Pattern and cost of growth and nutrient deposition in fish and shrimp: Potential implications and applications.[1]

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ABSTRACT: Growth is a factor of prime importance in aquaculture. A better understanding of growth could result in significant benefits in terms of productivity, sustainability and profitability for aquaculture operations, provided this greater understanding is translated into relevant and simple applications. The use of growth models, for example, offers an objective and practical way of describing pattern of growth and predicting production. Growth involves the accretion of body components. The amounts of body components deposited and the cost of depositing these components are the main factors determining feed requirement and waste outputs of fish, shrimp and other aquatic animals. This paper examines growth and nutrients deposition and utilization of fish and, to some extent, shrimp under aquaculture conditions. Simple approaches or models for describing and predicting growth, body composition, and feed requirement of fish and shrimp under aquaculture conditions are presented.

KEY WORDS: Growth, nutrient deposition, cost, fish, shrimp.

INTRODUCTION

Growth is a parameter of obvious importance in fish and shrimp culture. It has been the topic of numerous studies yet careful examination of the current scientific and technical literature shows that it is still poorly understood by many scientists and aquaculturists.

Growth involves the accretion of body components (deposition of nutrients). The amounts of body components deposited and the cost of depositing these components (and/or nutrient utilization efficiency) are the main factors determining feed requirement and waste outputs of fish, shrimp and other animals. Consequently, better understanding of the processes could result in significant benefits in terms of productivity, sustainability and profitability for aquaculture operations, provided this greater understanding is translated into relevant and simple applications.

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The purpose of this paper is to examine growth and nutrients deposition and utilization of fish and, to some extent, shrimp under aquaculture conditions. Some simple approaches or models for describing and predicting growth, body composition, and feed requirement of fish and shrimp under aquaculture conditions are presented.

Growth of fish and shrimp

Growth is defined as a change in magnitude. The change can be in size (weight and/or length), in tissue, chemical composition, number, etc. In this paper, the term growth is utilized to signify an increase in weight (mass), since this is generally the most significant parameter in aquaculture.

Because fish and shrimp are poikilothermic (cold-blooded) animals, temperature of their rearing environment has a determinant effect on their metabolism and growth potential (Brett, 1979). Within a same species, different families or groups of individuals (strains) have different genetic make up and often differ in terms of growth potential.

Growth involves accretion of body components (water, protein, phospholipids, triglycerides, nucleic acids, glycogen, minerals, etc.). Growth requires exogenous inputs from dietary (nutrients) or environmental (oxygen, water, certain minerals) origins that are used as building blocks (body components) and/or «fuel» sources to cover the cost of maintaining life processes and accretion of body components. Supply of sufficient quantity of a balanced diet in the proper form and at proper timing is, therefore, essential to realization of growth potential.

There are numerous other factors, such as water quality, diseases, stress, photoperiod, etc., that have different effects (limiting, directing, masking effects) on growth potential (reviewed by Brett, 1979). Examination of the effects of these factors is outside the scope of this paper. Rational approaches of estimating the impacts of such factors are nevertheless suggested in following sections.

It is common for nutritionists to believe that diet quality and quantity is the factor driving growth. It may be more appropriate to recognize that animals have a genetically determined target for body size (and, perhaps, composition) and that they are capable of recognizing whether the target is achieved or achievable given current environmental and nutritional circumstances. Animals will seek to eat a sufficient amount of an appropriately balanced diet to allow them to achieve their target or preferred performance unless limited by constraints or overridden by an externally managed intervention (Oldham *et al.,* 1997). The constraints can be related to dietary factors (nutrient composition, physical characteristics, bulk density, antinutritional factors), husbandry practices, or environmental factors (temperature, salinity). External interventions may involve manipulation, such as hormonal treatments, photoperiod manipulation, eyestalk ablation, etc. Improved understanding of growth should first involves better understanding of the mode or pattern or growth, or more simply put, understanding what the animal is able of achieving (or wants to achieve) given its own biology and the prevailing conditions.

The use of mathematical model (growth models) offers an objective and practical way of describing pattern of growth. Growth models can be of great usefulness from a production planning and management points of view (Iwama and Tautz, 1981). Proper models can allow intrapolation of growth data to estimate weight at time between sampling intervals. This may be very helpful for the accurate estimation of the standing biomass and the amount of feed to be distributed. Growth models can also be used to forecast (extrapolate) weight at a certain point in time past sampling interval. This may be helpful, for example to estimate time required to achieve a given target weight (e.g. market weight). An example is presented in Table 1.

Table 1. Predicted number of days needed to reach harvest weight of rainbow trout strains with different growth potentials, expressed as thermal-unit growth coefficient (TGC).

Fish strain	**A**	**B**	**C**
Growth potential (TGC[1])	**0.153**	**0.174**	**0.203**
Initial weight, g/fish	10	10	10
Target harvest weight, g/fish	1000	1000	1000
Average water temperature, °C	8.5	8.5	8.5
Number of days to harvest	603	530	455

[1] TGC = 100 x (Final body weight$^{1/3}$ - Initial body weight$^{1/3}$)/ Sum(Days * Temp (°C))

Describing growth of fish

Growth of fish is in many ways similar to growth of higher vertebrates, such as mammals and birds. However, growth of fish is said to be more plastic. Fish do not appear to have finite size like mammals and birds do. Most fish species appear to have the potential to grow as long and they live if conditions are favorable. Fish can survive starvation for extended periods of time (days to months) and lose very significant amount of weight and remain able to resume their growth, without ill-effect, when conditions become more favorable again (Weatherley and Gill, 1987).

There have been many attempts to mathematically describe growth of fish using a large diversity of approaches and concepts (Iwama and Tauz, 1981; Muller-Feuga, 1990). It is common to find growth expressed as centimeters per month, instantaneous growth rate, percentage of change in weight, often without reference to temperatures, ration, or culture conditions (Iwama and Tautz, 1981).

Since growth rate is highly dependent on species, genetics, nutrition, environment, husbandry and others factors, it is essential to calculate growth rate for a given aquaculture condition. Production records are very valuable starting points when trying to determine most appropriate growth model, and, consequently, predicting the growth of the fish (Cho and Bureau, 1998). Applying any growth model blindly is risky and defeats the purpose of the exercise.

The main criteria for choosing a growth curve are quality of fit and convenience (Iwama and Tautz, 1981). Ideally, growth models for fish and shrimp should offer possibility for comparing growth rates of animals of various sizes reared at various temperatures.

In aquaculture, several models applicable to the concave portion of the growth curve have been used. The model most widely used is the instantaneous growth rate or specific growth rate (SGR) based on natural logarithm of body weight.

Specific Growth Rate (SGR) = 100 x (ln FBW- lnIBW)/D

where:
FBW is final body weight (g) (weight at the end of the time interval studied)
IBW is initial body weight (g) (weight at the beginning of the time interval studied)
D is number of days

Despite its very wide use, SGR is not an appropriate growth model. It is widely recognized that SGR decreases with size of the fish and length of the time interval used in the calculation. This indicates that the natural logarithm does not correspond to the pattern of growth curve of most fish species reared under optimal conditions. Figure 1 shows that use of the SGR model to predict growth pattern of salmonids results in an underestimation of the weight gain between the weights (e.g. IBW and the FBW) used in the calculation. It also grossly overestimates predicted body weight (BW) when data are extrapolated (Fig. 1). SGR is dependent on fish weight and this results in meaningless comparisons of growth rates among different groups unless live weights are similar. Given the large body of evidence that the SGR is not an appropriate growth model, it is very strange to see that SGR is still used by most fish nutritionists and biologists and accepted by most scientific journal editors. This situation is unacceptable and it is imperative that these professionals critically examine the relevance of using of SGR (or any other growth model) for their growth data.

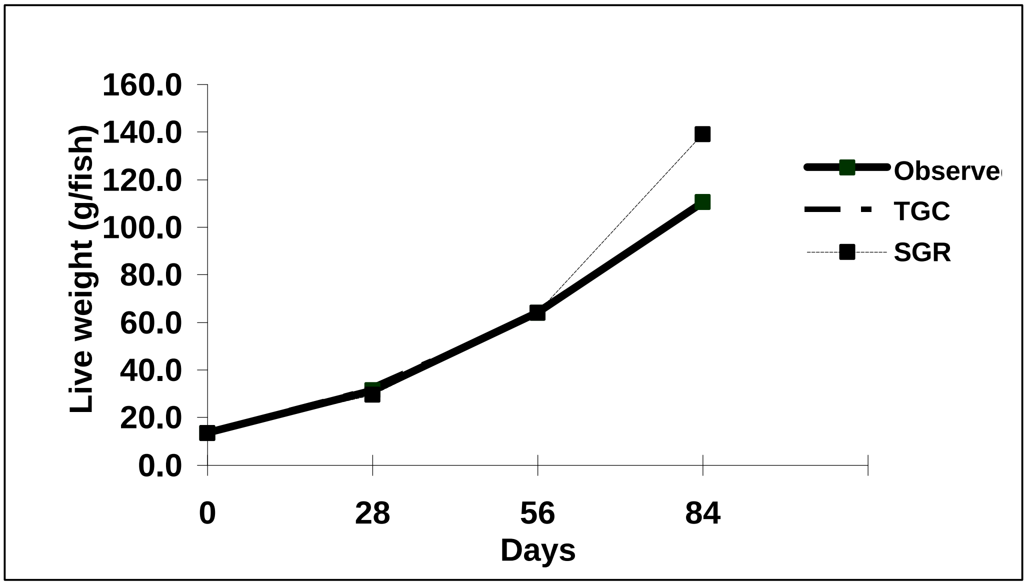

Figure 1. Growth curve of rainbow trout fed to near-satiation and reared at 15°C and comparison of two growth models, the specific growth rate (SGR) and the thermal-unit growth coefficient (TGC). (Data from Azevedo *et al.*, 1998).

There is strong evidences suggesting that, at constant water temperature, cubic root of live weight of salmonids increases linearly with time when the fish are reared under optimal conditions (Iwama and Tauz, 1981). Figure 2 present live weight and corresponding cubic root as a function of time (days) for rainbow trout fed to near-satiety and reared at 8.5°C. This figure clearly show that for rainbow trout (weighing between 150 and 600 g) fed to near-satiation, cubic root of live weight increases in a highly linear fashion as a function of time ($P<0.001$). Therefore, the slope of cubic root of live weight vs. time is the same regardless of the live weight of the fish and time interval used in the calculation. The slope of the cubic root of live weight vs. time is an appropriate and simple mode of growth rate comparison (i.e. gives a constant growth rate value regardless of live weight of fish and time interval used in calculation). This observation was translated into the following equation, commonly known as the daily growth coefficient (DGC) (Cho, 1992):

$$\text{Daily growth coefficient (DGC)} = 100 \times (FBW^{1/3} - IBW^{1/3}) / D \qquad (1)$$

where:

FBW is final body weight (g)
IBW is initial body weight (g)
D is number of days

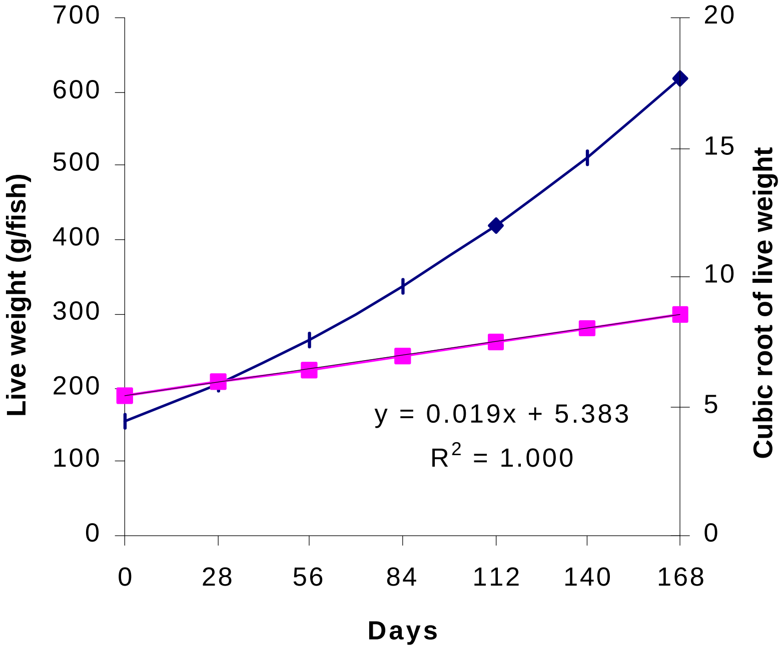

Figure 2. Live weight and cubic root of live weight of rainbow trout fed to near-satiation and reared at 8.5°C growing from 158 to 621 g live weight in 120 days. (Data from Bureau *et al.*, unpublished observations)

Data from Iwama and Tauz (1981) also show that slope of cubic root of live weight vs. time increases linearly with temperature over a wide range of temperature. Data from Azevedo *et al.* (1998) also support this conclusion (Fig. 3 and 4). This observation was translated into the following equation, commonly known as the thermal-unit growth coefficient (TGC) (Iwama and Tauz, 1981, Cho, 1992):

$$\text{Thermal-unit Growth Coefficient (TGC)} = [FBW^{1/3} - IBW^{1/3}] / [T \times D] \times 100 \qquad (2)$$

$$\text{Predicted Final Body Weight} = [IBW^{1/3} + (TGC/100 \times T \times D)]^{3} \qquad (3)$$

where:

FBW is final body weight (g)
IBW is initial body weight (g)
T is water temperature (°C)
D is number of days

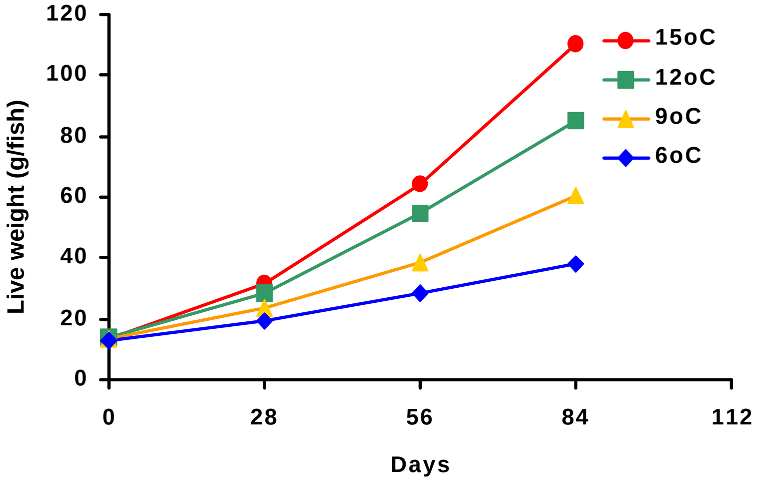

Figure 3. Live weight of rainbow trout fed to near-satiation and reared at four temperatures. (Data from Azevedo *et al.*, 1998)

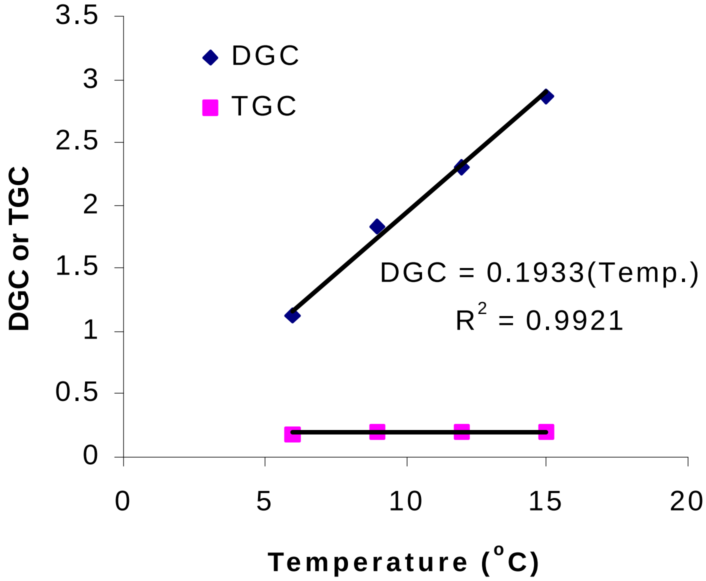

Figure 4. Daily growth coefficient (DGC) and thermal-unit growth coefficient (TGC) of rainbow trout as a function of temperature. (Data from Azevedo *et al*., 1998)

This model equation has been shown to represent very faithfully the growth curves of rainbow trout, Arctic charr, lake trout, brown trout, Chinook salmon and Atlantic salmon over a wide range of temperatures. Extensive test data are presented by Iwama and Tautz (1981). An example of the good agreement of the live weight values predicted with the TGC model and actually observed live weight values at varying water temperature environment is shown in Figure 5 (Cho and Bureau, 1998).

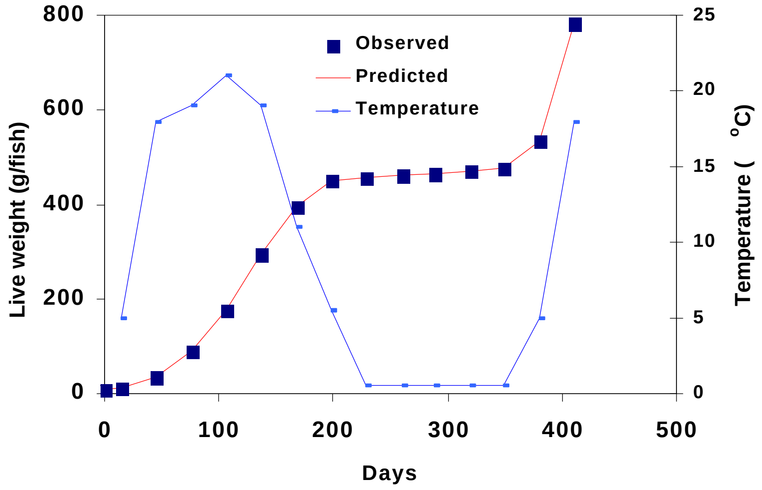

Figure 5. Live weight of rainbow trout reared under variable temperature regimen for 410 days and predicted weight using TGC model. Data from Cho and Bureau, 1998)

The TGC model consequently offers a simple mode of growth rate comparison for salmonids since it is a standardized measure of growth that is unaffected by live weight, time interval and water temperature. It therefore allows comparison of performance amongst culture operations, strains, production years, slots, sampling intervals, etc. It can also be used as a yardstick in scientific studies to determine if fish have achieved their growth potential or determine the effect of different dietary and environmental factors.

While it has only been demonstrated to be valid for salmonids, preliminary observations suggest that TGC model also faithfully represent the growth curve of some non-salmonid fish species, such as the Nile tilapia, *Oreochromis nilotica* (Fig. 6).

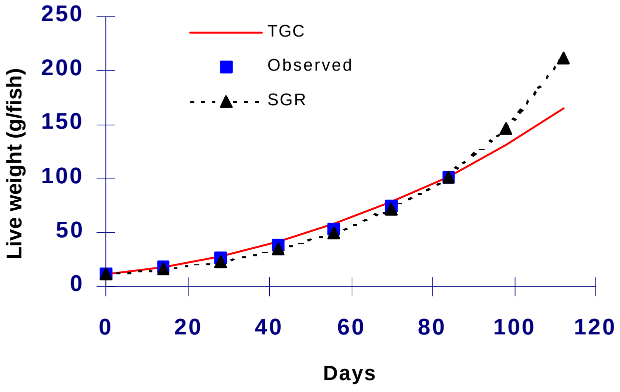

Figure 6. Growth curve of Nile tilapia reared at 29 °C (± 2 °C) and comparison of two growth models, the specific growth rate (SGR) and the thermal-unit growth coefficient (TGC). (Data from Huipeng *et al.*, 1987).

Pattern of growth of shrimp and other crustaceans

Growth of crustaceans and other invertebrates differs significantly from that of vertebrates, such as fish. Although tissue growth is essentially a continuous process in crustaceans, the accompanying increase in external dimensions is discontinuous (Hartnoll, 1983). This proceeds by a series of molts or ecdyses, when the old integument is cast off and a rapid increase in size occurs before the new integument hardens and becomes inextensible. These molts are separated by intermolts, periods when the integument is hard and no external growth occurs. During periods of growth the intermolts are relatively short, and are termed diecdyses (as opposed to anecdysis). There are two variable components of growth, the intermolt period (time between two molts) and molt increment (size increase during molting) (Hartnoll, 1983). At 27ºC, *P. vannamei* and *P.stylirostris*, molts about every 10-12 d when growing from 1 to 10 g live weight then every 15-21 d between 12 and 20 g live weight. This represents a total of about 12-15 molts over a 4-5 months grow out cycle (1 to 20 g live weight) (Cuzon *et al.*, unpublished observations).

Most crustacean species appear to have a finite size or grow toward an asymptotic weight (Hartnoll, 1983). In this regard, pattern of growth of crustaceans may be more comparable to that of birds and mammals than that of fish. Hartnoll (1983) presents series of curves representing the growth (in size) of various crustaceans throughout their life cycle but these may not be very relevant to shrimp culture. There have been few attempts to model growth of crustaceans under aquaculture conditions.

Jackson and Wang (1998) adapted the Gompertz growth model, a model that has frequently been used to describe growth of poultry and mammals, to *Penaeus monodon* under aquaculture conditions. This model accounts for the effects of temperature, mortality and pond age. While not fully validated, the model appears to faithfully represent growth of *Penaeus monodon* and represents a significant step in the right direction. However, it is difficult to understand how pond age and survival can truly be used as objective independent variable of growth into a generalized, widely applicable, growth model.

Figures 7, 8 and 9 present growth curves of various penaeid shrimp reared at constant temperature under laboratory conditions. These data suggest that live weight or cubic root of live weight increase linearly with time. Consequently, DGC or a simple linear growth models appear to be quite highly appropriate for a very large part of the growth curves of *P. monodon* (Figure 7), *P. vannamei* (Figure 8) and *P. stylirostris* (Figure 9). These models may not fit the whole growth curve (which is between 1 and 20 g under semi-intensive farm conditions). Different growth coefficients may need to be used for different parts of the growth curve (i.e. growth curve may need to be divided into stanzas). These expressions of growth are nevertheless very easy to use (easier than the Gompertz curve). They could also be very relevant and practical for shrimp culture, since the most of the production costs are incurred for the linear or concave part of the growth curve of the animal. Rearing of the various life stages are often done in different facilities (Rosenberry, 1998). Different growth models can be used for these different production stages.

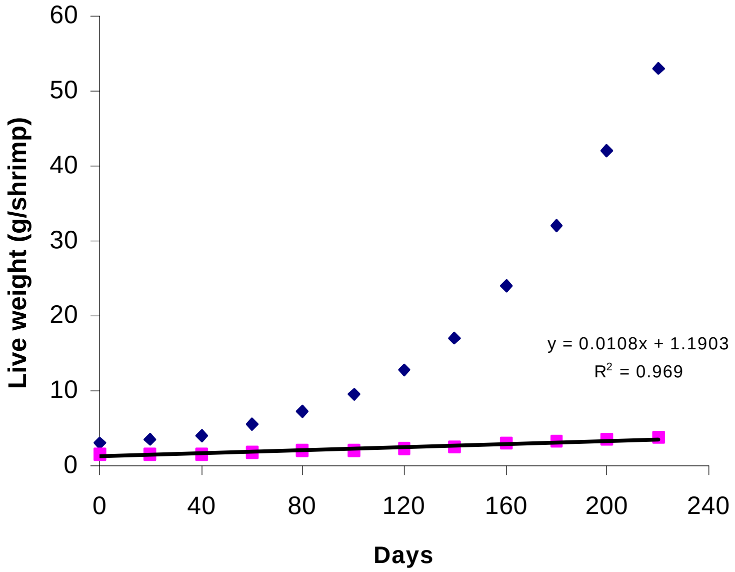

Figure 7. Live weight and cubic root of live weight of *Penaeus monodon*. (Data from Danish Aquaculture Institute)

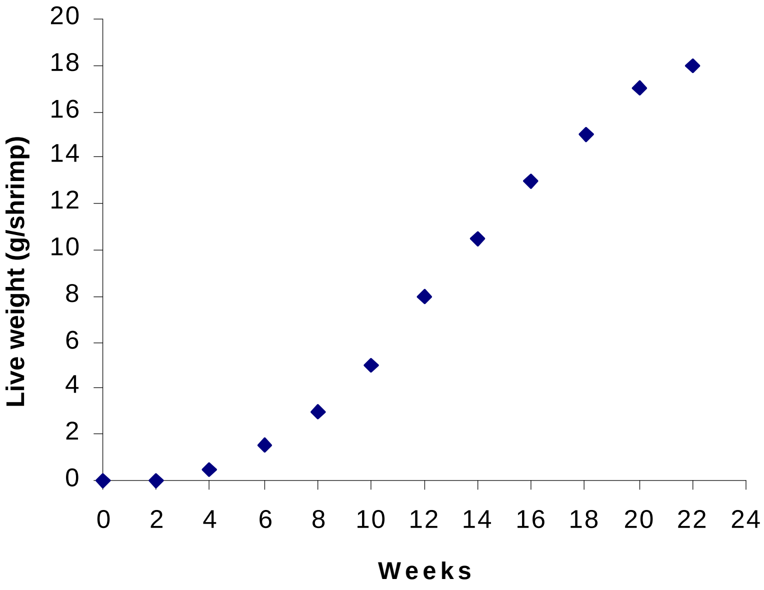

Figure 8. Growth curve of *Penaeus stylirostris* reared for 22 weeks at 27°C (Data from Aquacop and Garen, 1992)

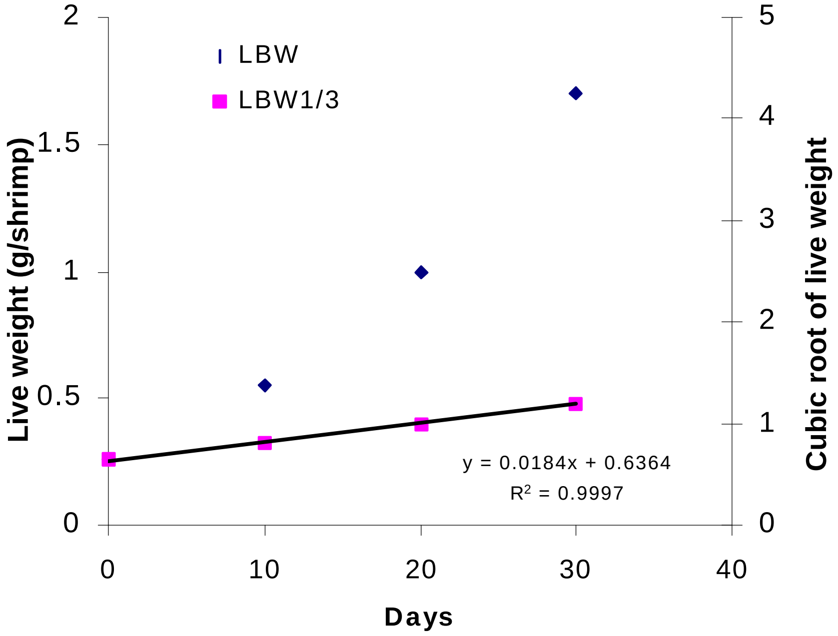

Figure 9. Live weight and cubic root of live weight of *Penaeus vannamei* growing from 0.26 to 1.7 g live weight (LBW). (Data from Civera *et al.* 1996)

Since crustaceans are poikilothermic animal, water temperature is expected to have a similar effect on their growth as that seen in fish. For larvae of *P.stylirostris*, for example, increasing water temperature from 28°C to 30°C shorten larval development period by about 10 days (Aquacop, unpublished observations). Maguire and Allan (1992) observed that growth of *Penaeus monodon* was maximized at temperature of 27 to 33ºC and decreased with decreasing temperatures up to the lowest temperature studied (18°C). Similarly, Jackson and Wang (1998) observed that growth rates of *Penaeus monodon* increased steeply from 18 to 28°C. These authors calculated that at 30°C shrimp reach 34 g after 180 days whereas at 20°C it reach only 15 g. Victoria (1998) observed that daily weight gain of *Penaeus californiensis* (initial weight ca. 0.05 g) was 0.004, 0.0017 and 0.026 g d^{-1} at 19, 23 and 27°C respectively. These data suggest that a temperature-corrected growth coefficient similar to the TGC may be developed for penaeid shrimp. However, more detailed studies on the effects of temperature on growth pattern of shrimp need to be conducted. It might be worth noting, however, that in practice, temperature variation may be relatively limited (e.g. 27+/- 2°C) during production cycle (4-5 months) under tropical conditions, where most shrimp farms are located.

Pattern of deposition of nutrients

Live weight gain is associated with the accretion of water, proteins, carbohydrates, fats, minerals, etc. The amount of these components deposited per unit of live weight gain is not constant but rather changes with fish species and size, feed used, etc.

Patterns of nutrients deposition have received little attention in the past. Experimental evidences (e.g. Shearer, 1994; Azevedo *et al.*, 1998; Lupatsch *et al.*, 1998) suggest that nutrient and energy deposition, and consequently carcass composition, follow rational patterns. Recognizing the rationality and predictability of patterns of nutrient depositions could help explain several phenomena and lead to the development of applications.

Figure 10 and 11 shows absolute (g or kJ per fish) and relative composition (% or kJ/g) of rainbow trout of various size fed practical diet with 20-22 g digestible protein (DP) per MJ digestible energy (DE). Figure 10 shows that the absolute contents of water, protein, lipid and gross energy of fish increase in a highly linear fashion with weight of the animal. Figure 11 show that when expressed in as relative composition (e.g. % of body weight), protein content of the fish increases slightly then remains approximately constant. Moisture tends to decrease rapidly with fish size up to about 100 g live weight, then decreases slowly. Lipid and gross energy (GE) increases very rapidly with size also up to 100 g live weight then increases linearly very slowly. Similar observations were made by Shearer (1994) and Lupatsch *et al.* (1998).

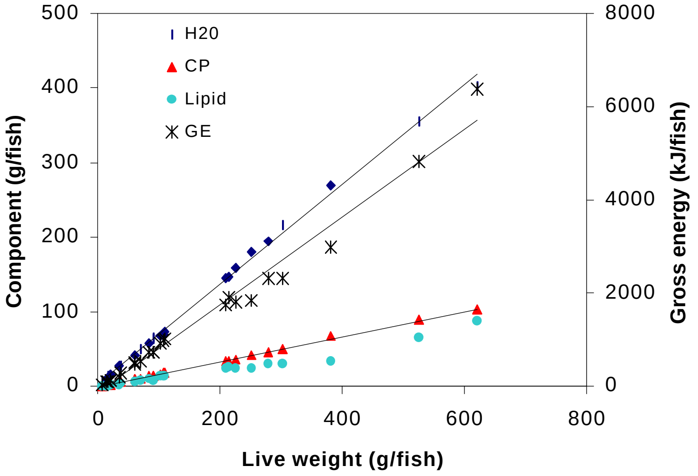

Figure 10. Chemical composition (absolute amounts, g/fish or kJ/fish) of rainbow trout over various sizes fed practical diets.

Regressions:

H_2O (g/fish) = 0.670 live weight (g/fish) – 3.13 R^2=0.997
Crude protein (CP) (g/fish) = 0.169 live weight (g/fish) – 0.07 R^2=0.999
Lipid (g/fish) = 0.125 live weight (g/fish) – 2.52 R^2=0.960
Gross energy (GE) (kJ/fish) = 8.6 live weight (g/fish) – 40.1 R^2=0.979

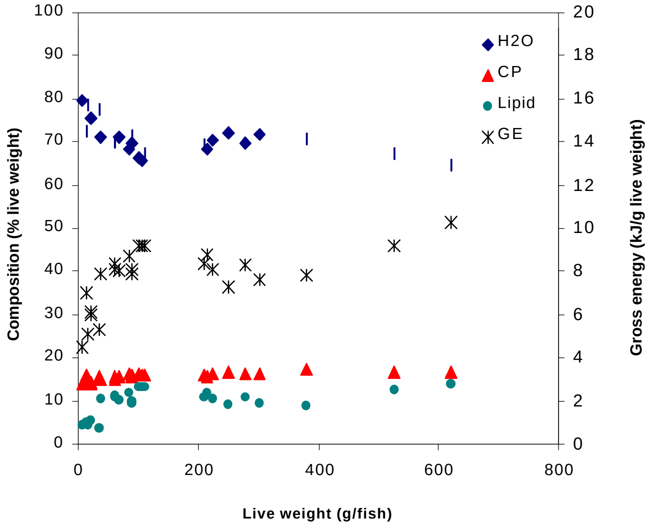

Figure 11. Chemical composition (relative amounts, % or kJ/g) of rainbow trout over various sizes fed practical diets.

This has serious implications since it explains the gradual decreases in feed efficiency of fish with increasing live weight. Larger fish contain more dry matter (protein, lipid, mineral, gross energy) per unit of live weight than smaller fish. One gram of live weight gain represents greater amounts of nutrient deposited for a large fish compared to a smaller one. If the cost of depositing nutrient is similar in smaller and larger fish, then feed requirement per unit of live weight gain should increase with fish size. This effect should be most dramatic before 100g live weight. Numerous examples of this can be seen in the literature.

The results from a number of studies clearly show that this increase in lipid content of fish of increasing body weight is not due to enhanced deposition of lipid compared to that of protein as the animal increases in size. Azevedo *et al.* (1998) observed that rainbow trout deposited protein and lipid according to the same ratio regardless of fish size (10-110 g live weight) and water temperature (6 to 15°C). Similar proportionality of protein and lipid deposition at increasing feed intakes has been reported in domestic animals (Boekholt *et al.*, 1994; 1997). It is apparent that the increase in lipid content (% of carcass) of fish of increasing live weight is the result of the low lipid and relatively high protein contents (expressed as % of body weight) of the body of fish at first feeding. Proportionally constant protein and lipid depositions will result in little change in the protein content (expressed as % of body weight) of the fish carcass but very significant increase in the lipid content (also expressed % of body weight).

Shearer (1994) concluded that the protein content of growing salmonid is determined solely by fish size, that lipid level is affected by both endogenous (fish size, growth rate) and exogenous (dietary, environmental) factors and that ash content is homeostatically controlled. The protein or ash contents of the whole body appear to vary little with growth of a given species of fish whereas whole body lipid and energy contents vary considerably over time.

There are three to six grams of water associated with each gram of protein tissue deposited (Cho and Kaushik, 1990). When lipid is deposited in tissues, it generally substitutes water. Consequently, protein gain generally results in significant live weight gain whereas lipid gain generally results in little or no weight gain. It is apparent from this that understanding of growth of fish resides in understanding of pattern and factors affecting protein deposition.

Severe feed restriction can result in significant alteration of the protein to lipid deposition ratio in fish. Protein deposition has, in general, priority over lipid deposition. Several studies have shown a linear relationship between DE and carcass protein and lipid gains (Figure 12). However, at zero energy gain (maintenance), both protein deposition and live weight gain are positive. Fish fed a maintenance ration (ration resulting in zero energy deposition), catabolize non-protein energy yielding nutrients of the diet and mobilize carcass lipids to support protein deposition and, consequently, live weight gain.

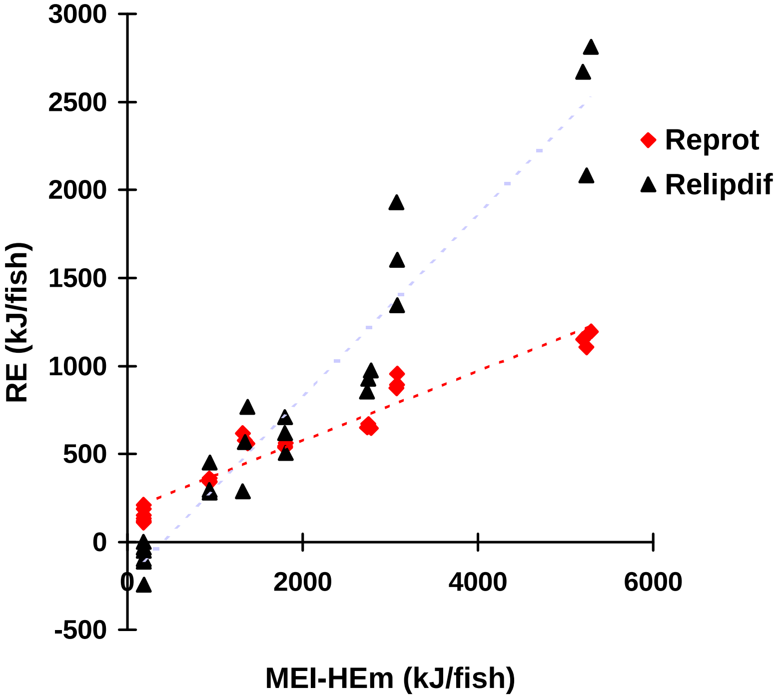

Figure 12. Energy gain (RE) as protein (Reprot) and lipid (Relipdif) as a function of metabolizable energy intake above maintenance (ME-HEm). (Data from Bureau *et al.*, unpublished observations)

The relative importance of protein and lipid deposition depends upon a great number of other nutritional factors. The balance of the available amino acids, particularly essential amino acids, in the dietary protein, and the digestible protein to digestible energy ratio in the diet are the major factors. Proteins of high biological value may promote greater protein deposition than those of lower value. High energy and low protein intakes result in the deposition of a larger proportion of lipid. Seasonal changes in body composition, in relation to specific physiological stages or endocrine status are also known to occur

(Shearer, 1994). There are also considerable inter-specific differences in lipid deposition and tissue distribution. Nutrient deposition and temporal changes in body composition of fish, and effect of all the factors mentioned above, should be examined more closely.

Energy gain, (or recovered energy, RE) has been used as a measure of nutrient deposition and growth in most feed requirement models (Cho, 1992; Cho and Bureau, 1998; Cui and Xie, 1999) and as proven very useful. However, RE is not always a quantitative measure of weight gain because deposition of lipid reduces the water content of the body thus changing the energy value per unit weight of the living animal. The great difference in the energy value of lipid and protein also exaggerates the difference in the energy content of body weight gain. However, RE remains a useful and simple measure of growth and nutrient deposition provided one recognize its limitations.

Information on patterns of nutrient deposition in shrimp reared under aquaculture conditions is very limited. This is related to the fact that chemical composition of shrimp is too seldom analyzed in scientific studies. An outline of the composition of shrimp at different life stages is presented in Table 2. It is quite probable that the nutrient deposition processes in shrimp bear of lot of similarity to those of fish. The dramatically different body structure of these invertebrates is bound to introduce significant differences. Shrimps only have a small capacity to store lipids and are, consequently, fed feeds that are low in lipids. Changes in relative moisture and lipid contents of shrimp are consequently much more limited than what is seen in fish. The presence of an exoskeleton results in higher carbohydrate (amino sugars) and mineral contents than what is generally seen in fish. Molting results in the periodical losses of body components when exoskeleton is shed (Read and Caulton, 1980). Dry weight of exoskeleton was estimated at 200 and 300 mg, respectively *for P.stylirostris* (11.2 g live weight) and *P.vannamei* (7.1 g live weight) (Cousin *et al.*,1996). A large proportion of this exoskeleton can be mineral, especially in large decapods. The energy loss as exoskeleton during molting was estimated at about 1.5% of total digestible energy intake of *Penaeus monodon* by Warukamkul *et al.* (2000) and less than 3% of GE intake for *Penaeus stylirostris* and *Penaeus .vannamei* (Cousin,1995).

Table 2. Estimates of the chemical composition of penaeid shrimp (data from various sources) expressed on a live weight basis.

Stage	Live weight g	Moisture %	CP %	Lipid %	NFE %	Ash %	GE kJ/g
Post larvae	1	79	11	1	5	4	3.8
Juveniles	5-20	74	12-16	2-3	2-7	4	5.2
Broodstock	30-35	70	12	4	10	4	6.6

Cost of depositing nutrients

The maintenance of life processes (integrity of the tissues of the animal, osmoregulation, respiration, circulation, swimming, etc.) and the accretion of body components (and the utilization of nutrients to achieve this accretion) have costs in terms of nutrient and feed energy. This cost is frequently expressed as energy cost. This type of approach is not perfect but is used in this section for simplicity sake. Readers are invited to refer to review on nutritional energetics (e.g. NRC, 1981; Cho and Kaushik, 1990; NRC, 1993; Kaushik and Médale, 1994; Cho and Bureau, 1995; Cho and Bureau, 1998) for more detailed information and review of methodological approaches.

Maintenance of life processes

Animals require a continuous supply of energy for those functions of the body immediately necessary for maintaining life regardless of whether or not feed is consumed. A major portion of this energy is spent for basal metabolism (HeE), a smaller portion of energy is also spent for voluntary or resting activity such as minor bodily movements and muscular activity. HeE represents use of energy for such things as the circulation of the blood, pulmonary ventilation, repair and replacement of cells, membrane transport of ions (especially of sodium and potassium), and muscle tone. Under basal conditions, all the energy released by these processes appears as heat. In fish, HeE is known to be related to both body weight and temperature.

In order to make comparisons between animals or between species, the conditions under which the measurements are made must be standardized. This is achieved by attempting to measure a minimum rate of heat production free of the effects of any controlling factors known to increase it. The object of standardization is to ensure comparability of estimates rather than to establish some absolute minimum value of metabolism that is compatible with life. A number of terms have thus arisen to describe these standardized measurements of "minimal metabolism". With domesticated animals, and hence fish under aquaculture conditions, what is usually measured is the fasting heat production (HEf) (Blaxter, 1989). HEf has been regarded as a close approximation of HeE (Cho and Kaushik, 1990; Cho and Bureau, 1995). In fish, oxygen consumption of free swimming animals fasted for 3 to 7 days to eliminate the effect of the consumption of feed and its subsequent metabolism is the most common approach to measuring basal metabolism (Kaushik and Médale, 1994; Cho and Bureau, 1995).

Fish

Available data on the HEf of fish show that, for a given weight, they are five to twenty-fold lower than that of terrestrial vertebrates. Data from Cho (1991) and Kaushik and Gomes (1988) suggest approx. 30-40 kJ per kg $BW^{0.824}$ d^{-1} for rainbow trout between 15 and 18°C whereas 170 to 590 kJ (kg $BW^{0.75})^{-1}$ d^{-1} has been reported for domestic animals (Blaxter, 1989). Such low energy needs for survival can be attributed to the lack of expenditure for thermoregulation, lower sodium pump activity, their aquatic mode of life, and the mode of nitrogen excretion (ammoniotelism).

HeE in absolute term (kJ $animal^{-1}$ day^{-1}) increases with the mass of the animal. The logarithm of the HeE increases in a linear way with the logarithm of the body mass (Blaxter, 1989). However, the slope of this relation is lower than 1. This means that in all the species, animals of smaller size spend more energy per unit of mass that the animals of larger size. For example, on a kilogram basis, a large shark produces around 1000 times less heat than fish larvae (Guillaume *et al.*,1999).

The relationship of body weight to metabolic rate in animals can be described by the general equation Y = aWb, where Y is the metabolic rate, W is the body weight, and a is a constant which is dependent on species and temperature. The value of the exponent for fish has been described as ranging from 0.50 to 1.00. Detailed observations by several authors with different fish species suggest that across species the exponent is more than 0.7 and less than 0.9.

Water temperature is the major factor determining HeE of fish. Based on a mathematical analysis of oxygen consumption data from several trials, Cho and Kaushik (1990) estimated that HeE of rainbow trout as a function of water temperature could be described as:

$$HeE = (-1.04 + 3.26T - 0.05T^2)\ (BW^{0.824})^{-1}\ \ d^{-1}$$

where

T is water temperature (°C)
BW is body weight (kg)

Clarke and Johnson (1999) observed a curvilinear relationship between metabolic rate and temperature based on analysis of data from 69 teleost fish species. This suggests that HeE of warm water species (e.g. tropical species) is considerably higher than that of cold water fish (e.g. arctic fish species). This, however, does not appear to be the case when one examine experimental evidences with salmonids (Cho and Kaushik, 1990) and other cold and warm water fish species such as Githead sea bream, seabass and grouper (Kaushik, 1998; Lupatsch *et al.*, 2000). At their optimal growth temperature HeE of these cold or warm water species appear to be similar, that is about 30-50 kJ (kg $BW^{0.824}$ $)^{-1}$ d^{-1}.

Maintenance energy requirement (HEm) is generally defined as the amount of energy required for an animal to maintain zero energy balance (zero energy gain, RE=0). HEm is estimated HeE plus extra energy is allocated to account for heat increment of feeding (HiE) associated with feeding a maintenance ration. There are numerous evidences that the efficiency of utilisation of metabolizable energy (ME) varies with the chemical nature of the energy-yielding nutrients absorbed (Blaxter, 1989). When a fasting animal is refed, nutrient absorbed by the animal replace body constituents as the source of energy. The efficiency of utilization of ME is in proportion to the ATP yield per unit of enthalpy of combustion of the nutrients absorbed (Blaxter, 1989).

Shrimp

The fasting oxygen consumption of the 30 g crayfish, *Cherax tenuimanus* (Smith) at 22°C was estimated at about 0.04 mg O2 min^{-1} (Villarreal, 1990), corresponding to HeE of about 26 kJ kg BW-^{1} d^{-1}. Tchung (1995) observed that the heat production of fasting *Penaeus stylirostris* (weighing 20-28 g) at 28°C was about 62 kJ (kg $BW^{0.66}$)$^{-1}$ d^{-1} during the intermolt period. Data from Gauquelin (1996) suggest that fasting oxygen consumption of *Penaeus stylirostris* weighing between 20-30 g was 3.3 g O_2 kg BW^{-1} d^{-1} which corresponds to HeE of 45 kJ kg BW^{-1} d^{-1}. These data suggest that at their optimal temperature HeE and HEm of shrimp and other crustaceans are similar to that of fish, something that is quite expectable.

The effect of temperature on fasting oxygen consumption has been studied by Victoria (1998) with *Penaeus californiensis* in the intermolt stage. Fasting oxygen consumption increased from 0.19 to 0.35 to 0.43 mg g^{-1} h^{-1} when temperature increased from 19 to 23 to 27°C, respectively. This suggests that the effect of temperature on HeE in shrimp is similar to that seen in fish (Cho and Kaushik, 1990).

There are several studies on fasting oxygen consumption of crustaceans scattered in the literature. Several approaches and nomenclatures have been used. The available experimental evidences should be reviewed and analyzed in a critical manner using approach that have been applied to higher vertebrates.

Cost of Accretion of Body Components or Nutrient Utilization Efficiency

Most theoretical and experimental evidences suggest that the energy losses associated with transformation of the substrates and their retention in tissues represent a very large proportion of the cost of growing in animals. Theoretical efficiency of transformation or retention of substrates in tissue have been calculated for higher vertebrates (Blaxter, 1989). Since the metabolism of fish and shrimp is very similar to that of higher vertebrates, it may be assumed that these theoretical costs are also valid for fish and shrimp, with some minor exceptions. Converting glucose into glycogen costs 5% of the energy of glucose as heat whereas converting glucose into lipids entails a heat loss equal to about 30% of its GE (Blaxter 1989). Conversion of dietary lipids into body lipids is, in theory, about 96%, therefore 4% of GE of lipids is dissipated as heat. Conversion of dietary amino acids into body proteins is, in theory, 86% efficient (Blaxter, 1989). Conversion of amino acids into body lipids is, in theory, only 66% efficient and 34% energy is lost as heat.

Fish

Determining the cost of nutrient deposition and interconversion in practice is not an easy task. Many studies have approached the problem in an empirical manner by trying to relate ME or DE intakes to recovered energy (RE). Studies involving the rearing of fish under the variety of conditions (water temperature, feeding level, fish size, etc.) have shown that efficiency of energy utilization (i.e. slope of RE as a function ME intake) was, surprisingly, fairly constant and, consequently, fairly easily predicted. (Cho and Kaushik, 1990; Azevedo *et al.*, 1998; Lupatsch *et al.*, 1998; Ohta and Watanabe, 1998; Rodehutscord and Pfeffer, 1999). A relatively large number of studies have showed a highly significant linear relationship between ME intake (or feed intake) and carcass energy gain (RE). Efficiency of energy utilization (Kpf, RE/ME intake) was found to be between 0.5 and 0.75 in most studies (e.g. Fig. 13). This suggests that, in practice, cost of nutrient deposition can easily be calculated as a constant proportion of energy deposited regardless of fish size and water temperature. This approach has been used in most feed requirement models (Cho, 1992; Cho and Bureau, 1998; Cui and Xie, 1999).

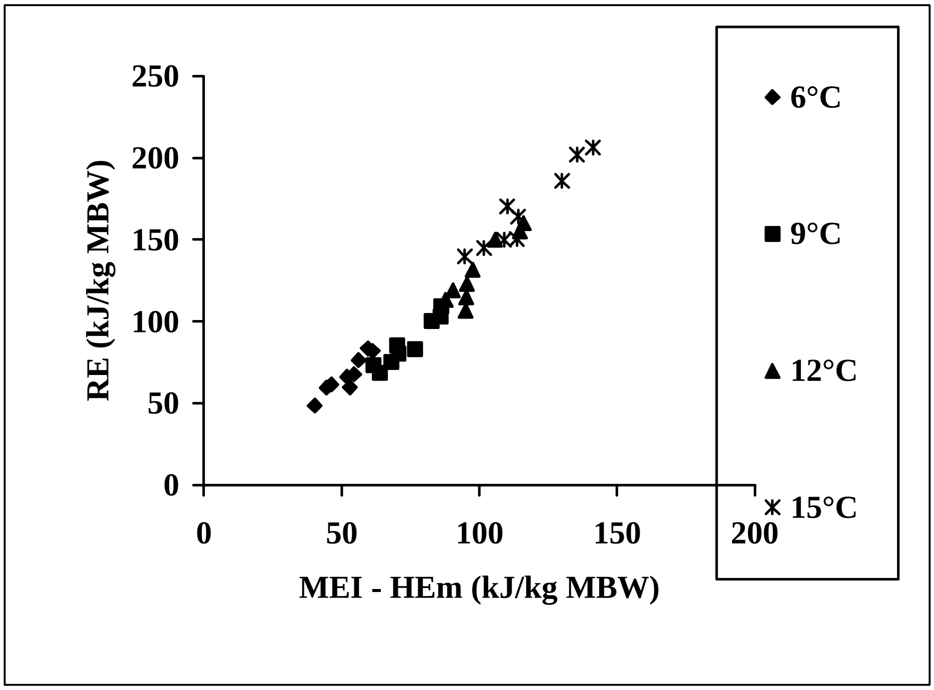

Figure 13. Energy gain (RE) as a function of metabolizable energy intake above maintenance (MEI-HEm). (Data from Azevedo *et al.*, 1998)

While very practical and useful, calculating cost of nutrient deposition as a sole function of RE may not be appropriate. Animal is depositing nutrients and the utilization and deposition of nutrients depends on the nature of these nutrients, not just the energy content of these nutrients. Studies have looked into more specific systems based on actual nutrient deposition. The most popular approach is a factorial one that has been first proposed by Kielanowski (1965). In this classical approach, the energy cost for lipid and protein deposition is simply defined as ME required to promote a defined increment in body protein or lipid. The partial efficiency of ME utilization for whole body growth (kpf), protein deposition (kp), and lipid deposition (kf) is the ratio of net energy retained to the corresponding ME intake components.

$$ME = HEm + REp/Kp + REf/Kf$$

Using this type of approach, Emmans (1994) concluded that the net energy cost for protein retention is 2.54 kJ per kJ of protein retained (that is 1.54 kJ of heat expended for each 1 kJ of protein deposited) equivalent to a Kp of 39.5%. According to Emmans (1994), when all related factors are accounted for in the analysis, the energy cost for protein deposition does not appear different between different species. The calculated energy cost for lipid retention was 1.4 kJ and 1.1 kJ per kJ lipid deposited (i.e. heat losses of 0.4 or 0.1 kJ per each 1 kJ lipid deposited) when deposited from non-lipid or lipid respectively. These are equivalent to a kf = 90% when deposited from lipid and kf = 70% when deposited from non-fat substrates.

A few studies have been conducted with fish on these lines. Partial efficiencies of ME utilization for protein deposition (Kp) of 0.56 and lipid deposition (Kf) of 0.72 were calculated for common carp (Schwartz and Kirchgessner, 1995). Results from Rodehutscord and Pfeffer (1999) suggest a Kp of

0.54 when a Kf of 0.9 is assumed. Lupatsch *et al.* (2000) observed Kp of 0.53, 0.47 and 0.44 for *Dichentrarchus labrax*, *Sparus aurata and Epinephelus aeneus*, respectively. Kf were 0.90, 0.66 and 0.60 in the same study for *Dichentrarchus labrax, Sparus aurata* and *Epinephelus aeneus*, respectively.

These studies suggest that cost of protein deposition is relatively similar amongst species and that cost of lipid deposition is relatively highly variable. These evidences are, nevertheless, highly empirical and these differences could well be related to several factors, including overt simplicity of the mathematical approach used. More studies are required to better understand costs of body components accretion. However, the available information is sufficiently accurate to determine cost of growth and feed requirement under most conditions.

Shrimp

Reliable information of cost of nutrient deposition in shrimp are very limited. One major problem is that leaching of nutrient from feed affect both estimates of the digestibility and nutrient utilization. A bottom up approach where efficiency of energy utilization is calculated from RE and heat production (or nutrient deposited and catabolized) appears very desirable for shrimp. Most studies that have used this approach have major methodological deficiencies and are of questionable relevance to shrimp culture conditions. In most studies, measurement of heat production (estimated from oxygen consumption) is based on fasting animal refed a single meal. A clear increases in oxygen consumption is observed following feeding (post-prandial peak) return to fasting oxygen consumption level (Tchung, 1995; Gauquelin, 1996; Victoria, 1998). This type of approach has been used for many studies with fish but observations by Cho *et al.* (1982) indicate that this type of approach does not produce results that are representative production conditions (i.e. when animals are fed intensively). The animals should be fed intensively as done under culture conditions and oxygen consumption (estimate of heat production, HE) measured, then fasting oxygen consumption (or more appropriately HEf) should be measured after 2 to 7 d fasting (to estimate HeE). Heat increment of feeding (HiE) is calculated as the difference between HE and HeE.

A recent well-conducted respirometric study suggests that Kpf of *Penaeus monodon* is somewhere around 0.5 for a 35% crude protein feed (Warukamkul *et al.*, 2000). These values appear to be similar to what is observed for fish. It may be worth to mention that apparent digestibility of the gross energy of the diet was estimated at only 44%. This value appears very low but, perhaps, not impossible given the high levels of poorly digested materials (grains, shrimp meal) are incorporated in most commercial shrimp feeds. These poorly digested materials dilute useful nutrients (Cho and Bureau, 1997). Low digestibility and low nutrient density of the feed used apparently explain, in large part, the high feed conversion ratio (FCR, feed:gain) observed for shrimp (1.8-2.5) under most farm and laboratory conditions compared to the FCR of fish of similar size (0.7-1.0), especially since evidences suggest that 1) chemical composition and 2) maintenance and cost of nutrient deposition are fairly similar for fish and shrimp.

Basic understanding of growth and nutrient utilization by shrimp and fish is definitely an area for which we know much less than what we should as we enter the 21st Century. Hundreds of studies have focused on diet composition (% nutrient in diet) but few have rationally look at quantitative aspect of nutrient utilization (g nutrient/unit of weight gain). Moreover, it is very difficult to go back to published studies and examine nutrient utilization *a posteriori* because the inadequate experimental approaches used in many studies. Inadequate feeding practices, such as feeding fish at a certain fixed feeding levels regardless of whether feed wastage is occurring or not, lack of definition of the digestible nutrient contents of the diets, and failure to determine the chemical composition of the experimental animals, are all too common practices in shrimp nutrition studies. The same comments also applied to fish nutrition studies. There is a need for more detailed and rigorous studies on nutrient and energy utilization in shrimp. Critical analysis of results using rational, yet practical, approaches (e.g. Emmans, 1994; De Lange, 1997; Azevedo *et al.*, 1998; Cho and Bureau, 1998; Lupatsch and Kissil, 1998; Lupatsch *et al.*, 1998; Rodehutscord and Pfeffer, 1999) could also prove very valuable.

Applications

The knowledge gained and/or models derived from research should ideally be translated into recommendations and applications for the industry. There is much to be gained for both sides from this type of transfer of technology, since it can provide the industry with useful tools and R&D specialist with constructive feedback on their research.

Feed Requirements Models

Many producers rely on feeding charts provided by feed manufacturers or found in various publications. One must be extremely cautious in applying these charts. The wide ranges of fish (or shrimp) species, genetic stocks, feed composition, water temperature, rearing conditions, and growth rates encountered on aquaculture operations make it impossible for anybody to develop feed chart that would be correct for all individual farm situations (Cho, 1992). Indiscriminate use of feed chart or careless feeding practices (e.g. poorly adjusted and monitored demand feeders) may result in significant feed wastage, waste outputs and economic losses, affecting both economical and environmental sustainability of the operation. Under most farm situations, hand feeding or the use of labour intensive feeding device (e.g. camera, feeding trays) is not possible or economically viable. The scientific estimation of feed requirement (allowance) of the animal may be the best possible approaches to objectively monitor feed use and minimize feed wastage. Used properly, scientific growth and feed requirement models could become a valuable management tool for commercial fish culture operations, notably by providing yardsticks to compare current performance (example: feed conversion ratio, FCR) with what is estimated to be biologically achievable. This information can then be used to improve husbandry practices (Cho and Bureau, 1998). The development of site or situation-specific feed requirement models may require some efforts by potential users, namely aquaculture producers and feed manufacturers, but this represents time and money well-spent.

Feed requirement is generally governed by how much nutrients (e.g. protein, lipid) or energy the animal deposits in its body and the biological cost of depositing these nutrients or energy (e.g. HEm and Kpf). Scientific feed requirement models can, therefore, be constructed based on this simple principle. Cho and Bureau (2000) suggested that this rational approach be divided into five steps

1) DIET Selection

The amount of feed required by a fish depends firstly on the composition of the feed used. In general, a greater amount will be required of a lower nutrient density feed than a higher nutrient density feed to achieve the same performance level (Table 3), if two feeds have similar protein and energy balance. Composition of the feed can also affect the composition of the fish produced and this, in turn, affects the amount of feed required.

Table 3. Performance of Atlantic salmon fed diets of different nutrient densities (but same protein to energy ratio) for 16 weeks and reared at 15°C.

Diet	**Grower**	**HND**
Digestible protein (DP), %	**37**	**44**
Digestible energy (DE), MJ/kg	**18**	**22**
DP/DE, g/MJ	**20**	**20**
Initial weight, g/fish	7.0	7.0
Final weight, g/fish	40.4	40.6
Feed served, g dry weight/fish	29.7	24.3
Feed Conversion Ratio (Feed/Gain)	0.82	0.67

Source: Azevedo (1998).

2) *GROWTH Prediction*

The accurate prediction of the growth of the animal over the period for which the feed requirement is calculated is probably the most critical factor for the accurate prediction of feed requirements. Growth involves the deposition of nutrients (accretion of body components) which is “real” factor determining feed requirement. Fish growing at different rates will deposit nutrients at different rates and, consequently, have different feed requirements. While this should be quite obvious, a careful examination of the current scientific and technical literature suggests that this concept is poorly understood by many in the fields of aquaculture and fish biology.

Production records are very valuable starting points when trying to predict the growth of the fish or shrimp for which one wants to calculate ration allowance. Once the growth pattern is known, then nutrient deposition can quite easily be predicted using simple models (as shown by Figure 10 and 11, for example). Development of such models can be done relatively easily by fish and shrimp producers. It simply involves sampling animals at different sizes and determining their chemical composition. A number of private laboratories can perform, at very reasonable cost, the basic chemical analyses required (moisture, protein, fat, energy) on fish or shrimp samples.

3*) WASTE Estimation*

The maintenance of life processes (integrity of the tissues of the animal, osmoregulation, respiration, circulation, swimming, etc.) and the deposition of body components have costs in terms of nutrient and feed energy. Sufficient data on growth process and nutritional energetics are now available to allow cost of nutrient deposition and efficiency of nutrient and energy utilization to be computed for salmonid fish species as well as a number of marine fish species (Cho and Bureau, 1998; Kaushik, 1998; Lupatsch and Kissil, 1998; Lupatsch *et al*, 1998).

4) *RATION Allowance*

Calculation of the ration can be done by simply to adding all the different components calculated above (body components deposited + waste produced) per unit of time (day, week) to calculate total cost. This cost is generally expressed as digestible energy (DE). Provided a feed is well-balanced nutritionally, knowledge of the DE content of that feed allows calculation of the amount of feed to be served or the feeding level to be used. This calculated amount of feed generally represents the minimum amount of feed required to achieve the predicted growth of the fish.

5) *FEEDING Strategies*

Any model, as good as it is, cannot replace common sense when feeding fish and it is up to the producer to determine how much feed to serve and how to serve it depending on the prevailing conditions. Feed should be served in manner that allows adequate opportunity (time or space-wise) for the fish to consume the determined ration and achieve their growth potential while minimizing feed wastage.

Applying these principles to fish

Using this conceptual framework, Cho (1992) and Cho and Bureau (1998) developed a series of bioenergetic models to predict growth and energy requirements and determine feed requirement and expected feed efficiency. These models have been used with much success for numerous studies at the University of Guelph Fish Nutrition Laboratory and Alma Aquaculture Research Station (Table 4).

Table 4. Observed performance of rainbow trout and Atlantic salmon lots fed rations calculated using the «Fish-PrFEQ» approach of Cho and Bureau (1998).

Species	**Feed composition**	**Duration of trial**	**Water temp.**	**Initial weight**	**Final weight**	**TGC**	**FCR**
	DP/DE[1]	**days**	**°C**	**g/fish**	**g/fish**		**Feed/gain**
Salmon	41/20	168	15	5	88	0.109	0.83
Trout	40/18	84	15	7	61	0.161	0.85
Trout	44/21	140	8.5	17	92	0.163	0.74
Trout	41/20	84	15	17	215	0.271	0.84
Trout	42/19	112	15	35	278	0.194	0.84

[1] DP = digestible protein (%), DE= digestible energy (MJ/kg)

The approach of Cho and Bureau (1998), with slight modifications to some of the models (based on recent results), is presented below using a practical example.

1) Diet selection

Define composition of feed:

Practical diet
44% digestible protein, 20 MJ digestible energy, DP/DE: 22 g/MJ

2) Growth prediction

Predict growth of fish :

Fish species:	Rainbow trout
Thermal-unit growth coefficient	0.220
Initial weight:	20.0 g
Water temperature:	12 °C
Time period:	7 days
Number of fish in tank:	10,000

Predicted final weight = $[((20)^{1/3} +((0.220/100)\ (12)\ (\ 7))]^3 =$ 24.4 g at d7

Predict energy gain (RE):

Based on equation derived from in Figure 10
Gross energy content of fish:

$GE_{d0} = 8.6\ (20.0)\ -\ 40 = 132$ kJ/fish
$GE_{d7} = 8.6\ (24.4)\ -\ 40 = 170$ kJ/fish

RE= 170-132 = 38 kJ/fish

3) Waste estimation

Predict maintenance need:

HeE = (- 1.04 + 3.26(10) - 0.05(12)^{2}) (0.020$^{0.824}$)$^{-1}$ d^{-1} = 1.2 kJ fish^{-1} d^{-1}
HeE = (1.2 kJ fish^{-1} d^{-1}) (7 d) = 8.4 kJ/fish

Predict heat increment of feeding (HiE):

From Azevedo (1998), Kpf above maintenance can be estimated at 0.6, therefore
For every 0.6 kJ of RE or HeE, 0.4 kJ is expended as HiE,
then HiE can be estimated as 0.4/0.6 = 0.67

HiE = 0.67 (HeE+RE) = 0.67 (8.4+38) = 31 kJ/fish

Predict non-fecal energy losses (UE+ZE):

UE+ZE = 0.08 (RE+HeE+HiE) = 0.08 (38+8.4+31) = 6 kJ/fish

4) Ration allowance

Calculate digestible energy requirement:

DE requirement (RE+HeE+HiE+UE+ZE)= (38+10+31+6)= 85 kJ/fish over 7 days

DE content of feed: 20 MJ/kg or kJ/g
Rational allowance = (85 kJ/fish) / (20 kJ/g)
= 4.25 g feed per fish over 7 days
= 0.61 g fish^{-1} d^{-1}

= 0.61 g fish^{-1} d^{-1} (10,000 fish)

= 6.1 kg feed tank^{-1} d^{-1}

Expected feed efficiency = live weight gain / feed = 4.4/4.25 = 1.04
Expected FCR = feed / live weight gain = 4.25/4.4 = 0.97

Applying these principles to shrimp

These principles will also be applied to shrimp even if constraints, such mortality, molting, etc., are more numerous and less reliable information is available on nutrient deposition and utilization of shrimp than on fish. A preliminary estimate of feed requirement of shrimp using the approach described above is presented below.

1) Diet selection

Define composition of feed:

40%CP, 8% lipid and 30% carbohydrate, 17 MJ/kg digestible energy.

2) Growth prediction

Predict weight gain of :

Species:	*Penaeus vannamei*
Daily weight gain:	2 g shrimp^{-1} week^{-1}
Initial weight:	10 g
Water temperature:	26 °C
Time period:	7 days
Number of shrimp in pond:	10,000

Predict energy gain (RE):

Based on Table 2:

Based on equation found in Figure 10:

Gross energy content of shrimp = 5.2 kJ/g
Weight gain = 2 g/shrimp

RE= (5.2) (2) = 10.4 kJ shrimp^{-1} week^{-1}

3) Waste estimation

Predict maintenance need:

from Gauquelin (1996)
HeE = 45 (0.010)$^{-1}$ d^{-1} = 0.45 kJ shrimp^{-1} d^{-1}
HeE = (0.45 kJ fish^{-1} d^{-1}) (7 d) = 3.2 kJ/fish

Predict heat increment of feeding (HiE):

Interpretation of data from Warukamkul *et al.* (1998) suggest Kpf can be estimated at about 0.5, therefore, for every 0.5 kJ of RE or HeE, 0.5 kJ is expended as HiE.
HiE can, therefore, be estimated at: 0.5/0.5= 1.0

HiE = 1.0 (HeE+RE) = 1.0 (10.4+3.2) = 13.6 kJ shrimp^{-1} week^{-1}

Predict molting energy losses (HxE)

25% of RE accumulated in intermolt is expended due to GE lost of metabolic cost of molting (Read and Caulton, 1980).

HxE = 0.25 (RE) = 0.25 (10.4) = 2.6 kJ shrimp^{-1} week^{-1}

Predict non-fecal energy losses (UE+ZE):

UE+ZE = 0.08 (RE+HeE+HiE+HxE)
= 0.08 (10.4+3.2+13.6+2.6) = 2.4 kJ shrimp^{-1} week^{-1}

Predict surface loss, exuviae (SE)

Data from Cousin *et al.* (1996) suggest
SE = 3% (RE+HeE+HiE+HxE)
= 0.9

4) Ration allowance

Calculate digestible energy requirement:

DE requirement = (RE+Hem+HiE+HxE+(UE+ZE)+SE)
= (10.4+3.2+13.6+2.6+2.4+0.9) = 33.1 kJ shrimp^{-1} week^{-1}
DE content of feed: 17 MJ/kg or kJ/g

Rational allowance = (33.1 kJ shrimp^{-1} week^{-1}) / (17 kJ/g)
= 1.95 g feed per shrimp over 7 days
= 0.28 g shrimp^{-1} d^{-1}
= 0.28 g shrimp^{-1} d^{-1} (10,000 shrimp)
= 2.8 kg feed pond^{-1} d^{-1}

Expected feed efficiency = live weight gain / feed = 2.00/1.95 = 1.03
Expected FCR = feed / live weight gain = 1.95/2.00 = 0.98

If a lower quality feed is used:

For example if DE content of feed is only 14 MJ/kg instead of 17 MJ/kg, then:

DE requirement = (RE+Hem+HiE+HxE+(UE+ZE)+SE)
= (10.4+3.2+13.6+2.6+2.4+0.9) = 33.1 kJ shrimp^{-1} week^{-1}

Rational allowance = (32.2 kJ shrimp^{-1} week^{-1}) / (14 kJ/g)
= 2.36 g feed per shrimp over 7 days
= 0.34 g shrimp^{-1} d^{-1}
Expected feed efficiency = live weight gain / feed = 2.0/2.36 = 0.85
Expected FCR = feed / live weight gain = 2.36/2.0 = 1.18

It is important to note that the above example is only theoretical or conceptual. However, this type of approach can be extremely useful and help improve of our knowledge of feed utilization by shrimp. Comparison with feed conversion ratio obtained in reality can help identify area where our knowledge needs to be improved (e.g. definition of cost of nutrient deposition). It can also help provide clues as to the potential impact of numerous constraints associated with feeding management of shrimp.

This theoretical model suggest, for example, that the high feed conversion ratio (1.5 to 2.5) observed for penaeid under most laboratory and farm conditions appear to be due to:

1) Low nutrient density or sub optimal composition of the feed used ((low digestible protein, low digestible energy, high starch and fiber feeds)
2) Extensive feed wastage due to poor control of feed delivery (even if feeding trays are used)
3) Extensive leaching of nutrients due to slow feeding response, mode of feed ingestion and physical characteristics of the feed.

The results from type of models always need to be interpreted and used carefully. They may not applicable yet at field level since numerous parameters still not under control, such as survival, the impact of natural productivity, and variation in appetite of the animal. The impact of parameters can still be accounted for. Survival can often be calculated using simple rules of thumb, at least under intensive system (Aquacop, unpublished observations). Impact of natural productivity appears to contribute to the feed budget only during the first month of the growing cycle in an earthen pond. At field level, appetite of shrimp can be monitored using feeding trays. Models are no magic bullet but can be useful tools if they are properly applied and integrated as part of the production management.

Better understanding of deposition and utilization of nutrient and energy may allow nutritionists, feed manufacturers and aquaculturists to look at feeding practices and feed cost under a new light. For example, when presented with accurate nutrient and energy utilization data, one may reconsider the use of low nutrient and energy density feeds (low cost feeds but not necessarily cost-effective feed) for the rearing of “omnivorous” fish (channel catfish, tilapia, carp) and shrimp. Current knowledge on energy requirement and nutrient utilization clearly indicates the use of low nutrient and energy density feeds is the main reason for the very poor feed conversion ratio (1.5 and 3) observed under most conditions. Anecdotal evidences suggest that omnivorous fish, such as tilapia, consistently achieve low FCR (around 1) when fed with higher nutrient density feed (e.g. 36-44% CP, 15-20 MJ/kg DE) than lower nutrient density feeds. Production cost using low nutrient density (low digestibility) feeds (e.g. 28-32% CP, 14 MJ/kg DE) may not be so advantageous as often touted when one accounts for amount of feed needed per kg weight gain, the cost of feed manufacturing (e.g. pelleting and extrusion) and transport, and the potential negative impact of the high organic waste output on the productive capacity of rearing environment.

It is imperative to move from a narrow vision of nutrient requirement or utilization as “% of the diet” to a more integral vision which takes into account diet composition (e.g. digestible protein to digestible energy ratio, digestible nutrient and energy levels), nutrient or energy gain, and nutrient and energy requirement per unit of live weight,. The challenges are numerous, the task very significant, but tangible progress can rapidly be made if investigators and aquaculturists adopt rational approaches.

REFERENCES

Aquacop., Garen, P., 1992. Elevage intensif de crevettes peneides-Le point technique au C.O.P. Rapport interne IFREMER COP, 12pp

Azevedo, P.A. , 1998. Effects of Feeding Level, Water Temperature and Diet Composition on Growth and Efficiency of Feed Utilization in Two Salmonids. M.Sc. thesis, University of Guelph, Guelph, Ontario, Canada, 116 pp.

Azevedo, P.A., Cho, C.Y., Leeson, S., Bureau, D.P., 1998. Effects of feeding level and water temperature on growth, nutrient and energy utilization and waste outputs of rainbow trout (*Oncorhynchus mykiss*). Aquatic Living Resources 11, 227-238.

Blaxter, K., 1989. Energy metabolism in animals and man. Cambridge University Press, Cambridge, UK.

Boekholt, H.A., Schreurs, V.V.A.M., Verstegen, M.W.A., 1994. Composition of daily growth in young growing animals receiving increasing amounts of energy. In: Aguilera, J.F. (Ed.), Proceedings of the 13th Symposium on Energy Metabolism of Farm Animals, September 18-24, 1994, Mojacar, Spain., pp. 229 - 232.

Boekholt, H.A., Schreurs, V.V.A.M., ten Doeschate, R.A.H.M., 1997. Partitioning of energy in protein and fat retention at increasing energy intakes in growing animals. In: McCracken, K.J., Unsworth, E.F., Wylie, A.R.G. (Eds.). Energy Metabolism of Farm Animals, CAB International Press, Wallingford, UK., pp. 327-330.

Brett, J.R., 1979. Environmental factors and growth. In Hoar, W.S., Randall, D.J. and Brett, J.R.. (Eds.) Fish Physiology, Vol. VIII, Bioenergetics and Growth. Academic Press, New York, pp. 599-667 .

Cho, C.Y., 1992. Feeding systems for rainbow trout and other salmonids with reference to current estimates of energy and protein requirements. Aquaculture 100, 107-123.

Cho, C.Y., Bureau, D.P., 1995. Determination of the energy requirements of fish with particular reference to salmonids. Journal of Applied Ichthyology 11, 141-163.

Cho C.Y., Bureau D.P. ,1997. Reduction of waste output from salmonid aquaculture through feeds and feeding. Progressive Fish Culturist 59, 155-160.

Cho, C.Y., Bureau, D.P., 1998. Development of bioenergetic models and the *Fish-PrFEQ* software to estimate production, feeding ration and waste output in aquaculture. Aquatic Living Resources 11, 199-210.

Cho, C.Y. , Bureau, D.P., 2000. Nutrition, energetics and growth of fish: Current challenges and approches. Proceeding of the NATO Symposium on Mariculture, 12-17 September 1998, Porto, Portugal (in press).

Cho, C.Y., Kaushik, S.J., 1990. Nutritional energetics in fish: energy and protein utilization in rainbow trout (*Salmo gairdneri*). World Rev. Nutr. Diet. 61, 132-172.

Cho C.Y., Slinger, S.J., Bayley, H.S., 1982. Bioenergetics of salmonid fishes: Energy intake, expenditure and productivity, Comp. Biochem. Physiol. 73B, 25-41.

Civera, R., Villarreal, H., Goytortua, E., Rocha, S., Vega, F., Nolasco, H., Pasten, J, Camarillo, T., 1996. Uso de la langostilla (Pleuroncodes planipes) como fuente de proteina en dietas experimentales para camaron. Tercer Simposium Internacional de Nutricion Acuicola, 11-13 Noviembre 1996, UNAL, Monterrey, Mexico.

Clarke, A., Johnson, N.M., 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. J. Animal Ecology 68, 893-905.

Cousin, M., 1995. Contribution à l'étude de l'utilisation des glucides et du rapport proteine/énergie *chez P.vannamei et P.stylirostris*. Thèse INA/PG. Paris, pp. 201

Cousin, M., Cuzon, G., Guillaume, J., Aquacop, 1996. Digestibility of starches in *P.vannamei*. *In vitro* and *in vivo* study on 8 samples of various origin. Aquaculture 150, 361-372.

Cui, Y., Xie, S., 1999. Modelling growth of fish.. In: Theodorou, M.K., France, J. (Eds.), Feeding Systems and Feed Evaluation Models. CABI Publishing, CAB International, Wallingford, UK, pp. 413-434.

De Lange, C.F.M., 1997. Modelling energy intake and utilization in grower-finisher pigs. Canadian Feed Industry Association Eastern Nutrition Conference 1997, May 6-7, 1997, University of Guelph, Ontario, pp.96-108.

Emmans G.C., 1994. Effective energy: a concept of energy utilization applied across species, Br. J. Nutr. 71, 801-821.

Gauquelin, F., 1996. Effets du taux de protéines alimentaires sur la croissance, la consommation d'oxygène et l'excrétion ammoniacale de la crevette *Penaeus stylirostris*. Mémoire de Stage, Maîtrise de Sciences et Techniques, Université de Corse, France, 37 pp.

Guillaume, J., Kaushik, S.J., Bergot, P., Métailler, R., 1999. Nutrition et alimentation des poissons et des crustacés. Collections Du Labo au Terrain. Éditions INRA, Paris, France, 489 pp.

Hartnoll, R.G., 1983. Strategies of crustacean growth. In: Lowry, J.K. (Ed.). Papers from theConference on Biology and Evolution of Crustacea. The Australian Museum Memoir 18, Australian Museum, Sydney, Australia.

Huipeng, L., 1987. Evaluation of a practical tilapia diet for small-scale farmers. M.Sc. Thesis, Asian Institute of Technology, Bangkok, Thailand. 51 pp.

Iwama, G. K., Tautz, A.F., 1981. A simple growth model for salmonids in hatcheries. Can. J. Fish. Aquat. Sci. 38, 649-656.

Jackson, C.J., Wang, Y.-G., 1998. Modelling growth rate of *Penaeus monodon* Fabricius in intensively managed ponds: effects of temperature, pond age and stocking density. Aquaculture Research 29, 27-36.

Kaushik, S.J., 1998. Nutritional bioenergetics and estimation of waste production in non-salmonids. Aquatic Living Resources 11, 211-217.

Kaushik, S.J., Médale, F., 1994. Energy requirements, utilization and dietary supply to salmonids. Aquaculture 124, 81-97.

Kielanowski, J., 1965. Estimates of the energy cost of protein deposition in growing animals. In: Blaxter, K.L. (Ed.). Proceedings of the 3rd Symposium on Energy metabolism, May 1964, Troon, Scotland, Academic Press, London, UK, pp 13 - 20.

Lupatsch, I., Kissil, G. Wm., 1998. Predicting aquaculture waste from gilthead seabream (*Sparus aurata*) culture using a nutritional approach. Aquatic Living Resources 11, 265-268.

Lupatsch, I., 2000. Comparison of efficiency of energy deposition among some fish species: a factorial approach. Second Workshop on Energy Metabolism of Fish. Efficiency of Energy Utilization: Methodological Considerations and Effects of Dietary, Biological and Environmental Factors, 22 May 2000, Miyazaki, Japan (abstract).

Lupatsch, I., Kissil, G. Wm., Sklan, D., Pfeffer, E., 1998. Energy and protein requirement for maintenance and growth in gilthead seabream (*Sparus aurata* L.). Aquaculture Nutrition 4, 165-173.

Maguire, G.B., Allan, G.L., 1992. Effets of temperature on gorwth, food consumption and food conversion of *Penaeus monodon*, *Penaeus plebejus* and *Metapenaeus macleayi*. IN: Allan, G.L., Dall, W. (Eds.). Proceeding of the Aquaculture Nutrition Workshop, 15-17 April 1991, Salamander Bay, NSW, Australia. pp. 97-99.

Muller-Feuga, A.,1990. Modélisation de la croissance des poissons en élevage. Rapports scientifiques et techniques de Ifremer,n°21, 58pp

National Research Council (NRC), 1981. Nutritional Energetics of Domestic Animals & Glossary of Energy Terms. National Academy Press, Washington, D.C. 54 p.

National Research Council (NRC), 1993. Nutrient Requirements of Fish, National Academy Press, Washington, 114pp.

Ohta, M., Watanabe, W., 1998. Effect of feed preparation methods on dietary energy budgets in carp and rainbow trout. Fisheries Science 64, 99-114.

Oldham, J.D., Emmans, G., Kyriazakis, I., 1997. Limits and limitations to nitrogen use in farm animals. Proceedings of the Nutrition Society 56, 535-545.

Read, G.H.L., Caulton, M.S., 1980. Changes in mass and chemical composition during the moult cycle and ovarian development in immature and mature *Penaeus indicus* Milne Edwards. Comp. Biochem. Physiol. 66A, 431-437.

Rodehutscord, M., Pfeffer, E., 1999. Maintenance requirement for digestible energy and efficiency of utilisation of digestible energy for retention in rainbow trout, *Oncorhynchus mykiss*. Aquaculture 179, 95-107.

Rosenberry, R., 1998. World Shrimp Farming 1998. Number 11. Shrimp News International, San Diego, CA.

Shearer K.D., 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. Aquaculture 11, 63-88.

Schwartz. F.J. , Kirchgessner, M., 1995. Effects of different diets and levels of feeding on retention and efficiency of utilization of energy and protein by carp. J. Appl. Ichthyol., 11, 363-366.

Tchung, B., 1995. Effet de la nourriture sur le métabolisme de la crevette *Penaeus stylirostris*. Mémoire de Diplôme d'Études Approfondies, Université Française du Pacifique,. Polynésie Française., 52pp.

Victoria, L.O., 1998. Energia metabolizable y eficiencia neta de crecimiento baja el efecto de variaciones medioambientales en el camaron. IV Simposium Internacional de Nutricion acuicola, Noviembre 15-18, 1998, La Paz, B.C.S., Mexico.

Villarreal, H., 1990. Effect of temperature on oxygen consumption and heart rate of the Australian crayfish *Cherax tenuimanus* (Smith). Comp. Biochem. Physiol., 95A, 189-193.

Warukamkul, P., Viyakarn, V. Nitithamyong, C., Piyatiratitivorakul, S., 2000. Effects of salinity and protein levels on energy budget of juvenile black tiger prawn, P*enaeus monodon*. IX International Symposium on Nutrition and Feeding of Fish, May 21-25, 2000, Miyazaki, Japan (abstract O56).

Weatherley, A.H., Gill, H.S., 1987. The Biology of Fish Growth. Academic Press, London, U.K. 443p.