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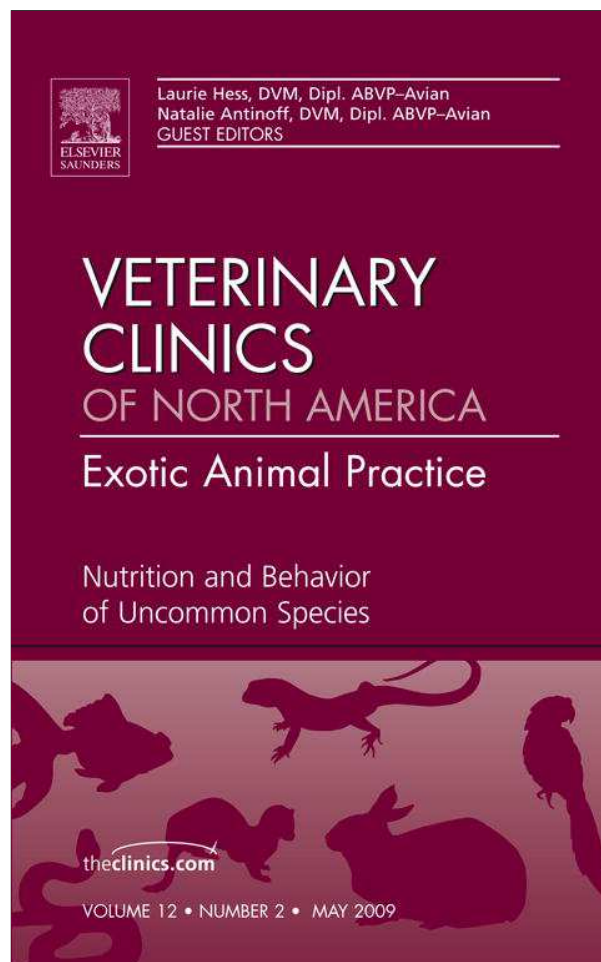
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# Nutrition, Feeding, and Behavior of Fish

Santosh P. Lall, PhD<sup>\*</sup>, Sean M. Tibbetts, MSc

## KEYWORDS

• Fish • Nutrition • Feeding • Behavior • Feeds • Diet

Nutrition and feeding influence growth, reproduction, and health of fish and their response to physiologic and environmental stressors and pathogens. The basics of fish metabolism are similar to those of warm-blooded animals in that they involve food intake, digestion, absorption, and transport of nutrients to the various tissues. Fish, however, being the most primitive form of vertebrates, possess some distinguishing features, such as the absence of a stomach in certain species, lack of mandibular teeth, and nondifferentiated small and large intestines. Some major physiologic and metabolic differences between other vertebrates and fish include the mechanisms involved in intestinal cell wall absorption by pinocytosis, metamorphosis in larval fish development, and the shift in osmoregulation in salmonids during sea water adaptation, carbohydrate metabolism, nitrogen excretion, and skeletal development. Unlike warm-blooded animals, which are homoeothermic, fish are poikilothermic, so their body temperature and metabolic rate depends on the water temperature. Environmental temperature influences energy expenditure and nutrient intake. At low temperatures, the cell membranes of fish remain fluid because of the incorporation of high amounts of polyunsaturated fatty acids from dietary fish oils and other lipid sources. Many fish efficiently use protein and lipid for energy rather than carbohydrates. Fish are also unique among vertebrates in their ability to absorb minerals not only from their diets but also from water through their gills and skin.

## NUTRIENT REQUIREMENTS OF FISH

All the essential nutrients for other animals, including amino acids, fatty acids, vitamins, minerals, and energy-yielding macronutrients (protein, lipid, and carbohydrate), are important for fish also. A diet must supply all the essential nutrients and energy required to meet the physiologic needs of growing animals or for successful reproduction of broodstock. The rapid growth of global aquaculture has resulted in the production of more than 123 finfish species in intensive and extensive culture systems. Despite considerable advances reported over the past 5 decades, the quantitative

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Institute for Marine Biosciences, National Research Council of Canada, 1411 Oxford Street, Halifax, Nova Scotia, Canada B3H 3Z1

\* Corresponding author.

E-mail address: [santosh.lall@nrc-cnrc.gc.ca](mailto:santosh.lall@nrc-cnrc.gc.ca) (S.P. Lall).

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requirements for all essential nutrients for most farmed fish species are not well established. The criteria of nutrient adequacy for approximately 40 specific nutrients and their quantitative nutrient requirements have been made for rainbow trout, Pacific salmon, channel catfish, tilapia, and common carp, while partial nutrient requirements have been established more recently for numerous other fish species.<sup>1,2</sup> Although the minimum nutrient requirements established promote growth and prevent deficiency signs, higher intakes of vitamins, minerals, amino acids, and essential fatty acids increase buildup of their reserves in the tissues. The continued intake of certain nutrients in excess amounts causes saturation of various coenzymes. Certain fat-soluble vitamins (eg, vitamin A) and trace elements (eg, copper, selenium) are toxic when taken in excess. Deficiencies or excesses of each of the major dietary components, including proteins, fats, total calories, vitamins, and trace elements may have profound effects on disease development and the survival of the fish, largely through their effects on host defense mechanisms. Nutritional deficiencies may influence the integrity of skin and epithelial tissues, alter the composition of tissues and body fluids, and reduce mucus secretions, consequently predisposing the fish to infections. Major nutrient deficiency and toxicity signs are summarized in **Table 1**.

### **Macronutrients**

Protein is an important component of fish diets, and to satisfy this dietary requirement a well-balanced mixture of amino acids from various animal and plant protein sources is critical to ensure proper growth and health of the fish. Protein is the most expensive component of the diet and levels greater than that needed to satisfy requirements result in elevated nitrogenous waste excretion into the surrounding waters. Excessive levels of protein in the diet are thus economically and environmentally undesirable. Most herbivorous and omnivorous fish require 25% to 35% protein in their diet but

<b>Table 1</b>		
<b>Major nutrient deficiency and toxicity signs in fish</b>		
<b>Symptom</b>	<b>Nutrient Deficiency</b>	<b>Nutrient Toxicity</b>
Fin erosion	Riboflavin, niacin, vitamin C, inositol, lysine, tryptophan, zinc	Vitamin A, leucine, cadmium
Fin and skin hemorrhage	Vitamin A, vitamin K, vitamin C, thiamin, riboflavin, pantothenic acid, niacin, inositol	Oxidized fish oil
Scoliosis and/or lordosis	Vitamin C, tryptophan, magnesium, phosphorus, essential fatty acids	Vitamin A, lead, cadmium, oxidized fish oil
Exophthalmia	Vitamin A, vitamin E, pantothenic acid, folic acid, niacin	Oxidized fish oil
Fatty liver	Choline, inositol, essential fatty acids, excessive dietary fat (mainly gadoids)	Oxidized fish oil
Cataracts	Vitamin A, riboflavin, methionine, histidine (mainly salmon smolts), tryptophan, zinc	Choline, oxidized fish oil
Skeletal deformity	Phosphorus, manganese, zinc	Vitamin A, oxidized fish oil
Anemia	Folic acid, iron	Oxidized fish oil
Nephrocalcinosis	Magnesium	Selenium
Convulsions	Thiamin, magnesium	—

carnivorous species require higher levels of protein ranging from 40% to 55% of diet.<sup>1</sup> This difference seems to be related to the limited use of carbohydrate as an energy source by carnivorous fish, which in turn use dietary protein for energy purposes. The efficient use of dietary protein in these fish is also attributable to the mechanism by which ammonia, produced by deaminated protein, is excreted by way of the gills with limited expenditure of energy. Energy density of the diet and the ratio of energy to protein in the diet also influence dietary protein requirements. The dietary requirement for protein is essentially a requirement for the amino acids contained within the protein. Ten amino acids, namely arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine, are considered indispensable (essential) for most fish species studied to date. Among the dispensable (nonessential) amino acids that commonly make up protein, two are particularly important for their ability to partially replace or spare indispensable amino acids. Tyrosine can spare approximately 50% of phenylalanine in meeting the total aromatic amino acid requirement of fish and cystine can replace a similar amount of methionine as part of the total sulfur amino acid requirement.

No dietary requirement for carbohydrates has been demonstrated in fish; however, if carbohydrates are not provided in the diet, a higher percentage of protein and lipid are catabolized for energy. The ability of fish to use dietary carbohydrate for energy varies considerably, with most carnivorous species having more limited ability than herbivorous or omnivorous species. The amount of soluble carbohydrate included in prepared diets for carnivorous species is generally less than 20%, whereas diets for omnivorous species generally contain between 25% and 40% soluble carbohydrate. Non-starch polysaccharides, such as cellulose, hemicellulose, and chitin, are essentially indigestible by most fish species.

Lipids supply essential fatty acids (EFAs) and energy in the diet of fish and the EFA requirement of most fish can only be met by supplying the long-chain unsaturated fatty acids of linolenic (18:3 n-3) and linoleic (18:2 n-6) series. Salmonid and marine fish tissues contain eicosapentaenoic acid, 20:5 n-3 and/or docosahexaenoic acid, 22:6 n-3, particularly in cell membranes. This finding reflects a high dietary requirement for these fatty acids (20:5 n-3 and/or 22:6 n-3). These fish seem to have limited ability to chain elongate and desaturate 18:3 n-3 and 18:2 n-6 to meet their requirement, unlike many freshwater fish that have been shown to meet their requirements for these essential fatty acids.<sup>3</sup> Dietary lipids also serve as precursors of steroid hormones and prostaglandins in fish and provide a vehicle for intestinal absorption of fat-soluble vitamins. Lipid from the diet deposited in the flesh may affect the flavor and storage quality of edible products derived from the fish, particularly when the dietary oils are oxidized.

### ***Micronutrients***

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Fish have unique physiologic mechanisms to absorb and retain minerals from their diets and from the surrounding water.<sup>4</sup> The knowledge of trace element requirements and their physiologic functions and bioavailability from feed ingredients is limited. Although the main functions of minerals involve skeletal structure maintenance, cellular respiration, oxygen transport, immune function, and regulation of acid-base equilibrium, they are also important components of hormones, enzymes, and enzyme activators. An excessive intake of minerals either from the diet or from gill uptake causes toxicity, and therefore maintaining a fine balance between mineral deficiency and surplus is vital for aquatic organisms to maintain their homeostasis either through increased absorption or excretion. Quantitative dietary requirements have been reported for phosphorus, magnesium, zinc, iron, copper, manganese, iodine, and selenium for selected fish species. Dissolved minerals in the aquatic environment may

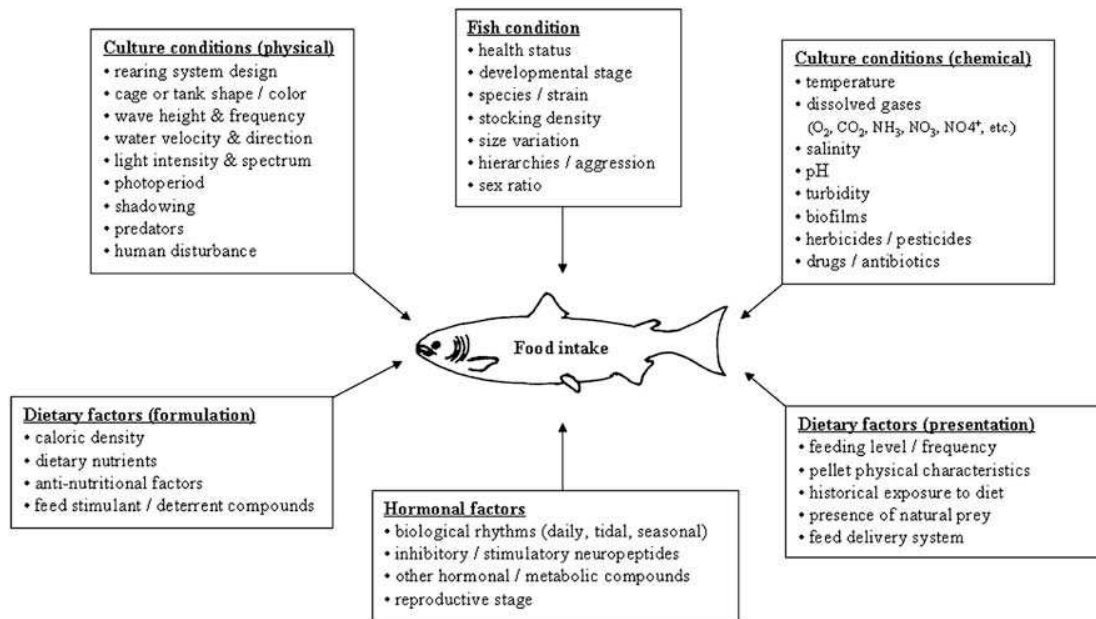
contribute to satisfying the metabolic requirements of fish and interact with dietary sources. In particular, fresh water of moderate hardness ( $\sim 50$  mg/L as  $\text{CaCO}_3$ ) has been shown to provide fish with adequate calcium to sustain metabolic functions in the presence of low levels of dietary calcium. Chloride, potassium, and sodium are other minerals that may be present in fresh water at concentrations sufficient to partially meet the metabolic requirements of fish. Dietary deficiencies of most of the macrominerals generally have been difficult to produce in fish because of the presence of these minerals in the surrounding water. Supplementation of phosphorus in fish diets, however, is often critical because its presence in the water is limited and the availability from common plant feed ingredients is low. Although supplementation of practical diets with other microminerals has not been shown to be necessary in most fish species, a mineral premix is typically added to most nutritionally complete diets to ensure adequacy.

Most vitamins that are considered essential for terrestrial animals are also required by fish. Quantitative dietary requirements for fat-soluble (vitamin A, D, E, and K) and water-soluble (thiamine, riboflavin, pyridoxine, pantothenic acid, folic acid, niacin, biotin, vitamin B<sub>12</sub>, vitamin C, and choline) vitamins have been determined for channel catfish, tilapia, common carp, rainbow trout, and Pacific salmon, while partial vitamin requirements have been established for some other fish species as well. The functions and dietary deficiencies of many of these vitamins are well documented<sup>1,2</sup> (see **Table 1**). These requirement values have been used to provide guidelines for vitamin supplementation for those fish species for which such information is not available.

## FEEDING BEHAVIOR

The feeding behavior of fish is complex and has been studied extensively in cultured fish and wild fish from ecological perspectives.<sup>5,6</sup> Several behavioral responses have been linked to methods of feeding, feeding habits, frequency of feeding, mechanisms of food detection, and food preferences. The food organisms consumed by fish in natural environments may range from algae, plants, and detritus to small prey, such as crustaceans, mollusks, polychaetes, and other fish. It is well recognized that various combinations of sensory systems during the different phases of gustation and feeding are required to achieve desired food consumption; however, the acceptance or rejection of feed is physiologically dependent on inputs from chemoreception.<sup>7</sup> Fish possess several chemosensory systems, which include gustation (taste), olfaction (smell), and chemical sensory and chemoreceptor cells. The role of each system is often difficult to distinguish because each system responds to aqueous chemical stimuli, some of which may be common in these different systems. It seems that the gustatory system is the most important in acquisition and ingestion of food and with the rejection of potentially harmful and toxic substances.<sup>8</sup> The gustatory system, which is highly developed in several fish species, also consists of taste buds in the epithelia of the oropharynx **Fig. 1, Table 2**.

Like all animals, food intake in fish is controlled by a central feeding system in combination with a peripheral satiation system regulated by various key neuropeptides and hormones.<sup>9–11</sup> Various endocrine and metabolic factors convey information regarding nutritional status to the fish's brain, either directly or indirectly by way of the vagus nerve.<sup>12</sup> The information is then processed by the brain and neuropeptide signaling systems are triggered to secrete factors that either initiate or terminate feeding.<sup>13–15</sup> Although most neuropeptides down-regulate feeding behavior, a smaller number have a stimulatory effect.<sup>10,11</sup> Certain biochemical factors that control food intake to some extent in fish are cholecystikinin, gastrin-releasing peptide, ghrelin, glucagon-like peptides, insulin, amylin, and leptin; these have been discussed in detail elsewhere<sup>9</sup>



**Fig. 1.** The complexity of factors affecting feeding behavior in fish.

and are beyond the scope of this section. With the exception of the gastric factor ghrelin, all of these factors serve as satiety signals to reduce food intake and feeding behavior. Certain nutrients or related compounds, such as carbohydrates, peptides, amino acids, and lipids, may also affect food intake. For example, glucose administration induces hyperglycemia in fish and intraperitoneal injections of glucose cause a decrease of food intake and increase in food latency time in carp and tilapia.<sup>16</sup>

## FEEDING RHYTHMS

The major factors that can influence feeding behavior of fish, such as stocking density, sex ratio, reproductive status, and biologic rhythms, have been subject to limited investigation and results often conflict between and within species.<sup>17</sup> Endogenous clock mechanisms may control some of these rhythms, but environmental factors, such as day length or temperature, may either control others or act as time setters or synchronizers. Rhythmic feeding activity, whether based on days, weeks, or months, is generated within the fish and the extent to which the external factors can influence feeding rhythms is complex. The anticipatory behavior seems to persist in fasting animals; thus it seems that there are internal timing mechanisms in fish similar to birds and mammals. The practical implications are that fish may adjust to the feeding of meals at set times, and there are likely optimum feeding times for each species. One important topic is whether the presence of rhythms can influence not only the amount of food consumed but also the efficiency with which food is converted into somatic growth. Recent developments in improving the understanding of the physiologic rhythms in farmed fish are providing useful information that allows selection of proper times for feeding fish to maximize growth, improve feed efficiency, and reduce feed wastage and fecal output to minimize the environmental impacts of aquaculture.

The three predominant feeding rhythms that affect food consumption in fish are diel (daily), annual (seasonal), and tidal (lunar) rhythms. Most fish in culture systems have diel feeding rhythms whereby they are either diurnal feeders (eat during the day) or nocturnal feeders (eat at night). Many fish species change their preferred time of feeding throughout the day based on the influences of biotic factors<sup>18</sup> (such as threat of predation) and abiotic factors<sup>19</sup> (such as lighting conditions). In a culture situation, it

Influencing Factor	Culture System			
	Pond	Cage	Tank (Outdoor)	Tank (Indoor)
<b>Rearing system characteristics</b>				
Shape	+	+	+	+
Color	-	-	+	+
<b>Light</b>				
Intensity	-	-	+	++
Photoperiod	-	-	+	++
Spectrum	-	-	+	++
Shadowing	+	+	+	++
Water temperature	-	-	+	++
<b>Waves</b>				
Height	-	-	+	n
Frequency	-	-	+	n
<b>Water flow</b>				
Velocity	+	-	++	++
Direction	+	-	++	++
<b>Water chemistry</b>				
Dissolved oxygen	+	+	++	++
Nitrogenous compounds (NH <sub>3</sub> , NO <sub>3</sub> , NO <sub>4</sub> <sup>+</sup> , and so forth)	-	-	+	+
Other dissolved gases	-	-	+	+
pH	-	-	-	-
Salinity	-	-	+	+
Toxicants or pollutants (drugs, antibiotics, biofilms, pesticides, herbicides, and so forth)	-	-	+	+
Turbidity	-	-	+	+
Stocking density	++	++	++	++
<b>Social structure</b>				
Size variability	++	++	++	++
Sex ratio	-	-	-	-
Dominance hierarchy (aggression)	+	+	+	+
Predators	-	-	+	++
<b>Human disturbances</b>				
Acute (weighing, sampling, cleaning, disease treatment, transferring, and so forth)	+	+	+	+
Chronic (prolonged noise or vibration, and so forth)	+	+	+	+
<b>Feeding rhythms</b>				
Diel (diurnal or nocturnal)	+	+	++	++
Tidal and lunar	-	-	+	n
Annual (seasonal)	-	-	-	n

(continued on next page)

Influencing Factor	Culture System			
	Pond	Cage	Tank (Outdoor)	Tank (Indoor)
<b>Nutritional factors</b>				
Pellet physical characteristics	++	++	++	++
Dietary nutrients	+	+	+	+
Caloric density	+	+	+	+
Feeding stimulants	+	+	+	+
Deterrent compounds	+	+	+	+
Antinutritional factors	+	+	+	+
Access to natural prey	–	–	+	++
Feed delivery system	++	++	++	++
Historical exposure (adaptation)	++	++	++	++
Feeding level/frequency	++	+	++	++
<b>Neurologic factors</b>				
Inhibitory neuropeptides	–	–	–	–
Stimulatory neuropeptides	–	–	–	–
Hormones	–	–	–	–
Species/strain	++	++	++	++
Health status	+	+	++	++
<b>Age</b>				
Developmental stage	++	++	++	++
Reproductive stage	+	+	+	+

Factor is easily controllable (++), controllable (+), difficult to control (–) or not a factor (n).

is important to know the optimum time of day to feed the fish when their appetite is highest to promote high growth rates and minimize feed wastage.

The feeding preference of fish can also be affected by other environmental rhythms, such as annual (seasonal) changes and tidal (lunar) rhythms.<sup>17</sup> Annual or seasonal changes are often predictable because they are closely correlated with other environmental factors, namely water temperature and day length. Most cold-water fish (eg, Arctic char, rainbow trout, Atlantic salmon, and turbot)<sup>19–23</sup> and warm-water fish (eg, European sea bass, catfish, and goldfish)<sup>24–27</sup> cultured under ambient water temperatures with access to natural light and photoperiods typically increase their feeding behavior in the spring and throughout the summer months when the days are longer and water temperatures higher. They gradually reduce feeding in the autumn and into the winter months as water temperatures fall and day length decreases. This cycle generally holds true for most fish in the growth phase before sexual maturation, but is often broken by the onset of sexual maturity and preparation for spawning, at which time feeding activity may diminish or completely cease.<sup>28–31</sup> Tidal or lunar rhythms have little or no effect on fish cultured in indoor or outdoor tank systems with artificial lighting and sufficient filtration to minimize natural prey items from entering the culture water. In open surface outdoor tank systems and in ponds and cage/net pen systems, however, the daily tidal and lunar cycles can significantly affect feeding behavior of fish.<sup>17</sup> The mechanism is most frequently associated with the abundance of natural prey items present in seawater during incoming and high tides. This phenomenon is illustrated in killfish,

wherein stomach fullness has been directly correlated with the high-tide cycle.<sup>32</sup> Similar observations have been made with other fish species also,<sup>33–35</sup> although it is not always clear whether the effect is due to the high-tide abundance of food or the lunar effects of increased light for foraging during a full moon. It is likely that during periods of full moon and high tides both factors are working together synergistically.

### FEEDING STIMULANTS AND DETERRENTS

Fish primarily detect food in the natural aquatic environment through olfaction (smell) and sight; however, appearance, feel, and taste of the diet are key factors in determining whether food will be swallowed or rejected by fish held in captivity.<sup>36</sup> A well-defined and species-specific tuning of the taste receptors of fish for particular cues is known to be present in their food items. Generally, various substances are added to fish feeds in an effort to enhance palatability and feed acceptance. The use of feeding stimulants is particularly important in the production of larval and starter feeds, wherein feed acceptability is a major concern. Four major chemical characteristics of feeding stimulants for fish have been identified: (a) low molecular weight (<1000), (b) nitrogen-containing, (c) nonvolatile and water soluble, and (d) simultaneous acid and base properties or amphoteric.<sup>37</sup> Several compounds are known to act as feeding stimulants in carnivorous and omnivorous species, including betaine and amino acids, notably glycine and alanine or mixtures of L-amino acids, and the nucleotides inosine or inosine 5'-monophosphate. Some dipeptides elicit a greater feeding response in combination than either of the constituent amino acids presented alone.<sup>38</sup> Limited data exist on feeding stimulants for herbivorous species; however, organic acids along with certain amino acids and dimethyl- $\beta$ -propiothetin were found to be stimulatory for carp and tilapia.<sup>39</sup> In general, the following patterns related to feeding stimulants have emerged from laboratory studies: (1) carnivores show a positive response to alkaline and neutral nitrogenous substances (such as glycine, proline, taurine, valine, and betaine) and (2) herbivores respond more to acidic substances (such as aspartic acid and glutamic acid). Studies conducted on common feed ingredients used to produce fish feeds for cold-water fish show that certain high-quality fish, crustacean, krill, and squid meals or their hydrolysates stimulate feeding behavior in salmonids and marine fish.

Fish have the ability to discriminate between high-quality and poor-quality feeds and refuse to ingest the latter. Certain compounds present in feeds are known as feeding deterrents. Trimethylamine (or its oxidation products), produced in decaying fish flesh, is known to cause a decrease in food consumption when added to the diet. Highly oxidized oils and fish meals in salmonid and marine fish feeds are also known to cause food aversion. Improper storage and use of poor-quality feed ingredients in feed manufacture are the common cause of rancidity in commercial feeds. The presence of aflatoxins, produced by molds growing on improperly stored feed, depress feed intake and can result in death if consumed by the fish in significant amounts. In addition, the presence of adventitious toxins (antinutritional factors) such as gossypol in cottonseed meal, protease inhibitors in soybean meal, glucosinolates in canola/rapeseed meals, and numerous others results in anorexia due to inactivation of digestive proteases and reductions in digestion, absorption and physiological utilization of dietary nutrients.

### FEED INTAKE

Generally, hunger stimulates feeding behavior in fish. When feed is offered, fish may initially feed at a faster rate and slowly decrease or stop with a gradual decline of appetite. Environmental factors, such as light, temperature, water velocity, social factors, predators, and disturbance by humans, may also influence fish feeding behavior.

Feeding practices, such as the even distribution of the feed into the water, can also affect the fish's chances of gaining access to food. There may thus be numerous combinations of biotic and abiotic factors that can have an important influence on feeding behavior of fish. Often, fish suddenly stop feeding for no apparent reason and the rates of feeding can either decrease or increase over a period of days. A better understanding of the factors that can influence feeding may allow for better feed management and the allocation of food, and reduce the variability in feeding and growth rates that are usually evident among individuals and among groups of fish.

It is generally accepted that fish feed to satisfy their energy requirements. Fish fed a diet low in energy content are forced to increase their consumption rate and gastric evacuation rate to compensate for the lower caloric diet. Other nutrients also impact feed intake, however, with anorexia being a common symptom of nearly all nutrient deficiencies.<sup>1</sup> Particle size is closely related to feed intake and the correct feed particle size induces a positive behavioral response. Feed particles must be sufficiently small to be ingested, while being large enough to be consumed without expending too much energy in the process.

To increase the efficiency of farming systems through proper feed management, the prediction of feed intake and growth under a wide range of environmental and culture conditions is necessary. Several environmental, genetic, and physiologic factors have been identified that correlate with feed intake and are considered as regulators of feed intake. When food availability is unlimited, the amount of food eaten is referred to as the voluntary feed intake (VFI). One key feature of VFI is the description of regulatory feedback mechanisms, which are not clearly identified for most fish. In particular, the identification of multiple feedback signals and their integration into specific responses may ultimately control the feeding behavior. Biologic factors, including fish size, physiologic stage, and genotype, are known to influence VFI. Among the environmental factors, both water temperature and photoperiod control feed intake. Feed intake is also under close metabolic, endocrine, and neuronal control, all of which are intimately related to the nutritional status of the animal. Several techniques are available to monitor individual feed intakes and the passage of feed through the digestive tract. They include radiography and analysis of gut contents.<sup>40,41</sup>

Like higher vertebrates, when there is an increase in the energy density of the feed, the VFI is reduced at any given production level. If the feed provides a lower ratio of protein to energy than required, fish may increase feed intake to obtain sufficient protein. There is growing evidence that fish are capable of adjusting their VFI depending on the quality of the diets and especially on the dietary digestible energy (DE) content.<sup>42,43</sup> Excessive DE in the diet may affect VFI and cause lower intake of other nutrients, which may cause metabolic imbalance and accentuate marginal nutrient deficiencies. Knowledge of nutrient and energy balance in diets is therefore considered important to better understand the mechanisms involved in the control of feed intake. Feeding tables have been developed for the major farmed fish species that take into account the water temperature, fish size, genotype, growth rate, dietary energy density, and nutrient concentration, but few take into account the principles of nutritional bioenergetics in fish.<sup>44</sup>

## FEEDS AND FEEDING

Feeds and feeding of fish depend on the type of culture system used: extensive, semi-intensive, or intensive. In the first two systems, fish derive all or a substantial part of their nutrients from natural food organisms in culture ponds. Fish maintained in intensive fish culture systems (tanks, raceways, and cages) are totally dependent on the provision of nutritionally complete diets produced in dry, semi-moist, or moist forms. Diets fed to fish are subject to leaching of nutrients while they remain in the water

column or at the bottom of the culture system. This leaching creates a challenge for feed manufacturers, particularly when small-sized granules or flakes are used to feed larval and small fish, often referred to as fry or fingerlings. Formulated dry feeds are more common and produced either by steam or cold compression pelleting or by a cooking extrusion process to produce feed in various physical forms and shapes, and of different buoyancy (floating, slow sinking, or fast sinking). Catfish, salmon, and shrimp, for example, require floating, slow-sinking, or fast-sinking feeds, respectively, because of their different preferred feeding habits in the water column. Extrusion technology is widely used to produce feeds of cold-water salmonids and marine fish. Application of extrusion technology allows for the production of feeds with high energy contents based on high levels of lipid (~20%–40% of the diet). The heat processing associated with extrusion also inactivates antinutritional components that can be present in plant ingredients and increases the digestibility of protein, carbohydrate, and other nutrients. Gelatinization of starch during extrusion processing also increases feed stability and allows for higher absorption of lipid into the pellets.

Proper feed distribution is necessary to achieve good feed efficiency. The amount of feed offered to fish per day has been based on feeding tables developed on the basis of a percentage of body weight and water temperature. Young fish require feed at a greater percentage of their body weight per day (>5%) than older fish. Demand or *ad libitum* feeding is commonly used in hatcheries where demand feeders dispense small quantities of feed when activated by the fish. Automatic feeders or hand feeding are used to feed fish in tanks or sea cages where fish feeding behavior can be monitored manually or on video camera. Frequency of feeding is important, with larval fish and fry offered a small amount of feed more than 12 times per day and the frequency is gradually decreased to 1 to 4 times per day. Additional time is required to feed fish at cold temperatures when their metabolic rate and appetite are lower.

Because fish live in aquatic environments, water quality affects their feed consumption, growth, survival, and health. Overfeeding results in feed wastage and deterioration in water quality, particularly when there is an increase in suspended particles and lower dissolved oxygen levels. Generally, undigested protein or carbohydrate produces suspended solids and this increases biologic oxygen demand, which should be kept minimized. The principal excretory end products of protein catabolism, an ionized and a nonionized form of ammonia, are excreted through the gills and the latter is toxic to fish. Fat not properly retained in the feed may leach out producing a thin film on the surface water causing respiration problems.

Feeding of larval fish requires special consideration because their digestive systems are not fully developed after hatching. Currently, larviculture depends on feeding live food organisms (eg, brine shrimp [*Artemia*], rotifers, and other planktonic organisms) that have been enriched with specific nutrients (essential fatty acids, vitamins, amino acids) to improve their nutritional value. Manufactured dry feeds are becoming increasingly important in hatcheries because diets can be tailored to provide optimum levels of nutrients and incorporate ingredients that adapt to larval digestive and metabolic needs (eg, hydrolyzed protein). Visual and chemical stimuli are important considerations for capture and acceptance of artificial food by larvae. Larvae are gradually weaned onto highly digestible, water-stable microparticulate dry feeds of appropriate particle size (~100–600  $\mu\text{m}$ ) or flakes and attractive color and organoleptic properties.

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