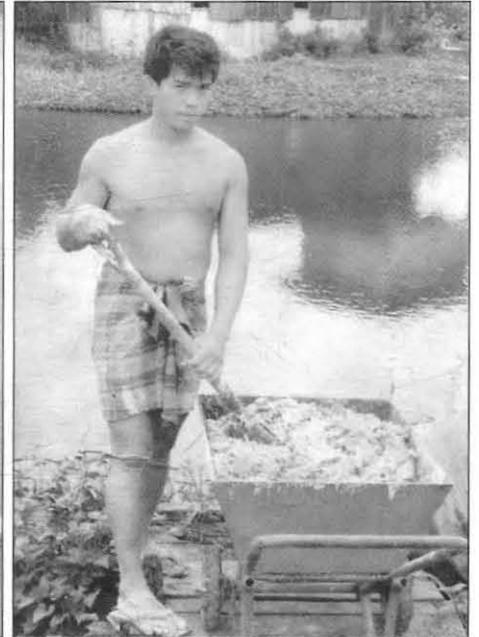
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2. PHYSIOLOGY OF DIGESTION IN FISHES AND SHELLFISHES

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CONTENTS

1.   INTRODUCTION

The knowledge of food and feeding habits and the physiology of digestion of any organism is most essential for development of artificial feed in culture practices. Fish and shellfish being the poikilothermous animal, the digestion process is somewhat different than the terrestrial animals. Similarly, the mechanism of digestion and absorption process is quite different in fishes and shellfishes. The details of the physiology of fishes and shellfishes are discussed below.

2.   DIGESTION OF FISHES

2.1   Nature of food of fishes

Some fish feed on plants, some on animals and a third group derives its protein, carbohydrate, fats, vitamins and minerals from both plant and animal sources. Some fishes live on blood and tissue fluid of other fishes (eg. *Petromyzon*). Some fishes feed on plankton during part of their life and some throughout life. Others feed on weeds. Many other feed on zooplankton and also on other larger animals like annelid worms, snail, mussel, clams, crustaceans, insect, birds, mammals, reptiles and amphibians. Even human beings are found in the stomach.

2.2   Feeding habit

Fish generally change their feeding habits depending upon availability of food. So according to their feeding habits fishes are classified into different categories viz., predators, grazers, strainers, suckers and parasites.

i.   **Predators :** They have well developed grasping and holding teeth. Presence of well defined stomach with strong acid secretions. Intestine is shorter than herbivorous. Nocturnal fishes rely largely on smell, touch, taste and also on their lateral line to locate and catch the prey.

ii.   **Grazers :** They develop biting habits, just like cows and sheep.

iii. **Strainers :** Here food objects are selected by size and not by kind. They can filter the water @ 1-2 gallons/minute through gill rakers to retain plankton. In such fishes filtering organs (Gill rakers) are well developed.

iv. **Suckers :** They are mostly bottom feeding fishes. Presence of inferior mouth and sucking lips. Fishes that suck in mud to extract organism in it may not get good mouthful of food with each ingestion.

v. **Parasites :** It is perhaps the most highly evolved feeding habit. Parasites suck the body fluid from the host fish after making a hole in the side of the body. The males of some deep sea fishes are obligatory parasites on females of the same species. Shortly after hatching the male finds a female and attach by his mouth in her body. The female oblingly responds by developing a fleshy papilla from which the male fish can absorb nutrients as it can not take free living food.

2.3 Feed adaptations

2.3.1 Modification of lips, mouth shape, teeth, gill rakers and digestive tube

Not all the fishes have stomach, i.e. a portion of digestive tube with a typically acid secretions and a distinctive epithelial lining different from that of intestine. For example, in plant feeding roach epithelial tissue of the oesophagus grades directly into that of the intestine. In other grazers such as parrot fishes analogous conditions are found. Some carnivores also have lost their stomach. The primary criterion for being able to do without the stomach does not seem to be whether fish is a herbivore or a carnivore but whether accessory adaptations for trituration and very fine grinding of food exist either in the form of teeth or a grinding apparatus such as gizzard. Where stomach exists, most pronouncedly in carnivores, they are characterised by a low pH and the prominent presence of pepsin among other digestive juices.

The intestine too, has many variations. It is shortened in essential carnivores perhaps because meaty food can be digested more readily than vegetable ones. On the other hand it is often elongated and arranged in many folds predominantly in herbivores. In certain fishes the intestine itself seems to undergo digestion (*autolysis*) in fishes that cease feeding as sexual maturity and breeding arrive. Once the functional digestive tract becomes mere thread with practically no lumen by the time the spawning is over and death approaches.

2.3.2 Stimuli for feeding

Two kinds of stimuli we come across.

i. The factors affecting the internal motivation or drive for feeding, these factors can be season, time of day, light intensity, temperature, time and nature of last feeding any internal rhythm.

ii. Food stimuli perceived by senses like smell, taste, sight and lateral line system.

The interaction of these two factors determine the feeding of fish.

2.4 What is digestion

The basic function of digestive system is to dissolve foods by rendering them soluble so that they can be absorbed and utilized in the metabolic process. The system may also function to remove dangerous toxic properties of certain food substances.

2.4.1 Movement of food in the tract

It is similar to that of higher vertebrates, by peristaltic waves of muscular contraction. In anterior part of the tract movement is voluntary due to presence of skeletal muscles.

The tongue is not mobile by itself. Many predatory fishes appear to regurgitate large food items from the stomach with great facility. This is possible because of pronounced development of striated muscles in the wall of the oesophagus to stomach.

2.4.2 Intestinal surfaces

The mouth cavity, oesophagus and stomach are lined with soft mucus membrane as is in the rest of the tract. There are no salivary glands except in parasitic lampreys. However, tract wall is liberally supplied with glands that secrete mucus which lubricates passage of food material and protects the gut lining. The gut is highly elastic and permits larger size food masses. The lining of the small and large intestine are highly absorptive. The absorptive capacity of these areas is increased by throwing the walls into lengthwise folds (typhosole), transverse folds (rugae) and finger like projections (villi). Along the course of the tract there are many gland cells that contribute digestive enzymes.

2.4.3 Glands and digestive enzymes

There are no digestive juices secreting into the oesophagus. The food passes very quickly from oesophagus into the stomach. Gastric glands occur in most of the predatory fishes. These glands secrete gastric juice which contain HCl and pepsinogen, effective in combination to split large amount of protein molecules. In some carnivorous fishes gastric acidity of pH 2.4 to 3.6 have been measured. Evidence for stomach enzymes other than peptidases are not clear. Some fishes (minnows) lack gastric gland and on this basis, may not possess true stomach. Similarly fish gizzard does not have digestive glands. HCl produced in the stomach facilitates in

i.   disinfecting action killing bacteria
ii.   converts disaccharides to mono saccharides.
iii. ,   it activates pepsinogen to pepsin. pepsin is a proteolytic enzyme and hydrolyses the protein complex food into simple protein molecule in presence of HCl.

Pyloric caeca may have digestive/absorptive function, as absorpture or both. An enzyme *lactase* and high levels of *saccharase* (invertase) has been found in pyloric caeca in trout, and carp which mainly feed on vegetable matter. Pyloric caeca and intestinal mucosa are sources of an enzyme *lipase* which breaksdown fats into fatty acid and glycerol.

The liver is the largest gland of the body which secrete bile - a product of both excretory and secretory activities of the organ. The bile is secreted by the hepatic cells into the bile capillaries and then it is collected into hepatic ducts which join to form a common bile duct. A cystic duct connects it to the gall bladder. Gall bladder acts as a store house for continuously secreting bile.

In some fishes, only vestigeal gall bladder is present and in others gall bladder is completely absent. The bile contains the fat emulsifying bile salts alongwith bile pigments, biliverdin and bilirubin that originates from the breakdown of RBC and haemoglobin. This is done in the liver. Biliverdin (green) and bilirubin (red) are the pigments responsible for the colour of the bile. While bile reaches the intestine, changes in the bile pigment take place owning to bacterial action. Bilirubin is reduced to mesobilirubinogen which on further reduction gives stercobilinogen. This on oxidation gives stercobilin (Brown) and this is responsible for the colour of faeces. The bile salts may not only help to hydrolize the fats but also to adjust the digestive juices of the intestine to the proper alkalinity for the action of digestive enzymes. (Fat digestion is facilited by bile juice. Waxes are not digested. Waxes digestion in some birds and insects is again due to symbiotic bacteria).

Besides its role in digestion, the liver also act as storage organ for fats and carbohydrates. It has further important functions in blood cell destruction and blood chemistry, as well as other metabolic functions such as production of urea and compounds concerned with nitrogen excretion. Liver also acts as a storage organ for fats and vitamin A and D. The content of vitamins in the liver of tunas is so high that persistant eating of their liver may lead to *hyper-vitaminosis*.

Pancreas is a glandular organ lying close to the duodenum. It is formed of exocrine and endocrine tissues. The exocrine tissue produce pancreatic juice which is carried by the pancreatic duct into the duodenum. It is neutral to alkaline and is important in digestion of food. Pancreatic juice contains enzymes for the digestion of proteins, carbohydrates and fats and nucleic acids. The pancreatic secretion is a complete digestive juice because it contains CHO-splitting, fat-splitting and protein-splitting enzymes.

The carbohydrate splitting enzymes from the pancreas is pancreatic *amylase* and it acts upon starch and glycogen in a similar but even more effective way than salivary amylase of mammals, completing the conversion of starch into maltose. The fat splitting enzyme is pancreatic *lipase*. It hydrolyzes each molecule into one molecule of *glycerol* and three of *free fatty acids*. The work of lipase is facilitated by the action of bile. There are no digestive enzymes in the bile. It breaks up large globules of fat into very small ones, giving much more surface for the enzyme to act on. The protein splitting enzymes of the pancreatic juice are *trypsin* and *chymotrypsin*. Trypsin is secreted in an inactive form, *trypsinogen*. This substance is converted into active trypsin by the action of another enzyme present in the intestinal fluid called the *enterokinase*. *Trypsin* and *chymotrypsin* continue the breakdown of large protein and polypeptide molecules into smaller molecules. This process is by hydrolysis with two enzymes acting inside the molecules (endopeptidases) rather than at the ends. Following this action, the polypeptides are broken into much smaller units made up of 2,3,4 or more aminoacids linked together. This is accomplished through the action of enzyme *carboxypeptidase*. This enzyme is also present in pancreatic juice.

(**Note** : The cellulose digestion in all vertebrates is done due to enzymes of bacterial origin. No vertebrate is able to produce enzyme cellulase. Rumen in cow and buffallows has got strong actions of bacteria on the cellulose and thus they derive large amount of energy.

The intestinal fluid contains, in addition to *enterokinase* mentioned above, several enzymes which are necessary to complete digestion of food to simple absorbable substances. The small intestine secretes a group of aminopeptidases and *dipeptidases* (*Erepsin*) which complete the breakdown of proteins into aminoacids, each enzyme being quite specific as to which amino acid it will split off. The intestinal fluid also contains three inverting enzymes by which the *disaccharides* are split into monosaccharides. They are *maltase* splitting maltose into glucose, *lactase* splitting lactose to glucose and galactose and sucrase, splitting sucrose to glucose and fructose.

2.5   Absorption and assimilation of food

Absorption can be defined as "the passage of food through the lining of the digestive tract into the blood". In order for digested food to be absorbed, they must be in aqueous solution, hence, they themselves must be soluble. The component molecules must further be of a size that will enable them to cross the membrane of the cells lining the tract, pass into the circulatory system and ultimately be carried to and enter cells that need them and store them. It is interesting to note in this context that fat absorption is intensified in the pyloric stomach of some fishes and pyloric caeca of others. Fats have been shown to enter into the lymph ducts in these regions without being split into their component fatty acid and glycerol molecules upon which intestinal absorption depends. No absorption takes place in mouth. Not much absorption in the stomach also except for simple molecules of glucose to some extent if at all they are present.

2.5.1 Mechanism of absorption

Nearly all organic and inorganic compounds are absorbed in small intestine. Modifications of gut facilitate the process of absorption. The lining of the small and large intestine are highly absorptive. The absorptive capacity of these areas is increased by throwing the walls into length wise rugae or villi(typlosole). These folds are covered with epithelium within which is a net work of blood capillaries and also lymph vessels. In absorption, material passes from the lumen of the intestine through the epithelium and into the capillaries or lymph vessels by process known as *active transport*. The active transport involves movement of materials against concentration gradient and needs energy. Some substances on the otherhand penetrate passively and diffuse through these folds.

2.5.2 Absorption of proteins

The amino acids formed due to digestion of proteins in the intestine, do not accumulate there but are absorbed into the intestinal capillaries and these enter the portal veins, to be carried into the general circulation by the way of liver. Absorption is more rapid than simple diffusion. Some absorption of protein derivatives has been shown to occur. It has been shown that the smallest units into which the proteins are broken down in the intestine are dipeptides. They apparently leaves to intracellular digestion for the final breakdown of proteins into single building blocks (amino acids) from which the fish proteins are resynthesized. The aminoacids absorbed into the blood diffuse through the body fluids and so reach all the tissue cells. At the same time, most of the tissue proteins are continually undergoing disintegration to release amino acids which also enter the circulation and this become the "amino acid pool". From this pool amino acids are taken up by the cells to be built up into the cell structure as required. If the cell takes up as much amino acid as it looses, it is the state of *dynamic equilibrium* If the loss is greater, the cell wastes and if the gain is greater the cell grows.

2.5.3 Absorption of carbohydrate

The absorption of sugars from the stomach and colon is very slight. The proximal part of the small intestine seems to be the chief site for absorption of sugars. Simple diffusion can play some part no doubt in the absorption, when concentration in the gut exceeds that in blood, but the main features of absorption can only be explained by active transport, requiring energy. The absorption of sugars also depends upon the presence of Na+ ions, probably also on Na:K ratio. However, their remains much to be found about the details of sugar absorption.

2.5.4 Absorption of fats

Fat absorption from the intestine is not clear. It is shown that long chained fatty acids are absorbed very largely into the lymph, whereas, short chained fatty acids enter the portal blood. It has also been pointed out by some that efficient fat absorption requires both lipase enzyme and bile salts.

3. PHYSIOLOGY OF DIGESTION IN SHELLFISHES

In the aquatic environment, particularly in the sea, the crustacea have exploited every type of niche and this ecological diversity is paralleled by the diversity of food eaten. The micro-crustaceans typically feed on microalgae, whereas larger crustaceans range from burrowing detritus feeders to active predators of molluscs and fish. Most of our knowledge of digestive physiology is derived from the larger decapoda, although there has been appreciable research on the Amphipoda and Isopoda. Earlier knowledge of function was fragmentary, but over the last 3 decades experimental research on digestive physiology, using modern methods has grown considerably. However, there are still very large gaps in our knowledge and much remains to be done.

3.1 The principal regions of the gut and their general functions

There is a considerably body of older literature describing the anatomy of the gut of Crustacea. Many recent publications, however, describe detailed investigations of regions of the gut, particularly foregut and the ultrastructure or histochemistry of the midgut.

The gut in Crustacea is basically a simple tube running virtually the length of the body, from the anteroventral mouth to the anus at the end of the last body somite. The foregut and hindgut, derived from embryonic ectoderm are lined with cuticle and only the midgut, derived from embryonic endoderm, has cells in direct contact with the lumen of the gut. Storage, trituration and early digestion may therefore take place in the foregut. It has been reported that up to 12% sugars may pass through the walls of foregut but it is probable that most absorption normally occurs via the midgut. Various glands associated with oesophagus have been described, but their function appears to be lubricatory rather than digestive. Secretion of enzyme is limited to the midgut, while faecal formation and defecation is the usual role of the hindgut. In larger Crustacea, a mechanism is needed to mix the much larger mass of food in the foregut with the digestive enzymes from the midgut. If the food particles are large, digestive efficiency will be improved by trituration and complex gastric mills have evolved in the Decapoda.

3.2 The foregut : Structure and Function

Structure : The foregut or proventriculus is always divided into an anterior distendable part that usually serves as a crop in macrophagus feeders. The posterior end of this chamber constructs as a gastric mill, comprised principally of median dorsal ossicle and two lateral ossicles. The gastric mill leads into posterior part of the proventriculus, which is in turn divided into dorsal and ventral chambers. The dorsal chamber, which bears lateral grooves, leads into the midgut or directly into the hindgut. The ventral chamber contains the filter press (W-shaped) which leads into the digestive gland. The floor of the anterior proventriculus bears a median groove and two ventro-lateral grooves, with fringing dense setae. The ventro-lateral grooves lead to the filter press. There is a complex system of muscle attachment over the surface of the proventriculus, particularly around the gastric mill.

Function : As the food enters the anterior chamber of the proventriculus it is penetrated by the fluid from the digestive gland that flows towards dorso-laterally in grooves in the posterior chamber. Trituration and further mixing with fluid occurs at the gastric mill ossicles. The food mass is continually being manipulated by the lateral plates of the anterior chamber and forced into the gastric mill. Eventually the fluid passes from the food mass into the ventral grooves of the anterior chamber. Dense setae exclude larger particles and the fluid passes backward through the filter-press which excludes particles above 1um and finally into the openings of the digestive gland. Fluid from the digestive gland is pumped dorsally into the dorso-lateral grooves, joined by the fluid squeezed from the food mass in the posterior chamber. Some fluid is also pumped in and out of the anterior diverticulum of the midgut. The combined fluid then pass forwards to the anterior chamber. The circulation is driven by the pumping action of filter press and associated structures. We do not know what happens to the fluid that enters digestive gland. Probably dissolved nutrients are absorbed and the fluid with addition of more enzymes returns to proventricular circulation. This will be the fruit area of research to be investigated.

3.3 The midgut : Cell structure and Function

The digestive gland is comprised of a large number of simple, fragile tubules, each tubule is invested with only a thin layer of connective tissue. (therefore autolysis is rapid). Because the midgut serves the dual role of enzyme secretion and absorption of digested food. The epithelial layer is differentiated into two cell types one with microvilli border i.e. absorptive cells (R) and other without i.e. secretory cells (F). Both these cells actually arise from E cells (embryonic cells).

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                    ┌─────────────────────────┐
                    │   R Cells (absorptive)  │
                    └─────────────────────────┘
                   ╱
┌──────────────────┐
│        E         │
│ (Embryonic cells)│
└──────────────────┘
                   ╲
                    ┌─────────────────────────┐
                    │   F Cells (Secretory)   │
                    └─────────────────────────┘
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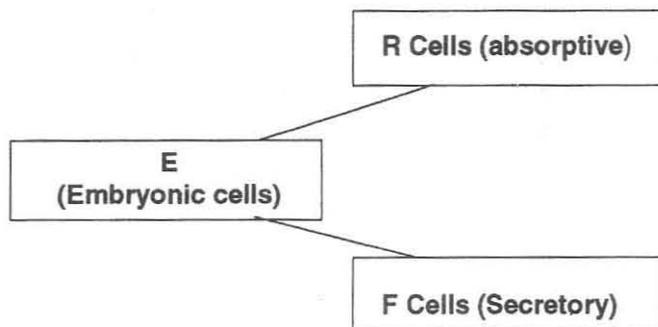
Sometimes the F cells appear to develop into B cells with a large single vacuole containing digestive enzymes. R-Cells absorb and store nutrients and F-Cells synthesise digestive enzymes. The secretion is of holocrine in nature (whole things liberated into lumen).

3.3.1 Digestive enzymes

Proteolytic enzymes : Crustaceans contain proteolytic enzymes similar to mammalian enzymes. There are reports of absence of some enzymes e.g. Chymotrypsin but controversy still exists. There are reports about the presence of trypsin. They are similar to mammalian trypsin in many characters.

The crustacean enzymes have an acidic iso-electric point and they are irreversibly inactivated in acid solutions, they do require ca+ for stability and they are resistant to autodigestion. The crustacean trypsin like proteinases differ from mammalian trypsin in that they attack undenatured protein. Apart from trypsin there are other proteinases in crustacea but very less work on this has been done. In *Homarus* seven proteolytic enzymes have been reported. The presence of various *peptidases* has been reported mainly based on studies with synthetic substrates and crude mixtures. Presence of *carboxypeptidases, acrylamidase,* and *dipeptidase* have been reported in the foregut and digestive gland. The dipeptidases may be associated with the brush border of the absorptive cells in the digestive gland, *zymogens*. No zymogens of crustacean proteolytic enzymes have been found. If this so, how do the secretory cells protect themselves from proteolytic activity. Whether zymogens are synthesized in crustacean is still open question.

3.3.2 Lipid digestion

The digestion of lipids has been given less attention than protein digestion. *Lipase* and *esterase* activities have been demonstrated in many crustaceans. *Lipase* has been partly purified from the foregut of lobster and shown to have molecular wt.43,000 which is similar to that of hog pancreatic lipase. Lipase helps to breakdown long fatty acids into β-diacyglycerol and x-monoacyglycerol, in this form only probably they are absorbed in the gut. Micelles of *sterols* and *lecithins* and readily formed by a *fatty acyltaurine* thus promoting their absorption.

3.3.3 Carbohydrate digestion

Hydrolysis of carbohydrate is a complex process involving *transglycosylation* and condensation. Some *glycosidases* have been also determined. Thus many of the different *carbohydrases* that have been reported as present in the digestive tract of Crustacea may not exists. The glycosidases actually attack dissacharides and oligo-saccharides and make them absorbable.

Starch and similar compounds : x-Amylase activity has been demonstrated in all Crustacea. For digestion of starch and glycogen two other enzymes viz oligo x-1-6 *glucosidase* and *maltase* have been isolated.

Cellulose : *Cellulase* enzyme hydrolysases the cellulose component. The main components are endo β*1,4 glucanase* and *exo* β*-1,4 glucanase* and β-*glucosidase*. Detailed studies have not been made on cellulolytic enzymes in Crustacea. Probably many Crustacea synthesize *cellulases* but cellulase activity may be due to microorganism in the gut and in food prior to ingestion. Cellulase may have two functions in digestion 1) to convert cellulose to glucose as energy source and 2) to enable other digestive enzymes to penetrate a plant cell wall.

Glucans : Glucans are structural polymers present in many algae, fungi, protozoans, therefore potenital source of energy for crustaceans that feed on algae or micro-organism. *Glucanases* enzyme occurs in crustacea together with *cellulases, amylases* and *chitinases* for digestion of carbohydrates.

Chitin : Chitin is the main structural carbohydrate in crustacean skeleton and many of them they eat their own exuviae. This is digested by an enzyme *chitinase* and *chitobiase*. The removal of digestive fluid together with rise in pH and association of other compound such as *mucopolysaccharide* with peritrophic membrane may inhibit residual chitinase activity.

3.3.4 Micro-organisms in the digestive tract

Bacteria are found in the digestive tract of most crustaceans and they derive very little benefit from them. Micro-organism may be a good sources of digestive enzymes for polysaccharides that can not be digested by animals itself. Other possible function of microbial activity in the digestive tract is the supply of vitamins and essential amino acids.

3.3.5 Peritrophic membranes

Peritrophic membranes are formed in large number of crustacea. In decapoda the cylindrical peritrophic membrane is secreted by midgut epithelia cells just behind the digestive gland opening and contains the feces in a characteristic long pellets. It is shown that peritrophic membrane is thought to protect the gut from abrasive material in the feces. Usually the membrane disintegrates soon after its egestion.

3.4 The Hindgut

In higher crustacean the hindgut is a long tube and has internal longitudinal folds containing longitudinal muscle bundles with an outer layer of cuticular muscle. In penaeid shrimp six-smooth surface pads containing spongy tissue fill the lumen of the gut. These pads taper posteriorly to longitudinal ridges of the muscle.

The obvious function of the hindgut is defecation. In shrimp the congitudinal pads grasp the fecal pellet in its peritrophic membrane and rhythmically expel it. The muscular hindgut also pump water into the gut. Anal drinking of water has been also observed in many crustacean. This is mainly to assist defecation process but it also assist in removal of electrolytes excreted into the gut. Further research is needed to assess the exact functions.

4. CONCLUSION

In order to propagate aquaculture activities, more and more species, we need to cultivate in capture condition. Hence the knowledge of the physiology of digestion is most essential. Unfortunately we have not much information covering such aspects and there is good scope for future development.

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6. SELF ASSESSMENT QUESTIONS

I   Answer the following.

i.   What is digestion ? What kind of modification occurs in gut system in response to different feeding habits ?

ii.   Write the mechanism of digestion of food in crustacean animals.

II   Fill in the blanks.

i.   Some fishes feed only on phytoplankton throughout their life cycle, they are called as _____ _planktofeeders_ .

ii.   The food grinding apparatus present in stomach fish is known as __ _gizzard_ __.

iii. The absorptive capacity of the intestinal surfaces is increased by throwing the walls of intestine into lengthwise folds, such folds are termed as __ _typhosole_ __.

iv.   Trypsin is secreted in an inactive form called __ _trypsinogen_ __

v.   If the cell takes up much amino acid as it looses it is the state of __ _dynamic Eq._ __.

III   State whether true or false.

i.   The embryonic (E) cells present in the digestive gland of crustaceans give rise to R and F cells.

ii.   An enzyme *chymotriypsin* is absent in crustaceans. (T)

iii. The cellulase activity in the digestive tract of crustaceans may be due to presence of bacteria. (F)

iv.   The chitin is the structural protein predsent in crustacean exoskeleton. T

v.   The peritrophic membrane is secreted by midgut eprithelia cells just behind the digestive gland opening.
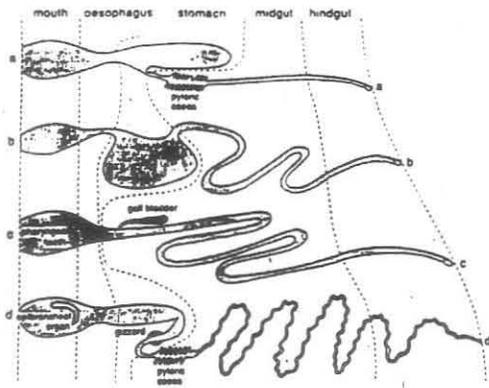
Fig.1: The digestive systems of four fish described in the text, arranged in order of increasing gut length. (a) Rainbow trout (carnivore). (b) Catfish (omnivore emphasizing animal sources of food). (c) Carp (omnivore, emphasizing plant sources of food). (d) Milkfish (microphagous planktivore). (From Smith, 1980.)
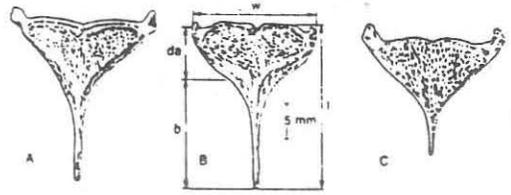
Lower pharyngeal bones of: A *Oreochroms niloticus*
B *Sarotherodon galilaeus*
C *Tilapia rendalli* – da is dentiferous area
b the blade, I the length and w the width

Fig.2: Lower pharyngeal bones of three cichlids – *Oreochromis niloticus* (A), *Sarotherodon galilaeus* (B) and *Tilapia rendalli* (C) and their dentition. (From Pullin, 1988).
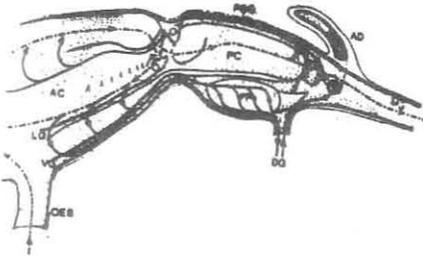

Fig.3: Hypothetical generalized diagram of circulation of digestive gland fluid in the decapod proventriculus, based on Powell's (1974) model (the anatomical features shown are based on that of penaeid shrimp but the general layout is applicable to many Decapods; setae have been ommitted).Dotted lines path of solid food; solid lines,path of fluid. AC. anterior chamber; AD,anterior diverticulum of midgut;DG.digestive gland opening; FP, filter-press; LG.lateral grooves; MG. midgut,O. ossicles of gastric mill; OES, esophagus; PC, posterior chamber; PCG. dorsolateral grooves of posterior chamber;VG,ventral grooves. (For explanation of function, see text).
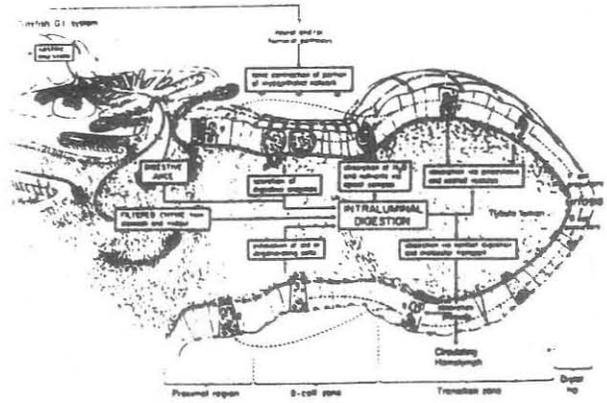

Fig.4: Scheme of digestive gland function showing the differentiation of cell types (see text), secretion of enzymes,and cellular absorption. Relative zone lengths are not drawn to scale. Proximal region and B-cell zone have been reduced 9x. (from Loizzi, 1971).

Fig.5: Schematic drawings of transition zone and B-cell zone in the digestive gland tubule showing ultrastructural details.B, F, R, cell types (see text); ac, apical complex; bi, basal invaginations; bl, basal lamina; cm, circular muscle fiber;cv, clear vesicle; dv, dense-core vesicle; Fe, iron granule in supranuclear vacuole; gly, glycogen; gol, Golgi body; NEM, blood surrounding tubule; ld, lipid droplet; lm, longitudinal muscle fiber;Lu,lumen of tubule; myo,myoepithelial network; np? possible neurosecretory process; pin, pinocytic channels and vesicles; sec, surface enteric coat; vac, vacuole (From Loizzi, 1971).