ENERGETICS

Energetic Models

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Glossary

Abiotic The chemical and physical (nonbiological, physical) variables of the environment (e.g., temperature).

Absorption Passage of nutrients across the gut and into the blood; uptake of fluid and solutes by cells and tissues.

Alkaloids A large group (*c.* 6000 are known) of toxic, basic nitrogenous compounds found in plants. The term alkaloid has not been precisely defined, but the group encompasses heterocyclic nitrogen bases derived from the amino acids – ornithine, lysine, phenylalanine, tyrosine, and tryptophan.

Amino acids Molecules with an amine group, a carboxylic group, and one of 20 R groups that are the building blocks of proteins.

Ammonotelic Excreting nitrogen mainly as ammonia (i.e., NH_3 or the ammonium ion, NH_4^+), as in most teleost fish and aquatic invertebrates. Total ammonia nitrogen (TAN) is the sum of the ammonia–nitrogen found in the unionized (NH_3) and ionized (NH_4^+) form.

Anti-nutritional factor (ANF) A substance that reduces the value of a feed or feedstuff, primarily via interference with the digestion, absorption, or metabolism of nutrients.

Ash The mineral residues remaining after combustion of feeds, feedstuffs, or plant and animal tissues at 450–500 °C.

Bioavailability (biological availability) Describes the proportion of a nutrient in a feed or feedstuff that may be utilized by an animal. Bioavailability of a nutrient can be subdivided into three constituent phases: availability in the intestine for absorption, absorption and/or retention in the body, and utilization. Bioavailability is studied to evaluate the quality of feeds and feedstuffs, and to provide data for establishing nutritional requirements.

Biotic factors Biological factors such as availability of food, numbers of conspecifics and competitors, and predators, etc., that affect the abundance, distribution, and life histories of individuals and species.

Carbohydrates Compounds containing carbon, oxygen, and hydrogen, and having the general formula $C_x(H_2O)_y$ (although some compounds classifed as carbohydrates do not comply with this general definition). The group includes simple sugars (monosaccharides) and their derivatives, oligosaccharides and polysaccharides, such as starch and cellulose.

Carnivore Generally applied to animals that feed upon other animals, although there are also carnivorous (flesh-eating) plants that trap and digest insects and other small animals.

Crude fiber The insoluble carbohydrates remaining after boiling a feed or feedstuff in acid and alkali; this fraction represents the carbohydrates that are not readily available to, and are poorly utilized by most animals.
Crude protein The content of nitrogen in a feed, feedstuff, plant, or animal tissue multiplied by a factor (usually 6.25, since most proteins contain about 16% N) to provide an estimate of the protein content; this only gives a crude estimate of protein content because variable amounts of nonprotein nitrogen will be present in analyzed samples.
Digestion The process of solubilization and hydrolysis of ingested nutrients in the gastrointestinal canal into constituent molecules and elements suitable for transport across the intestinal wall.
Ectotherm (adj. ectothermic) An organism whose body temperature is largely determined by heat exchange with its surroundings. It does not produce and retain enough metabolic heat to elevate its body temperature above ambient temperature, but may use behavioral mechanisms to regulate body temperature.
Endocrine Mode of secretion in which a chemical is released by a cell into extracellular fluid then enters the blood.
Endotherm An animal that uses its own metabolism as the major source of heat to maintain its body temperature greater than that of the surrounding environment.
Energy budget The balance of energy input and use in a biological system, expressed in terms of consumption (intake or ingestion), production (growth), respiration, fecal losses, and excretory losses.
Ether extract The portion of a feed, feedstuff, or tissue that is soluble in ethyl ether and is removed by extraction in this solvent; it represents the majority of the lipid fraction of a feed.
Excretion The elimination of waste materials from the body; specifically the elimination of waste materials produced by metabolism, for example, nitrogenous excretion refers to the elimination of nitrogenous compounds (ammonia, urea, uric acid, etc.) resulting, primarily, from the metabolism of proteins and nucleic acids.
Feces The undigested feed residues, plus some endogenous digestive secretions, sloughed cells of the intestinal lining, and bile metabolites that are expelled from the gut via the anus.
Feed efficiency Wet weight gain per unit feed consumed; it often calculated as gain divided by the amount of feed provided, thereby including an error relating to unconsumed feed waste; it may also be termed feed conversion efficiency or feed utilization (cf. feed:gain ratio).
Feed:gain ratio The term used in commercial aquaculture to express the quantity of feed required to produce a given weight gain; it is the reciprocal of feed efficiency.
Heat of combustion The heat produced when organic material is completely oxidized in an oxygen atmosphere to yield carbon dioxide, water, and oxides of nitrogen and sulfur; it is usually measured using a bomb calorimeter, and referred to as the gross energy of a feed or feedstuff.
Herbivore An animal that feeds exclusively on plants.
Homeotherm An animal that maintains a more or less constant body temperature regardless of external temperature variations; it is generally endothermic, being able to generate its own body heat.
Lipids Group of naturally occurring hydrophobic compounds including fats, oils, waxes, phospholipids, and others.
Macronutrients Substances required in relatively large amounts for normal growth and development; the macronutrients present in animal feeds are the proteins, lipids, and carbohydrates.
Maintenance requirement The amounts of food, or specific nutrients, needed to meet metabolic requirements, without any gain or loss of body weight; it is the level of intake that provides for the continuation of life processes but allows for no increase in biomass.
Metabolic rate A measure of the rate of metabolic activity within an organism; it is the rate at which an organism uses energy to sustain life processes. It is most usually measured as heat production or oxygen consumption (sometimes together with carbon dioxide production), but the latter only gives an estimate of the contribution of aerobic metabolism.
Metabolism An integrated network of biochemical reactions that occurs in living organisms; the biochemical processes by which the absorbed nutrients are transformed and stored (anabolism), broken down and energy made available for the performance of work (catabolism).
Micronutrient Nutrients needed in very small amounts.
Nitrogen-free extract (NFE): One of the six fractions in the system of proximate analysis; it is calculated by difference when the sum of the percentages of moisture, crude protein, ether extract, ash, and crude fiber is subtracted from 100. NFE is a complex mixture of compounds that may include cellulose, hemicelluloses, lignin, sugars, starch and pectins, organic acids, resins and tannins, pigments, and water-soluble vitamins.
Nutrient A substance used by an organism for maintenance, growth, and reproduction; it is designated as macronutrients (proteins, lipids, and

carbohydrates) and micronutrients (vitamins and trace elements), depending upon the amounts required.
Nutrient requirement Minimum amount of a nutrient that is needed for the maintenance of growth, health, and reproduction, with no safety margin.
Omnivore An animal that feeds upon a mixed diet comprising both plants and animals.
Phytate Hexaphosphoinositol, the phosphate derivative of the sugar alcohol inositol, is found in plant seeds as the main storage form of phosphorus; fish are unable to digest phytate so the phosphorus is not bioavailable; phytate can inhibit the action of digestive enzymes, and can chelate with di- and trivalent metal ions, thereby reducing their biological availability; it is considered an important anti-nutritional factor (ANF) in plants used to manufacture fish feeds.
Poikilotherm An organism that cannot regulate body temperature except through behavioral means. An animal whose body temperature fluctuates with that of the environment.
Protease inhibitor A substance, often a protein (such as the trypsin inhibitors), that inhibits the actions of proteolytic enzymes, thereby reducing the efficacy with which an animal can digest protein.
Protein An organic molecule consisting of chains of amino acids, and containing chiefly C, H, O, N, and S. One or more polypeptide chain may comprise it, and such chains may also be associated with nonprotein components (prosthetic groups). It is essential in living organisms as enzymes and structural constituents of tissues.
Secondary metabolites (compounds) Compounds produced by microbes, plants, and some animals (e.g., antibiotics, alkaloids, and tannins) that are usually not essential to the growth of the organism, but may have other functions, for example, in chemical defense.
Spectroscopy Encompasses a range of techniques for acquiring information about atomic and molecular structure via the study of patterns of absorption or emission of electromagnetic radiation. Near-infrared spectroscopy is a technique that is used for the rapid analysis of the chemical composition of feeds and feedstuffs, and instruments that measure either reflectance (NIRS) or transmission (NIT) have been developed.
Tannins These are complex, soluble, phenolic secondary metabolites that play a prominent role in the general defense strategies of plants. They are believed to be by-products of the metabolism of the aromatic amino acid phenylalanine.
Vitamins These are organic compounds required by animals in small amounts for the maintenance of a variety of metabolic functions; these are classified as lipid soluble (vitamins A, D, E, and K) or water soluble (ascorbic acid, myo-inositol, choline, and the vitamin B complex). Vitamins are essential nutrients that must be obtained via the diet, and a lack of a vitamin will lead to the development of a deficiency disease.

Animal Bioenergetics

Experiments in bioenergetics were first carried out during the eighteenth century, and eventually the discipline matured to the stage where it was applied to solve problems within human and animal nutrition. This role for bioenergetics was initiated early in the twentieth century. Bioenergetics has been widely applied in animal science, where one of the major aims is to produce edible muscle. Interactions between farmed animals and their environments are often stressed, with research focusing on:

- the relationships between gas exchange and heat production;
- examination of the causes of energy expenditure, and the costs associated with the performance of various activities; and
- the establishment of a basis for the evaluation of feed ingredients and compound feeds in relation to energy requirements and expenditures.

The results of these various lines of research have been used to estimate the energy requirements of farmed animals, to predict the growth of animals on different feeding regimes and to assist in the development of compound feeds for terrestrial livestock and farmed aquatic animals. A major goal of aquaculture is the effective production of edible fillet (myotomal muscle), so it is important to know about the interactions of environmental and nutritional factors on muscle development and growth (Figure 1). Modern bioenergetics studies can increase this understanding.

Defining Bioenergetics: Energy Flow and Partitioning

Bioenergetics is the quantitative study of energy partitioning induced by the metabolic processes that occur in organisms for them to stay alive, grow, and reproduce; it includes events taking place at the

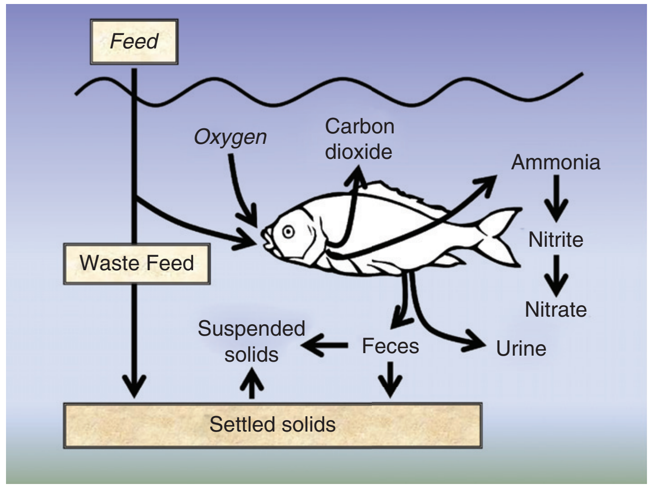

Figure 1 Two-way interactions between farmed fish and the environment may have marked influences upon the characteristics of the water (i.e., water quality) in which they are held. Adapted from Le Francois et al. (eds.) (2010) *Finfish Aquaculture Diversification.* Wallingford: CABI.

molecular and cellular level, as well as those that can be studied in whole organisms, populations, or ecosystems. In the broadest sense, a descriptive factorial scheme (Figure 2) can depict the fate of energy intake, and mathematical modeling or graphical representation can be used to investigate thef interrelationships among energy intake, metabolism, and energy retention.

Animals expend energy in the performance of physical activity, but even when resting animals may expend a considerable amount of energy to maintain the metabolic integrity of their body functions. For example, there is transport of substrates and metabolites in and out of cells, and chemical work is needed for tissue renewal and repair; the latter involves the turnover of proteins and the biosynthesis of lipids and carbohydrates (**see also Energetics**: General Energy Metabolism).

How much energy animals are required to expend, and how much of their energy intake they retain as production is under the influence of a wide range of environmental factors (Figure 3; **see also Swimming and Other Activities**: Cellular Energy Utilization: Environmental Influences on Metabolism). The environmental factors can be broadly divided into two main types, abiotic and biotic. Abiotic factors are those that relate to the nonliving, physical environment. For fish, and other aquatic animals, the abiotic factors include temperature, light intensity and day-length

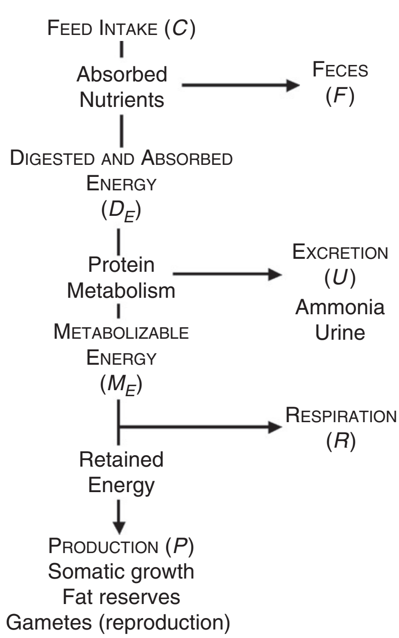

Figure 2 Flow diagram illustrating the factorial scheme of energy partitioning and dissipation in the study of animal energetics.

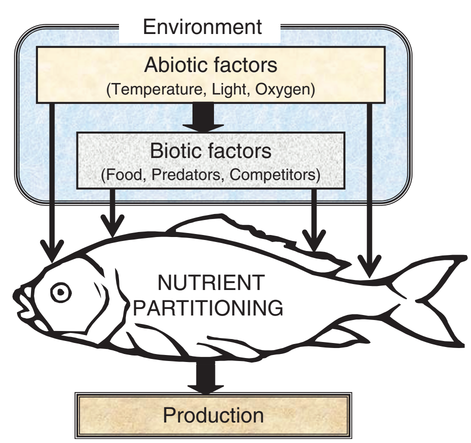

Figure 3 A wide variety of biotic and abiotic environmental factors influence energy partitioning and production of fish.

(photoperiod), oxygen concentration, water flow and currents, salinity, and other chemical properties of the water in which the animals live. The biotic factors, on the other hand, relate directly to the effects that organisms sharing habitats have on each other; biotic factors include the prey, predators, competitors, and parasites of the fish.

A Simple Model of Energy Partitioning

Food energy (C) is gross intake, usually expressed as a daily rate, but not all of this is available to the fish. Some is voided in the feces (F), and there are also losses as urinary excretion (U) and via diffusion from the body surface, including the gills of fish. From this, two quantities can be defined: digested and absorbed energy (D_E) and metabolizable energy (M_E) (**Figure 2**). D_E is the difference between food energy and fecal losses (i.e., $D_E = C - F$). M_E is the difference between food energy and the sum of losses in the feces, urine, and across the body surface, so $M_E = C - (F + U)$. In other words, M_E is the energy available for meeting the demands for staying alive, and for growing and reproducing.

The metabolic expenditure by an animal is often measured as the amount of heat produced (**see also Energetics**: General Energy Metabolism); this is usually called respiration (R). The difference between M_E and R is retained energy, usually termed production (P): $M_E - R = P$. When an animal is deprived of food ($C = 0$), body tissues are catabolized in order to support R, P is negative, and the animal loses body mass. On the other hand, if an animal eats some food but energy retention is zero over time (i.e., $P = 0$), there is an equilibrium and the animal is meeting its maintenance requirement (**Figure 4**).

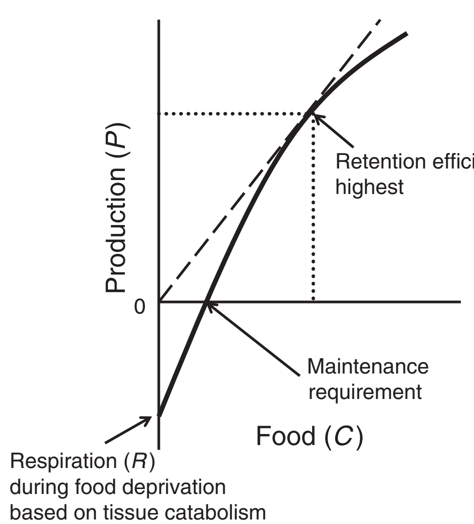

Figure 4 The relation between production and food intake, illustrating key points relating to energy retention.

As C increases so does R; R is greater at maintenance than it is in animals that are deprived of food, and as C increases above maintenance, R continues to increase. In a growing animal, an increase in C results in a proportion (r) of M_E being retained as P and a proportion ($1 - r$) being lost in respiration (R). In other words, r is a measure of the efficiency with which energy is retained as production, or the energy utilization efficiency. Energy utilization efficiency is not constant but varies with the amount of food consumed. If the relationship between P and C is nonlinear, retention efficiency is highest at the point where a line drawn through the origin intersects with the plotted line that depicts the relationship between P and C (**Figure 4**). The efficiency with which C is retained as P is usually expressed as a percentage, the food conversion efficiency. In farming practice, the reciprocal of food conversion efficiency is sometimes used, that is, the amount of food required to produce a given unit of production or gain, the feed:gain ratio.

Units of Measurement

Bioenergetics is the study of biochemical transformations using units of energy as the common currency. In common parlance, for example, when we are undergoing weight reduction regimens we will often say that we are watching, or counting, our calories; the calorie is a unit used to measure energy, but the joule (J), an SI unit, has replaced the calorie in the scientific literature. The joule is named after James Prescott Joule, who was the first to demonstrate the equivalence of heat, work, and the various forms of chemical energy. The kilojoule ($1\ \text{kJ} = 10^3\ \text{J}$), rather than the joule, is most often the unit of choice in studies of animal energetics ($1\ \text{kJ} = 0.239\ \text{kcal}$; $1\ \text{kcal} = 4.186\ \text{kJ}$).

Bioenergetics involves the examination of biological rates, and power units (the watt in the SI system) are the appropriate ones to use when referring to such rates. The convention, however, is to retain the kilojoule and express rates in direct relation to periods of time. For example, food consumption is generally expressed as kilojoules per day (kJ d^{-1}) and energy expended on activity as kilojoules per hour (kJ h^{-1}).

Although bioenergetics relies upon energy units as common currency, it must be borne in mind that animals eat, digest, absorb, and metabolize food that is made up of chemicals. Animals have a requirement for, transform, and store macronutrients (proteins, lipids, and carbohydrates) and micronutrients (vitamins, minerals, and trace elements). As such, nutritional energetics revolves around the investigation of the absorption, biochemical transformation, and partitioning of nutrients. In the study of fish bioenergetics, the focus is most often on the fluxes and fates of energy, proteins, and lipids (**see also Energetics**: General Energy Metabolism).

Chemical Analyses and Energy Determination

Assessments of the chemical composition and energy value of feedstuffs, feeds, and animals are central to the study of the energetics and nutrition of farmed animals, including fish. The major energy sources in feeds are the organic macronutrients: lipids, proteins, and carbohydrates. These can be completely oxidized in a bomb calorimeter to yield carbon dioxide, water, oxides of nitrogen and sulfur, and heat. The three macronutrients yield different amounts of heat energy when completely oxidized: approximately 39 kJ g^{-1}, 23.5 kJ g^{-1}, and 17 kJ g^{-1} for lipids, proteins, and carbohydrates, respectively.

Chemical composition is measured using a variety of techniques. Some methods enable determinations to be made of individual amino acids, fatty acids, vitamins, and mineral elements, but the chemical analyses undertaken are not usually so comprehensive. Chemical composition is most frequently given as proximate composition in which six major fractions are recognized: moisture, crude protein, ether extract, ash, crude fiber, and nitrogen-free extract. Proximate analysis is time consuming and expensive, large samples are required, and the analyses are destructive. Alternatives can provide quick, nondestructive, quantitative assessments of the constituents of biological materials. These include X-ray computed tomography, total body electrical conductivity, near-infrared reflectance spectroscopy (NIRS), and near-infrared transmittance. NIRS has attained popularity because it is rapid and nondestructive, equipment costs are relatively low and the equipment is quite easy to use. NIR spectra can give information about physical and chemical properties, and NIRS is being used for assaying the chemical composition (protein, moisture and oil/fat) of feed ingredients, feeds and animal tissues, for species identification and for food authentication purposes.

Energy Budgets: Growth Trials and the Biological Evaluation of Compound Feeds

Chemical analyses provide a great deal of information about the nutritional properties of feeds, but biological trials are required to reveal the full value of feeds and their ingredients. For example, studies of digestion and absorption are required for the assessment of the bioavailabilities of nutrients to fish. Moreover, growth trials are fundamental for feed assessment, and for the determination of nutrient requirements. When conducting growth trials for feed assessment, it is seldom that data relating to all components of the energy balance equation are collected. Emphasis is usually placed upon the monitoring of food intake (C), fecal losses (F), and the energy and nutrients retained as production (P). Practical problems relating to the measurement of respiration (R) and excretion (U) over prolonged periods of time often preclude their inclusion in the assessment (**see also Energetics**: General Energy Metabolism).

Although neither R nor U is usually monitored in growth trials, their importance in determining the outcome of trials is recognized. For example, mammals and birds are homeothermic endotherms, whereas fish are poikilothermic ectotherms; these animals differ in metabolic characteristics and rates of energy expenditure. Homeothermic endotherms generate body heat and maintain a body temperature that differs from that of the environment. They have high metabolic rates and their maintenance requirements are high; if deprived of food, they lose body mass rapidly, and they have low starvation resistance (**Table 1**). Given that mammals and birds have relatively high maintenance requirements, the proportion of feed nutrients directed toward production may be low and so these animals are generally characterized as having relatively low retention efficiencies. Fish, being poikilothermic ectotherms, have a body temperature that changes as environmental temperature changes, and the main source of their body heat is the environment. Fish have lower metabolic rates than mammals and birds of similar size, and the maintenance requirements of fish are accordingly low. Fish are relatively efficient at converting food to body tissue, and have higher retention efficiencies than do mammals and birds of similar size.

Table 1 Comparison of metabolic characteristics and growth efficiencies of fish (poikilothermic ectotherms) and mammals (endothermic homeotherms)

	Fish	*Mammals*
Metabolic rate	Low	High
Starvation resistance	High	Low
Maintenance food requirement	Low	High
Food use for growth	High efficiency	Low efficiency

This comparison between mammals, birds, and fish can be extended to include generalizations about nutritional requirements and feed compositions. Most farmed mammals and birds are either herbivorous or omnivorous, and they are capable of digesting and metabolizing feeds that contain high concentrations of complex plant carbohydrates. Feeds formulated for these animals, such as poultry and pigs, usually have high carbohydrate content and relatively low protein and lipid contents (**Table 2**). Carbohydrates are an abundant and inexpensive energy source, so poultry and pig feeds are largely comprised of relatively cheap feed ingredients. In contrast to terrestrial farmed animals, many of the high-value, intensively farmed fish species are carnivorous. They are unable to digest and metabolize large amounts of dietary carbohydrate. These carnivorous fish rely upon feeds that contain relatively high proportions of proteins and lipids. Feed ingredients that contain these nutrients are more expensive than those that are rich in carbohydrate. Consequently, fish feeds are typically more expensive than those prepared for terrestrial livestock.

Monitoring Feed Intake

Effective feeding of farmed fish poses several problems not encountered when feeding terrestrial livestock. The feeds are exposed to water prior to being ingested, so they must be water stable with minimal loss of nutrients. Disintegration of feed will make it unavailable, and leads to undesirable water fouling. In addition, feeds should have physical and chemical characteristics that make them easy to detect and capture. As such, attempts are usually made to manufacture feeds that float at the water surface, or sink through the water column at prescribed rates that suit the fish's feeding preferences. A large proportion of the cost of aquaculture production is related to feeds and feeding, so feeds must be correctly formulated, and the quantities given to the fish should meet demand, without excessive wastage.

There are numerous factors that interact to influence feeding (**Figure 5**). Therefore, it is extremely difficult to predict when and how much a fish will eat. On intensive fish farms, feeding is usually highly automated, and several types of feeding systems have been developed. On-demand feeders are designed to circumvent problems arising from the unpredictability of feeding responses. The purpose of using on-demand feeders is to feed the fish effectively by presenting feed at the correct time and in sufficient quantity. On-demand feeders operate on the principle that both the timing and quantities of feed released are controlled by the fish: on-demand feeders are either self-feeders or interactive feeding systems.

When self-feeding, the fish control the delivery of feed by activating a trigger system. The trigger is activated either by the fish biting on, or displacing, the tip of a rod, or by pulling on a small bead or pellet-shaped object attached to a string. When the fish activates the triggering system, a portion of feed is released from a hopper.

Interactive feeding systems usually rely upon the detection of waste feed to control the amount delivered. The fish are provided with feed at regular intervals and registration is made as to whether or not the feed is consumed. This may be done by direct observation of the feeding responses of the fish, by following the fate of feed pellets using video recording, or by using special optical (infrared) or hydroacoustic (sonar or Doppler) sensors to monitor the distributions of the fish or detect uneaten pellets. Feed delivery is stopped or modified according to feedback signals from the sensor system, so the delivery of feed is controlled in relation to the willingness of the fish to eat.

When feed assessment studies are conducted, it is important to collect accurate information about food intake. Measurements are usually made by combining automatic feeding with the collection of waste feed to get information about the amount of food eaten by a

Table 2 Comparisons of feeding habits and feed compositions of selected terrestrial livestock species and farmed fish

	Terrestrial livestock (pigs and chickens)	*Carps and tilapias*	*Salmonids and sea basses*
Feeding habits	Omnivorous	Herbivorous Omnivorous	Carnivorous
Metabolic substrates	Carbohydrates Fats	Carbohydrates Fats	Fats Proteins
Feed components (nutrient composition)	High carbohydrate Low protein (*c*. 20%) Low fat (*c* 10%)	High carbohydrate Medium protein (*c*. 30%) Low fat (*c*. 10%)	Low carbohydrate (up to *c* 20%) High protein (38+%) Medium-to-high fat (up to *c* 35%)
Feed costs (per kg feed)	Low Cheap ingredients with high carbohydrate content	Low-to-medium	High Expensive protein-rich ingredients

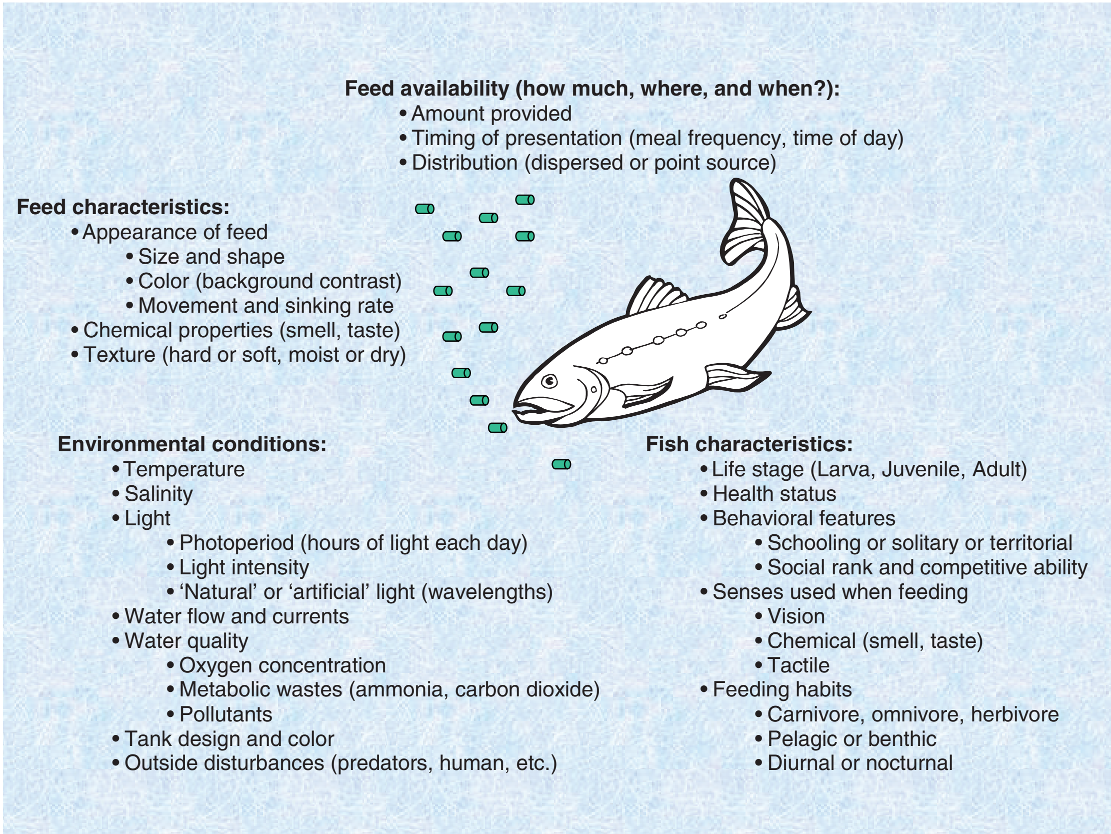

Figure 5 The wide variety of factors that influence feeding in fish make prediction of food intake extremely difficult. From Le Francois et al. (eds.) (2010) *Finfish Aquaculture Diversification.* Wallingford: CABI.

group of fish. Techniques are also available that enable the food intake of individual fish to be monitored.

Assessment of Nutrient Bioavailability

Realistic assessments of feeds require that information is collected about the digestion and absorption of nutrients, that is, measurement of nutrient bioavilability is an important aspect of feed evaluation. In principle, $D_E = C - F$, so information about both C and F is required for the calculation of D_E. It is difficult to collect accurate information about food consumption and it is virtually impossible to collect all of the feces produced by fish during a growth trial. This means that D_E cannot be measured directly, and alternative indirect marker methods must be used for the estimation of nutrient bioavailability.

Many ingredients are used for preparing fish feeds. Some feed ingredients are now in short supply and are being replaced by alternatives. In particular, there is increased replacement of animal proteins, such as fish meal, with terrestrial plant proteins. The replacement of animal proteins with plant proteins presents several problems, particularly in feeds for carnivorous fish. Feeds given to carnivorous fish usually contain at least 38% protein, limiting the use of ingredients that contain moderate amounts of protein; plant protein sources usually have less protein than do animal products. Consequently, fractionation of plant materials is often carried out to increase the protein concentration in the feed ingredient.

In addition to their low protein concentration, many plants contain secondary compounds that reduce their value as feed ingredients. These compounds act as antinutritional factors (ANFs) by suppressing feeding or by interfering with the digestion, absorption, and utilization of nutrients. ANFs may interfere with protein digestion and absorption, bind to minerals and reduce their bioavailability, act as anti-vitamins, interfere with metabolic pathways, or disrupt endocrine signaling. The ANFs include protease inhibitors, alkaloids, tannins, phytate, and plant fibers. Some ANFs are heat labile, so thermal processing may be used to destroy them. ANFs present in the outer hulls or seed coats of plants may be removed and deactivated using de-hulling and heat treatment. Other ANFs are more resistant, and their removal or destruction may require treatment of plant materials with organic solvents or enzymes. Thus, a range of processing and fractionation technologies, including dehulling, heat treatment, enzyme treatments, aqueous or organic solvent extraction, and protein purification, may be applied to plant products to increase their value as feed ingredients.

Metabolic Rates: Energy Expenditure and Rates of Nitrogenous Excretion

There are many biotic and abiotic factors that influence energy expenditure and rates of excretion of poikilothermic ectotherms; temperature, oxygen availability, activity, and feeding are among the most important (**see also Energetics**: General Energy Metabolism and **Swimming and Other Activities**: Cellular Energy Utilization: Environmental Influences on Metabolism). For example, an increase in environmental temperature results in an increase in energy expenditure that is reflected in an increase in oxygen consumption. Aquatic hypoxia is a state of reduced oxygen availability. In fish farming, attempts are made to minimize exposure of fish to hypoxic conditions to avoid the negative effects this has on feeding, energy expenditure, and growth.

Increases in swimming speed result in increases in rates of energy expenditure (**see also Swimming and Other Activities**: Energetics of Fish Swimming). Given the high energetic cost of activity, it is surprising that fish of some species grow faster and more efficiently when swimming against a modest water current than they do when reared in tanks with less pronounced water flows. This is most probably related to behavioral changes that result from exposure of fish to flowing water. The fish often form schools, and do not spend as much time and energy on exploratory activities and aggressive behaviors when engaged in directed swimming activity.

Energy expenditures of fed fish are higher than those of fish deprived of food; fed fish may be more active than unfed fish and this may contribute to their elevated metabolic rates. Food search and capture may lead to some increase in energy expenditure, but metabolic rates are elevated whenever there is food in the gut; metabolic rates are usually highest a few hours after feeding has ceased. As such, the increase in energy expenditure that follows feeding may largely result from the energy requirements for

- physical processing of food, digestion, and the absorption of nutrients;
- biosynthesis, turnover, and deposition of tissue macromolecules; and
- deamination of amino acids and synthesis of excretory products.

Following the ingestion of food there is an increase in motor activity of the gut, and digestion and absorption involve the synthesis and secretion of digestive enzymes and transport of nutrients across the gut wall; all result in increased energy expenditure. Tissue constituents are in a dynamic state; quite a large proportion of the energy expenditure associated with the ingestion of food is related to turnover, synthesis, and deposition of macromolecules (primarily protein, but also lipids and carbohydrates; Figure 6; **see also Food Acquisition and Digestion**: Cost of Digestion and Assimilation. Rates of nitrogenous excretion also increase following feeding, so amino acid deamination and the synthesis of nitrogenous excretory products contribute to energy expenditure. Fish excrete most of their waste nitrogen as ammonia, that is, they are ammonotelic. Ammonia excretion increases following feeding and protein-rich feeds induce greater ammonia excretion than feeds of lower protein content. Although fish mostly excrete ammonia, they also excrete some urea, amino acids, uric acid, creatine, and creatinine; the amounts of the different nitrogenous compounds excreted vary with species and life-history stage, feeding conditions, feed composition, and environmental factors (**see also Food Acquisition and Digestion**: Cost of Digestion and Assimilation).

Growth and Nutrient Retention Efficiency

Feeds are evaluated according to whether or not they are utilized effectively to sustain production. Information is collected on feed composition, amounts eaten, and animal production, and used to calculate how efficiently nutrients are retained. The calculation of an efficiency requires that there is both a numerator and a denominator, and it is imperative that the terms and units in which both are expressed are clear. The numerator is production and the denominator is feed consumption, but expressions of retention efficiency differ in sophistication and complexity. The crudest expression of retention efficiency sets the weight gain of the animal as the numerator and the weight of feed consumed as the denominator. This is an unsatisfactory estimate because it takes no account of possible differences in energy concentrations and chemical compositions between the feeds and the animals that consume them.

If the aim is to express retention efficiency in terms of energy or a specific nutrient, such as protein, it is essential to have information on the chemical compositions of each feed and of the animals at the beginning and end of a growth trial. Once information on chemical composition has been obtained, the numerator is either the energy or amount of nutrient accrued as production, and the denominator is feed consumption expressed in appropriate terms. The units expressing feed consumption can be the weight of a given nutrient that has been eaten, the total amount of gross feed energy consumed, consumption expressed in terms of digested and absorbed nutrients or energy, or the amount of metabolizable energy consumed by the animal.

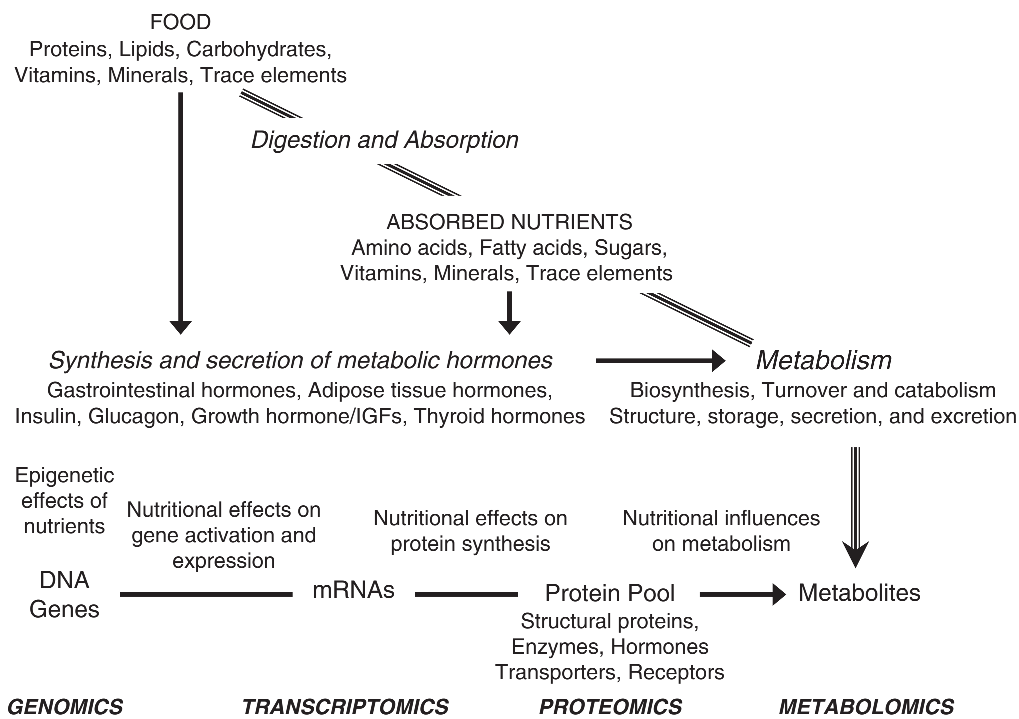

Figure 6 Food nutrients induce changes in gene activation and transcription, protein synthesis and turnover and nutrient metabolism. Transcriptomic (gene expression profiling), proteomic (protein expression analysis), and metabolomic (metabolite composition analysis) monitoring provide holistic assessments of these changes.

Many expressions are used to describe the efficiency of animal production. This can cause confusion, and it also means that care must be exercised when comparing results among studies to ensure that the metrics and estimates are equivalent and comparable.

Past and Future

The biochemical transformations that sustain life and support production are a form of combustion, and this is the basis of bioenergetics. This discovery paved the way for experiments that combined the study of food digestion and absorption with measurements of heat loss, energy expenditure, production, and energy retention. These studies contributed to the development of schemes used to predict animal performance and food requirements, and provided guidelines for use in feed formulation. As such, bioenergetics is established as an important area of applied animal sciences.

On the negative side, the focus on energy as the common currency may overshadow the facts that nutrients have different fates within the animal body, and that energy partitioning is governed by how the different nutrients are transformed during their progress through metabolic pathways. In-depth understanding requires knowledge about the roles of specific nutrients and their metabolism, but such knowledge is fragmentary for the nutritional energetics of fish. This type of information must be obtained if dynamic response models are to be updated and improved in the face of new challenges. These challenges include concerns about the environmental impacts of farming systems, shortfalls in supplies of some traditional feed ingredients, an increased focus on product quality, and the pressure to develop production systems that are sustainable in the long term.

The applied animal sciences have now entered the '-omics' era: genomics, transcriptomics, proteomics, and metabolomics (Figure 6). The techniques developed in support of these disciplines provide powerful tools for the examination of the biochemical networks involved in metabolic regulation. These '-omics' disciplines integrate to provide a holostic overview of the information stored in the genes, the biochemical transformations resulting from enzymatic activity and the actions of metabolic hormones, and compositional changes that accrue from the retention and elimination of metabolites. This integration provides new insights into the factors that control the need for, and use of, nutrients and energy that are a prerequisite for the advance of nutritional energetics. For example, '-omics' techniques make it possible to study the effects of abiotic factors and nutrients on the activation or suppression of genes that code for metabolic enzymes, examine effects on protein translation, and discern rates of nutrient fluxes through metabolic pathways. Metabolomics allows mapping of the fates of nutrients via global monitoring of the metabolites present within cells and tissues. Such studies may lead to the identification of biomarkers that could have utility in growth trials, and the identification of specific nutrients that exert strong biological effects. Further, the large data sets generated by the '-omics' technologies, together with bioinformatics (analysis of metabolic pathways using a systems biology approach), are expected to instigate development of mathematical models to describe and predict the cellular responses to nutrients. This, in turn, should allow progress toward solving several of the problems facing the animal production industries.

See also: **Energetics**: General Energy Metabolism. **Food Acquisition and Digestion**: Cost of Digestion and Assimilation. **Swimming and Other Activities**: Cellular Energy Utilization: Environmental Influences on Metabolism; Energetics of Fish Swimming.

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