CHAPTER

Feeding Habits and Digestive Physiology of Fishes

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Introduction

This chapter provides basic information on the feeding habits and behavior, and physiology of fishes and crustaceans. The mechanisms that control the movement and digestion of food, methods of assessing digestibility of feed, factors affecting digestion and absorption of food nutrients, and feeding processes in fish are discussed. An understanding of the feeding habits, feeding mechanisms, and the digestion and absorption processes can help fish farmers and nutritionists maximize the use of feed. The rate at which fish digest their food is of primary importance in determining feeding rates, frequency, and ration size. Knowledge of the digestive physiology of fish is also necessary for an effective feed formulation and in choosing a proper feeding regime.

This chapter aims to teach the reader: the feeding habits and behavior of fishes and crustaceans; the structural adaptation in the anatomy of the digestive tract; the various organs of the digestive systems of fishes and crustaceans and their functions; nutrient digestion and absorption by fishes and the fate of digested and undigested food; the factors that affect the rate of digestion and absorption; and the feeding process in fish.

Feeding Habits and Behavior

The feeding habits and behavior of fishes refer to the process of the search for and ingestion of food. This also includes the manner and the stimuli for feeding.

Fishes can be classified according to their food and diet, which refer to the materials they habitually eat as:

Herbivores – those that feed exclusively on plant materials
Carnivores – those that feed exclusively on animal matter
Omnivores – those that derive their nutrients from both plants and animals
Planktivores – those that feed on plankton, the microscopic plant and animal life in water including bacteria
Detritivores – those that feed on decaying matter

Food availability is a key factor in determining what the fish will eat. Most fishes are highly adaptable in their feeding habits and utilize the most readily available foods. Table 3.1 summarizes the natural food and feeding habits of commonly cultured species of fish and shrimp.

Table 3.1. Feeding habits and natural food of some juvenile fish and shrimp

Fish	Feeding Habit	Natural Food
Milkfish	microphagous planktivore	Microplankton (lab-lab), benthic algae (filamentous green algae)
Seabass	carnivore	Fish of same species or other fish
Grouper	carnivore	Fish of same species or other fish
Snapper	omnivore	Fish, crabs, stomatopods, mollusks, crustaceans and other bottom dwellers
Rainbow trout	carnivore	Fish
Channel catfish	omnivore	Insects, snails, worms, plants and general organic debris in muddy bottom
Common carp	omnivore	Plants and other organic debris in muddy bottoms
Siganid	herbivore	Macroalgae
Mullet	omnivore	Small algal cells and other organic debris
Shrimp	omnivore	Small crabs, shrimps, mollusks, fish, polychaetes, algal matter, and debris

Another classification of feeding behavior of fishes according to the manner of feeding are:

1. **Predators** are fishes that feed on macroscopic animals. They may either be constantly on the move, hunting and pursuing their prey, or lie-on-wait to catch prey that stray into their territory. Some predators feed upon small fishes or insects found at or near the water surface. Predators mainly use vision to hunt for prey, although sharks, eels, and other predatory fishes that feed at night may also rely on smell, taste, and lateral line sense organs to locate their prey.
2. **Grazers** feed on bottom organisms or planktons that are selectively consumed. Some grazers feed on algae or nibble on coral reefs to eat polyps. The actual taking of food is by bites while browsing continuously.
3. **Strainers** are those which filter organisms, mainly diatoms and crustaceans from water. These fishes swim through rich plankton beds, filter the water, and swallow the soup-like concentrate. Strainers normally have numerous, fine, and elongated gill rakers.
4. **Suckers** are those which suck in mud or food-containing material to obtain their food. Sometimes, food items are separated from the sediments before being swallowed, although in some catfishes, food is ingested together with flocculent bottom deposits.
5. **Parasites** such as lampreys and hagfishes, are very different from other finfishes in their behavior. They obtain nutrients by sucking body fluids of host fish.

Anatomy and Physiology of the Digestive System

In nature, there is a wide variety of food available on which fish and crustaceans depend. Fish adapt to their food differences by anatomic as well as behavioral means. Thus, there are many differences in the anatomy and physiology of digestion in fish. There is a strong correlation between the anatomical structure of the digestive tract and the feeding habits of the fish. Herbivorous fish that depend on fibrous foods such as phytoplankton and macrophytes differ anatomically and behaviorally from carnivorous fish that consume meat and other more digestible feeds. Carnivorous fishes have a relatively simple and short gut, with thick mucosa for absorption. Herbivorous fishes have an accessory masticatory apparatus or other physiological adaptation to help in breaking down plant cell walls before the digestion process starts, and a long, thin gut to increase gut retention time and enhance digestion and absorption.

A. Fishes

The digestive system of fish includes the mouth, esophagus, stomach, pylorus, intestine, liver, and pancreas. An illustration of the digestive tract of four commonly cultured fishes that differ in their food preferences is shown in Figure 3.1. The digestive tract is tubular in structure. The whole digestive tract is often referred to as the gut and in fish, the gut usually has four divisions: these are the headgut, foregut, midgut, and hindgut. The **headgut,** which is the most anterior part includes the mouth (oral or buccal cavity)

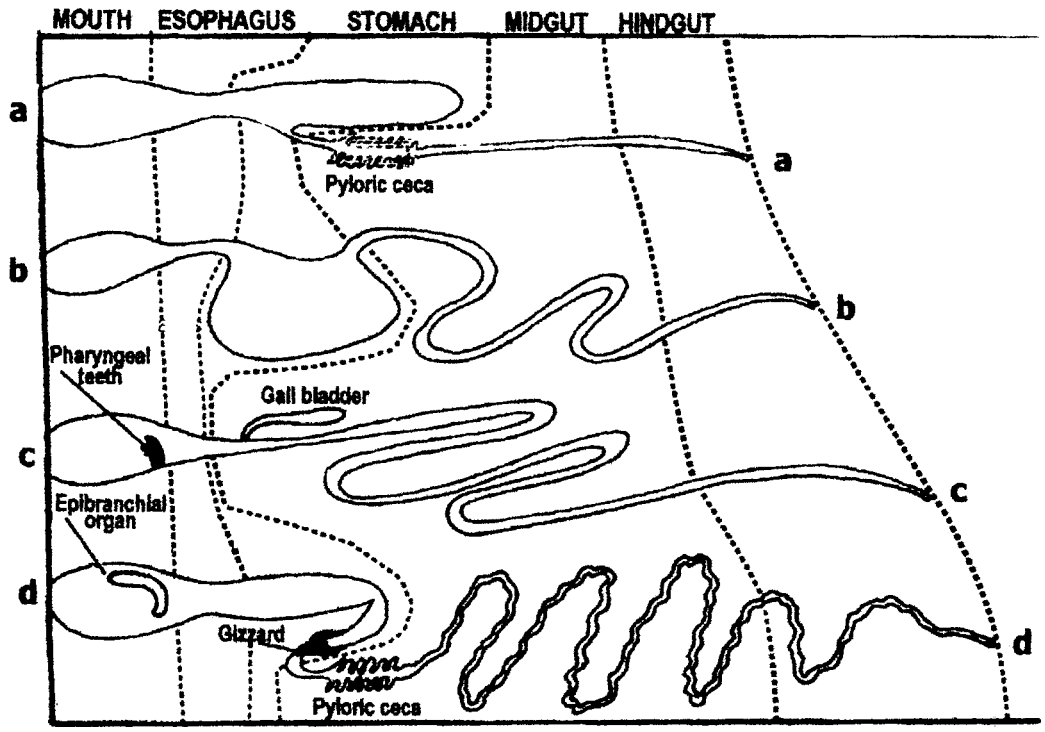


Figure 3.1
Diagrammatic representation of the digestive systems of four fishes, arranged in order of increasing gut length. a) Rainbow trout (carnivore); b) Catfish (omnivore, eating more of animal source); c) Carp (omnivore, eating more of plant source); d) Milkfish (omnivore, microphagus planktivore).
Source: Smith 1989

and gills (branchial or pharyngeal cavity). The **foregut** begins at the posterior edge of the gills and includes the esophagus and stomach. The **midgut** consists of the intestines and pyloric caeca, if present. The midgut is the longest portion of the gut and may be coiled into complicated loops. The **hindgut** includes the enlarged portion of the intestines and the rectum or anus. Each portion of the gut has a very variable structure for adaptation. The liver and pancreas are organs involved in digestion but are found outside the tubular structure.

1. Headgut

Mouth and various ingestion mechanisms

The first phase of digestion is the ingestion of food into the mouth. The mouth has a variety of adaptations for capturing, handling, and sorting of food before entry into the stomach. Figure 3.2A shows the different shapes of mouth in response to their food adaptations. Fish have teeth that vary in type, number, and arrangement. They serve to catch and hold the prey. The arrangement and structure of the teeth are related to the kind of food that the fish normally eat. There is a strong correlation among kind of teeth, feeding habits, and food eaten.

Generally, the more active feeders have strong jaws with sharp teeth to bite and shred the food. Some major kinds of jaw-teeth are the following: cardiform, villiform, canine, incisor and molariform (Figure 3.2B). Those feeding on mollusks and crustaceans have short heavy teeth, strong enough to crush the mollusk shell. Zooplankton feeders and most planktivores have practically no teeth. The shredding of food is most often done in the throat or pharynx. Here, another set of specialized teeth may be found. Again, the structure, size and shape of the pharyngeal teeth are also variable. Plankton feeders have fine rows of pharyngeal teeth, while mollusk eaters have large but flat crowned teeth, which is better adapted to crushing their food.

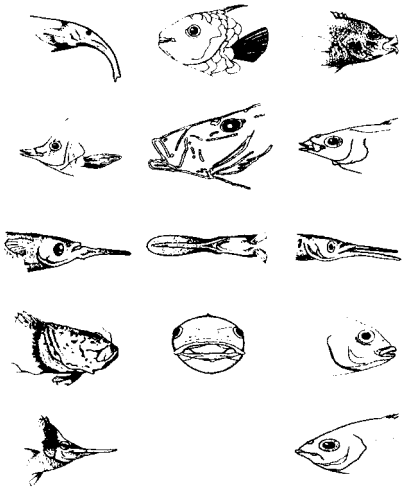


Figure 3.2A
Variations of the mouth structure in fishes.

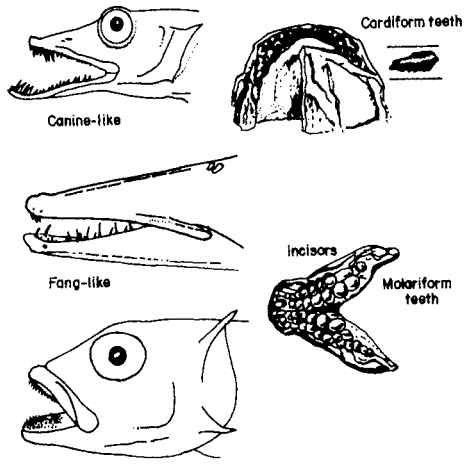


Figure 3.2B
Some major kinds of jaw teeth.

2. Foregut

Esophagus

Most fish have short, wide esophagus that serves as a transitional area between the striated muscles of the mouth and the smooth muscles of the gut. Mucus producing cells are present in the esophagus. In general, the esophagus serves only as a passage way, however, enzyme activity has been detected in the esophagus of some fishes indicating a more active role of the esophagus in the digestion process in these species.

Other fishes with long, slim body shapes like the seawater-adapted eels have a long esophagus. Osmoregulation may take place in the esophagus if mucus is present. The mucus is much thicker anteriorly than posteriorly and is electrically charged. Some reports have suggested that both passive and active transport of ions into the blood may also take place in the esophagus without addition of water such as the dilution of ingested seawater in freshwater eels.

Stomach

The stomachs of fishes vary greatly in their anatomical structure due to adaptations to specific foods. There are four general configurations or shapes of fish stomachs. These include:

a. a straight stomach with an enlarged portion
b. a U- or J-shaped stomach
c. a stomach shaped like a Y on its side where the stem faces the caudal portion
d. stomachless fish, such as in carps and other cyprinids

The stomach has a configuration or shape which is convenient for containing food in the shape in which it is ingested. Food is temporarily stored in the stomach while the rest is gradually being processed through the other portion of the digestive tract. The size or capacity of the stomach in relation to the body weight varies between species and is usually related to the interval between feedings and to the size of food particles. Generally, fish that eat relatively small, soft particles have small stomach whereas fish that eat large food particles, e.g. whole fish, or eat at infrequent intervals have larger stomach.

The cecum of the Y-shaped stomach is adapted to stretch posteriorly to accommodate large food particles or prey. In contrast, the absence of a stomach has been suggested to benefit fish adapted to freshwater (low chloride concentration) where stomach acids impose added osmoregulatory pressure. This is to avoid acidifying large amounts of alkaline food, as in omnivorous fish that eat plant sources, corals, shells, and others.

In milkfish, the stomach can be divided into cardiac and pyloric portion. The cardiac portion is often more enlarged while the pyloric stomach is highly muscular (Figure 3.3). The pyloric stomach intensely grind the food particles resulting in chyme (a paste like mass).

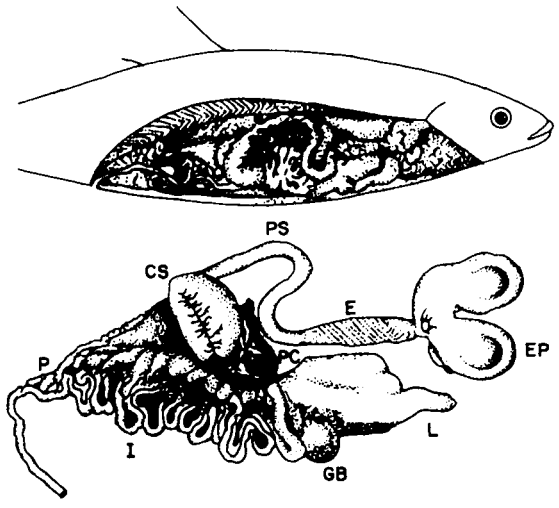


Figure 3.3
Regions of the digestive tract of milkfish *Chanos chanos*. EP-epibranchial organ; E-esophagus; CS-cardiac stomach; PS-pyloric stomach; PC-pyloric caeca; I-intestine; L-liver; GB-gall bladder; P-pancreas.

The capacity or volume of the stomach in relation to the body weight varies between species and reflects the size of the meal that can be taken voluntarily. It can vary from as small as 10% of body weight and as large as 50% of body weight in a single feeding.

3. Midgut

The digestion process actively continues into the intestines after preliminary digestion in the stomach. All fishes have intestines. The length of the intestines varies from as low as 1/5 to as high as 20 times the body length. In some fish, the intestines may be short and straight while it can be long, folded, and looped in others. In general, herbivores have longer intestines than carnivores. Although there are some cases of overlaps, some general statements can be made on gut length in relation to feeding habits of fish (Table 3.2). Within the same fish species, the relative gut length can change as feeding habit of the fish changes. Gut length is directly more related to the amount of indigestible material in

Table 3.2 General observations on feeding habits and relative gut lengths (ratio of intestine to body length) in fish

Feeding habits	Relative gut length
Carnivores	0.2 - 2.5
Omnivores	0.6 - 8.0
Herbivores	0.8 - 20.0

Feeding habit and relative gut length in some fishes

Species	Food or feeding habit	Relative gut length
Gobio gobio	Invertebrates	0.80
Chelethiops elongatus	Zooplanktons	0.75
Elopichthys bambusa	Carnivores	0.63
Borilius meorei	Carnivores	0.65- 0.80
Catla catla	Plants, insect larvae	4.7
Garra dembensis	Algae, invertebrates	4.5
Cirrhina mrighala	Algae, detritus	8.0
Gadus morhua	Carnivores	1.05 - 1.50
Labeo calbasu	Herbivores	3.75 - 10.0
Labeo horie	Detritivores	15.0 - 21.0
L. niloticus	Algae, detritus	16.9
L. variegatus	Algae, detritus	16.9
L. lineatus	Algae, detritus	16.1
Ctenopharyngodon idella	Plants	2.5
Doras grypus	Plants	2.8
Hypophthalmichthys molotrix	Herbivores	4.6 - 7.1
Micropterus salmoides	Carnivores	0.7 - 0.9
Salmo salar	Carnivores	0.73 - 0.80

the food rather than whether the food source is of plant or animal origin. Fish that ingest large amounts of detritus have gut lengths similar to those of herbivores.

Some fishes possess pyloric caeca. There are conflicting reports on the functions of the **pyloric caeca** in fish. Histologically, the pyloric caeca resembles the intestines. Most studies indicate that it serves as an extension of the intestines thus increasing the effective surface area for digestion and absorption. Other studies show that it acts as an accessory food reservoir, for temporary storage, possibly a devise for saving space. It is clear, however, that rainbow trout caeca takes up amino acids and sugars across the apical membrane of the epithelial cells. Electron microscopy has shown that both intestinal and caecal cells are involved in lipid absorption, with caecal cells being more active.

The structure of the absorptive cell of the intestines reflects its specialized function in digestion (Figure 3.4). The cell contains many mitochondria, which provide energy for metabolic processes; endoplasmic reticulum, where proteins (including digestive enzymes) are assembled, and golgi bodies where carbohydrate side chains are attached to proteins. Tight junctions and desmosomes bind the absorptive cells into a single sheet on the surface of the mucosa. The nucleus lies deep in the cell. The most striking feature of the cell is the presence of a brush border, a prominent structure on the surface facing the lumen of the intestine. The brush border is composed of minute projections called microvilli. On the membrane of the microvillus are found several kinds of digestive enzymes and transport proteins.

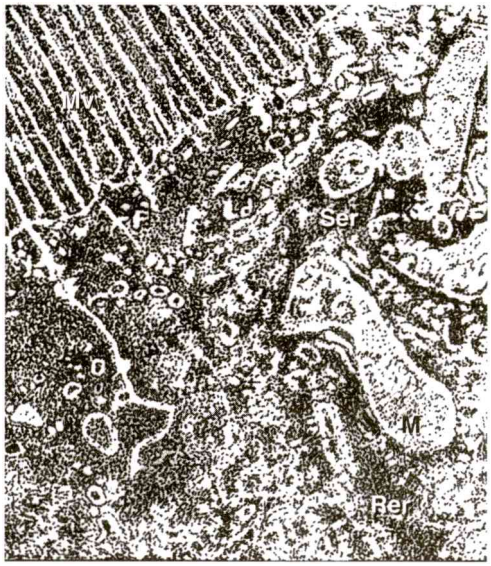


Figure 3.4
Schematic representation of a portion of an absorptive cell from the intestine, Mv-microvilli, M-mitochondrion, Ser- smooth endoplasmic reticulum, Rer-rough endoplasmic reticulum.

4. Hindgut

The hindgut is an extension of the midgut. Digestion has been shown to continue in the hindgut although with a gradually diminishing digestive or absorptive function, an increased secretion of mucus and a pH near neutral. Histological sections show a sudden change from columnar secretory and absorptive to a squamous epithelium that produces mucus.

5. Liver

The liver is an important metabolic organ. It aids in digestion by secreting bile, a greenish fluid with strong emulsifying properties. The bile is stored in the gall bladder and is composed of a mixture of bile salts, taurocholate, glycocholate. Bile acids are derived from metabolism of cholesterol, and degradation products of hemoglobin, bilirubin and biliverdin. Bile serves to emulsify lipids in the gut and may contain other waste products. The bile duct opens into the anterior intestines or into the pyloric caeca if present. Fish can reabsorb bile in the hindgut even though most lipid uptake occurs in the anterior intestine. The liver is also a storage organ for lipids and glycogen or stored starch. In some fishes, large amounts of lipid is stored in the liver to help maintain buoyancy. In other fishes, glycogen is the major stored nutrient.

6. Pancreas

The pancreas is involved in many important functions in digestion. Pancreatic morphology is variable in many bony fishes. In most fishes, unlike in land animals, there is no discrete pancreas. The pancreas is diffused, scattered, and embedded in the mesenteries, in the liver, and clustered around the bile duct, or in combinations of sites. In a diffused pancreas, several small ducts open into the intestine and the pyloric caeca. In other cases where the pancreas is found inside the liver, the pancreas delivers its secretions directly into the gallbladder. The pancreas produces insulin and digestive secretions, principally proteases and bicarbonates. Insulin stimulates uptake of amino acids from the intestine and may stimulate growth. In the northern pike, insulin decreases blood amino acids with uptake into skeletal muscles, while in cod, insulin decreases blood glucose.

B. Crustaceans

The crustacean digestive tract is mostly straight and consists of the foregut, the midgut, and the hindgut (Figure 3.5). The foregut and the hindgut are lined with chitin. The midgut arises from the endoderm and the innermost layer adjacent to the lumen is the mucosa lined with epithelial cells which is composed of simple columnar cells. These are supported by a basement membrane, a layer of circular muscles and then by a layer of longitudinal muscles. These muscle layers are surrounded by a layer of fibrous connective tissue or serosa and contain a network of arterial hemolymph vessels.

In the anterior portion of the midgut epithelium are simple columnar cells with medial nuclei. The surface adjacent to the lumen also contains microvilli. Many mitochondria, secretory granules and golgi bodies are present in epithelial cells. In contrast, the posterior portion of the midgut epithelium contains many squamous cells which secrete mucus. The cell surface facing the lumen also contains microvilli.

In almost all crustaceans, the midgut is made up of one or more pairs of glandular appendages called the **hepatopancreas**. The hepatopancreas contains a wide range of digestive enzymes which hydrolyze food nutrients and aid in breaking down by the gastric mill. The hepatopancreas is composed of simple blind-ending tubules or diverticula which open into secondary secretion ducts. These ducts, in turn, open into the primary secretion or collecting duct, through which the secretion is poured into the midgut, behind the stomach. The lumen of the hepatopancreatic tubule contains granular material and cells lining the mucosa are covered with a microvillus brush border. The tubules are lined with an epithelium in which different cell types are present. The apex of the tubule contain undifferentiated embryonic or **E-cells**. Farther away from the apex, cells begin to differentiate into developing absorptive, storage or **R-cells**. In the proximal region of the

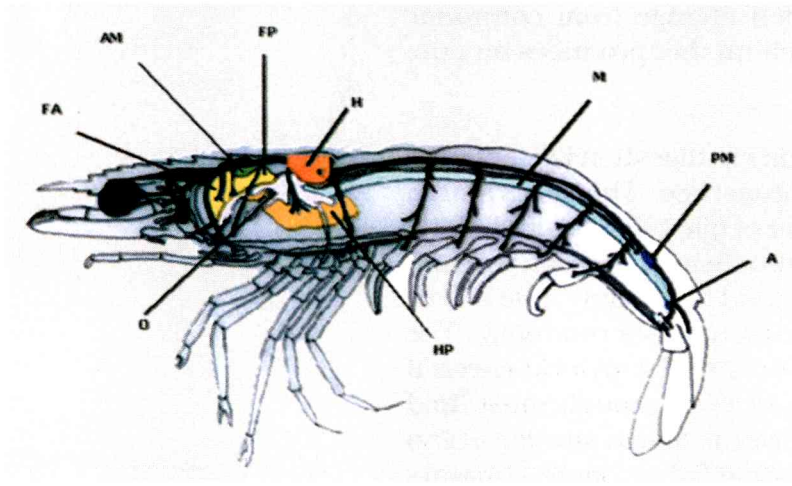


Figure 3.5
Diagram of the digestive system of shrimp with gills and musculature removed to show major organ systems. FA-foregut (anterior chamber); AM-anterior midgut cecum; FP- Foregut (posterior chamber); H- heart; O- ovary; HP- hepatopancreas; M-midgut; PM-posterior midgut cecum; A-anus

hepatopancreatic tubule, in addition to the E and R cell types, are found large distinctive secretory or **B-cells** (Figure 3.6).

The contents of the gut of crustaceans are moved forward by peristaltic or contractile movements of the longitudinal muscles. Peristalsis occurs in the esophagus, midgut, and hindgut. Absorption occurs in the anterior part of the midgut and digestion in the posterior part. Therefore, it is necessary that strong anti-peristaltic movements also take place in the midgut from the posterior end to the anterior portion. In decapods, if mandibles armed with sharp teeth for chewing food are absent, there is a gastric mill with movable teeth fixed to platelike ossicles that serve as substitute for grinding the food. The gastric mill is an adaptation to a sedentary existence. It allows crustaceans to swallow their food first, then chew at leisure while hidden from other animals.

The digestive juice is produced chiefly by the cells of the hepatopancreas and transported to the stomach. In some species, the pH is about 5 during hunger and rises to pH 6.6 on feeding. In others species, the pH is neutral

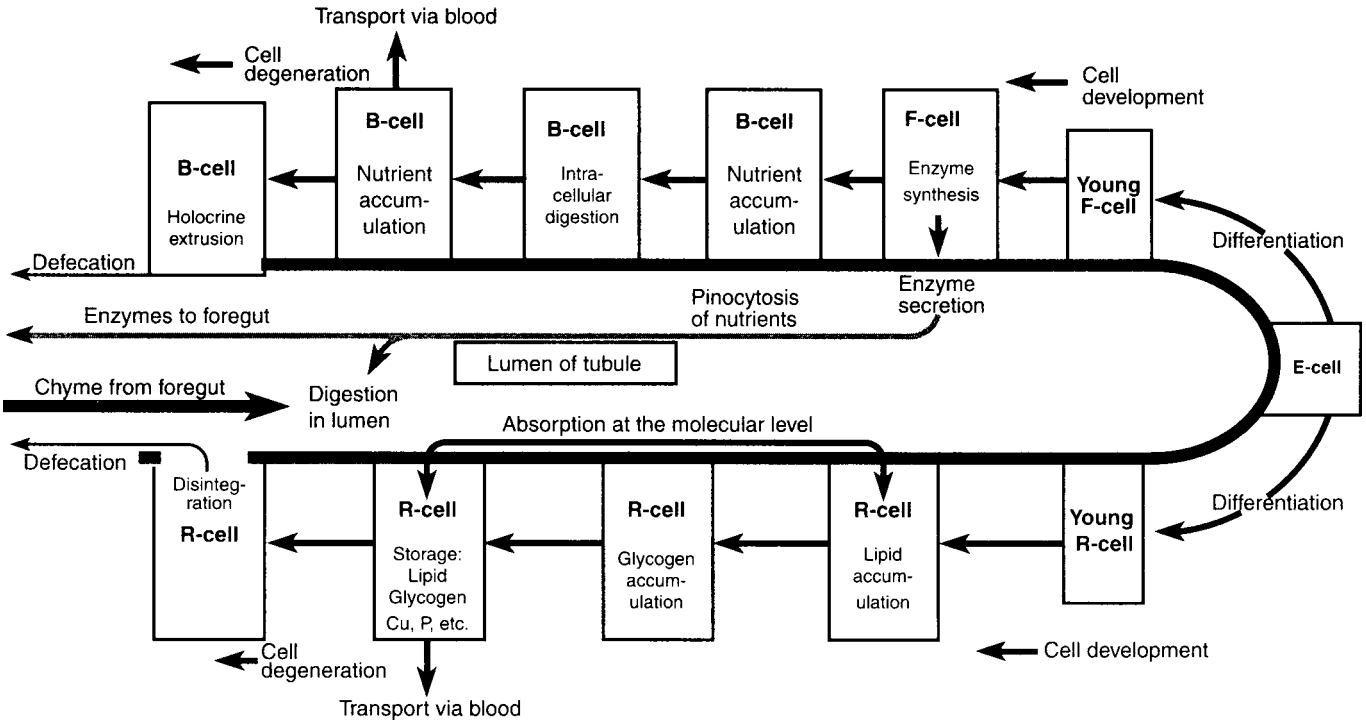


Figure 3.6
Scheme of differentiation and function of the digestive gland tubule. The E-cells differentiate into F-cells (fibrillar) or R-cells (storage). F-cells secrete enzymes and differentiate into B-cells. B-cells absorb small particles by pinocytosis. R-cells absorb nutrients and store lipids, glycogen, copper, phosphorus and other substances.
Source: Dall, 1992

in the hungry animals and increases to pH 7.5 after feeding. The digestive juice contains various digestive enzymes and bile salts that act in emulsifying fats.

Absorption occurs mainly in the hepatopancreas and in the anterior part of the midgut. The R-cells of the hepatopancreas have the capacity to absorb nutrients.

Digestion and Absorption

Digestion is a process whereby ingested food nutrients such as proteins, lipids and complex carbohydrates are broken down into units that are small enough to be absorbed across the gut wall. The process is accomplished through the action of digestive enzymes. The ability of fish to digest feed depends on the secretion of adequate quantities of the appropriate types of enzymes. Many of the enzymes are stored in an inactive or proenzyme form. Once secreted into a favorable environment for digestion, usually influenced by pH, these inactive enzymes are converted to the active form ready to perform their specific digestive function. When various nutrients have been adequately digested, they are then absorbed primarily in the midgut.

There are several mechanisms of nutrient absorption in fishes-**simple diffusion, active transport, and pinocytosis.** In simple diffusion, solutes pass through the membrane from an environment of high to low solute concentration without using energy. Active transport differs from simple diffusion as it requires a continuous supply of energy and transports solutes only in one direction from low to high solute concentration. A carrier system that utilizes Na^+ and ATPase activity is needed in the active transport of glucose and some amino acids. Pinocytosis (cell drinking) is the process by which materials are taken into the cell through an invagination and subsequent dissolution of a part of the cell membrane. This process enables the cell to absorb some proteins and lipids in intact form. Absorptive cells of the midgut are capable of undergoing pinocytosis.

A. Digestion and absorption of proteins

Proteins are hydrolyzed into amino acids or polypeptide chains of a few amino acids with the help of enzymes known as **proteases**. The process can occur in acidic or basic pH.

1. Pepsin

Pepsin and hydrochloric acid play important roles in protein digestion in fish stomachs. The pH optimum for pepsin is about pH 2.0. Pepsin is synthesized in the gastric gland in the inactive form called **pepsinogen**. Hydrochloric acid converts the inactive pepsinogen to the active pepsin. Pepsin is an endopeptidase and cleaves or cuts most peptide bonds in the interior region particularly where linkages are formed by aromatic amino acids (phenylalanine, tyrosine, and tryptophan), and acidic amino acids (aspartic and glutamic acid).

2. Trypsin and Chymotrypsin

Trypsin and chymotrypsin are involved in the alkaline digestion of proteins. These enzymes are synthesized, stored and secreted in an inactive form by the pancreas and transported to the midgut and the pyloric caeca. **Trypsinogen** is activated in the intestine by enterokinase, an enzyme secreted from the intestinal mucosa. When activated, trypsinogen becomes **trypsin.** In turn, trypsin, activates **chymotrypsinogen** to **chymotrypsin**. Both trypsin and chymotrypsin are endopeptidases but cleave different linkages in a protein. Trypsin cleaves peptide linkages which are formed by basic amino acids, arginine, lysine, and histidine. Chymotrypsin cleaves linkages with aromatic amino acids, phenylalanine, tyrosine, and tryptophan.

In milkfish, both tryptic and chymotryptic activities are higher in the posterior intestines than in the anterior part. The pyloric caeca also contains high activities of both enzymes. Milkfish intestinal protease activity appear to have two pH optima, one at pH 7.0 to 7.6 and another at pH 9.5 to 10.0. It also has a temperature optimum of about 50° to 60°C.

PEPSINOGEN	TRYPSINOGEN	CHYMOTRYPSINOGEN
⇓ HCl	⇓ enterokinase	⇓ trypsin
PEPSIN	TRYPSIN	CHYMOTRYPSIN

Conversion of pepsin, trypsin, and chymotrypsin from their inactive forms

3. Carboxypeptidases

Carboxypeptidases are also secreted from the pancreas in the inactive form. These are exopeptidases which cleave the C-terminal amino acid of peptides or proteins. There are two types: carboxypeptidase A and B. **Carboxypeptidase A** is active towards proteins with aromatic C-terminal amino acids (phenylalanine, tyrosine, and tryptophan) while **carboxypeptidase B** acts preferentially on those peptides with basic amino acids (lysine and arginine).

4. Aminopeptidases

Aminopeptidases are exopeptidases that act on N-terminal peptide of proteins.

In summary, because of the complexity of proteins, their complete digestion has to proceed in a number of steps (Figure 3.7). The protein molecule is first hydrolyzed into relatively large polypeptide fragments by endopeptidases. These fragments are then hydrolyzed by enzymes acting on the amino and carboxyl bonds and finally dipeptidases reduce the protein to its constituent amino acids.

Proteins can be absorbed as whole proteins, peptides, or free amino acids. Protein macromolecules may be absorbed in the gut epithelium via pinocytosis. Rainbow trout have granule cells in the lamina propria of the intestine just under the mucosa which could be part of this uptake system.

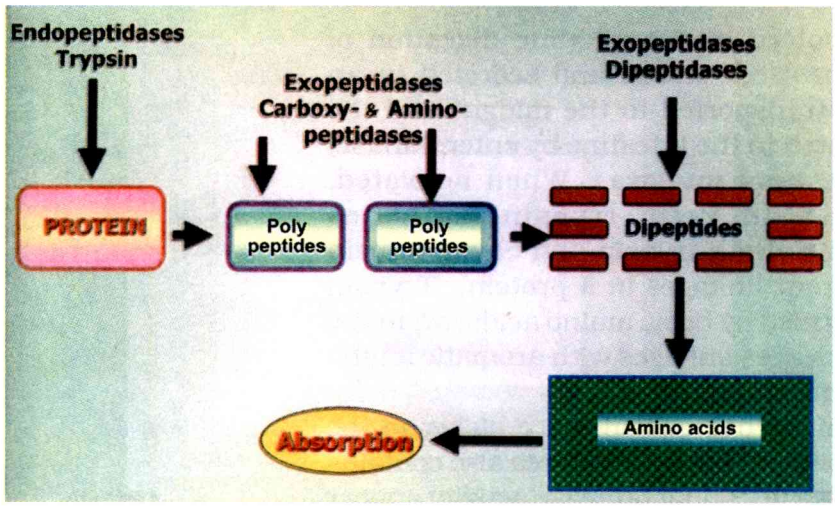


Figure 3.7
Sequence of protein digestion. The protein molecule is first hydrolyzed into polypeptides by endopeptidases. Polypeptides are further hydrolyzed to smaller dipeptides and finally into constituent amino acids.

For completely digested proteins, each amino acid has its own uptake characteristics. In rainbow trout, L-leucine uptake is shown to be specific for the L-isomer, active and sodium-dependent and could be inhibited by other neutral amino acids such as L-valine and L-methionine. Lysine uptake is slowed down by the presence of glucose and hastened by ATP. Some amino acids may be taken up by simple diffusion; others may be transported by carriers in a sodium-independent system which usually occur in the basolateral membrane.

B. Digestion and absorption of carbohydrates

Carbohydrases digest complex carbohydrates and are found in fish intestines. They are very important in herbivorous fish because of the high levels of carbohydrate in plants. The enzyme **amylase** catalyses the digestion of starch. There are two forms: **α-amylase** which acts randomly cleaving the chain from within and **β-amylase** which cuts the chain at every two glucose units. At the branched point, another enzyme, **dextrinase** does the work. The amylase and dextrinase produce maltose. Maltase hydrolyses maltose to give glucose, the final product of starch digestion (Figure 3.8). Most fish have amylase; in herbivorous fish, such as tilapia, it may be present in all parts of the digestive tract, whereas in carnivorous fish it may be found only in the pancreas, pyloric caeca and intestines. In milkfish (an omnivore), extracts from the intestines, pancreas, pyloric ceca and liver showed high levels of amylase activity. In addition, maltose, trehalose, dextrin, starch, and glycogen are rapidly hydrolyzed in the presence of crude extracts from the intestines and pyloric caeca of milkfish.

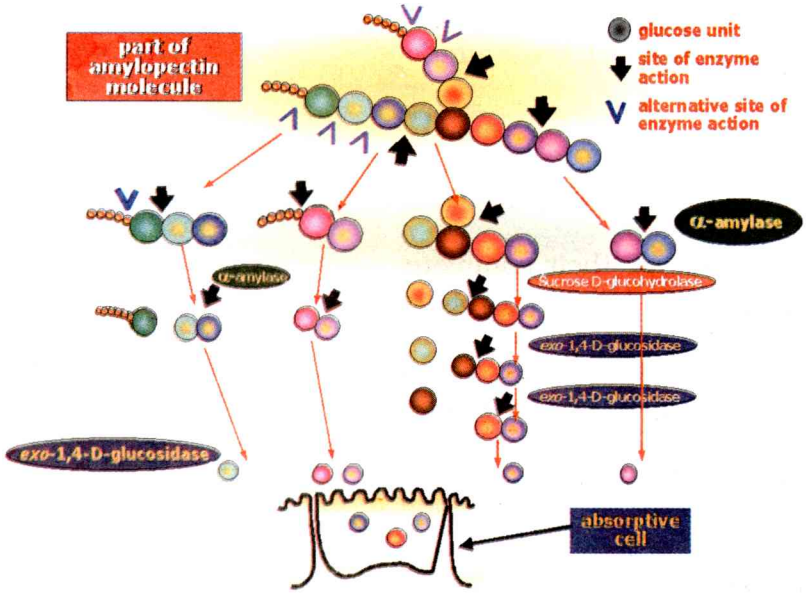


Figure 3.8
Representation of digestion and absorption of carbohydrates.

Other complex carbohydrates that are potential sources of energy but are not readily digested are cellulose, a constituent of plant cell wall, and chitin, a component of crustacean exoskeleton. The complete digestion of cellulose is mediated by two enzymes: **cellulase** and **cellobiase**. **Cellulase** hydrolyses cellulose to

disaccharide cellobiose, which is then acted upon by **cellobiase** producing the final breakdown product, glucose. Very few fish have cellulase activity, most likely the intestinal microflora actively provide the cellulase. Cellulytic bacteria are widely distributed in nature.

Carbohydrate absorption has been tested by measuring the uptake of glucose, the usual final end product of carbohydrate digestion. Glucose transport appears to be lowest in carnivores (e.g. catfish) and highest in herbivores (e.g. carp).

C. Digestion and absorption of lipids

Lipases hydrolyze ester linkages in triglycerides. The end products of lipase activity are glycerol and fatty acids. Lipases are detected in the pancreas, pyloric ceca, intestine, and liver. In milkfish, lipase has also been detected in the esophagus. Milkfish intestinal and pancreatic lipases appear to have two pH optima- pH 6.8 to 8.0; and pH 6.4 to 8.6, respectively. The detection of two well-defined pH optima, one at slightly acidic and the other at alkaline pH for both the intestinal and pancreatic lipases suggests a physiological versatility for lipid digestion in milkfish. **Phospholipases** are enzymes that hydrolyze phospholipids.

Lipids are taken up by the intestinal and cecal epithelium, partly as fatty acids, mostly as mono-glycerides and partly as droplets, and transferred into blood and lymph vessels (Figure 3.9). In the intestinal cell, fatty acids are re-esterified to triglycerides and are transported as very low density lipid particles into lymph vessels. In the blood, triglycerides are transported as chylomicra. The lipid absorption process in fish, although much slower than in mammals, does not differ fundamentally.

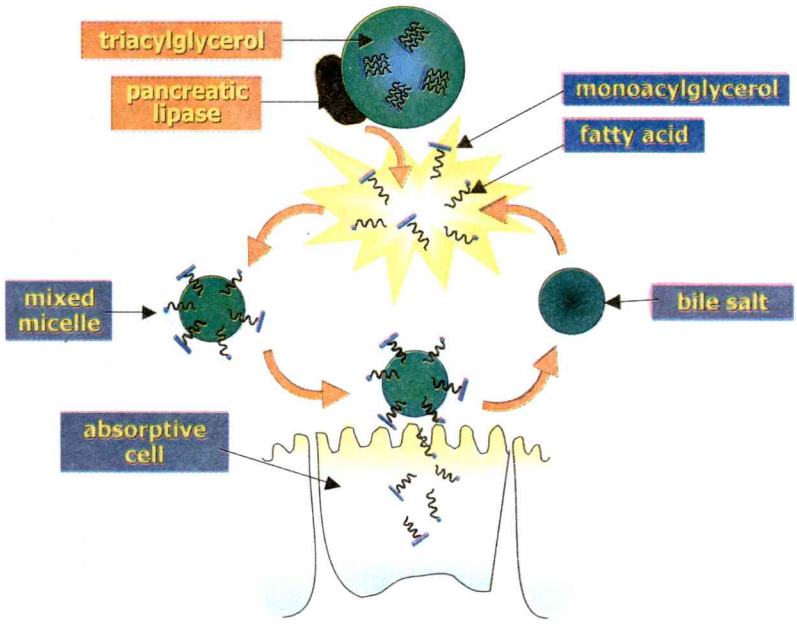


Figure 3.9
Diagrammatic representation of digestion and absorption of lipids.

Measurements and Analysis used in Digestion Studies

A. Measurement of Stomach Contents

Analysis and measurement of stomach contents can give information on the feeding preferences of a particular species as well as its frequency of feeding. Several methods are used to measure stomach contents. however, all of these methods have their limitations.

1. The occurrence of a particular type of food in the fish stomach can be determined qualitatively as in web studies but the quantity of the food present cannot be obtained by this method.

2. Each kind of individual food organism in the stomach can be counted to show the choice of the fish for certain food types from a general population of potential food organisms. The method can not be used in cases where the food is chewed or when the food is not in distinct units as with detritus.
3. The use of stomach flushing methods measures the displacement volume of a food type or of the total food volume and is most applicable if the food is in liquid form.
4. Measurement of the wet weight or the dry weight of food as a percentage of the body weight is another procedure for determining stomach contents. This method may give inaccurate results when heavy items such as mollusk shells, sand or mud are present.
5. Estimate of fullness- half, third, quarters, etc.- of the stomach by appearance is an inexact method but useful under practical conditions.

Gastric emptying rate and food passage rate may be determined in a number of ways. This can be done by killing or not killing the fish to obtain stomach contents. In many cases, a certain number of fish is fed a known amount of food. Samples are obtained periodically by serial slaughter to determine gastric emptying rate. One limitation of this method is that it assumes that all the fish ate exactly the same amount. An alternative procedure is to feed an individual fish a known amount of food, and then after a certain period stomach contents are removed from the fish under anesthesia. The stomach contents may be flushed out with water using a variety of gadgets. Other methods of measuring the amount of food in the stomach or intestines without removing food involve feeding fish a diet with a marker like barium sulfate or iron powder and using an x-ray to view the labelled food at various times. This is useful in fish that are too small for other methods.

B. Measurement of digestibility

The first step in evaluating the potential of a feedstuff for inclusion in a diet is to determine or measure its digestibility. Digestibility can be measured either by *in vivo* or *in vitro* methods.

1. In vivo methods

The most common method of measuring digestibility is to add to the diet a marker, such as chromic oxide or iron powder that is neither digested nor absorbed. The diet is fed to the fish and the concentration of the marker is followed through the digestive tract as the indigestible components are excreted. Feces from the fish is collected by one of the following methods: netting, fecal settling, and stripping or dissection of the hindmost part of the digestive tract (Figure 3.10).

Some technical problems arise in each of these methods. Vigorous stripping may remove parts of the digestive tract. Fecal collection is difficult if the excreta is soft and cannot be collected as a solid. The amount that leaches out from the feces as they stay in the tank bottom or in a collecting device is quite difficult to determine. Therefore, care should be taken that the best fecal collection method for a particular species is used.

Endogenous markers such as cellulose, hydrolysis resistant organic matter, and acid-insoluble ash may also be used.

The apparent protein digestibility (%APD) of a feed is defined as:

$$\textbf{APD (\%)} = 1 - \left[\frac{(\%F_p)}{(\%D_p)} \times \frac{(\%D_i)}{(\%F_i)} \right] \times 100$$

where:

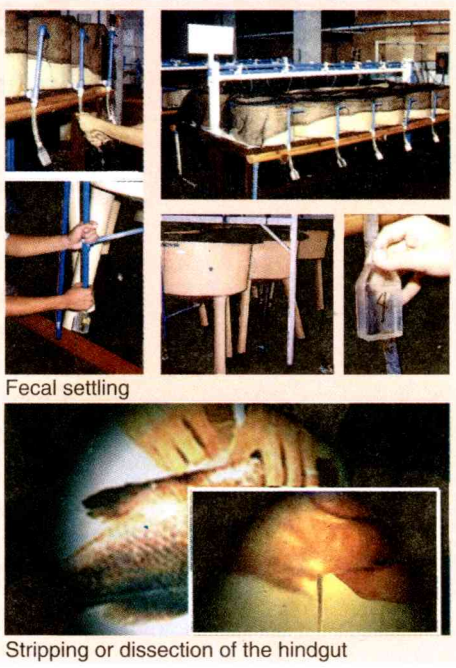
F_p = protein in feces or intestinal content
F_i = indicator in feces or intestinal content
D_p = protein in diet
D_i = indicator in the diet

True protein digestibility (%TPD) of a feed is obtained by correcting the amount of protein in intestinal contents or feces with protein of endogenous origin with the use of the formula:

$$\textbf{TPD (\%)} = 1 - \left[\frac{(\%F_p)}{(\%D_p)} \times \frac{(\%D_i)}{(\%F_i)} + \frac{(\%D_i)}{(\%F_{ci})} \times \frac{(\%F_{cp})}{(\%D_p)} \right] \times 100$$

where:

F_{cp} = protein in feces or in intestinal content of control fish (fish fed a non-protein diet)
F_{ci} = indicator in feces or intestinal content of control fish


Fecal settling

Stripping or dissection of the hindgut

Figure 3.10
Experimental set-up for *in-vivo* digestibility measurement.

2. *In vitro* assays

In estimating protein digestibility by *in vitro* assays, test rations are incubated with intestinal extracts of fish at an optimum temperature for a specified length of time (e.g. 24 h). The proteolytic activity in the intestinal extract will digest the protein component of the diet. The *in vitro* digestibility is computed using the formula:

$$\textbf{\textit{In vitro} protein digestibility (\%)} = \frac{(Nr - Ni)}{Nr} \times 100$$

where:

Nr = protein in ration
Ni = indigestible protein

The conditions under which *in vitro* techniques are carried out are highly unphysiologic, thus caution must be exercised in extrapolating the results of such experiments to the *in vivo* condition. At best, the value of digestibility obtained using this technique is only an estimate of true digestibility.

Factors Affecting Digestion and Absorption

In fish, as in all animals, both extrinsic and intrinsic factors can alter the efficiency of digestion and absorption. These are those involving the feed itself, feeding practices, as well as the prevailing condition of the digestive tract.

Feed composition, digestibility, and preparation influence digestion and absorption. Dietary fiber is highly indigestible in non-herbivores due to the absence of the enzymes necessary to breakdown the complex cell walls found in the feed. Roughage are high in fiber, thus their use is limited in practical feed for non-herbivores. Plant proteins are known to vary in their digestibility in fish because of differing amino acid composition and secondary as well as tertiary structures of the proteins. In addition, if a certain type of feed is known to pass quickly through the digestive tract of an animal, the feed will not be adequately digested because of inadequate exposure to the digestive enzymes.

The presence of antinutritional factors in feed such as trypsin inhibitors and tannins will also decrease the efficiency of protein digestion and absorption. Processing the feed such as cooking soybean to destroy the trypsin inhibitor is necessary before the feed can be utilized by fish. Dehulling or removal of the seed coat of some legumes will increase the digestibility of the feed because unbroken seed coats are not easily digested and in some cases contain high levels of tannin. Furthermore, excessive amounts of feed given to the fish decrease digestibility.

The efficiency of digestion and absorption is also affected by the condition of the digestive tract, pancreas, and the liver in fishes or hepatopancreas in crustaceans. Nutritional diseases and bacterial infections of the digestive system can diminish the digestive and absorptive functions in fishes and crustaceans.

Feeding Process in Fish

The cycle of feeding process in fish is shown in Figure 3.11.

Appetite and Satiation

Appetite is the state that initiates arousal and feeding behavior. Knowledge on the factors that trigger appetite and satiation are very important to fish farmers who want to maximize feed consumption, growth, and conversion efficiencies of their fish stock by adjusting feeding schemes. Appetite, which is controlled by the hypothalamus, is stimulated by the gut fullness and or other metabolic changes which affect food consumption. In general, stomach expansion after feeding inhibits appetite and gastric evacuation stimulates appetite. The optimal interval between meals has been estimated to correspond to gastric evacuation.

Several factors both biotic and abiotic tend to affect the appetite of the fish and shrimp.

The biotic factors include:

1. Food availability and food distribution, which may be seasonal in nature;
2. Competition. More aggressive fish in a stock affect the appetite and or feeding and hence the growth of subordinates. Generally, size differences

of the stock and dominance cause increased variation in body sizes. To avoid such occurrence, periodic size grading, to ensure that no fish is 1.5 times larger than another, should be done to prevent cannibalism. In addition, increasing the frequency of feeding or better dispersal of feed may help the inferior fish to obtain food. The presence of competing species may entail a shift to other "less desirable food";

3. The presence of predators may inhibit feeding;
4. Physiological condition such as starvation or motivation level, and circadian rhythm of the animal may dictate feeding time and amount of food ingested;
5. Selection of prey
   a) Choice of prey or food eaten, in terms of size and form, is limited by the mouth gape of the fish.
   b) The "optimal foraging theory" states that the natural selection favors those fish that maximize efficiency of prey capture. Since energy is spent in searching, pursuing, handling and digesting prey, an optimal foraging strategy must balance these factors such that the total energy expenditure is minimized and the net energy gain from the captured prey is maximized.
6. Handling causes stress in fish. Brown trout refuse to feed for three days after handling while rainbow trout, milkfish, or sea bass resume feeding the next day.

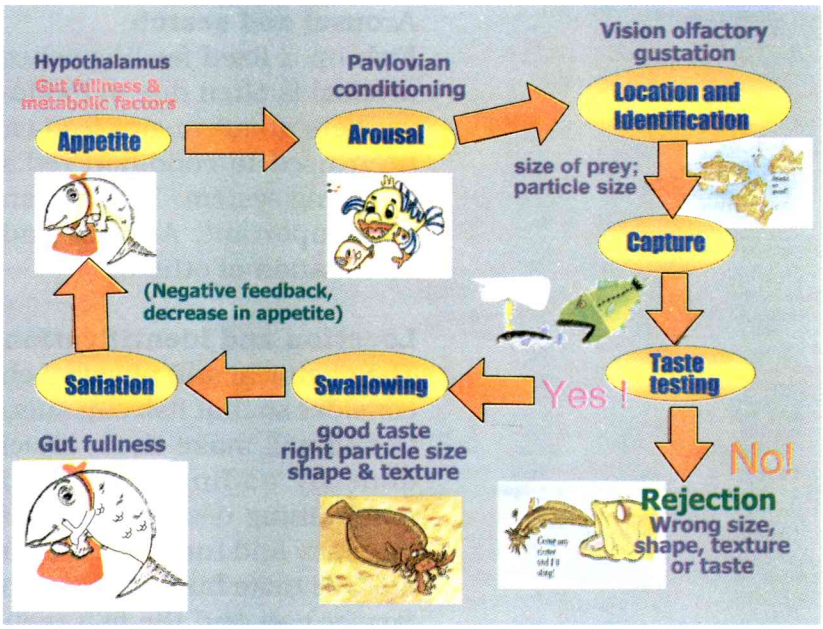


Figure 3.11
Feeding process in fish.
Source: Modified from Knight 1985

The abiotic factors include:

1. Dissolved oxygen (DO) is one of the most important abiotic factors affecting feeding behavior of fishes. Low DO levels lead to decreased feeding activity. Milkfish and shrimps raised in ponds cease feeding when DO levels drop below 1.5 and 3.0 ppm, respectively.
2. In most fish species, daily and seasonal water temperature fluctuation affect food intake. For milkfish, a tropical species, ambient temperature does not affect feeding activity in ponds, however, extreme temperature fluctuations affect feeding activity of milkfish. Shrimps are also affected by extreme temperature fluctuations.
3. Light intensity also influences feeding activity of most fish, especially larval fish, which rely on vision to recognize food particles.
4. Unionized ammonia (NH_3) levels of about 0.1 ppm inhibits growth in most species. However, appetite could be inhibited at ammonia levels high enough to cause serious physiological and morphological damage.

Arousal and search

Fish on a fixed feeding schedule can learn to anticipate feeding times but arousal is often due to **Pavlovian** conditioning. The sight or sound of farm workers about to give feed can stimulate feeding. Sound (200-700 Hz) has been used to condition red sea bream to come to a feeding spot in a sea ranching system. The influence of social interaction among fish in a stock is also important. Arousal and feeding of one or a few usually lead to the stimulation of others.

Location and identification

The chemical and physical characteristics of food particles are important to consider so that fish can successfully locate food. Making food more obvious to fish will make them easier to locate in the water column. This can be done by adding chemical attractants, providing color and contrast, maintaining desirable size and shape of particles, and manipulating light intensity and turbidity. Vision, olfaction, and gustation (sense of taste using surface taste bud) are all important in finding and locating food items. The farmer can feed the fish regularly in a set area of the farm or the tank and encourage fish to aggregate. It is a usual practice in shrimp farms to provide feeding trays at several places where shrimp can come to eat.

Capture

In carnivores, small particles can be ingested whole by being sucked into the mouth from a distance. Capture success in the wild depends on prey size and avoidance behavior, but this is not applicable in culture using complete or supplementary feed. However, movement in water currents may cause problems in getting at the food. Food particle size is a factor in capture success. Big particles not eaten immediately will disintegrate and be wasted. However, in general, some fish and shrimp will continue to nibble big food particles until ingestion is possible.

Taste Testing

Once the food is captured inside the mouth, the fish or shrimp tastes the food leading to swallowing or rejection. Not all materials taken into the mouth are swallowed, they are tested for suitability by taste receptors inside the mouth, gill arches, gill rakers, and in the tissue surrounding the pharyngeal teeth.

Swallowing or Rejection

Food which tastes good and have optimal particle size, shape, and texture will be swallowed by fish. More rejections and disintegration occur in pellets that are hard, abrasive and are much longer than their diameter. Large particles are usually ejected through the mouth with a "coughing" action. Therefore, feeds should have the correct size and texture for the species in culture. Delays in the ingestion of food due to repeated spitting out of food particles by the fish lead to increased energy expenditure and food wastage.

The overall practical implications of the knowledge on feeding process to fish culture are: encounter rates should be maximized by concentrating food availability in time and space; food supply must be matched to appetite; and chemical and physical characteristics of food particles need to be related to fish species, size, and sensory abilities to aid location, identification, and capture.

Summary

The rate at which fish digest their food is of primary importance in determining frequency, feeding rates, and ration size. Fishes can be classified according to their diet or food they habitually eat as herbivores, carnivores, omnivores, planktivores, and detritivores. A classification based on the manner of feeding or food getting includes predators, grazers, strainers, suckers, and parasites.

Fish adapt to their food differences by anatomic as well as behavioral means. There is a strong correlation between anatomical structure of the digestive tract and the feeding habits of the fish and the food eaten. The mouth has a variety of adaptations for capturing, handling and sorting of food before entry into the stomach. Fish have teeth that vary in type, number, and arrangement. The arrangement and structure of the teeth are related to the kind of food that the fish normally eat.

The stomach of fishes has a configuration or shape which is convenient for containing food. The size or capacity of the stomach in relation to the body weight varies between species and is usually related to the interval between feedings and to the size of food particles. All fishes have intestines. The length of the intestines varies from as low as 1/5 to as high as 20 times the body length. Carnivores have a relatively simple and short gut, with thick mucosa for absorption while herbivores have a long and thin gut to increase gut retention time and enhance digestion and absorption.

Digestion is a process whereby ingested food nutrients such as proteins, lipids, and carbohydrates are broken down into units that are small enough to be absorbed across the gut wall. The process is accomplished through the action of digestive enzymes. Enzymes that aid in digestion of proteins are known as proteases. For carbohydrate digestion, the enzymes involved are carbohydrases. Lipid digestion is facilitated by enzymes lipases and phospholipases.

The main difference between fish and crustacean digestion is that, in the latter, enzymes are secreted by the hepatopancreas. The hepatopancreas also acts as storage organ for glycogen, fat, and contains enzymes for secretion of bile acids. The crustacean hepatopancreas to a great extent fulfills the role of the liver in vertebrates.

Analysis and measurement of stomach contents gives information on the feeding preferences as well as frequency of feeding of a particular species. Digestibility measurements can be done through *in vivo* and *in vitro* methods.

Knowledge of feeding process in fish and shrimp is useful to maximize food location, capture, and ingestion.

Guide Questions

1. What correlation exists between anatomy of the digestive tract and feeding habits of fishes?
2. What are the four types of feeding behavior of fish in their natural habitat?
3. What are the different parts and functions of the digestive system of:
   a) fish
   b) crustaceans

4. What are the four general configurations or shapes of the fish stomach?
5. Discuss the relationship between gut length and feeding habits of fishes?
6. Differentiate the four types of epithelial cells found in the hepatopancreatic tubule of the crustaceans.
7. Define and explain digestion.
8. Describe the steps and enzymes involved in:
   a) protein digestion
   b) lipid digestion
   c) carbohydrate digestion in fishes and crustaceans
9. Discuss the methods used to measure stomach contents of fishes and digestibility of feeds.
10. Discuss the factors that may affect digestion and absorption in fishes.
11. Explain the different stages in the feeding process in fish

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