ponds; and also that larger dikes can be used to cultivate vegetables irrigated with pond water, a far safer practice for both producers and consumers than irrigation with raw sewage.
- As an increased supply of wastewater to ponds would lead to higher fish production, farmers should be willing to pay for wastewater, thereby providing cost recovery to the city.

The single largest threat to the system, filling in the ponds for urban / industrial development, is likely to be reduced by the recent listing of the complex as a Ramsar site as it carries a Government obligation to ensure conservation and wise use. The latter is defined as sustainable utilization for human benefit compatible with maintaining the natural properties of the ecosystem, in this case wastewater-fed (agro) ecosystem. On-going wastewater development projects do not threaten the wastewater supply from the core area of the city to the fishponds. A World Bank project is renovating the sewers; and a project to desilt the main sewage canal that feeds the fishponds will increase the flow of sewage to the ponds. Kolkata sanitary engineers recognize the value of the ponds as a low-cost sewage treatment system; in the words of a local engineer "if at any time the city authorities think of introducing conventional technology, it will be a very very foolish step".

Cultivating vegetables on a wastewater fed fishpond dike at Mudialy Fishermen's Co-operative Society

Aquaculture Fundamentals

Getting the most out of your feed Part II: The role of macronutrients

Simon Wilkinson, NACA

The role of energy in nutrition

All animals require energy in order to perform a variety of biochemical, physiological and mechanical activities that are essential to their survival, growth and reproduction. In any animal, the costs of these activities place competing demands on the available supply of energy[1]. Ultimately it is the availability of energy that determines the capacity of an animal for growth and this has a substantial influence on the way in which fish utilise and respond to feed. The energy budget in fish may be considered in the following terms[2]:

$$C = F + U + R + G$$

Where C is energy intake through food consumption, F is loss of energy in faeces, U is energy lost in nitrogenous excretory products, R is energy lost through metabolism and G is energy stored in tissues (growth). Growth can be regarded as the difference between food consumption and other components of the energy budget, ie. Growth = C - F - U – R[3]. The proportion of energy expended on growth varies widely according to the behaviour and physiology of the species.

Ration size and growth

The relationship between ration size and growth rate has been summarised by De Silva and Anderson[4]. Weight loss occurs until the ration meets the minimum energy demands of the fish. This level is known as the maintenance ration. At feed levels below the maintenance ration, assimilated nutrients are fully utilised to provide energy and fish catabolise their own fat reserves and tissues to compensate for the energy shortfall[5,6].

Growth rate increases with ration in excess of the maintenance level, although the rate of increase diminishes towards the maximum ration. The utilisation efficiency (feed conversion ratio) also improves to an optimum point, and then decreases towards the maximum ration due to a reduction in absorption efficiency[4,7]. This decline may also be partially caused by increased heat of activity at high ration[4] as fish have more energy to allocate to discretionary activities. For example, the Roach *Rutilus rutilus* has been shown to adjusts its level of swimming activity in response to changes in energy demand associated with gonad development[1].

Digestible energy content

The gross (potential) energy value of a food to a fish depends on its heat of combustion as determined by its chemical composition. However, the realised energy value of a food is also dependent on its digestibility and this will vary between species[2,8,9]. This is because part of any particular nutrient may be present in an indigestible form and its energy value unavailable to the fish[8]. Undigested components of feed pass through the digestive tract to be voided as faeces[5].

Digestibility may also vary with life stage since some fishes do not have fully developed stomachs during the larval phase or may have different dietary requirements. Therefore it is of critical importance to consider the relative digestibility of feed components to a species and / or age class when formulating a diet[10]. A measure of digestibility, the coefficient of digestion, can be calculated from the following equation[8]: Coefficient of digestion = (nutrient intake - nutrient in faeces X 100) / nutrient intake.

Digestible energy content and essential nutrient concentration of feed and feeding frequency

A negative correlation has been reported between the rate of consumption and digestible energy content of feed, indicating that fish feed primarily to satisfy their demand for energy. However, this also means that the quantity of essential nutrients that are consumed will also be negatively correlated to the energy content of the feed[5]. More frequent feeding over the course of a day can enhance the growth rate of some species. However, this is not always the case and the effect varies with species[4], meal size and feeding time[12].

Growth and dietary composition

Fish obtain energy principally through the digestion, absorption and catabolism of proteins, fats and carbohydrates in their diet. However, in addition to providing an energy source, these materials are also required as structural components for the formation of new tissues[5]. The relative proportions and quality of proteins, fats and carbohydrates affect the allocation of these dietary components between catabolism for energy and use in the formation of tissues.

Effect of dietary protein levels on growth

The growth rate in juvenile Tilapia has been reported to increase as dietary protein content is raised until a plateau is reached at around 30-34%. Further increases in protein dietary protein content past this optimum point led to a decline in growth rate thereafter[13]. Similar trends in the mussel *Mytilus edulis*[6]. In both cases the rate at which growth rate increases slows as dietary protein content approaches the maximum, such that there is little difference in growth rate across a wide range of dietary protein levels.

Essential amino acid balance and protein synthesis

Protein synthesis is dependent on the presence of the correct ratio of essential amino acids required for the formation of complete protein molecules. When a shortfall in one amino acid occurs the rest are rendered unavailable for growth and are deaminated to provide energy instead[4]. This indicates that the potential utilisation efficiency of ingested proteins is limited by their quality in terms of meeting the essential amino acid requirements of the animal[5]. Therefore the concentration of protein in the diet needed for maximum growth is not, it itself, an indication of protein requirement in fish[13].

Protein sparing

In the absence of a non-protein source of energy in the diet, some of the protein consumed will have to be degraded in order to support the energy demands for tissue synthesis and metabolism[1,4,6]. This will obviously reduce the quantity of protein that is available for growth. Carbohydrates and lipids serve as alternative sources of dietary energy, thereby reducing the proportion of dietary protein that must be catabolised in order to meet energy demand[4]. This is known as the protein sparing effect. Lipids have a greater energy content than carbohydrates and exert a greater protein sparing effect than carbohydrates[11], which are often of limited digestibility to fish[4].

Protein : Energy ratio

The effectiveness of the protein sparing effect of carbohydrates and lipid is related to the ratio of protein to energy in the diet (P/E ratio). The optimum ratio varies with species and with protein source[10]. Variation away from the optimum ratio will result in either the catabolism of protein for energy, or the production of fatty animals[4]. Both scenarios result in suboptimal feed efficiency[14].

Hajra et al.[14] investigated the optimum dietary protein : energy ratio of the tiger prawn Penaeus monodon by manipulating carbohydrate content. Under constant protein levels growth rate, feed efficiency and protein utilisation all increased with energy content up to an optimum. Protein efficiency ratio remained negatively correlated to P/E ratio up to the optimum dietary energy level. This was attributed to a protein sparing effect associated with increasing levels of carbohydrate in the test diets.

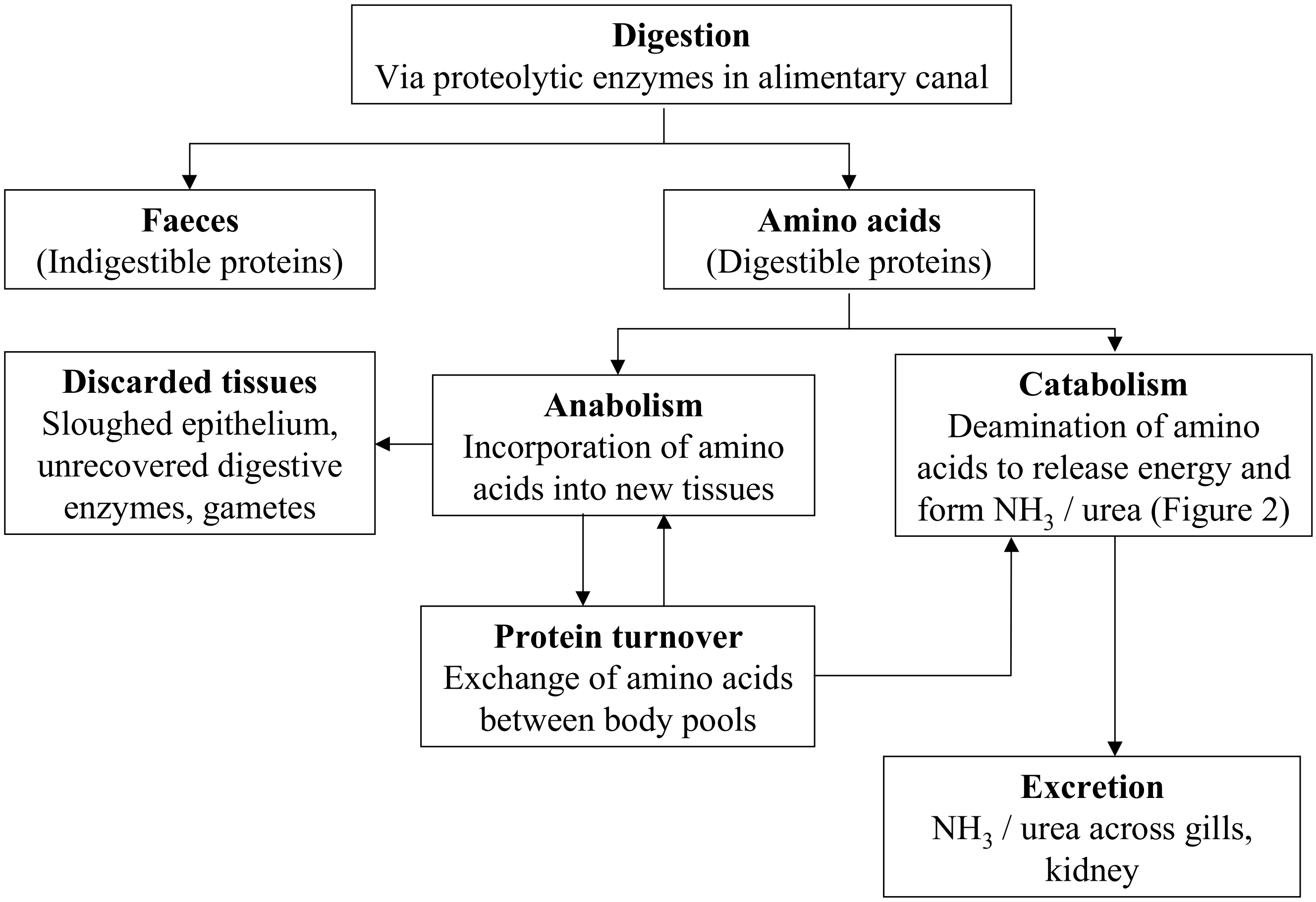
Similarly, De Silva et al.[11] reported that per cent average daily growth, food conversion ratio and protein efficiency ratio increased with dietary lipid content up to a maximum of 18% in the Red tilapia hybrid *Oreochromis mossambicus* x *niloticus*. The optimum lipid level that enhanced growth increased with increasing dietary protein level. Carcass lipid content was positively correlated to dietary lipid content, but the effect diminished with increasing dietary protein level.

Both studies found that increases in dietary energy content past the optimum level had no further beneficial effects, and resulted in reduced growth rates, feed conversion efficiency and protein efficiency ratio.

The fate of ingested protein

The fate of an ingested protein varies with the energy needs of the fish at the time of digestion, its digestibility and quality in terms of meeting essential amino acid requirements and the rate of protein/tissue turnover. Protein may also be lost or shed in tissues and reproductive material. These possibilities are summarised in Figure 1 and those not already dealt with are explored in more detail below.

Fate of ingested protein



Digestion of proteins

Digestible proteins are broken down to release their free amino acids which are then used either for the synthesis of new proteins in body tissues or for energy[10]. The digestion of proteins is catalysed by proteolytic enzymes, principally pepsin and trypsin, that are secreted into the lumen of the alimentary canal[8]. Amino acids suffer one of three fates in an organism, they are either degraded for energy, modified to form another compound, or they are used in protein synthesis[10].

Catabolism and formation of nitrogenous excretory products

The metabolism of amino acids is summarised in Figure 2[10]. There are three stages, the third of which occurs only in elasmobranchs. These are:

1. deamination, where amino groups of amino acids are removed from the carbon skeleton and converted to either ammonia or aspartate;
2. conversion of amino acid carbon skeletons to common metabolic intermediates; and
3. incorporation of ammonia and aspartate nitrogen atoms into urea.

Amino acids are principally deaminated through the transfer of their amino group to an alpha-keto acid through reaction 1, catalysed by transaminases. The amino group of glutamate is transferred to oxaloacetate in a second transamination reaction yielding aspartate in reaction 2. Net deamination principally occurs through the breakdown of glutamate, as per reaction 3 which notably results in the production of ammonia. The regulation of deamination reactions is probably most likely occurs in response to the concentrations of substrates and products.

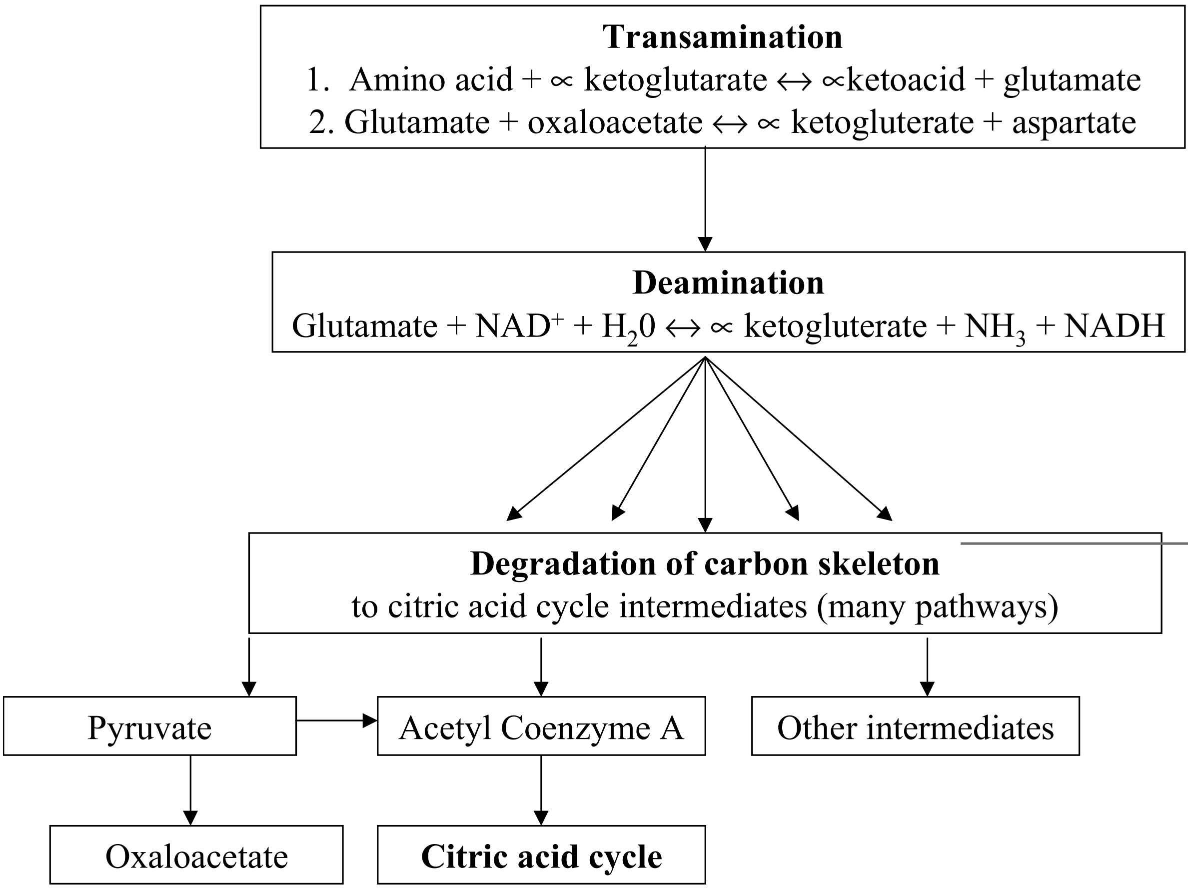
Energy from amino acids is obtained through the degradation of the carbon skeleton following deamination. The carbon skeletons are converted to pyruvic acid, acetyl coenzyme A or intermediates of the citric acid cycle[15] where they are metabolised or used in gluconeogenesis[10].

The nitrogenous end product of protein catabolism in fishes, except for elasmobranchs, is the toxic waste product ammonia, which is excreted across the gills or urine. The provision of a diet of an inappropriate amino acid balance can therefore cause an excessive loss of nitrogen through the gills or urine pathways[5,6]. The catabolism of body proteins during periods of starvation will similarly result in elevated excretion of ammonia[6].

Anabolism and shedding of tissue

Assimilated amino acids that are not catabolised for energy are available for use in growth. Amino acids are linked to form linear polymers of amino acids joined by peptide bonds between the amino group of one amino acid and the carboxyl group of the next. The structure

Metabolism of amino acids



Derived from Anon. (1999)

of the protein determined by the sequence of amino acids and this is under genetic control[4]. Assimilated protein may be shed or released as sloughed structural components, for example epithelial cells or in gametes, or as unrecovered digestive enzymes lost in the faeces[10].

Protein turnover

Tissue proteins are constantly undergoing synthesis and degradation with continual exchange of amino acids between those that are incorporated into protein, free in tissues and free in blood[4]. Amino acids deposited in protein are therefore not 'locked up' but may renter circulation for catabolism as an energy source or be recycled directly into protein synthesis[6].

Conclusion

An understanding of the bioenergetics of a cultured animal and the interaction of dietary components is essential to the provision of an adequate and cost effective diet. From a nutritional point of view, the digestibility of feed components to the target species is a key consideration since this dictates the realised energy and nutrient value of the feed to the animals. The availability of dietary protein for growth is also contingent on the provision of adequate energy levels and on its quality in terms of meeting the essential amino acid profile of the fish. Protein sources that more closely meet the essential amino acid requirements of the animal will promote more effective growth. From an economic point of view the protein-sparing action of fat and carbohydrate energy sources offers the aquaculturist an opportunity to significantly reduce feed costs.

References

1. Koch, F. and Wieser, W. (1983). "Partitioning of energy in fish: Can reduction of swimming activity compensate for the cost of production ?". Journal of Experimental Biology, No. 197, pp 141-146.
2. Cui, Y. and Liu, J. (1990a). "Comparison of energy budget among six teleosts - I. Food consumption, faecal production and nitrogenous excretion". Comparative Biochemical Physiology, V 96A, No. 1, pp 163-171.
3. Cui, Y. and Liu, J. (1990c). "Comparison of energy budget among six teleosts - III. Growth rate and

London, 319pp.

5. Cho, C.Y.; Slinger, S.J. and Bayley, H.S. (1982). "Bioenergetics of salmonid fishes: Energy intake, expenditure and productivity". Comparative Biochemical Physiology, V 73B, No. 1, pp 25-41.
6. Hawkins, A.J.S. and Bayne, B.L. (1991). "Nutrition of marine mussels: Factors influencing the relative utilisations of protein and energy". Aquaculture, No. 94, pp 177-196.
7. Soofiani, N.M. and Hawkins, A.D. (1982). "Energetic costs at different levels of feeding in juvenile cod, Gadus morhua L.". Journal of Fish Biology, V 21, pp 577-592.
8. Kapoor, B.G.; Smit, H. and Verighina, I.A. (1975). "The alimentary canal and digestion in teleosts". Advances in Marine Biology, V 13, pp 109-239.
9. Hidalgo, M.C.; Urea, E. and Sanz. A. (1999). "Comparative study of digestive enzymes in fish with different nutritional habits. Proteolytic and amylase activities". Aquaculture, Vol. 170: 267-283.
10. Anon. (1999). "Nutrition and Growth in Aquaculture". Study Guide SQQ636, Deakin University, Geelong.
11. De Silva, S.S., Gunasekera, R.M. and Shim, K.F. (1991). "Interactions of varying dietary protein and lipid levels in young red tilapia: evidence of protein sparing". Aquaculture, No. 95, pp 305-318.
12. Azzaydi, M.; Martinez, F.J.; Zamora, S.; Sanchez-Vazquez, F.J. and Madrid, J.A. (1999). "Effect of meal size modulation on growth performance and feeding rhythms in European sea bass Dicentrarchus labrax", Aquaculture, Vol. 170: 53-266.
13. De Silva, S.S.; Gunasekera, R.M. and Atapattu, D. (1989). "The dietary protein requirements of young tilapia and an evaluation of the least cost dietary protein levels". Aquaculture, No. 80, pp 271-284.
14. Hajra, A.; Ghosh, A. and Mandal, S.K. (1988). "Biochemical studies on the determination of optimum dietary protein to energy ratio for the tiger prawn Penaeus monodon (Fab.), juveniles". Aquaculture No. 71, pp 71-79.
15. Keeton, W.T. and Gould, J.L. (1985). "Biological science". 4th edition, W.W. Norton and Company, New York, 1175pp.