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Review

Development of bioenergetic models and the Fish-PrFEQ software to estimate production, feeding ration and waste output in aquaculture

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Abstract – Feeding guides for salmonid fishes have been available from various sources for many years. These feeding guides have originated in one way or another from earlier feeding charts of the 1950–60s when meal-meat mixture diets were widely used. Few of the feeding guides available today are based on actual bioenergetics data at different water temperatures and are adapted to high energy diets. New feeding standards have been developed based on principles of nutritional energetics in which the digestible energy content of diet, digestible protein and energy ratio and the amount of digestible energy required per unit of live weight gain are taken into account. The gain expressed as retained energy in carcass and maintenance energy at different water temperatures is the main criteria for energy and feed allocations. Series of bioenergetic models were developed based on these principles and a stand-alone multimedia program was written to facilitate computation of the models. This program predicts growth and energy, nitrogen and phosphorus retention, requirements and excretions to determine feeding standards, waste outputs and effluent water quality based on a biological method. The models require initial and final body weights, water temperature, growth coefficient, carcass energy content and waste coefficients to estimate input and output. Accurate determinations of the thermal-unit growth coefficient, apparent digestibility coefficients and retention efficiencies are essential and these coefficients are determined by biological experiments in the laboratory and field. Oxygen requirement is included to aid environmental control in fish culture system. The Fish-PrFEQ program also contains modules for production records, performance calculations and data base management for input and output data which may be exported for further data and graphic manipulations. © Ifremer/Elsevier, Paris

Bioenergetics / growth model / feeding / solid waste / phosphorus / nitrogen / oxygen / salmonid aquaculture

Résumé – Développement de modèles bioénergétiques et du logiciel Fish-PrFEQ afin d'estimer la production, les rations alimentaires et les déchets en aquaculture. Des guides d'alimentation des salmonidés sont disponibles depuis de nombreuses années. Ils ont été établis à partir de diagrammes d'alimentation dans les années 1950–1960, lorsque des régimes à base de mélanges de viande étaient largement utilisés. Peu de guides sont basés sur les données actuelles bioénergétiques à différentes températures et adaptés à des aliments hautement énergétiques. De nouvelles normes d'alimentation ont été développées, basées sur des principes de besoins énergétiques nutritionnels dans lesquels le contenu en énergie assimilable de l'aliment, les protéines assimilables, le taux énergétique assimilable et le niveau d'énergie sont évalués par unité de poids vif. Le gain exprimé en énergie retenue dans la carcasse et en énergie de maintenance à différentes températures est le principal critère pour l'énergie et les distributions de nourriture. Des séries de modèles bioénergétiques ont été développées, basées sur ces principes et un programme multimédia didacticiel a été écrit pour faciliter l'utilisation de ces modèles. Ce programme prévoit la croissance et l'énergie, la rétention d'azote et de phosphore, les besoins et l'excrétion pour déterminer des normes d'alimentation, les déchets et la qualité des eaux de rejets basée sur une méthode biologique. Les modèles nécessitent les poids initiaux et finals, la température de l'eau, le coefficient de croissance, le contenu énergétique de la carcasse et les coefficients de déchets pour estimer les entrées et sorties. Des déterminations précises du coefficient d'unité thermale de croissance, des coefficients de digestibilité apparente et d'efficacité de rétention sont essentielles et ces coefficients sont déterminés par des expériences biologiques en laboratoire et sur le terrain. La demande en oxygène est incluse afin de contribuer au contrôle environnemental dans la pisciculture. Le programme Fish-PrFEQ contient aussi des modules de données de production, des calculs de performances de croissance et de bases de données pour des données d'entrées et de sorties, qui peuvent être exportées vers d'autres traitements graphiques et analyses. © Ifremer/Elsevier, Paris

Bioénergie / modèles de croissance / alimentation / déchets solides / phosphore / azote / oxygène / aquaculture de salmonidés

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1. INTRODUCTION

Feeding systems may be defined as all feeding standards and practices employed to deliver nutritionally balanced and adequate amount of diets to animals for maintaining normal health and reproduction together with efficient growth and/or work performance. Until now, the feeding of fish has been mostly based on folkloric practices while the main preoccupation has been to develop 'magic' diet formulae. Many 'hypes' such as mega-fish meal and mega-vitamin C diets have come and gone, and we are now in the age of the 'Norwegian Fish Doughnut' (> 36 % fat diet)! Whichever diet one decides to feed, the amount fed to achieve optimum or maximum gain is the ultimate measure of one's productivity in terms of biological gain, economical benefit and/or environmental sustainability.

Scientific approaches have been used in the feeding of land animals for over a century. The first feeding standard for farm animals was proposed by Grouven in 1859, and included the total quantities of protein, carbohydrate and ether extract (fat) found in feeds, as determined by chemical analysis. In 1864, E. Wolf published the first feeding standard based on the digestible nutrients in feeds [26].

Empirical feeding charts for salmonids at different water temperatures were published by Deuel and his colleagues [18] and were likely intended for use with meat-meal mixture diets widely in use at that time. Since then several methods of estimating daily feed allowance have been reported [5, 21, 22, 32]. Unfortunately all methods have been based on the body length increase or live weight gain, and dry weight of feed and feed conversion, rather than on biologically available energy and nutrient contents in feed in relation with protein and energy retention in the body. These methods are no longer suitable for today's energy- and nutrient-dense diets, especially in the light of the large amount of information available on the energy metabolism of salmonids.

Many problems are encountered when feeding fish, much more so than when feeding domestic animals. First, delivery of feed to fish in a water medium requires particular physical properties of feed together with special feeding techniques. It is not possible in the literal sense to feed fish on an 'ad libitum' basis, like it is done with most farm animals. The nearest alternative is to feed to 'near-satiety' with very careful observation over a predetermined number of feedings per day; however, this can be very difficult and subjective. Feeding fish continues to be an 'art' and the fish culturist, not the fish, determines 'satiety' as well as when and how often fish are fed. The amount of feed not consumed by the fish can not be recovered and, therefore, feed given to them must be assumed eaten for inventory and feed efficiency calculations. This can cause appreciable errors in feed evaluation as well as in productivity and waste output calculations. Meal-feeding the fish pre-allocated amounts by hand or mechanical device may be the only logical choice. Uneaten feed represents an economical loss and becomes 100 % solid and suspended wastes! However, meal-feeding a pre-allocated amount of feed calculated based on the theoretical energy requirement of the animal may not represent a restricted feeding regime as suggested by some [19] since the amount of feed calculated is based on the amount of energy required by the animal to express its full growth potential.

There are few scientific studies, based on nutrition and husbandry, on feeding standards and practices; however, there are many duplications and 'desktop' modifications of old feeding charts with little or no experimental basis. Since the mid-1980s, development of high fat diets has led to most rations being very energy-dense, but feeding charts have changed little to reflect these differences in diet composition. This, not withstanding the fact that fish, like other animals, eat primarily to meet energy requirements. Most feeding charts available today tend to overestimate feed requirements and this overfeeding has led to poor feed efficiencies under most husbandry conditions, and this represent a significant, yet avoidable, waste of resources for aquaculture operations. In addition, it may result in self-pollution which in turn may affect the sustainability of aquaculture operations. Recent governmental regulations imposing feed quota, feed efficiency guidelines and/or stringent waste output limits may somewhat ease the problem. Sophisticated and expensive systems, such as underwater video camera or feed trapping devices, have been developed to determine fish satiation or the extent of feed wastage and are promoted by many as a solution to overfeeding [1]. However, regardless of the feeding system or method used, accurate growth and feed requirement models are needed in order to forecast growth and objectively determine biologically achievable feed efficiency (based on feed composition, fish growth, and composition of the growth). These estimates can be used as yardsticks to adjust feeding practices or equipment and to compare the results obtained.

The development of scientific feeding systems is one of the most important and urgent subjects of fish nutrition and husbandry because, without this development, nutrient dense and expensive feeds are partially wasted. Sufficient data on nutritional energetics are now available to allow reasonably accurate feeding standards to be computed for different aquaculture conditions. Presented here is a summarized review of the basis of a nutritional energetic approach for estimating feed requirement and waste output of fish culture operation as well as the development of the Fish-PrFEQ computer program. Results obtained from a field station are presented and provide a framework to examine the type of information that can be derived from bioenergetic models and generate a feed requirement scenario for the next production year (Note: all the terminology and abbreviations used are listed in *table VI*).

2. PRODUCTION RECORDS

Evaluating and/or predicting growth performance of a fish culture operation or a stock of fish first requires production records of past performance. These records may become databases for calculating growth coefficients, temperature profiles during growth period and feed intake and efficiency for various seasons etc. One such production record for a lot of rainbow trout from a field station is shown in *table I*. A lot of 100 000 fish was reared over a 14-month (410 days) production cycle between May 1995 and June 1996. Cumulated live weight gain (fish production) was 72 tonnes with a feed consumption of 60 tonnes which gave an overall feed efficiency (gain/feed) of 1.19 (ranged between 1.11–1.22). Water temperature ranged from 0.5 °C in winter to 21 °C in summer which is typical of most lakes in Ontario. In spite of the wide fluctuation in water temperature, the thermal-unit growth coefficient (TGC) was fairly stable ranging between 0.177–0.204. Total mortality was around 9 % over 410 days.

From the production record (*table I*), one can extrapolate an overall growth coefficient of 0.191 and this coefficient can be used for the growth prediction of the next production cycle with the assumption that similar husbandry conditions and fish stock are used. Total feed requirement and weekly or monthly feeding standards can be computed on the basis of this growth prediction plus the quality of feed purchased (see *table V*).

3. PROCEDURES FOR THE ESTIMATION OF FEED REQUIREMENT AND WASTE OUTPUT

Using production records as a starting point, feed requirements and waste output can scientifically be estimated based on the following three concepts:

- prediction of growth and nutrient and energy gains;
- estimation of excretory and feed waste outputs;
- quantitation of energy and nutrient needs.

3.1. Prediction of growth and nutrient and energy gains

Accurate prediction of growth potential of a fish stock under given husbandry condition is an inevitable prerequisite to the estimation of energy or feed requirement (e.g. weekly ration). The formula most commonly used for fish growth rate expression is instantaneous growth rate known as 'specific growth rate (SGR)' which is based on the natural logarithm of body weight:

$$\mathrm{SGR} = (\ln \mathrm{FBW} - \ln \mathrm{IBW}) / \mathrm{D} \qquad (1)$$

where FBW is final body weight (g), IBW initial body weight (g), and D number of days.

Brett [3] employed this expression and the SGR has been widely used by most biologists to describe growth rate of fish. However, the exponent of natural logarithm underestimates the weight gain between the IBW and the FBW used in the calculation and it also grossly overestimates the predicted body weight at weights greater than the FBW used. Furthermore, the SGR is dependent on the IBW, making meaningless comparisons of growth rates among different groups unless the IBWs are similar.

Table I. Rainbow trout production records from a field station. Fish were reared in 1 200 L fibreglass tanks with 1–2 exchanges/h flow-through water system. TGC: Thermal-unit growth coefficient.

Month-end	Days	No. Fish	Weight (g/fish)	TGC	Total biomass (kg)	Total feed (kg)	Gain/ feed	T (°C)	Flow rate ($\mathrm{L \cdot min^{-1}}$)
1995									
Initial		**100 000**	**10**						
May	15	98 900	12	0.184	1 192	167	1.22	5.0	2 500
June	30	95 000	36	0.189	3 463	2 000	1.18	18.0	6 000
July	31	95 000	90	0.197	8 535	4 300	1.18	19.0	10 000
Aug.	31	94 500	177	0.175	16 767	7 200	1.15	21.0	16 000
Sept.	30	94 000	296	0.184	27 848	9 500	1.18	19.0	20 000
Oct.	31	93 500	396	0.199	37 032	7 800	1.20	11.0	25 000
Nov.	30	93 200	451	0.197	42 036	4 300	1.19	5.5	25 000
Dec.	31	93 000	456	0.176	42 394	400	1.12	0.5	25 000
Jan.	31	92 000	461	0.178	42 391	400	1.14	0.5	25 000
Feb.	28	91 500	465	0.177	42 569	370	1.11	0.5	25 000
Mar.	31	91 200	470	0.184	42 900	420	1.12	0.5	25 000
Apr.	30	91 000	476	0.188	43 274	420	1.12	0.5	25 000
May	31	91 000	535	0.200	48 653	4 500	1.20	5.0	30 000
June	30	90 800	783	0.204	71 130	18 500	1.22	18.0	50 000
TOTAL	410 days			0.191		60 277 kg feed	1.19	13.5 10^6 $\mathrm{m^3}$ water used	

A more accurate and useful coefficient for fish growth prediction in relation to water temperature is based on the exponent 1/3 power of body weight. Such a cubic coefficient has been applied both to mammals [25] and to fish [23]. The following modified formulae were applied to many nutritional experiments [2, 6, 7, 10, 14]:

Thermal-unit Growth Coefficient (TGC) =

$$[FBW^{1/3} - IBW^{1/3}] / \Sigma [T \times D] \times 100 \qquad (2)$$

Predicted Final Body Weight =

$$[IBW^{1/3} + \Sigma (TGC/100 \times T \times D)]^3 \qquad (3)$$

where T is water temperature (°C). (NOTE: 1/3 exponent must contain at least 4 decimals (e.g. 0.3333) to maintain good accuracy).

This model equation has been shown, by experiments in our laboratory and several field stations, to represent very faithfully the actual growth curves of rainbow trout, lake trout, brown trout, chinook salmon and Atlantic salmon over a wide range of temperatures. Extensive test data were also presented by Iwama and Tautz [23]. An example of the relationship among growth, water temperature and TGC is shown in *figure 1*. Growth of some salmonid stocks used for our experiments in freshwater gave the following TGC [6]:

Rainbow trout-A	0.174
Rainbow trout-B	0.153
Rainbow trout-C	0.203
Lake trout	0.139
Brown trout	0.099
Chinook salmon	0.098
Atlantic salmon-A	0.060
Atlantic salmon-B	0.100

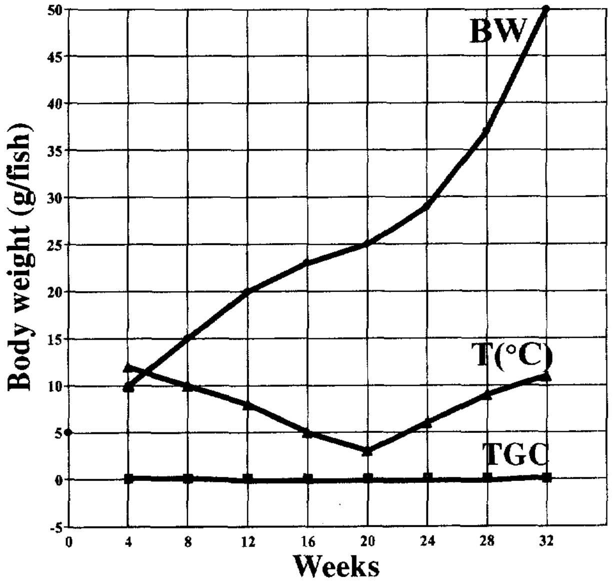

Figure 1. An example of the relationship among body weight (BW = 10–50 g/fish), water temperature (T = 3–12 °C) and thermal-unit growth coefficient (TGC = 0.17–0.18) of rainbow trout as a function of time.

Since these TGC values and growth rate are dependent on species, stock (genetics), nutrition, environment, husbandry and others factors, it is essential to calculate the TGC for a given aquaculture condition using past growth records or records obtained from similar stocks and husbandry conditions.

Once the expected TGC and water temperature profile during the production period are established, expected live weight gain (LWG) and recovered energy (RE), nitrogen (RN) and phosphorus (RP) on basis of dry matter (DM, 20–35 % of live body weight) in carcass can be computed in the following manners:

$$LWG = FBW - IBW \qquad (4)$$

$$RE \text{ (or RN, RP)} = LWG \times DM \times GE \text{ (or N, P)} \qquad (5)$$

where LWG is live weight gain (g), FBW is final body weight (g), IBW is initial body weight (g), RE, RN, RP are the recovered energy (kJ), nitrogen (g) and phosphorus (g), respectively, DM is dry matter content (%) of the fish, GE, N, P is gross energy (kJ), nitrogen (%) and phosphorus (%) content of dry matter, respectively.

Because a large proportion of the nutrients (e.g. protein, lipid) and, consequently of the dietary energy, consumed by fish is retained as carcass body constituents, carcass energy gain is a major factor driving dietary energy requirement of the fish. Carcass moisture, protein and fat contents in various life stages dictate energy level of fish. These factors are influenced by species, genetics, size, age and nutritional status [29]. The dry matter and fat contents of the fish produced are, in general, the most variable factors and have a determinant effect on energy content of the fish. For example, relatively fatty Atlantic salmon and rainbow trout may require more dietary energy per unit of live body weight than leaner salmonids such as brown trout, lake trout and charr. Fish containing less moisture (more dry matter) and more fat require more energy allocation in feeding standards.

The simplistic assumption of the constant body composition within a growth stanza in certain published models [19] is not necessarily valid for different species and sizes. Dry matter and energy content of fish can increase dramatically within a growth stanza, especially in the case of small fish. Underestimation or overestimation of the feed requirement is likely to occur if constant carcass energy content is assumed in calculations. Reliable measurements of carcass composition of fish at various size are essential. Nutrient and energy gains should be calculated at relatively as short a size interval as possible, at least for small fish (see *tables IV* and *V*). Additionally, composition of the diet, notably the digestible protein to digestible energy ratio and the lipid content of the diet, can have a very significant influence on the composition and energy content of the carcass. Estimation of carcass composition and energy content should rely on data obtained with fish fed diets similar to those one intends to use.

3.2. Estimation of excretory and feed waste outputs

Waste output loading from aquaculture operations can be estimated using simple principles of nutrition and bioenergetics [15, 16]. Ingested feedstuffs must be digested prior to utilization by the fish and the digested protein, lipid and carbohydrate are the potentially available energy and nutrients needed by the animal for maintenance, growth and reproduction. The remainder of the feed (undigested) is excreted in the faeces as solid waste (SW), and the by-products of metabolism (ammonia, urea, phosphate, carbon dioxide, etc.) are excreted as dissolved waste (DW) mostly by the gills and kidneys.

The total aquaculture wastes (TW) associated with feeding and production is made up of SW and DW, together with apparent feed waste (AFW):

$$\mathrm{TW} = \mathrm{SW} + \mathrm{DW} + \mathrm{AFW} \tag{6}$$

SW, DW and AFW outputs are biologically estimated by:

$$\mathrm{SW} = [\text{Feed consumed} \times (1 - \mathrm{ADC})] \tag{7}$$

$$\mathrm{DW} = (\text{Feed consumed} \times \mathrm{ADC}) - \text{Fish produced (nutrients retained)} \tag{8}$$

$$\mathrm{AFW} = \text{Actual feed input} - \text{Theoretical feed requirement} \tag{9}$$

in which ADC is the apparent digestibility coefficient of diets. Measurements of ADC and feed intake provide the amount of SW (settled and suspended, AFW-free) and these values are most critical for accurate quantification of aquaculture waste. ADC for dry matter, nitrogen and phosphorus should be determined using reliable methods by research laboratories where special facility, equipment and expertise are available. More information on the equipment and procedures may be obtained from the website www.uoguelph.ca/fishnutrition.

Dissolved waste, DW (N or P) can be calculated by the difference between digestible N or P intake and retained N (RN) or P (RP) in the carcass if this information is available, or by using a digested nutrient retention efficiency (NRE = Retained/Intake). Reliable NREs are necessary and should be determined or estimated for each type of diet used by research laboratories where expertise is available. However, controlled feeding and growth trial(s) with particular diets at production sites are essential to validate and fine-tune the coefficients from the laboratory. Dissolved nitrogen output depends very much on dietary protein and energy ratio and amino acid balances [33] and rate of protein deposition by the fish; therefore, all coefficients must be determined on a regular basis, particularly when feed formulae are changed. Assuming constancy of many coefficients is a dangerous exercise.

Accurate estimation of total solid waste (TSW) requires a reliable estimate of AFW. Feeding the fish to appetite or near-satiety is very subjective and unfortunately TW contains a considerable amount of AFW under most fish farming operations. The use of 'biomass gain x feed conversion' as an estimate of real feed intake of the fish to calculate waste output used in certain waste output prediction models [19] can grossly overestimate the feed intake in many operation where overfeeding is common and results in an underestimation of the TSW output.

It is very difficult scientifically to determine the actual feed intake by fish in spite of many attempts (mechanical, radiological and biological) that have been made by biologists. Since estimation of AFW is difficult and almost impossible, the best estimates can be made based on energy requirements and expected gain [6] in which the energy efficiency (energy gain/intake) indicates the degree of AFW for a given operation. The theoretical feed requirement (TFR) can be calculated based on nutritional energetic balance as follows:

$$\mathrm{TFR} = \text{Retained} + \text{Excreted} \tag{10}$$

and the amount of feed input above the TFR should be assumed to be AFW and all nutrient contents of the AFW must be included in solid waste quantification. This approach may yield relatively conservative estimates.

Biological procedures based on the ADC for SW and comparative carcass analyses for DW were shown to provide very reliable estimates [16]. Biological methods are flexible and capable of adaptation to a variety of conditions and rearing environments. It also allows estimation of the theoretical feed requirement and waste output under circumstances where it would be very difficult or impossible to do so with a chemical/limnological method (e.g. cage culture). Properly conducted biological and nutritional approaches to estimate aquaculture waste outputs are not only more accurate but also more economical than the chemical/limnological method [8, 15, 16].

The waste outputs from the field station (see *table I*) are tabulated in *table II*. SW was estimated at 10 610 kg (fish production 72 t; 60 t feed input over 14 months). SW represented 90 % of TSW, since AFW (actual feed input – theoretical feed requirement) was estimated at 1 201 kg or 2 % of feed input (60 277 kg in *table I*). The TSW outputs were equivalent to 164 kg per tonne fish produced. Phosphorus waste was 5.11 $\mathrm{kg \cdot t^{-1}}$ fish produced and nitrogen 30.64 kg. Total water consumption during 14 months was 13 469 10^6 L; therefore the average effluent quality can be estimated at: solid

Table II. Model estimation of waste outputs and effluent quality from the rainbow trout production operation in *table I.*

Waste output Total load estimate	Solid (kg)	Nitrogen (kg)	Phosphorus (kg)
Feed wastage (2 %) *	1 201	80.69	12.01
Solid	10 610	356.49	212.19
Dissolved	-	1 764.60	143.23
TOTAL	11 811	2 201.79	367.43
- per tonne fish produced	164.3	30.64	5.11
- % of dry matter fed	21.8 %	60.4 %	67.7 %
Average concentration ($mg{\cdot}L^{-1}$) in effluent (13 469 10^6 L) during 410 days	0.877	0.163	0.027

* Actual amount of feed fed – Theoretical amount of feed required.

0.877 $mg{\cdot}L^{-1}$, nitrogen 0.163 and phosphorus 0.027 (*table II*). The diet (MNR-95HG) and the procedures to estimate waste production as well as comparative data of chemical and biological estimations from field experiments at the Ontario Ministry of Natural Resources (OMNR) Fish Culture Stations are described elsewhere [8, 15, 16].

3.3. Quantitation of energy and nutrients needs

3.3.1. Dietary energy and protein requirements

A relatively large portion of dietary energy is expended for maintenance or basal metabolism, which is the minimum energy and nutrients required to maintain basic life processes. Maintenance energy requirement is approximately equal to the heat production of a fasting animal. This amount of dietary energy, represented as an absolute minimum of 'energy-yielding' nutrients, must be covered before any nutrients can be used for growth and reproduction of the animal. Otherwise body tissues will be catabolized because of a negative energy balance between intake of dietary fuels and energy expenditure. Poikilotherms, such as salmonid fish, require far less maintenance energy (approx. 40 kJ per kg $BW^{0.824}{\cdot}d^{-1}$ for rainbow trout at 15 °C) than do homeotherms (approx. 300 kJ per kg $BW^{0.75}{\cdot}d^{-1}$) [9, 26]. The most important component of the energy requirement estimation is this basal or maintenance energy requirement which can be approximated by using fasting heat production (HEf) values. Unfortunately, there is serious disagreement in the estimate of basal metabolism or HEf of fish in the literature. Some examples are shown in *table III*. Some of the data [30, 31] suggest, for example, that fasting heat production of rainbow trout at 15 °C is higher than that of homeotherm animals (36.5 vs 31.0 $kJ{\cdot}d^{-1}$ for a 50 g animal). More recently, Smith [30] revised his previous estimate of maintenance energy requirement. The use of this new estimate to calculate HEf of rainbow trout results in a value (see *table III*) which is now much lower than the estimate of Cho and Kaushik [9] for larger fish while similar for smaller fish. The selection of maintenance estimate of basal metabolism or HEf among published data is a very critical problem.

A review of available data suggest that a HEf of about 36–40 $kJ/kg^{0.824}$ per day appears accurate for rainbow trout at 15 °C, at least for fish between 20 and 150 g live weight with which most of studies have been conducted [4, 9, 11, 13, 24].

Water temperature has a major influence on basal metabolism of fish. The following equation estimates HEf of salmonids as a function of water temperature [7]:

$$\mathrm{HEf} = (-1.04 + 3.26T - 0.05T^2)\,(BW^{0.824})\,D^{-1} \quad (11)$$

where HEf is fasting heat production in kJ, T water temperature (°C), BW body weight (kg), and D number of days.

A slight modification of the equation above was performed recently since it underestimated HEf and feed requirement of salmonid at very low water temperatures (e.g. 0.5–2 °C):

$$\mathrm{HEf} = (-0.0104 + 3.26T - 0.05T^2)\,(BW^{0.824})\,D^{-1} \quad (12)$$

Ingestion of food by an animal which has been fasting results in an increase in the animal's heat production,

Table III. Comparison of fasting/basal energy requirements of poikilotherm and homeotherm ($kJ.d^{-1}$).

Body weight	Cho [7] (1)	NRC [28] (2)	Smith et al. [31] (3)	Smith [30] (4)	Kleiber [25] (5)
(g/fish)	Rainbow trout at 15 °C				Homeotherms
1	0.1			0.2	1.6
5	0.5	8.6	1.1	0.7	5.5
10	0.8	13.3	3.8	1.0	9.3
50	3.1	36.5	6.5	2.8	31.0
100	5.5		21.6	4.3	52.1
500	20.7			11.9	174.0
1 000	36.6			18.4	293.0

(1) 36.6 ($BW^{0.824}$) with BW in kg or $(-0.0104 + 3.26T - 0.05T^2)(BW^{0.824})$, T = 15 °C
(2) 241 ($BW^{0.63}$); (3) 201 ($BW^{0.75}$); (4) 18.4 ($BW^{0.63}$); (5) 293 ($BW^{0.75}$)

which is known as heat increment of feeding (HiE). The physiological basis of this increased heat production includes the post-absorptive processes related to ingested food, particularly protein-rich food and the metabolic work required for the formation of excretory nitrogen products, as well as the synthesis of proteins and fats in the tissues from the newly absorbed, food-derived substrates such as amino acids and fatty acids. The factors contributing to the HiE can be divided into three categories: i) formation and excretion of metabolic wastes; ii) transformation and interconversion of the substrates and their retention in tissues; and iii) digestion and absorption processes.

The HiE of rainbow trout fed a balanced diet was observed to be approximately 30 $kJ \cdot g^{-1}$ digestible N or the equivalent of 60 % HEf [9], but these relationships do not always hold true. Studies with farm animals suggest that HiE associated with growth may be more appropriately quantified as a factorial function of protein and lipid deposition rates [20]. Protein oxidation rate also appears to contribute to HiE [12]. Experimental observations suggest that HiE is approximately equivalent to 17 % of net energy intake, i.e. 0.17(RE + HEf) for rainbow trout and other salmonids. This value is used in the bioenergetic model presented here. Studies are underway to quantify HiE as a function of protein and lipid deposition and oxidation rates.

Biological oxygen requirement of feeding fish is equal to the total heat production (HEf + HiE / Qox) in which the oxycalorific coefficient (Qox) used in the model is 13.64 kJ energy per g oxygen [12]. This represent the absolute minimum quantity of oxygen that must be supplied to the fish by the aquatic system. Oxygen requirement per unit of BW per hour will vary significantly for different fish sizes and water temperatures. Calculated oxygen (mg per kg biomass per hour) and digestible energy requirements for fish of various size at three temperatures are presented in *table IV*.

3.3.2. Total energy requirement and calculation of feeding standard

The calculation of total energy requirement and consequently feed allocation of the animal can be accomplished as follows:

1) Calculation of expected live weight gain (LWG = FBW – IBW) and recovered energy (RE) based on carcass dry matter content (DM = 20–35 % of live body weight) and gross energy contents (GE = 25–30 $kJ \cdot g^{-1}$ DM):

$$\mathrm{RE} = \mathrm{LWG} \times \mathrm{DM} \times \mathrm{GE} \qquad (13)$$

2) Allocation of approximate maintenance or fasting energy requirement at a given water temperature (T):

$$\mathrm{HEf} = (-0.0104 + 3.26\mathrm{T} - 0.05\mathrm{T}^2)\,(\mathrm{BW}^{0.824})\,\mathrm{D}^{-1} \qquad (12)$$

3) Allocation of approximate heat increment of feeding for maintenance and growth ration:

$$\mathrm{HiE} = (\mathrm{RE} + \mathrm{HEf}) \times 0.17 \qquad (14)$$

4) Allocation of approximate non-faecal energy loss:

$$\mathrm{ZE} + \mathrm{UE} = (\mathrm{RE} + \mathrm{HEf} + \mathrm{HiE}) \times 0.09 \qquad (15)$$

or

5) Theoretical/minimum energy requirement:

$$\mathrm{TER} = 1) + 2) + 3) + 4) = [(\mathrm{RE} + \mathrm{HEf}) \times 1.2753 \qquad (16)$$

6) Feed allowance or feeding standard:

$$\mathrm{FA} = \mathrm{TER} / \mathrm{DE} \times \mathrm{Qfi} \qquad (17)$$

where TER is the theoretical/minimum energy requirement (MJ), FA feed allowance (kg), DE digestible energy content of the feed (MJ/kg), Qfi an adjustment factor. Qfi is an adjustment factor determined by the fish culturist to provide flexibility for estimating a realistic FA under a given husbandry condition (if one observes that more or less feed may be required than predicted by the model).

The minimum digestible energy requirement that should be fed to the fish is the sum of retained energy (RE) and energy lost as HEf + HiE + ZE + UE. The amount of feed can be estimated on a weekly or monthly basis, and recalculated if any parameter (growth rate, water temperature, etc.) is changed. The computed quantity of feed should be regarded as a minimum requirement under most conditions and fish culturists should fine-tune the feeding level to their own local conditions using the adjustment factor (Qfi).

The overall energy cost of producing one kg of rainbow trout is around 15–16 MJ DE, but this ranges from 10 MJ for fry to 20 MJ for fish of almost 3 kg (*table IV*). Even though maintenance energy requirement per kg BW is much higher in small than in large fish, overall energy cost of production is much higher in large fish because of high ‘growth-fattening cost’. This may become much more significant when feeding overly high energy (fat) diets, hence more than 50 kJ DE per g DP (or less than 20 g DP/MJ DE) is not recommended. Water temperature greatly affects heat production and oxygen consumption of poikilotherms and a growing fish of 100 g is expected to consumed 110, 210 and 300 mg oxygen/kg BW/h at 5, 10, 15 °C, respectively (*table IV*).

Growth rates can also affect the energy cost of production because the proportion of the maintenance energy requirement is higher with lower growth rate. Fish with a TGC of 0.14 may require 5–10 % more feed to attain a given size than a fish with a TGC of 0.19. The former will also require a 25 % longer period. A similar situation may occur at a lower growth rate due to lower temperature.

Table V summarizes the monthly fish sizes and feed rations predicted by the bioenergetic models program

Table IV. Model estimated growth rate and minimum oxygen and energy requirements by feeding salmonids at different water temperatures (TGC = 0.191 and Qox = 13.64 kJ·g^{-1}). An example. Dietary DP/DE ratio was 22 g digestible protein per MJ DE. Growth rate (TGC = 0.91) may be regarded as a higher range of growth performance.

Weeks	Body weight (g/fish)	Dissolved oxygen[1] (mg·kg^{-1}·h^{-1})	DE[2] (MJ·kg^{-1} gain)	Body weight (g/fish)	Dissolved oxygen[1] (mg·kg^{-1}·h^{-1})	DE[2] (MJ·kg^{-1} gain)	Body weight (g/fish)	Dissolved oxygen[1] (mg·kg^{-1}·h^{-1})	DE[2] (MJ·kg^{-1} gain)
	5 °C water temperature			10 °C water temperature			15 °C water temperature		
0	10			10			10		
1	11	164	10.92	12	311	10.57	13	441	10.24
2	12	161	10.97	14	299	10.66	17	414	10.37
3	13	158	11.02	17	288	10.75	21	392	10.49
4	14	155	11.06	19	277	10.84	26	372	10.60
5	15	159	12.59	22	282	12.40	31	373	12.20
6	17	157	12.64	26	272	12.48	38	357	12.30
7	18	154	12.68	30	264	12.56	45	342	12.40
8	19	151	12.73	34	256	12.64	53	328	12.50
9	21	157	14.65	38	263	14.59	62	335	14.48
10	22	154	14.70	43	256	14.67	72	323	14.57
11	24	152	14.74	48	249	14.74	83	312	14.66
12	26	150	14.78	53	243	14.81	95	302	14.75
13	28	149	15.26	59	240	15.31	108	296	15.26
14	30	147	15.30	65	234	15.37	122	288	15.35
15	31	145	15.34	72	229	15.44	138	280	15.43
16	34	142	15.38	79	224	15.50	154	272	15.51
17	36	140	15.42	87	219	15.57	172	265	15.58
18	38	139	15.46	95	214	15.63	192	259	15.66
19	40	137	15.49	103	210	15.69	212	253	15.73
20	43	135	15.53	113	206	15.75	234	247	15.81
21	45	134	15.96	122	204	16.20	258	244	16.27
22	48	133	16.00	132	201	16.26	283	239	16.34
23	50	131	16.04	143	197	16.32	310	234	16.41
24	53	129	16.08	154	194	16.38	338	229	16.48
25	56	128	16.11	166	190	16.43	368	225	16.54
26	59	126	16.15	179	187	16.49	400	220	16.61
27	62	125	16.18	192	184	16.54	434	216	16.67
28	65	124	16.22	205	181	16.59	469	213	16.74
29	69	122	16.25	219	179	16.65	506	209	16.80
30	72	121	16.29	234	176	16.70	546	206	16.86
31	76	120	16.32	250	174	16.75	587	202	16.92
32	79	118	16.36	266	171	16.80	630	199	16.98
33	83	117	16.39	283	169	16.85	675	196	17.04
34	87	116	16.42	301	167	16.90	722	193	17.10
35	91	115	16.46	319	164	16.95	772	190	17.16
36	95	114	16.49	338	162	17.00	824	187	17.21
37	99	112	16.52	358	160	17.05	878	185	17.27
38	103	111	16.55	379	158	17.09	934	182	17.33
39	108	110	16.59	400	156	17.14	993	180	17.38
40	113	109	16.62	422	154	17.19	1 054	178	17.44
41	117	108	16.65	445	153	17.23	1 117	175	17.49
42	122	107	16.68	469	151	17.28	1 183	173	17.54
43	127	106	16.71	494	149	17.33	1 252	171	17.59
44	132	105	16.74	519	148	17.37	1 323	169	17.65
45	138	104	16.77	546	146	17.42	1 397	167	17.70
46	143	104	16.80	573	144	17.46	1 474	165	17.75
47	149	103	16.83	601	143	17.50	1 553	163	17.80
48	154	102	16.86	630	141	17.55	1 635	161	17.85
49	160	101	16.89	660	140	17.59	1 720	160	17.90
50	166	100	16.92	691	139	17.63	1 808	158	17.95
51	172	99	16.95	722	137	17.67	1 899	156	18.00
52	179	99	16.98	755	136	17.72	1 992	155	18.05
53	185	98	17.01	789	135	17.76	2 089	153	18.09
54	192	97	17.04	824	133	17.80	2 189	151	18.14
55	198	96	17.07	860	132	17.84	2 292	150	18.19
56	205	96	17.10	896	131	17.88	2 398	149	18.23
57	212	95	17.13	934	130	17.92	2 508	147	18.28
58	219	94	17.15	973	129	17.96	2 620	146	18.33
59	227	94	17.18	1 013	128	18.00	2 736	144	18.37
60	234	93	17.21	1 054	127	18.04	2 856	143	18.42
61	242	92	17.24	1 096	126	18.08	2 979	142	18.46
62	250	92	17.27	1 139	124	18.12	3 105	141	18.51
63	258	91	17.29	1 183	123	18.16	3 368	139	18.59
64	266	90	17.32	1 229	122	18.19	3 368	138	18.59

1. Dissolved oxygen includes basal and heat increment of feeding requirements (mg·kg^{-1} BW·h^{-1}).
2. DE = minimum digestible energy cost required to produce a kg of live weight gain (MJ).

Table V. Model prediction of fish body weight and feed requirement based on the 1995 production records in *table I*. TGC: Thermal-unit growth coefficient; (**) Overall TGC = 0.191 from *table I* was used to predict body weight and total feed requirement.

Month-end	No. Fish	TGC (%)	Body weight (g/fish)	Total feed (kg)	Gain/Feed ratio	Body weight (g/fish)**	Total feed (kg)**	Gain/Feed ratio	T (°C)
	Actual production records					Predicted production scenario			
Initial	**100 000**		**10**			10			
May	98 900	0.184	12	167	1.22	12	120	1.81	5.0
June	95 000	0.189	36	2 000	1.18	37	1 498	1.68	18.0
July	95 000	0.197	90	4 300	1.18	88	3 446	1.47	19.0
Aug.	94 500	0.175	177	7 200	1.15	182	6 732	1.40	21.0
Sept.	94 000	0.184	296	9 500	1.18	310	9 495	1.35	19.0
Oct.	93 500	0.199	396	7 800	1.20	407	7 775	1.24	11.0
Nov.	93 200	0.197	451	4 300	1.19	461	4 602	1.19	5.5
Dec.	93 000	0.176	456	400	1.12	467	451	1.16	0.5
Jan.	92 000	0.178	461	400	1.14	472	454	1.16	0.5
Feb.	91 500	0.177	465	370	1.11	477	452	1.17	0.5
Mar.	91 200	0.184	470	420	1.12	483	453	1.18	0.5
Apr.	91 000	0.188	476	420	1.12	488	456	1.18	0.5
May	91 000	0.200	535	4 500	1.20	544	4 627	1.21	5.0
June	90 800	0.204	783	18 500	1.22	781	18 228	1.30	18.0

for the field station based on its production records (see *table I*). The feed requirements were calculated using a single TGC (0.191) for the whole production cycle (14 months) and actual temperature profile. The nutrient and energy gains used in the calculations were based on carcass composition values for rainbow trout of various sizes obtained in different laboratory trials at the University of Guelph. Nutrient and energy retention efficiencies (NRE and ERE) used were derived from previous studies at another fish culture station (Harwood Fish Culture Station, Harwood, Ontario) using comparable diets [16]. The main discrepancy is between the actual and predicted feed amount for the first four months with actual feed input being greater than predicted allocation. This may indicate that overfeeding occurred in 1995; however, real feed intake by the fish could be somewhere between the predicted amount and the actual amount. Using this information, the fish culturist can fine-tune the program in the next production cycle. In the remaining 10 months, the feed allocation estimated by the model was very close to the actual feed fed, the largest discrepancies (in terms of predicted/actual) occurring at very low water temperatures (0.5 °C).

This simulation may not be considered a perfect example of independent or objective validation of the model but is, nevertheless, an adequate demonstration of the realism of the predictions from bioenergetic models. Most of the parameters used in the calculations are fairly independent from the actual data. For example, the carcass composition data were from a number of laboratory trials which had nothing to do with actual data. The TGC and the temperature profile used in the calculation are not independent from the actual data because it is essential to use actual values or values from previous production cycle if these are available and repeatable. TGC and water temperature are the main inputs required by the models from the fish culturist. The predicted values from *table V* were calculated a posteriori and their main use is as production scenario for the following year based on the 1995 production performance. The predicted values can also be used as yardsticks to compare the results obtained with what was predicted to be biologically achievable and adjust feeding practices or equipment in the following production cycle.

4. DEVELOPMENT OF THE Fish-PrFEQ PROGRAM

A stand-alone multimedia program for the Windows 95^{TM} platform was developed in visual basic language with database functionality by the Ontario Ministry of Natural Resources. The program has 4 modules for fish production/growth prediction, waste output quantification, feed allowance estimation and oxygen requirement tables and is based on the bioenergetic models presented above. Feed composition, body weight, water temperature, flow rate and mortality are entered by the user but waste, retention and other coefficients are parameters that are locked and may only be revised with an authorized program update diskette. These coefficients should be determined by qualified nutritionists from feed manufacturers or research institutions since specific coefficients are required for each type of diets. The use of unrelated coefficients results in under- or overestimation of feed requirements and waste outputs. All input parameters required for and outputs from the modelling are listed in *table VI*.

The various outputs are printed and stored as popular MS-Access and dBase files so that further manipulation of the output data by users is facilitated. Live weight gain, feed efficiency, growth coefficients, solid, nitrogen, phosphorus in the effluent, total waste load, feed ration and oxygen requirements are some of the output parameters generated by the models.

Table VI. Terminology, abbreviations and input/output parameters for the bioenergetic models.

Categories	Abbreviations	Description	Units	Model parameters	
				Input	Ouput
Feed	ADC	Apparent digestibility coefficient		++	
	FA	Feed allowance	g or kg		x
	FE	Feed efficiency (live weight gain/feed input)			x
	NRE	Nutrient retention efficiency (retained/intake)		++	
	Qfi	Adjustment factor for feed input		+	
	TFR	Theoretical feed requirement	g or kg		x
Composition	DM	Dry matter	%	+	
	DP	Digestible protein	%	++	
	N	Nitrogen (crude protein/6.25)	%	+	
	P	Phosphorus	%	+	
	RN	Recovered nitrogen in carcass	%	++	
	RP	Recovered phosphorus in carcass	%	++	
Growth	BW	Body weight at given time	g or kg		x
	FBW	Final body weight at the end of period	g or kg		x
	IBW	Initial body weight at the beginning of period	g or kg	+	
	LWG	Live weight gain (FBW – IBW)	g or kg		x
	TGC	Thermal-unit growth coefficient		+	x
Energy*	DE	Digestible energy	kJ or MJ	+	
	ERE	Energy retention efficiency		++	
	HEf	Heat production of fasting animal	kJ or MJ	++	
	HiE	Heat increment of feeding	kJ or MJ	++	
	Qox	Oxycalorific coefficient (13.64 $kJ \cdot g^{-1}$ oxygen)	kJ or MJ	++	
	RE	Recovered energy	kJ or MJ	++	
	TER	Theoretical energy requirement	kJ or MJ		x
	UE	Urinary energy	kJ or MJ	++	
	ZE	Branchial energy	kJ or MJ	++	
Waste	AFW	Apparent feed waste	g or kg		x
	DW	Dissolved waste	g or kg		x
	SW	Solid waste, faeces	g or kg		x
	TSW	Total solid waste (= SW + AFW)	g or kg		x
	TW	Total waste (= SW + DW + AFW)	g or kg		x

* NRC nomenclature is used when available [27].
+ User input; ++ Coefficients input; x Results output.

5. INTEGRATION OF THE PREDICTION MODELS INTO FEEDING SYSTEMS

In spite of the widespread feeding practice of high fat (energy) diets for salmonids today, adjustment of old feeding charts has not followed and feed efficiency has not improved accordingly. Many salmonid aquaculture operations still entertain feed conversions (feed/gain) of nearly 1.5 [17]. These situations lead not only to high feed cost, but also create considerable aquaculture waste problems in rivers, lakes and coastal waters.

Regardless of approach and techniques employed to feed to appetite or near-satiety, the actual amount of feed intake under practical conditions can unknowingly be one of the five categories illustrated in *figure 2*.

Aiming for maximum gain and best feed efficiency may be desirable, but practising it under farming condition is a difficult and almost impossible basis even with the aid of computer programs and sophisticated feeding equipment [17]. True gain and actual feed intake are not known until the next inventory measurements, therefore maximum gain and best feed efficiency are mere conceptual figures in daily operations. Real feeding situation will still fall in one of the five categories as illustrated by the experimental results with rainbow trout fed 'old' low nutrient-dense diet (*figure* 2). In the feeding level of category 3.) the theoretical requirement will be maximum gain with best feed efficiency, however, this level in daily situation may be a 'moving target'. With the aid of the bioenergetic models, fish culturists can maintain the feeding levels between categories 2.) and 4.), and aim near category 3.) on a weekly or monthly basis.

Results from carefully conducted feeding trials in our laboratory with rainbow trout and Atlantic salmon [2, 4] suggest that feed efficiency improves to its maximum at moderate feed restriction (as low as 50 % of near-satiation) and this optimum is maintained up to near-satiation (maximum voluntary feed intake) of the fish. The recent hypothesis put forward by Einen et al. [19] that maximum feed efficiency is only attained at maximum intake and, therefore, not accurate. It might be important to note that as the feed offered approaches the amount corresponding to near-satiation for the fish, feed wastage may increase

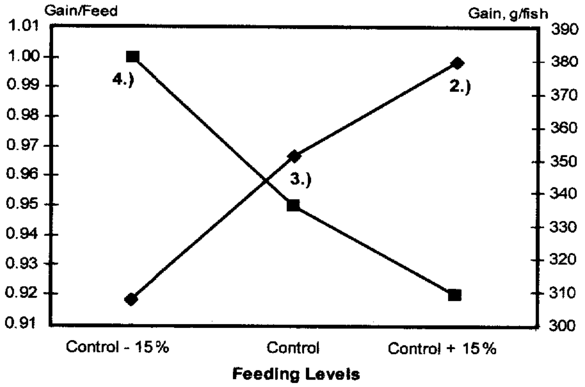

Figure 2. Effects of feeding level on gain and feed efficiency (gain/feed) of rainbow trout (10 g initial weight) fed a low nutrient-dense diet for 32 weeks at 15 °C. The figure illustrates 5 feeding categories: 1.) Overfeeding – feed waste (not in figure); 2.) Upper range of optimum feeding level – maximum gain; 3.) Most optimum feeding level – theoretical requirement; 4.) Lower range of optimum feeding level – best feed efficiency; and 5.) Underfeeding and restricted feeding – lower gain (not in figure).

because of slower response of the fish to the presentation of feed pellet [1]. This may result in a slight reduction of apparent feed efficiency (due to feed wastage) but slightly higher weight gain as observed in *figure 2*.

Quantitative minimal energy and feed requirement prediction models and computer software can not replace common sense when feeding fish, particularly when effective feeding method/practices are used. The bioenergetic models could represent a valuable management tool to help improve husbandry practices and may provide considerable benefits if one fine-tunes the model based on his own production records through adjustment factors. Ideally, such readjustment should be made on the basis of actual performance. Accurate growth and feed requirement prediction models can help in objectively examining one's performance by providing a yardstick with which performance can be compared and results obtained with the feeding system/practice in use validated. With nutritional energetics-based models and programs, production forecast, feed requirement, oxygen requirement and waste output can be estimated a priori. This may prove very useful for aquaculture operations when forecasting production and environmental impacts, negotiating yearly feed and oxygen supply contracts, etc.

Pre-allocated weekly amounts are divided into desired number of daily meals, but each meal must be sufficient in quantity for whole populations as long as total ration fed does not exceed the quantity estimated in advance. Properly sized feed should be dispensed over a wide water surface by hand or mechanical devices in such manner that the feed wastage is minimized. With any feeding system, dominant fish will probably consume enough feed to express their full growth potential; however, the effort made to ensure adequate feed intake of 'weakling' fish may dictate the extent of AFW. The goal of most feeding systems employed today is fast and maximum body weight gain and minimal concern for feed efficiency and wastage, but this approach is not always economical, and will not promote a lasting cohabitation of sustainable aquaculture and a cleaner environment.

Presented above are three relatively simple steps on how to feed fish using scientific principles of the nutritional strategies and management of aquaculture waste (NSMAW). The up-coming Windows 95™ multimedia program Fish-PrFEQ developed by the Ontario Ministry of Natural Resources will make easier predictions of growth rate, estimation of feed required and computation of waste output. Feeding fish using almost folkloric approaches must become something of the past. The largest portion of fish production costs (over 40 %) is expended on feed and fish feed is among the highest quality and most expensive types of animal feed on the market. Dispensing this expensive commodity using the most out-dated mode is an undeniably wasteful practice. Much more attention and time should be devoted to feeding systems and approaches to feeding fish.

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