

Energy Requirements and Feeding Behaviour of Salmonids in Culture

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Abstract

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This thesis deals with the feeding management of salmonids, from the calculation of the daily feed requirement to the presentation and delivery of that ration taking into consideration the feeding behaviour. The digestible energy need (DEN) to grow 1 kg of wet body weight was calculated for different farmed fish species. In general, the DEN increased with increasing body weight. Using this information, a feed ration model was created and tested using rainbow trout (*Oncorhynchus mykiss*). Fish fed using this model showed a high rate of growth and a good feed conversion ratio (FCR). The model accurately predicted growth in trout and can be easily applied as a method of calculating the daily ration. For comparison, 3 groups were fed using self-feeders. These groups showed a pattern of fluctuating trigger-biting activity across days and this type of pattern was further studied using time series analysis for groups of rainbow trout. Peaks in activity occurred in the morning and evening at lights on and lights off. Across days, peaks in activity are significantly higher every second day. This pattern is probably a result of an "hourglass" mechanism such as the time required for gastric evacuation and the return of appetite.

Knowing how much feed to give each day, one must then present it in an optimal way. Rainbow trout were fed the daily ration using various portion sizes and at different temperatures. At 5 °C, growth and FCR were best when small portion sizes were used. At higher temperatures, good growth rates and FCR were observed over a broader range, indicating a high level of plasticity in the trout's ability to adjust to different portion sizes at higher temperatures. To further evaluate feed presentation, Atlantic salmon (*Salmo salar* L.) were raised in sea cages, and fed using different combinations of pellet sizes and delivery rates. Treatment groups were compared using growth rate. No significant linear effect on growth due to pellet size or delivery rate could be detected. For pellet size, however, indications point to a non-linear relationship with growth rate. Salmon grew equally well irrespective of treatment further indicating a high level of plasticity in the salmon's ability to adjust to changes in feed presentation.

Keywords: feed management, energy requirements, feed budget, self-feeders, feeding behaviour, feeding intensity, portion size, pellet size

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To Albert & Arthur
'Tis in me blood'

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Appendix

Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Bailey, J. & Alanära, A. Digestible energy need (*DEN*) of selected farmed fish species. *Manuscript*.
- II. Bailey, J. & Alanära, A. 2001. A test of a feed budget model in rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Aquaculture Research* 32: 465-469.
- III. Bailey, J. & Alanära, A. Mapping the demand-feeding pattern of hatchery-reared rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Manuscript*.
- IV. Bailey, J. & Alanära, A. Effect of feed portion size on growth of rainbow trout, *Oncorhynchus mykiss* (Walbaum), reared at different temperatures. *Submitted*.
- V. Bailey, J., Alanära, A. & Crampton, V. Does delivery rate and pellet sizes affect growth rate in Atlantic salmon (*Salmo salar* L.) raised under semi-commercial farming conditions? Accepted in *Aquaculture*.

Papers II and V are reproduced with permission of the journal concerned.

Introduction

The food and agriculture organization (FAO) of the United Nations estimated aquaculture production in 1999 to be 32.9 million metric tonnes (mt) with the farming of salmonids making up approximately 900,000 mt (or 2.7 %) (FAO, 2000). Norway and Chile lead the way in production of mainly Atlantic salmon (*Salmo salar* L.) with 462,000 mt and 222,900 mt respectively. Norway's salmon exports of 8.3 million kilograms to the United States alone in 1999 held a value of 51 million US\$ (FAO, 2000). Slight changes in production efficiency of an industry of this magnitude will mean profits of millions of dollars. Feed costs account for about 50% of the total yearly production costs on large commercial farms. More efficient production will translate into more biomass for a smaller amount of feed. This will lead to further reductions in environmental impacts and, therefore, increased economic gains. The aquaculture industry is one of the few where direct economic gains can be realised through a decrease in pollution.

A fish farmer's primary objective is to produce high quality, disease-free fish in as short a time as possible. The three principal factors that govern this objective are the physical environment of the fish, fish physiology, and behaviour. Throughout development, at least one of these factors, and most often an interaction of all three, is affecting fish growth and ultimately the cost of production of the final product.

As stated, feed costs are by far the principal expense a fish farmer has to deal with. Thus, it can be contended that the act of feeding is the single most important undertaking for the economy of the farming industry. The size of the daily ration, the nutritional and physical make-up of the feed, and the method by which the feed is delivered can have significant effects on farm economy. This thesis deals with some of these parameters.

The Daily Ration

If the act of feeding is the most important step for the fish farmer, then the part of that step that includes the calculation of the daily ration is perhaps the most difficult. An optimal ration will give maximal growth while maintaining a good feed conversion ratio (*FCR*), the ratio of feed ingested to body weight gained. One may assume that once the daily ration is known, that merely weighing up the daily amount as a proportion of the biomass of the fish to be fed, will be a simple procedure. However, fish species, individual fish size, water temperature, time of year, and an array of behavioural, physiological, and environmental variables can affect the daily and seasonal requirements of the fish (Farbridge & Leatherland, 1987; Langhans & Scharrer, 1992; Heggenes *et al.*, 1993; Jobling, 1994; De Silva & Anderson, 1995; Saether, Johnsen & Jobling, 1996; Tveiten, Johnsen & Jobling, 1996; Thetmeyer *et al.*, 1999).

Feeding fish on demand, either through fish feeding themselves (self-feeders) or by automatic cessation or reduction of feed delivery when feeding activity declines (interactive feedback system), has received much attention within the

aquaculture industry (Alanärä, Kadri, & Paspatis, 2001). Demand feeding systems operate on the premise that the fish themselves “decide” when and how much they will eat by providing direct and constant feedback to a computer-controlled device. Since they incorporate feedback from the fish, they are thought to take variations in appetite into account. These systems can, however, become expensive and complex and are not without their own problems. It has even been suggested that these systems may induce variation in daily appetite level (Paper III).

An effective means of calculating the daily ration should be based on the daily energetic requirements of the fish. Even if demand feeding systems are in place, theoretical calculations of the daily ration should be conducted on a regular basis as a control of the amount of feed delivered by these systems. Moreover, if feeding models are based on accurate calculations of growth, they can also be used in the calculation of detailed production plans, aiding farm management and planning.

Fish farmers who use automatic, timer-controlled feeders often rely on feeding charts or growth models for calculation of the daily feed requirements of the fish (e.g. Iwama & Tautz, 1981; Jobling, 1983; From & Rasmussen, 1984; Austreng, Storebakken & Åsgård, 1987; Cho & Bureau, 1998). These are frequently based on temperature and fish size and are often in very generalised form with little room for adjustments based on local conditions and the strain of fish being farmed. Using growth data readily available from previous production cycles, the farm manager can easily calculate his/her own feed budget model. Since this model will be based on local conditions, a very accurate value can be calculated for the theoretical daily requirements of the fish for one unit of biomass gain (g or kg).

Alanärä, Kadri, & Paspatis (2001) described a feed budget model that utilises the digestible energy need (*DEN*) for a 1 kg gain in wet body weight of the fish ($\text{MJ DE}\cdot\text{kg}^{-1}$). This can be written mathematically as:

$$DEN = \frac{(FI \cdot DE)}{(W_i)} \quad (\text{Equation 1})$$

where *FI* is the feed intake (kg), *Wi* is the increment of weight gain (kg), and *DE* is the digestible energy content of the feed ($\text{MJ}\cdot\text{kg}^{-1}$).

The energy budget of an organism can be described as:

$$C = F + U + R + P \quad (\text{Equation 2})$$

where *C* is the energy of the feed consumed, *F* is the energy lost in the faeces, *U* is the energy lost to excretion (urinary, gill, body surface energy loss), *R* is the energy used for metabolism, and *P* is the remaining energy deposited as growth (De Silva & Anderson, 1995). The energy budget can be described figuratively as shown in Fig. 1 and the relationship between this energy budget and Equation 1 can be described as follows:

$$DEN = \frac{(C - F)}{(U + R + P)} \quad (\text{Equation 3})$$

From a fish farmer's point of view, the details concerning where energetic expenditures occur are less important (Fig. 1). What is important is obtaining the maximum return (gain in biomass) per unit input (feed intake). The advantage with this view of the energy budget is that, since the values for F , U , and R need not be quantified, the fish can be raised under normal culture conditions when the estimation of DEN is performed. By doing so, energetic costs due to the ingestion and digestion of feed, and to swimming activity are more similar to those used in culture than to those used when a complete energy budget model, as that described in Equation 2, is used (Alanärä, Kadri, & Paspatis, 2001).

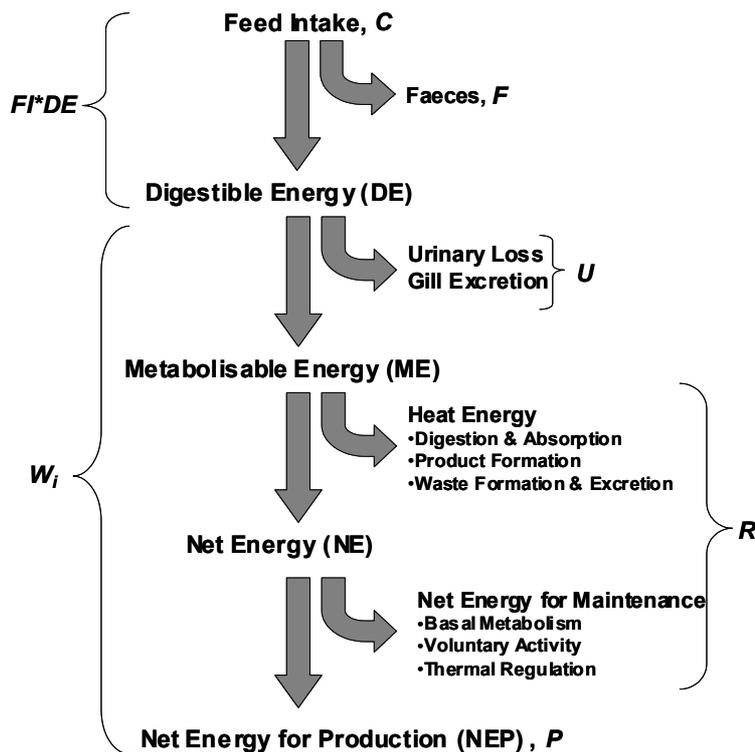


Fig. 1. Energy flow in fish. Arrows indicate the direction of energetic transfer. Large brackets to the left show the parts of the energy budget encompassed by the equation $DEN = (FI * DE) / W_i$ (see text). C , F , U , R and P make up the energy balance indicated by the equation: $C = F + U + R + P$, where C is the energy of the feed consumed, F is the energy lost in the faeces, U is the energy lost to excretion (urinary, gill, body surface energy loss), R is the energy used for metabolism, and P is the remaining energy deposited as growth (De Silva & Anderson, 1995).

Due to its ease and relatively low cost of calculation, the DEN can be estimated for a particular strain of fish and under local farm conditions, providing the farmer with a very specific method of evaluating the energetic requirements of the fish.

Variation in Feed Intake

Demand feeders have been used extensively in behavioural studies on salmonids (Landless, 1976; Boujard & Leatherland, 1992; Brännäs & Alanära, 1993; Alanära & Brännäs, 1993; Juell, Furevik, & Bjordal, 1993; Alanära, 1994; Alanära & Brännäs, 1996; Sanchez-Vazquez & Tabata, 1998). Time series plots of the feeding activity data obtained from these kinds of studies often display a variable pattern of peaks and troughs across days (Boujard & Leatherland, 1992; Brännäs & Alanära, 1993; Alanära & Brännäs, 1993; Alanära, 1994; Alanära & Kiessling, 1996). In general, peaks observed in the series on one day, are followed by troughs on the following day. It appears that these peaks in activity occur every second day (Paspatis & Boujard, 1996; Alanära, Kadri, & Paspatis, 2001) and that perhaps the demand feeding system itself may be causing this pattern through changes in stomach fullness and the time required for emptying (gastric evacuation time) (Grove, Loizides & Nott, 1978; Bromley, 1994).

Trout fed using demand feeders may also be consuming more than they need to cover their daily metabolic requirements (Bres, 1986). Appetite is controlled partly by stretch receptors in the gut and partly by the level of various metabolites in the blood system (Grove, Loizides & Nott, 1978; Dill, 1983; Juell *et al.*, 1994; De Silva & Anderson 1995). It has been suggested that if fish eat until the gut is full of pelleted feed, much of the energy might be unused and excreted undigested or stored as excess visceral and muscular lipid (Jobling, 1986; Storebakken *et al.*, 1991) although no studies have been conducted to fully support this suggestion. Bres (1986) and Alanära (1994) showed that rainbow trout were unable to distinguish between pellets of different energetic contents and were therefore unable to, or do not need to regulate their daily energetic intake in the range studied.

The high-energy pelleted feed used in salmonid aquaculture has a very low volume to energy ratio. Pellets used in today's aquaculture industry have as high as 4 or 5 times the energy value for an equivalent volume of wild food (Ruohonen & Grove, 1996) due, in part, to the low water content of pelleted feed. It follows logically that fish fed high energy diets require less feed in terms of volume, than do those fed low energy diets. However, fish fed using demand feeders often eat to satiation and the time required to digest this feed might be very long. Ruohonen, Grove, & McIlroy (1997) suggested that the longer time required for the gastric evacuation of pelleted feed is due to the time needed to moisten the feed in the stomach, creating a high lag time before digestion can continue. The variation in feed intake seen in rainbow trout fed using demand feeders, then, could be due to the time required for gastric evacuation and the return of appetite. If the time required for gastric evacuation is more than 24 hours as suggested by Ruohonen, Grove, & McIlroy (1997) and Grove, Loizides & Nott (1978), then the pattern of daily activity should reveal a period between peaks of 2 days. This may have implications on how the feed should be delivered using demand feeders and further strengthens the necessity of using a model to calculate energy need, even if demand feeders are in use. Perhaps restrictions on the amount available per day should be applied using the feed budget model as a guide so as to prevent excessive wastage.

In addition to the pattern in daily activity levels, recurring activity patterns have been shown to occur within days (Cuenca & de la Higuera, 1994; Alanärä & Brännäs, 1997; Sanchez-Vazquez & Tabata, 1998; Bolliet, Aranda & Boujard, 2001). These studies show that peaks in activity usually occur under conditions of changing light levels, at dawn and at dusk, probably as a result of evolutionary selection for activity when there is increased prey abundance and decreased predation risk (Eriksson & Alanärä, 1992). Some fish farmers have decided to adapt their feeding regimes around these patterns in activity, feeding the daily ration in the morning and evening, while others feed constantly throughout the day.

Feed Presentation

Alanärä, Kadri & Paspatis (2001) described a meal as the amount of food consumed in a single feeding bout, usually with a duration of between 30 min and 2 h. A meal can be made up of one to many “feed portions”, consisting of short, periodic feed delivery periods followed by a short pause. The size, rate of delivery and temporal spacing of these portions will affect the meal length and/or the feeding intensity of the daily ration. As these definitions are interrelated, a change in one parameter in the schedule will affect each of the other parameters.

Delivery Rate

Using a model to calculate the daily feed ration one must still face the problem of how to deliver the feed so that the fish can utilise it in an optimal way. Feeding schedules may vary in number of meals per day, number of portions in each meal, the time between portions and meals, the size of each portion, and the speed of delivery of each portion.

The delivery rate can be described in two ways: (1) the number and temporal spacing of portions given per day, often referred to as the feeding intensity, or (2) the delivery rate of the feeder itself, measured in number of pellets per unit time. Both approaches will likely affect the ability of the fish in catching pellets and consequently, growth, and so both should be considered when presenting feed to salmonids.

The number of feed items an individual fish can catch is related to its swimming activity and the temperature of the water (Brett, 1969; Alanärä, 1994; Jobling, 1994; Tang & Boisclair, 1995). In salmonids, activity level increases and the proportion of time spent hiding during daylight hours decreases as temperatures rise between *ca.* 4-8 °C (Cunjak, 1988; Elliott, 1975; Fraser, Metcalfe & Thorpe, 1993; Fraser *et al.*, 1995; Graham, Thorpe & Metcalfe, 1996; Rimmer, Saunders & Paim., 1985) dependent, of course, upon the acclimation history of the fish and the strain or species being considered. In aquaculture, decreased swimming activity may affect the rate of feed capture and feed delivery rate, therefore, should perhaps reflect this change in activity level at different temperatures.

Portion Size

With respect to portion size, fish are poikilothermic and at low temperatures, when fish are less active, many small feed portions will likely allow the fish to catch a larger proportion of the feed than if large portion sizes are used. At higher temperatures, the fish are more active and will likely be able to catch all pellets in the feed portions up to a point where the portion size becomes too large and waste occurs. It is suspected that the relationship between feed portion size and growth rate follows a quadratic function as shown in Fig. 2. Assuming that the ability to catch pellets is limited by the activity level of the fish, at different temperatures the optimal portion size should shift along the x-axis (Fig. 2). In addition, because swimming activity increases, the plateau of the quadratic function flattens as a broader range of portion sizes (*i.e.* larger and larger portion sizes) give equivalent growth rates as small portion sizes, assuming fish receive the same amounts of feed each day and energetic expenditures associated with feeding under longer periods are relatively insignificant.

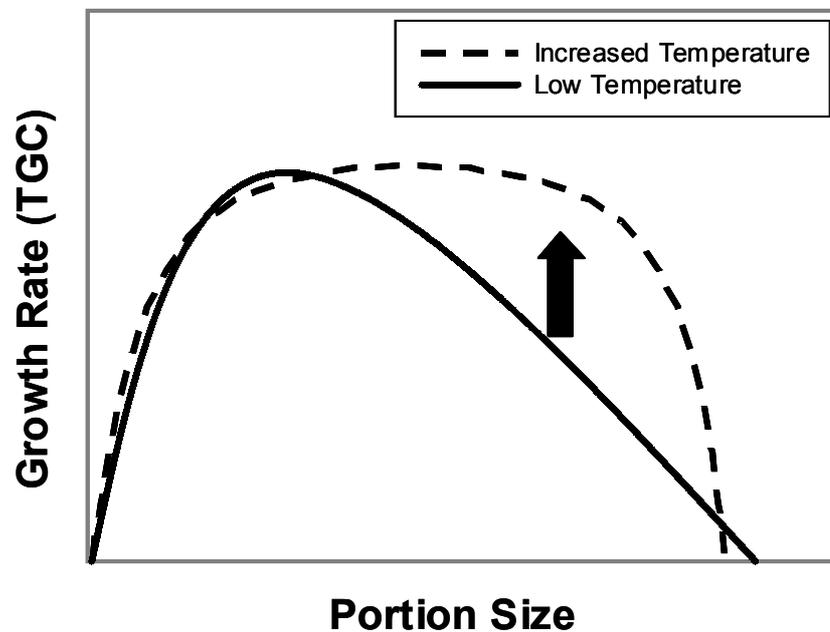


Fig. 2. Schematic relationship showing the effect of changes in temperature on the range of portion sizes giving good growth rates. At the low end of the normal range of growing temperatures, small portion sizes give highest biomass increases (solid curve). As temperatures increase, the range of portion sizes giving good growth increases as fish activity increases and more and more pellets in the larger portion sizes can be caught (dashed line).

Pellet Size

The size of the feed pellets and the rate at which they are delivered should also affect the amount of feed an individual fish can ingest over a period of time. The effects of pellet size on growth or feeding behaviour has been examined in

juvenile to adult (over 3 kg) Atlantic salmon (Stradmeyer, Metcalfe & Thorpe, 1988; Smith, Metcalfe & Huntingford, 1995) and Arctic charr (fork length 20-24 cm) (Linnér & Brännäs, 1994). Atlantic salmon appear to be rather plastic in their behavioural responses to different pellet sizes. In salmon a more immediate response to larger pellets was observed when compared to smaller pellets, but the former were more likely to be rejected than the latter. Smith, Metcalfe & Huntingford (1995) also found that pellets slightly smaller than the “normal” commercial size were eaten at the fastest rate, thereby indicating that the salmon are perhaps adjusting their feeding behaviour to compensate for a smaller feed pellet size. For Arctic charr reared under hatchery conditions, the optimal pellet size has been suggested to be around 2% of the fish’s length (Linnér & Brännäs, 1994). Others have suggested that for a range of fish species, the optimal feed size appears to be 25-50% of the mouth width (Wankowski, 1979; Tabachek, 1988). Pellets of sub-optimal size or pellets that are delivered at a high rate may cause wastage, as fish may be unable to catch large numbers of pellets before they sink through the net pen.

As a result of suggestions for an “optimal” pellet size based on fish length, salmonid farmers use many different sizes of feed pellets during the growout period. Each time the size is changed new calculations for the optimal number of pellets per fish and delivery must be done. It would therefore save both time and money if fewer sizes of pelleted feed can be used for larger parts of the growout period. Fewer sizes of pellets will also mean lower warehouse costs and more storage space for the farm operators as well as a reduced working capital for the salmon farming business.

Objectives and Aims

The objective of this thesis was to develop and test practical methodology in the various stages of feeding management for salmonid culture, specifically the calculation and presentation of the daily feed ration. In papers I-V, I have attempted to:

- 1) develop and test a reliable and practical method of calculating the daily ration of farmed fish using rainbow trout, *Oncorhynchus mykiss* (Walbaum), as a test species.
- 2) map the feeding activity patterns of rainbow trout fed using self-feeders and held under hatchery conditions.
- 3) examine the effects of altering methods of delivery of the daily ration under hatchery and commercial conditions using variation in pellet size, feed portion size, and delivery rate.

Materials & Methods

Fish and Rearing

Studies II and IV were conducted at UMF (Umeå Marine Research Centre; 63°35'N, 19°50'E) using rainbow trout under hatchery conditions in small tanks. Study V was carried out using Atlantic salmon in Norway and under semi-commercial farming conditions in sea cages. It was conducted under 2 trials and over a period of 2 years with salmon ranging in size between 1.25 and 5.0 kg. Rainbow trout used in the experiments (Papers II, III, and IV) weighed between 30-500g.

DEN Calculation

The digestible energy need (*DEN*) was required as part of the feed budget model tested in Paper II. For paper II, 12 trout were held individually in 170 l aquaria. These were individually hand-fed twice per day to satiation for three weeks at 10°C and feed intake (*FI*) was registered. The increment of weight gain (*W_i*) for these fish was measured. The digestible energy (*DE*) content of the feed (MJ·kg⁻¹) was estimated from its nutrient composition, supplied by the manufacturer, and apparent nutrient digestibility coefficients (*ADC*). The following values, from digestibility studies with Atlantic salmon, were used for calculation: protein, 20.9 kJ·g⁻¹; fat, 35.1 kJ·g⁻¹; and carbohydrate, 11.0 kJ·g⁻¹ (Hillestad, Åsgård & Berge, 1999). Based on Equation 1, the *DEN* was calculated to be 12.4 MJ DE·kg⁻¹ for the strain of rainbow trout used. In comparison, the calculated *DEN* for a rainbow trout strain of similar size in Canada was found to be approximately 15 MJ DE · kg⁻¹ (Cho & Bureau, 1998).

Due to ontogenetic changes in metabolism and body composition (Jobling, 1994), the *DEN* changes as fish grow. A juvenile fish has the possibility to grow faster and to use less energy to achieve this growth than an adult fish. In order to fully evaluate the relationship between body size and *DEN* for different fish species, a literature search was performed (Paper I). *FI*, average weight (*W_e*), *DE*, *ADC*, temperature, and species data were collected. *DEN* was calculated using equation 1 above, for 26 different species important for aquaculture.

DE content was chosen as the energy unit as it is a more reliable measurement to use in nutrition and production studies than gross energy or metabolisable energy (Jobling, 1983b). Apparent digestibility coefficients were collected for a large number of species, but the values varied markedly both within and between species (see appendix II) depending on experimental conditions and the content of the feed. Therefore, for estimating the digestible energy in the feed, the *ADC* values from Hillestad *et al.* (1999) were also used here. These values lie within the range of *ADC*s found in the literature for carnivorous fish and have been generally accepted by the Norwegian salmon farming industry (Hillestad *et al.*, 1999). However, from a practical point of view, and in lieu of the fact that variation in the *ADC*s and calculation of *DE* may be difficult, the *GE* might also be a suitable alternative for fish farmers.

Feed Budget Model

A feed budget model, which enables farmers to adapt a general model to local conditions, was tested on rainbow trout (Paper II). The model uses the theoretical daily energetic requirements of the fish and an estimation of growth to calculate the daily ration required. The advantage is that this model can be adjusted in relation to prevailing environmental conditions and the specific species or strain being farmed. Fish fed using self-feeders were used as a comparison to the results obtained using the model.

Time Series

Rainbow trout were organised into 10 groups fed using self-feeders (Paper III). The feeders incorporated the use of a trigger suspended 2 cm below the water surface. Biting the trigger caused a small feed portion to be delivered to the fish. Fish were allowed to feed unrestricted for about 60 days. Using the information collected in this way, within- and between-day trigger-biting datasets were prepared. The Fast Fourier Transform (FFT) (Cooley & Tukey, 1965) time-series analysis was used to analyse the trigger-biting activity of groups of fish on a daily and hourly scale (Paper III).

Feed Presentation

Groups of rainbow trout (Paper IV) and Atlantic salmon (Paper V) were subjected to variations of the method of presentation of the daily feed ration.

Feed Portion Size

In Paper IV, rainbow trout were fed using different portion sizes, measured in number of pellets per fish in each portion over a 25-day period and growth rate, *FCR*, and coefficient of variation of growth rate, were compared between groups. This was repeated for temperatures of 5, 10, and 15 °C and any changes in performance with temperature were analysed.

Feed Delivery Rate and Pellet Size

Atlantic salmon reared on a commercial farm site in Norway were arranged into 14 groups with various combinations of pellet sizes (0.03 - 2.68g) and delivery rates (82.5 - 1320 g·min⁻¹) (Paper V). The growth rate and *FCR* were used to compare differences between treatments.

Results – Summary of Papers

Paper I makes use of data from studies on various fish species common to aquaculture. The *FI*, *We*, *DE*, *ADC*, temperature, and species were collected from scientific journal articles and used to examine the relationship between *DEN*, and body size and temperature for different species. There seems to be a positive relationship between *DEN* and *log body weight* for salmonids and pleuronectids while no such relationship was found for percid fishes. In addition, no effect of temperature was found for either of the salmonid, pleuronectid, or percid Orders.

When examined by species, a significantly positive, linear relationship could be found between the body weight and the *DEN* for rainbow trout, Atlantic salmon, Atlantic halibut (*Hippoglossus hippoglossus*), and Arctic charr. No linear models were found to relate body weight, temperature, or a combination of both body weight and temperature to the *DEN* for sea bass (*Dicentrarchus labrax* L.), sea bream (*Sparus aurata* L.), turbot (*Scophthalmus maximus* L.) or tilapia (*Oreochromis* spp.).

In order to explore the effect of strain, a separate regression relating *body weight* to *DEN* was calculated using “Scandinavian” rainbow trout. Different strains of rainbow trout appear to have different abilities in converting the energy content of the feed into body mass gain, with data from Scandinavia being superior over data from North America. In addition, data taken from Larsson (2002) and Thodessen *et al.* (1999) and used to calculate the *DEN*, suggest that there may be an effect of selection on the utilisation of energy in feed. Larsson (2002) showed 2 strains of Arctic charr having different mean *DEN* and Thodessen *et al.* (1999) indicate that wild Atlantic salmon have a higher *DEN* than cultured strains.

Paper II was designed to test a feed budget model, which incorporated the idea of *DEN* as described above, and which farmers can use and adapt to local conditions. Rainbow trout fed using the model as a guide had a high rate of growth and good feed conversion. After 49 days the model accurately predicted growth of 300g rainbow trout to within 5g of the measured value. Growth of fish fed using self-feeders is presented for comparison with the results obtained using the model. During both growth periods, the fish fed by automatic feeders according to the model had higher rates of growth than those fed using self-feeders. The daily ration for self-fed groups in the second part of the experiment fluctuated around the ration level predicted by the model with what looked like an apparent frequency of about 2 days between peaks in activity.

In Paper II, a subjective analysis was made suggesting that the daily trigger-biting activity for self-fed groups fluctuated around the ration level predicted by the feeding model at a frequency of about 2 days. **Paper III** was designed to test this observation quantitatively using time series analysis. The self-feeding activity for groups of rainbow trout showed a repeating pattern recurring every second day. FFT analyses revealed peaks in activity for free-running rainbow at frequencies between 0.312 and 0.469. The period, *P*, is defined as the length of time required to complete one cycle and is the reciprocal of the frequency, *v*. This corresponds to periods between peaks in activity in a range of 2.1 and 3.2 days

(mean 2.4). Period values between 2.1 and 2.5 days are likely the result of leakage and should, therefore be considered as a period of 2. Although padding the series to 64 will help reduce the effects of leakage, a loss of power from frequency bands to adjacent spectral lines due to the limited number of frequencies over which the periodogram is estimated is inevitable.

When examined hourly, peaks in activity occurred at a period of 24 hours corresponding to the two crepuscular peaks in activity recurring at a period of 24 hours each. Two daily peaks in trigger activation occur at about lights on (dawn) and lights off (dusk).

In **Paper IV**, groups of 125 rainbow trout were fed using various portion sizes (0.23 – 4.29 pellets·fish⁻¹·portion⁻¹) at rearing temperatures of 5, 10, and 15 °C. It should be pointed out, however, that because this study did not use replicate groups, the results should be taken as preliminary indications in this question. The study does give an indication that portion size influences growth and variation in growth between individuals as temperatures change. At 5 °C, good growth and FCR were observed using a low portion size. However, the range of portion sizes where good growth was observed expanded with temperatures of 10 °C and 15 °C (0.52 - 3.11 pellets·fish⁻¹), possibly suggesting a high level of plasticity in the trout's ability to adjust to different portion sizes at higher temperatures.

In **Paper V** salmon were raised in commercial cages and fed using 14 different combinations of pellet sizes and delivery rates. No consistent pattern with respect to *TGC* and pellet size or delivery rate could be found using multiple regression analysis. Salmon performed equally well irrespective of treatment, having similar final sizes at the end of the experiment. Atlantic salmon showed a high level of behavioural plasticity in their ability to adjust to changes in pellet size and delivery rates without experiencing negative affects on growth or survival. That said, indications of a small effect of pellet size on the mean *TGC* for both trials were seen when a second-order plot was drawn of this data.

Discussion

The digestible energy need (*DEN*) changed with changes in body size for salmonid and pleuronectid fishes (Paper I) whereas no such relationship was found for percid fishes. The reason for this is unknown and an attempt to draw any broadly encompassing conclusions based on the limited information available will not be attempted here. A wide variety of uncontrollable variables as well as the relatively low number of samples likely contribute to the lack of relationship. In fact, it is suspected that such a relationship does exist for all fishes since, as stated, metabolic rates follow such an ontogenetic pattern (Jobling, 1994). Although metabolic processes are not directly measured for the calculation of *DEN*, it is understood that these metabolic processes are included in the final value of the *DEN*. Therefore, since metabolism has been shown to change exponentially with temperature (Brett, 1964; Brett & Groves, 1979) and allometrically with body weight (Jobling, 1994) for fish, *DEN* should also change similarly.

For all species where a model could be fit, temperature had an insignificant effect on *DEN*. This result can be explained by looking at the source of the growth and feed intake information. Most of the studies examined come from aquaculture-related studies where good growing conditions are simulated. Seldom are fish subjected to temperature extremes unless this is the purpose of the study. The effect of temperature around the optimal growing temperature of the fish is both linear and very small when compared to the effect of body size (Paper I). In addition, much more information is available in the literature for fish of different body size than for temperatures over a wide growing range, making an effect of body size easier to detect than an effect of temperature.

It was stated in the introduction that fish farmers could use the *DEN* to calculate their own feed budget models based on previous growth records. To illustrate how the energy requirements and daily feed allowance are calculated an example will be given using Atlantic salmon.

Suppose the group of salmon is made up of 50 individuals weighing approximately 200g each. The temperature of the water is 10°C. From growth information from previous growout years (or alternately through a preliminary growth study), the growth rate (expressed here using the *TGC*) is 2.50. Using this information the farm manager can calculate the weight of the fish after 1 day by using the formula for growth rate (in this case the *TGC*):

$$TGC = [(BW_f^{1/3} - BW_i^{1/3}) / (T \times D)] \times 1000 \quad (\text{Equation 4})$$

and rearranging to give:

$$BW_f = [BW_i^{1/3} + (TGC/1000 \times T \times D)]^3 \quad (\text{Equation 5})$$

where BW_f is the final body weight, BW_i is the initial body weight, T is the temperature, and D is the number of days (in this case 1). Filling in the available information:

$$\begin{aligned} BW_f &= [(200\text{g})^{1/3} + (2.50/1000 \times 10 \times 1)]^3 \\ &= 202.6\text{g} \end{aligned} \quad (\text{Equation 6})$$

The increment of weight gain (W_i) in kg after one day then is:

$$\begin{aligned} W_i &= BW_f - BW_i \\ &= 0.2026 - 0.2000 = 0.0026 \text{ kg} \cdot \text{day}^{-1} \end{aligned} \quad (\text{Equation 7})$$

The farm manager can calculate the *DEN* for the particular strain or stock of fish being farmed, but for simplicity the regression line for Atlantic salmon will be used to estimate the *DEN* for a 200g fish (Paper I).

$$\begin{aligned} DEN &= 10.77 + 1.05 \times \text{LN}(BW) \\ &= 10.77 + 1.05 \times \text{LN}(200\text{g}) = 16.3 \text{ MJ} \cdot \text{kg}^{-1}. \end{aligned} \quad (\text{Equation 8})$$

Since the *DEN* and the daily weight increase are known, the theoretical energetic requirement (*TER*) to achieve this growth can be estimated using:

$$\begin{aligned} TER &= 16.3 \text{ MJ} \cdot \text{kg}^{-1} \times 0.0026 \text{ kg} \cdot \text{day}^{-1} \\ &= 0.042 \text{ MJ} \cdot \text{day}^{-1} \end{aligned} \quad (\text{Equation 9})$$

The digestible energy content of the feed was estimated as $19.0 \text{ MJ}\cdot\text{kg}^{-1}$ and so finally, the daily feed allowance can be calculated using:

$$FA = (n \times TER)/DE \quad (\text{Equation 10})$$

where FA is the daily feed allowance and n is the number of fish, giving:

$$\begin{aligned} FA &= (50 \times 0.042)/19.0 && (\text{Equation 11}) \\ &= 0.111 \text{ kg} = 111 \text{ g day}^{-1} \end{aligned}$$

Table 1 shows an example of a feeding chart for Atlantic salmon. Feeding charts such as this one can be easily created for the particular species and stock of fish being farmed, and under the local farm conditions.

Table 1. An example of a feeding chart for Atlantic salmon (*Salmo salar* L.) constructed using fish sizes of 50 and 200 g, a TGC of 0.75 during autumn and 2.5 during spring, and DE of $19 \text{ MJ}\cdot\text{kg}^{-1}$. Amounts given are in $\text{g}\cdot\text{fish}^{-1}\cdot\text{day}^{-1}$

Temperature	Spring		Autumn	
	50g	200g	50g	200g
4	0.28	0.88	0.08	0.26
8	0.57	1.77	0.17	0.53
10	0.71	2.21	0.21	0.66
12	0.85	2.65	0.26	0.79

The feed ration model tested in Paper II and described above predicted the growth of rainbow trout extremely well, and good feed conversion indicated that there was little feed waste. These results can likely be attributed to the flexibility of the model. Both components of the model: (1) the calculated energy needed to grow one kg (DE_N) and (2) the growth data, come from calculations using the stock of fish used to test the model, and are based on local conditions. This is the biggest advantage of the present model when compared to other, similar models. Most feed budget models are based on either growth rate (*e.g.* Austreng, Storebakken & Åsgård, 1987) or energy requirement (*e.g.* Cho, 1992) estimates, but generally lack the flexibility to allow adjustments to be made in relation to local conditions. In practice, fish-farmers make somewhat arbitrary adjustments, without knowing how factors like temperature, fish growth, body composition, season, *etc.* influence the feed budget during each growth period. Using a model such as the one tested in Paper II, however, the farmer can adjust the daily ration more often and with more certainty.

The day-to-day variation in feed demand observed in the self-fed groups in Paper II is consistent with earlier observations on salmonids (Grove, Loizides & Nott, 1978; Juell, Furevik & Bjordal, 1993; Juell *et al.*, 1994). A plot of the daily self-fed activity with the amount predicted by the model (Paper II) shows variation of the self-fed amount around the predicted value. The reason for this variation is unclear, but it may be related to changes in stomach fullness and the time required for emptying (gastric evacuation time) (Grove, Loizides & Nott, 1978; Bromley,

1994). Using self-feeders with unlimited access to feed then, may cause fish to eat more than is energetically required for maximal growth every second day. Variation in feeding for groups of fish fed using automatic feeders at rates predicted by the model were not registered, but any such variations were probably minor since major variation would have resulted in feed waste and high *FCR* values.

In Paper III the daily variation in self-feeding activity for groups of rainbow trout was mapped using time-series analysis. It was concluded that a 2-day pattern between peaks in daily trigger-biting activity exists in rainbow trout weighing between 30 and 300g and held in 1m³ freshwater tanks. The implication of the 2-day period is not that trout fast every second day. On the contrary, trout activate the trigger every day, but the results suggest that the total biting activity is greater every other day. Whether the rhythmic pattern seen is controlled by some kind of internal clock or whether it is simply an artefact of the feeding system used is unknown. Whatever the cause of the pattern, fish farmers should perhaps adjust feed delivery to match feeding activity and thereby reduce overfeeding.

When the trigger-biting activity was examined within days, an interesting observation was made. As expected, the morning peak in activity always appears as trout probably initially associate the conditioned stimulus of lights on with the availability of food. As the study progressed under consistent photoperiod conditions, trout learned when “dawn” occurred and anticipated this by biting before the lights came on. A second and larger peak appeared in the evening, contrary to other studies showing the major peak occurring during the dawn in Atlantic salmon (Kadri *et al.*, 1991; Paspatis & Boujard, 1996). Eriksson & Alanärä (1992) suggested that the crepuscular activity (at dawn and dusk) of stream-living salmonids is due to a trade-off between food availability and predation risk. They explained that locomotory activity patterns of Atlantic salmon corresponded to organic drift of mayfly larvae. At the same time, lowered light levels impair the ability of visual predators on salmonids. However, since salmon are also visual predators, a trade-off must exist between predation risk and the efficiency of catching abundant prey; that time being at dusk and dawn. Although not the same species, the behavioural patterns observed in rainbow trout might also share these explanations.

From a fish farming point of view, it is obvious that the best feeding times should be at dawn and dusk, when fish-feeding activity is highest. However, fish-feeding schedules are often built around human convenience and the fish are therefore fed at various times of the day. It may be difficult, for example, to get to a remote farm-site at dawn and dusk every day to feed fish. In this capacity, timer-controlled automatic or demand-feeding systems might be used to feed at optimal times during the day.

Paper IV indicates that portion size may affect the growth rate and food conversion efficiency of rainbow trout held in small tanks. As temperatures increase from 5 to 15 °C, trout may be able to feed effectively over a broader range of portion sizes. The group fed using 0.52 pellets·fish⁻¹·portion⁻¹ grew at a high rate while maintaining good *FCR* throughout the study, however, due to the confounding effect of group it is difficult to determine if this effect is significant.

Groups fed using between 1.89 and 3.11 pellets·fish⁻¹·portion⁻¹ did not grow well and had a poor *FCR* at 5 °C. When temperatures were increased fish probably became more active and caught a larger proportion of the pellets in larger portions as reflected by improvements in growth rate and *FCR*. The positive result in terms of growth performance with increasing portion size at 10 °C and 15 °C would be expected, since, like other ectothermic animals, fish become sluggish at low temperatures. This is in agreement with studies on feeding and changes in swimming activity at different temperatures (Elliott, 1975; Rimmer, Saunders & Paim., 1985; Cunjak, 1988; Fraser, Metcalfe & Thorpe, 1993; Fraser *et al.*, 1995; Graham, Thorpe & Metcalfe, 1996).

While these results are interesting, the authors suggest some caution be taken in interpreting them due to the confounding effect of group in the experimental design. The results do give an indication of an effect of portion size on the growth and *FCR* of small rainbow trout and so are presented here in that context. However, further work will be required before suggestions are made as to exact portion sizes at different temperatures.

In this study, group 2, fed using a small feed portion size, gave good growth and *FCR* throughout the study. However, increasing temperatures increase the energy and feed demand of fish, and without a corresponding change in feed portion size, the fish-farmer is forced to feed the fish essentially throughout the entire day. A reduced period of feeding, however, would be beneficial from a practical viewpoint. Commercial farms using a feed barge, for example, would benefit from reduced feeding time at every cage. Thus, a better strategy would be to feed fish using feed portions that change in size with changes in temperature, large at high temperatures and small at low temperatures, thereby keeping meal length relatively constant over temperatures. In this way, the daily feed budget can be delivered in a much shorter time without decreasing performance. The increase in growth performance with larger portion sizes at higher temperatures as has been found in Paper IV supports this theory.

In Paper V the effects of delivery rate and pellet size were examined on a semi-commercial salmon farm. Fish reared in commercial aquaculture operations are sometimes fed at a relatively low intensity over prolonged periods (Alanära, Kadri, & Paspatis, 2001). This 'little-and-often' strategy has partly been the result of technical limitations in some of the feeding systems and partly because many farmers think that intense feeding will result in feed waste. In Paper V, fish were fed using one intense meal per day of approximately two hours duration. Other studies have shown that feeding fish using 1-4 meals per day under high intensity have resulted in good growth rates in salmonids (Elliot, 1975; Grayton & Beamish, 1977; Jobling, 1983; Juell *et al.*, 1994), and Cho (1990) suggested that 1-2 meals per day is sufficient for optimal growth in rainbow trout weighing over 200g. The 'little-and-often' feeding regime is probably associated with increased swimming activity and energy expenditures (Alanära, 1992; Johansen & Jobling, 1998), whereas the main positive effect of a 'large-and-seldom' regime is the inclusion of longer non-feeding periods during the rest of the day, as well as the aforementioned, practical benefits of reduced feeding time.

Assuming, according to the above, that the number or length of meals decrease, the rate at which feed is supplied must increase accordingly. Since salmon have been shown to be extremely flexible in adopting their feeding rate to the rate of delivery (Paper V), the fastest delivery rate that still produces little waste should be chosen in order to fulfil this requirement. In addition, the faster the supply rate the better in avoiding large variation in growth rates, because slow rates may allow feed monopolisation by more competitive individuals (Grant, 1993). As shown in Paper III, it appears that the optimal times for feeding in rainbow trout are for short periods in the morning and evening. A fish farmer should take advantage of this intense feeding activity period and feed at as high a rate as is possible without causing wastage.

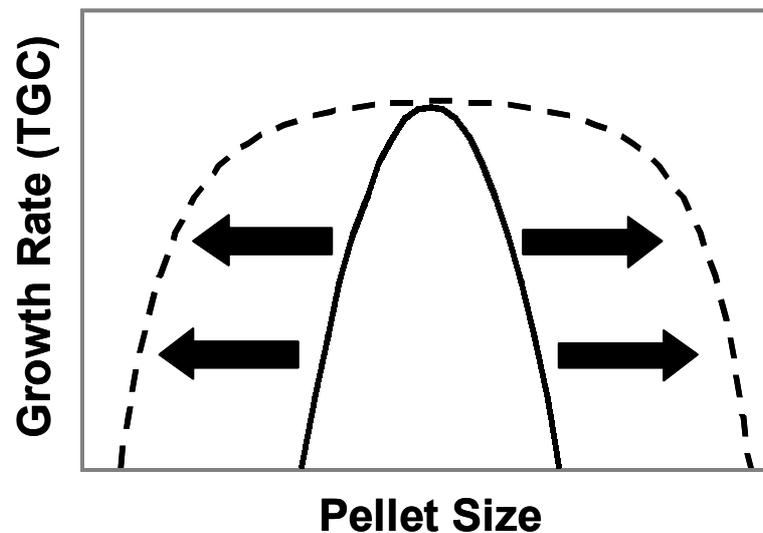


Fig. 3. Schematic illustration of plasticity in salmon feeding behaviour. The solid line shows the “preferred” pellet size for salmon of a given body size. The dashed line indicates the ability of the salmon to make adjustments in their behaviour and accept pellets of an inoptimal size without compromising growth.

As stated in the introduction, the relationship between portion size and growth rate should follow a quadratic function. Similarly, it was hypothesised that pellet size and growth rate should follow the same type of function. This type of plot was examined and indications of a small effect of pellet size on the mean *TGC* for both trials were seen. It is probable that this relationship exists but that the pellet sizes tested here were not large or small enough to fully challenge the salmon’s ability to adjust feeding activity. A “preferred” pellet size might exist but, under conditions where this size is unavailable, salmon display their remarkable ability to adjust, and show no decreases in growth rates (Fig. 3). The full effect of pellet size on the growth rate may have been masked by the long growout periods in the study and led to results seen as contradictory to previous work with Atlantic salmon (Stradmeyer, Metcalfe & Thorpe, 1988; Smith, Metcalfe & Huntingford, 1995). Pellet sizes that were very large for a particular fish size at the beginning of a ‘Period’ may have become only slightly oversized by the end of that same period due to fish growth. The results from Paper V, however, are seen as a testament to

the extraordinary ability of Atlantic salmon to adjust to changes in feed presentation. At some extreme, pellet size, for example, will obviously have an affect on fish performance. A pellet that is larger than the gape width of the fish or is so large that handling time becomes a limiting factor in the fish's ability to ingest enough pellets to maintain good growth will clearly have adverse effects. Within a reasonable range of pellet sizes and delivery rates, however, large Atlantic salmon raised in sea cages appear to adjust and grow relatively well regardless if the size/rate is ¼ to 4 times that which is recommended by the industry.

Conclusions

It has been emphasised throughout this thesis that the cost of feed is the highest returning expense in salmonid aquaculture. Therefore, in order for the business to be successful, it is paramount (1) to have access to an accurate model for calculation of daily feed requirements, including an understanding of how these requirements may change over time, and (2) that the feed is presented in a manner that is acceptable to the target species in order to ensure utilisation. Uningested or undigested feed translates directly into a reduction in the farm's economic viability and an increase in environmental loading.

The model used for the calculation of the daily feeding ration in Paper II was based on the amount of energy required by that strain of fish, reared under those particular conditions, and at that particular time of the year. The advantage with this model is that although it is based on energetics, direct calculation of a complete energetic budget is unnecessary. Farmers can use source information such as that presented in Paper I to estimate the digestible energy needed for a 1 kg gain in biomass, or may calculate this value specifically for the fish species and strain being farmed (Paper II). Information on annual growth cycles is often available from previous production years and so the farmer can adjust accordingly for changes in appetite throughout the year. Even if a demand feeding system is in place, the utilisation of a model to calculate the daily ration is useful to aid in feeding management.

As demonstrated in Paper III, fish appetite varies both within and across days. It has also been shown that this variation occurs on a seasonal basis (Rowe & Thorpe, 1990; Jobling & Baardvik, 1991; Eriksson & Alanärä, 1992; Thorpe, 1994; Sæther *et al.*, 1996). Within-day variation can be easily adjusted for, simply by feeding during times of the day when fish are most willing to accept feed. For rainbow trout, this appears to be during short periods in the morning and evening, under conditions of changing light (dawn and dusk). The feed ration model presented in Paper II does not regulate daily feed intake to account for daily variations in appetite. However, as shown in Paper II, it does calculate an amount of feed at the approximate midpoint between the peaks and troughs of the amount fed using demand feeders. Therefore, over a production period, the amount fed using demand feeders and that fed using the model should be approximately equal.

Papers IV and V demonstrate, probably more than anything, plasticity in salmonids. Although the feed delivery rates and pellet sizes were varied between ¼x and 4x that considered 'normal', no significant effect on growth rate was detected (Paper V). In Paper IV, a significant effect of portion size was found at 5 °C. At low temperatures, physiology and swimming activity is reduced and so fish have difficulty in catching all pellets in a large portion before they sink out of reach. At higher temperatures, fish could be fed, with good production results, using larger and larger portion sizes. It was suggested, therefore, that, if possible, to save time and reduce the length of the stressful feeding periods, that the largest possible feed portion be used at different temperatures.

The thesis began with some production figures presented by the FAO. It was stated that small advances in production efficiency for such a large industry would give large economic returns. Consider this: A farm having 12 cages each stocked with 20,000 Atlantic salmon weighing 500g each, giving a total of 120 mt. Production for the previous year gave an *FCR* of 1.0. Fish final size was 4kg (biomass 960 mt) and total feed used throughout the year was therefore 840 mt. Improvements in feeding management have lowered the *FCR* to 0.90 during the current production year. Assuming no mortality and the same final slaughter size, the farmer would have used 756 mt of feed; a reduction of almost 100 mt! Considerable economic returns for small changes in feed management practices and yet, further benefits from time saved through, for example, increased feed delivery rates or portion sizes are not included in this simple illustration.

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Given the only space where I am *risk-free* in expressing my own feelings, I choose to use the words of others. In this way unnamed names are never forgotten but remain unnamed with the unforgotten.

“In order to make an apple pie from scratch, you must first create the universe” (*Sagan, Cosmos*). Having seen that the work was already ‘published’, I proceeded to work on my own ‘pie’. Thank-you to my friends and co-workers at the Dept. of Aquaculture. You’ve made a foreign cook feel at home among the Swedish chefs (and even made me learn that crazy language “U putt de morn-y mort in de fishy dishy!”). Special thanks to the ‘*maître d’Vattenbruk*.’ Utan henne skulle vi inte klara oss! “Discovery consists of seeing what everybody has seen and thinking what nobody has thought” (*von Szent-Gyorgyi*). Thank you to my supervisor ‘Chef (Ankan) Alanära’ for sharing your ability to perform this task with me. Thanks also to Ewos and ‘Chef (Laksen) Crampton’ for the “salmon projects”.

Not everything can be explained by science. It’s been said that, “Only love can be divided endlessly and still not diminish” (*Lindbergh*). Varför kan jag “inte ens stå när du inte ser på?” (*Berg*). Tack för att du ser på. And, in stereo, “Yours are the sweetest eyes, I’ve ever seen” (*Taupin*)... Often “The best effect of fine persons is felt after we have left their presence” (*Emerson*) and meeting is a feeling like no other. “Nothing makes the earth seem so spacious as to have friends at a distance” (*Thoreau*). Sweden, Newfoundland, & Canada... the earth will always be huge to me. Thanks to all my friends!

Now, “Sooner or later we all quote our mothers” (*Williams*)... and fathers for that matter. I remember, “When I was 14 I thought my father was the dumbest human being alive. By the time I reached 24 I couldn’t believe how smart he had become in 10 years” (*Twain*). Sometimes we take our family for granted but I am forever indebted to my family for standing behind me through everything. What can I say?.. Other than, “Thanks, you’re the best!” I’ve been in school for some 25 years (it’s true!) but no amount of reading will ever make me as smart as my mother’s mother, who left school in Grade 8 to take care of her family. If there’s one thing I’ve learned from her it’s that “We do not stop playing because we are old, we grow old because we stop playing” (*Hayes*). She’s the youngest 91-year old in the world. Ginger tea, raison buns, and late night yarns at the kitchen table, where the beach still sings, the tides still change and the gulls still rise in the landwash. Those memories have both hurt me and helped me uncountable times during my studies here in Sweden.

Back to the Cosmos! “Ah, but a man’s reach should exceed his grasp - or what’s a heaven for?” (*Browning*). I have a tendency to fly away, hands clasping for everything in sight. Wanting to try everything at once. Thanks to everyone for keeping me grounded (or trying to?). Lastly, from one of the best: “Imagination is more important than knowledge” (*Einstein*). Words to live by.