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Development of a novel reference feed intake model for Atlantic salmon (*Salmo salar*) based on temperature and body weight

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ABSTRACT

Precision aquaculture requires the use of advanced technologies to optimize fish management. Substantial progress has been achieved in modeling Atlantic salmon (*Salmon salar*) growth and feeding behavior. However, there is still no simple mathematical model to predict feed intake that can be used for reference and benchmarking. This study aims to infer basic parametrized equations for Atlantic salmon feed intake using a minimal number of predictors: body weight and temperature. We used data from 64 previous publications and 25 commercial feeding tables. Various mathematical models were tested, incorporating different temperature functions and fitting methods. The following model provided the most accurate predictions under a wider range of temperatures and fish body weights:

 $FI = 0.006 \times BW^{0.80} \times e^{(0.287 \times temperature - 0.012 \times temperature^2)}$

where FI is the feed intake (g/fish/day), BW the average body weight of fish (g) and temperature the water temperature (°C). Using simple least squares and robust fitting methods yields better prediction capacities, while data from commercial feeding tables does not significantly enhance model accuracy. This basic reference model developed on this study can be readily used as an applied tool, e.g. estimating the feed amount required for production or trials, determining baseline feed intake when building more complex models accounting for other factors, developing growth models taking feed intake as input, evaluating current feeding practices. Its simplicity, adaptability, and broad applicability represent a valuable contribution to the field, providing a practical foundation for future model development and decision-making in Atlantic salmon farming management.

1. Introduction

Atlantic salmon (*Salmo salar*) is the predominant aquaculture species in Norway, with an export volume of approximately 1.5 million tons in 2023 (Fiskeridirektoratet, 2024), and it holds significant economic importance in other countries as well. Like other fish species, feed constitutes the largest operational cost in Atlantic salmon farming, often exceeding 50 % of total expenses (Buentello et al., 2000; Iversen et al., 2020). The current feeding management practices for Atlantic salmon primarily rely on biomass estimates and feeding tables outlining feeding rates based on fish size and water temperature classes. Administration of each meal, however, is largely guided by the intuition and experience of the individual farm personnel, supplemented by underwater cameras to monitor fish behavior as a proxy for appetite (Berckmans, 2017; Føre et al., 2018). Sonar systems are also sometimes employed to track feeding activity and fish distribution. These also provide essential data on biomass, size distribution, and density for effective farm management (Knudsen et al., 2004; Pettersen et al., 2019; Ubina et al., 2022). Despite these tools, current practices often lead to inaccuracies in feed intake estimates, frequently resulting in overfeeding (Webster et al., 2023). Farmers, cautious of underfeeding and losing growth potential, tend to provide excess feed, leading to resource waste and significant environmental, economic, and reputational impacts (Sun et al., 2016).

Mathematical modeling offers a promising solution to address these inefficiencies. Such models, when integrated into advanced frameworks like digital twins and decision systems, can improve the accuracy and

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efficiency of feed management strategies. Significant progress was achieved in developing models to estimate growth and feeding behavior in Atlantic salmon (Føre et al., 2013, 2016, 2017). Some simple models for feed intake have also been proposed (Gomes et al., 2023). However, there is currently no published model specifically designed to predict feed intake in this species using a minimum number of input variables. A baseline model designed with body weight and temperature as its primary variables is essential for advancing feed intake predictions. These predictors, chosen for their well-documented roles in feed intake regulation, ensure a balance between simplicity and biological relevance.

This simple reference model is crucial for several reasons. First, it can serve as the simplest benchmark for validating more complex models that incorporate additional factors, such as oxygen, salinity, pH, or meal frequency. Second, validation of nutrient-dependent or dynamic agent-based models requires matching their results with the data based on this baseline reference equation. For example, Føre et al. (2016) reported a nutrient-dependent agent-based feed intake model, but its validation failed to provide reliable predictions of feed intake.

For its development, the model uses existing published literature, providing a cost-effective and scientifically robust approach to mathematical modeling. This reduces the need for new experiments, aligning with the Reduction principle of the 3Rs (Replacement, Reduction, and Refinement) in animal research. It also enhances model replicability across diverse contexts ("large world modeling") rather than limiting it to specific trial conditions ("small world modeling"). For Atlantic salmon, ample datasets are available from feeding tables and prior studies, providing a strong foundation for model development.

The choice of candidate exponential equations was grounded in mechanistic insights into feed intake regulation. Furthermore, exponential equations with multiplicative components provide a general extensible framework to add further factors. More complex models can build on this baseline by adding multiplicative (or additive) components, enhancing our understanding of the physiological and environmental factors that influence appetite and feed intake. This, in turn, is crucial for growth models and feeding optimization. Cross-validation, involving fitting the model on one dataset and then testing it on an unrelated dataset (e.g., Rhinehart, 2016; Yates et al., 2023), ensures uncertainty estimation, generalization, and robust prediction.

By serving as both a practical tool and a benchmark, this baseline model aims to improve understanding of the factors influencing appetite and feed intake. For example, it can support trials of new feed ingredients by estimating satiation levels, thereby optimizing resource allocation and experimental design.

This study represents the first step toward developing a reference mathematical model to estimate feed intake in Atlantic salmon based on key predictors, specifically body weight and temperature. Using commercial feeding tables and published data, the model was developed to replace traditional feeding tables, support growth models, and serve as a benchmark for improving feeding practices in aquaculture.

2. Materials and methods

2.1. Data collection

The mathematical model was developed using data from published literature and online commercial feeding tables. Therefore, no experimental work was performed during this research. Data from 64 scientific publications published between 1991 and 2020 describing measured feed intake rates for Atlantic salmon was systematically gathered (see Supplementary material).

According to the description of each paper, the experimental conditions (temperature, number of trial days, initial and final weight) were recorded. The daily feed intake was calculated by distributing the cumulative feed intake over the trial period as a fixed proportion of the estimated daily body weight. The daily body weight was estimated using exponential interpolation between the measured body weights at sampling points. The range of temperatures and body weights covered by this data was 6.0–19.1 °C and 0.92–4075.84 g, respectively.

Commercial feeding tables, available online, were used to increase the range of body weight and temperature data. In total, 25 feeding tables from fry to adult life stages, ranging in body weight from 0.20 g to 5000 g and covering a temperature range of 2–20 °C. Feed intake (kg of feed per 100 kg fish per day) was directly retrieved from the information provided in the commercial feeding tables.

Fig. 1 provides an overall view of the body weight and temperature range from scientific publications and commercial feeding tables.

2.2. Model design

All the evaluated models followed the same general shape mathematically, wherein the effects of temperature and body weight (BW) are regarded as multiplicatively separable. The f(BW) function for every model exhibits a power-law connection (Eq. 1).

$$FI(BW, temperature) = a \times BW^b \times g(temperature)$$
(1)

Three different categories of models were considered with different relations for g(temperature); exponential (Eq. 2), log-quadratic (Eq. 3) and log-cubic (Eq. 4). Fig. 2 illustrates the distinct relationships of temperature function with the varying degrees of complexity.

Category 1

 $FI(BW, temperature) = a \times BW^b \times e^{(c \times temperature)}$ (2)

Category 2

$$FI(BW, temperature) = a \times BW^{b}$$

$$\times e^{(c \times temperature - d \times temperature^{2})}$$
(3)

Category 3

 $FI(BW, temperature) = a \times BW^{b} \times e^{(c \times temperature+ d} \times temperature^{2} - e \times temperature^{3})$ (4)

2.3. Model fitting method

An "inductivist" approach to modeling was used, considering a range of fitting methods with little a priori constraints. To test different assumptions of the underlying data structure different model fitting methods (implemented in R version 4.2.1) were used.

- 1) Least squares regression, ("simple" methods, using function lm()).
- Huber loss minimization ("robust" methods, using function MASS:: rlm()).
- 3) Mixed-effect modelling ("mixed" methods, source being the random effect, using function lme4::lmer()).

In addition, 3 variations of model fitting were performed:

- 1) Dynamic Energy Budget (DEB) theory, with fixed body weight exponent 2/3 ("fixed23" variants);
- excluding the auxiliary feeding table data during calibration ("i" variants). This method was not applied to mixed model-effect models, since the random effect applied was the source of the feeding table;
- 3) recalibrating the "a" parameter using only the data from scientific publications data ("r" variants).

Therefore, 33 different models with fitting combinations were tested in total.



Fig. 1. Violin plot of the range of body weight (g) and temperature (°C) of the scientific publications (light grey) and commercial feeding tables (dark grey).



Fig. 2. The distinct relationships of temperature function with varying degrees of complexity. A illustrates an exponential correlation of temperature with the equation $e^{(temperature)}$. B illustrates a log-quadratic correlation of temperature with the equation $e^{(temperature-temperature^2)}$. C illustrates a log-cubic correlation with temperature with the equation $e^{(temperature-temperature^2)}$. C illustrates a log-cubic correlation with temperature with the equation $e^{(temperature-temperature^2)}$.

2.4. Model evaluation and model analysis

To determine the best process to obtain reference models it was used the cross-validation method. Cross-validation is a robust statistical technique that assesses model performance by partitioning the dataset into multiple subsets (folds). In this technique, the model is trained on a subset of the data and validated on the remaining fold, with this process repeated multiple times to ensure each subset is used for validation at least once. Therefore, a series of 5-fold cross-validations with 5 repetitions (totaling 825 evaluations) using 454 data points was performed to estimate, for each model and fitting method combination, the expected mean absolute percentage error (MAPE; Eq. 5).

$$MAPE(\%) = \frac{100}{n} \sum_{i=1}^{n} \left| \frac{P_i - O_i}{O_i} \right|$$
 (5)

Where *n* is the number of predicted-observed value pairs, P_i is the predicted value, and O_i is the observed value.

The model evaluation was performed by assessing the MAPE values of each model and fitting method using cross-validation method. The smaller the percentage of MAPE value, the smaller was the deviation of the pattern predicted by the model from the observed data that was not used for model fitting. Subsequently, the three models with the lowest MAPE value of each category were selected to perform a model analysis. The model analysis consisted of evaluating the raw residual values of feed intake predictions and evaluating the predicted performance, by testing the models' prediction using different temperatures and body weights.

Additionally, model selection was further supported by using Information Criteria using Akaike Information Criterion corrected for small sample sizes (AICc; Eq. 6) values to assess the relative quality of the models, considering both their predictive performance and complexity.

$$AICc = n \ln\left(\frac{SEE}{n}\right) + \frac{2k(k+1)}{n-k-1}$$
(6)

Where n is the number of observations, SEE is sum of the square errors, and k is the number of parameters in the model.

3. Results and discussion

3.1. Model evaluation

The overall result of the cross-validation of the models (Table 1) indicates substantial unmodelled variation in feed intake rates, with MAPE values ranging from 28.19 % to 59.93 %, suggesting a variability in prediction accuracy across models and fitting techniques. The elevated MAPE can be attributed to the considerable variability in the

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Table 1

Mean absolute percentage error (MAPE) of each model, obtained through cross-validation on evaluation datasets.

Model/Fitting	MAPE (%)
FI3/robust_i	28.19
FI3/simple_i	28.45
FI2/simple_i	29.40
FI2/robust_i	29.51
FI1/robust_i	30.43
FI1/simple_i	30.44
FI2/simple_r	33.20
FI2/robust_r	34.62
FI3/simple_r	34.84
FI2/mixed_r	35.25
FI2/mixed	35.37
FI2/robust	35.75
FI3/robust_r	36.63
FI3/mixed_r	36.82
FI3/mixed	36.94
FI3/robust	37.21
FI1/robust	37.41
FI2/simple	37.61
FI1/simple	38.13
FI1/mixed	38.83
FI1/mixed_r	39.00
FI3/simple	39.10
FI1/simple_r	40.07
FI1/robust_r	41.01
FI2/mixed_fixed23	52.33
FI3/mixed_fixed23	53.56
FI1/simple_fixed23	54.57
FI2/simple_fixed23	55.19
FI1/mixed_fixed23	55.30
FI3/simple_fixed23	56.40
FI1/robust_fixed23	57.18
FI2/robust_fixed23	58.87
FI3/robust_fixed23	59.93

dataset derived from scientific publications. This extensive dataset contains a wide range in unmodelled factors influencing feed intake, such as daily meals, feeding schedules, and dissolved oxygen levels, contributing significantly to the error. Moreover, achieving a high level of prediction (very low MAPE) is hardly possible due to the inherent variability in fish behavior (Assan et al., 2021; Martins et al., 2011). We therefore used a value of 40 % as a cutoff defining satisfactory model prediction level.

The model "FI3/robust_i" exhibits the lowest cross-validation MAPE value of 28.19 %, that indicates the best accuracy of prediction. In general, models using the "simple" (Least squares regression) and "robust" (Huber loss minimization) fitting tended to have better prediction accuracy. The use of "mixed" (Mixed-Effect Modeling) did not provided any improvement on the quality of the model (MAPE). Consequently, including the feeding tables (as a random effect) did not provide any improvement to the accuracy of the model. Therefore, it can be concluded that for this model using simpler calibration methods, such as "simple" and "robust," resulted in better prediction capacity.

In addition, models ignoring the feeding tables (the "i" category) demonstrated a lower MAPE. This indicates that adding the data from the feeding tables may not have contributed to the model quality for a variety of reasons, e.g. high homogeneity of these data with minuscule deviations from the main biological pattern.

The models using the variation "fixed23" with fixed weight raised to the power of 2/3 had the highest MAPE values and, therefore, low prediction accuracy. Models based on DEB theory have been utilized with various aquaculture species in the Mediterranean region, including the European sea bass (*Dicentrarchus labrax*), seabream (*Diplodus sargus*), and gilthead seabream (*Sparus aurata*). In these models, the ingestion rates { \dot{p}_x } and assimilation rate { \dot{p}_A } were calculated as proportionally to the surface area of the structural body volume ($V^{2/3}$). This approach has allowed the development of models capable of quantifying feeding and growth dynamics for the species mentioned above (Serpa et al., 2013; Stavrakidis-Zachou et al., 2019). Furthermore, the application of the DEB theory model has been widely applied to bivalves in aquaculture, especially to the Pacific oyster (*Crassostrea gigas*). The assimilation rate { \dot{p}_A } has also a direct relation with the body volume ($V^{2/3}$), resulting in reliable growth models in various environments (Bourlès et al., 2009; Pouvreau et al., 2006; Van der Veer and Alunno-Bruscia, 2006).

A study that modeled the growth performance and feeding behavior of Atlantic salmon using a DEB model approach calculated feed intake depending on the maximum gut capacity (Føre et al., 2016). In addition, a model developed with a behavior approach in sea cages of Atlantic salmon used the stomach content to predict the fish's appetite and therefore the feed intake (Føre et al., 2009). Hence, the assumption of the assimilation rate directly proportional to ($V^{2/3}$) does not appear to hold consistently across Atlantic salmon, which can explain why the variable "fixed23" did not help to improve the model accuracy. In addition, the exponent value for species-specific and rapidly growing animals in agriculture has been questioned, which might be the case of the Atlantic salmon (Baldwin and Bywater, 1984; Kil et al. 2013; Thonney et al., 1976).

Furthermore, using the temperature as log-cubic seemed to improve the model accuracy: there was an improvement in prediction capacity by considering additional complexity on the temperature effect. First, the temperature range may have provided sufficient variability for the more complex models. Second, the log-cubic model (Eq. 4) defines a biphasic effect: increased FI up to a point and then reduction at exceedingly high temperature (see Fig. 2C). This agrees with the commonly observed suppression of feed intake at higher temperatures in the Atlantic salmon (Handeland et al., 2008; Kullgren et al., 2013).

By comparing the model "FI3/robust_i" with "FI2/robust_i" and "FI1/ robust_i", there was an increase in MAPE of approximately 1.32 % and 2.24 %, respectively.

3.2. Model analysis

Following model evaluation, the top-performing model from each model type (FI1, FI2, FI3) was selected for analysis of residuals (Fig. 3). The variables and corresponding values of these chosen models are outlined in Table 2. Notably, the "FI3/robust_i" model exhibited the lowest MAPE of 28.19 %, indicating the robust predictive performance. While the "FI2/simple_i" model demonstrated a MAPE of 29.40 % and "FI1/robust_i" model recorded a MAPE of 30.43 %. However, when analyzing the AICc values, it becomes evident that the "FI2/simple_i" model has the lowest AICc (595.44), indicating the best trade-off between goodness-of-fit and model complexity among the evaluated options.



Fig. 3. Box plots of the prediction error (PE%) for model "FI1/robust_i", "FI2/ simple_i" and "FI3/robust_i" respectively.

Table 2

Equations with parameter values for model "FI3/robust_i," "FI2/simple_i," and "FI1/robust_i", their mean absolute percentage error (MAPE) and Akaike Information Criterion (AICc) during the evaluation phase. Standard deviation errors were \pm 1.96, 1.93, and 2.15, respectively.

Model/Fitting	Equation	MAPE (%)	AICc
FI3/robust_i	$0.0000814 imes BW^{0.80} imes e^{(1.43 imes temperature - 0.11 imes temperature^20.003 imes temperature^3)}$	28.19	609.55
FI2/simple_i	$0.006 \times BW^{0.80} \times e^{(0.287 \times temperature - 0.012 \times temperature^2)}$	29.40	595.44
FI1/robust_i	$0.028 \times BW^{0.80} \times e^{(-0.004 \times temperature)}$	30.43	697.12

The distribution of Percentage Error (PE) values for the best models in each category is symmetrical and centered around zero, indicating that the models exhibit similar performance across the range of predictions, with errors evenly distributed around the mean. Additionally, approximately 75 % of the points exhibited a percentage error below 40 %. This indicates that, in most cases, the model's error falls within the pre-defined threshold of 40 %, which was established as the benchmark for satisfactory prediction accuracy prior to the development of this work.

3.3. Model performance evaluation

3.3.1. Temperature

Three different temperatures were selected to evaluate the prediction capacity of the models based on a previous study by Handeland et al. (2008) that investigated the effect of temperature on feed intake. The study found that fish reared at 6°C and 18°C had significantly lower feed intake, while 14°C was the optimal temperature for growth and feed intake. Consequently, for our evaluation, we chose temperatures of 5°C, 15°C, and 20°C, considering both the literature and the available data range of the dataset used to develop the models. To facilitate the visualization of the accuracy of the models a range of 20 % lower and 20 % higher than the reference temperature was defined. This enabled a clear comparison of the model predictions within a \pm 20 % margin around the chosen temperatures (Figs. 4 to 6).

When comparing the predicting performance of the models at 5°C, which is considered a temperature below optimal for Atlantic salmon cultivation, it is clear that "FI2/simple_i" has closer predictions to the data from the trials and auxiliary data from commercial feeding tables that were performed with temperature range from 4–6°C (Fig. 4). "FI1/ robust_i " and "FI3/ robust _i" overestimate and underestimate the feed intake, respectively.

At 15 °C, which is close to the optimal temperature for Atlantic salmon cultivation, all three models show similar predictions (Fig. 5). This temperature range is well-studied, with extensive data from both

scientific publications and commercial feeding tables. However, feed intake rates (g/fish/day) reported in scientific studies tend to be lower than those provided in commercial feeding tables.

Analysis of the prediction accuracy at the temperature 20 °C (which is above the optimal level for the Atlantic salmon) shows that model "FI3/robust_i" and model "FI1/simple_i" have better feed intake prediction capacity (Fig. 6) while "FI2/robust_i" underestimates the feed intake. Therefore, the Atlantic salmon's feed intake prediction is better performed by temperature described as a log-cubic or an exponential function.

In summary, the evaluation of model performance for predicting feed intake in Atlantic salmon cultivation reveals nuanced findings across different temperature conditions. At temperatures below optimal levels, such as 5 °C, the "FI2/simple_i" model demonstrates closer alignment with trial data compared to "FI1/robust_i " and "FI3/simple_i. At 15 °C, considered as optimal cultivation temperature, all three models produce similar predictions with a good fit. However, at 20 °C, above optimal levels, "FI3/robust_i" and "FI1/simple_i" outperform "FI2/robust_i" in predicting feed intake.

3.3.2. Body weight

We also evaluated the performance of each model to predict the feed intake under three different body weights, 10, 100, and 1000 g with variable temperature (Figs. 7 to 9).

First, the performance of the model "FI1/robust_i" was evaluated (Fig. 7). There was a slight decrease in feed intake from 5 to 20 °C. However, as previously stated, an increase in feed intake from 5 to 14 would be expected, followed by a decrease of feed intake at higher temperatures (Handeland et al., 2008).

The model "FI2/simple_i" performance was subsequently evaluated (Fig. 8). The model shows an increase in feed intake until 12 °C, the temperature at which the highest feed intake occurs, followed by a decline. Previous studies indicate that feed intake should peak at 14 °C, with lower intake at 6°C and 18°C (Handeland et al., 2008). Thus, while the model's peak occurs at 12 °C instead of 14 °C, it accurately



Fig. 4. Evaluation of the best-performing models for Atlantic salmon at 5°C (purple: "FI3/robust_i", green: "FI2/simple_i", yellow: "FI1/robust_i"). Black dots represent scientific publications, grey dots are from commercial feeding data, blue dots are scientific data within \pm 20 % of 5°C, and red crosses are commercial feeding data within the same range. The x-axis shows body weight (grams), and the y-axis shows feed intake rate (g/fish/day), both in log scale.



Fig. 5. Evaluation of the best-performing models for Atlantic salmon at 15°C (purple: "FI3/robust_i", green: "FI2/simple_i", yellow: "FI1/robust_i"). Black dots represent scientific publications, grey dots are from commercial feeding data, blue dots are scientific data within \pm 20 % of 15°C, and red crosses are commercial feeding data within the same range. The x-axis shows body weight (grams), and the y-axis shows feed intake rate (g/fish/day), both in log scale.



Fig. 6. Evaluation of the best-performing models for Atlantic salmon at 20°C (purple: "FI3/robust_i", green: "FI2/simple_i", yellow: "FI1/robust_i"). Black dots represent scientific publications, grey dots are from commercial feeding data, blue dots are scientific data within \pm 20 % of 20°C, and red crosses are commercial feeding data within the same range. The x-axis shows body weight (grams), and the y-axis shows feed intake rate (g/fish/day), both in log scale.

represents the overall pattern of feed intake variation with temperature, providing a good fit to the observed data.

When evaluating the model "FI3/robust_i" (Fig. 9), the feed intake increases from 5 °C to 10 °C, then decreases between 10 °C and 16 °C, followed by another increase up to 20 °C. However, according to empirical data, an increase in feed intake is expected from 5 °C to 14 °C, which differs from the model's predictions. This discrepancy highlights the need to refine the model further to align more closely with observed feeding behavior.

3.3.3. Overall evaluation of models

The final analysis concerns the evaluation of the models with all the three different variables, feed intake, temperature and body weight (Figs. 10 to 12). Fig. 10 illustrates the model "FI1/robust_i" pattern across the three dimensions. Given that the relationship between feed intake and temperature g(temperature) is exponential, it is evident that feed intake decreases as temperature increases. Consequently, in this

scenario, the highest feed intake is observed at a temperature of 5 $^{\circ}$ C and a body weight of 1000 g.

Fig. 11 shows the relationship between the three variables for model "FI2/simple_i." The feed intake behavior in this model is similar to Fig. 2 B due to the log-quadratic relationship. In this model, the highest feed intake occurred at a temperature of 12 °C and a body weight of 1000 g, indicating an optimal condition within the modeled parameters. Overall, the model "FI2/simple_i" shows the biphasic pattern with the optimal temperature effect that agrees best with the qualitative pattern observed in the Atlantic salmon trials (Handeland et al., 2008).

Finally, Fig. 12 shows the relationship between the three variables for model "FI3/robust_i". The feed intake behavior in this model is similar to Fig. 2 C due to the log-cubic relationship, which has inflection points where the curve changes concavity. In this model the highest feed intake occurred at temperature 20 °C and a body weight of 1000 g.



Fig. 7. Evaluation of "FI1/robust i" model relationship between temperature and feed intake in three different sizes of fish (purple: 1000 g; green: 100 g; yellow: 10 g). The vertical axis shows the feed intake in percentage of body weight per day. The horizontal axis shows the temperature in degrees Celsius. Grey shaded areas indicate suboptimal temperature ranges ($< 6 \degree C \text{ or } > 18 \degree C$), where feed intake should be reduced.



Fig. 8. Evaluation of "FI2/simple_i" model relationship between temperature and feed intake in three different sizes of fish (purple: 1000 g; green: 100 g; yellow: 10 g). The vertical axis shows the feed intake in percentage of body weight per day. The horizontal axis shows the temperature in degrees Celsius. Grey shaded areas indicate suboptimal temperature ranges (< $6 \degree C$ or > 18 $\degree C$), where feed intake should be reduced.



Fig. 9. Evaluation of "FI3/robust_i" model relationship between temperature and feed intake in three different sizes of fish (purple: 1000 g; green: 100 g; yellow: 10 g). The vertical axis shows the feed intake in percentage of body weight per day. The horizontal axis shows the temperature in degrees Celsius (°C). Grey shaded areas indicate suboptimal temperature ranges (< 6 °C or > 18 °C), where feed intake should be reduced.

4. Perspectives and conclusions

The model developed in this study offers a cost-effective and scientifically solid approach to mathematical modeling in aquaculture. It focuses on predicting feed intake, which is a key factor that directly affects fish growth. While many existing models in aquaculture are designed to predict growth based on environmental and physiological factors, they often treat feed intake as a fixed or known value. This model provides reliable prediction of feed intake under specific conditions, that can be used as a complement to growth models. In addition, while this model focuses explicitly on Atlantic salmon (*Salmo salar*), its structure is based on general principles that could be adapted to other



Fig. 10. 3D surface plot illustrates the relationship between feed intake (g/ fish/day), body weight (grams), and temperature (°C) according to the model "FI1/robust_i".



Fig. 11. 3D surface plot illustrates the relationship between feed intake (g/ fish/day), body weight (grams), and temperature (°C) according to the model "FI2/simple_i".

species in aquaculture, that can be adapted for other species and environmental conditions, showing its potential to be applied widely across different aquaculture systems.

Simple static models allow the prediction of feed intake through application of a single equation that relies on the most important factors: fish body weight and temperature. Our work demonstrates that, despite simplicity, such models can provide sufficient accuracy for the prediction of feed intake of Atlantic salmon. Unlike more traditional approaches, cross-validation assesses prediction accuracy on samples different from those used for fitting and provides a reasonable estimate of prediction error and uncertainty.

Simple and robust fitting methods had better prediction capacities, but adding data from commercial feeding tables does not significantly improve model accuracy. The comparisons across multiple models using various fitting methods suggest that many other factors, such as stress, dissolved oxygen, and dynamic behavioral processes, contribute to the high variability in the data points, reducing the model's prediction capacity. However, including every additional independent variable incurs increasingly high cost for practical applications. Our results demonstrate that the simplest models had sufficient accuracy for many practical purposes. Although the model "FI3/robust_i" exhibited the



Fig. 12. 3D surface plot illustrates the relationship between feed intake (g/ fish/day), body weight (grams), and temperature (°C) according to the model "FI3/robust_i".

lowest MAPE value, utilizing "FI2/simple_i" is recommended due to its closer alignment with the actual relationships between temperature, body weight, and feed intake, especially the biphasic temperature effect. Even though the log-cubic models generally display the same biphasic pattern, the predicted feed intake increases drastically when the model extrapolates to higher temperatures, which is not realistic.

Simple models allow to distill the most important factors influencing feed intake, assisting in various practical applications. This model relies only on body weight and temperature-two variables that are routinely monitored in production systems-it offers a practical and easily implementable tool for predicting feed intake in real-world farming conditions. Additionally, they can assist in evaluating the relative roles of additional factors like diet composition and dissolved oxygen on feed intake. In commercial fish farming activities, these models can aid in identifying over- or underfeeding scenarios and optimizing overall feed strategies. Their simplicity enables easy implementation across different platforms, rendering them versatile tools for both research and practical purposes. For instance, a salmon producer could use the model to adjust feeding schedules based on seasonal temperature changes, while a researcher could apply it to determine standardized rations across experimental groups. Feed conversion ratio (FCR) can also be used to estimate feed requirements, especially when modeled as a function of body weight and temperature (Handeland et al., 2008). Ultimately, the superiority of either approach depends on model performance when applied to the same dataset. Comparative validation using common input data and performance metrics is necessary to objectively assess their relative accuracy and usefulness. Moreover, in production settings, both FCR and feed intake models are often used in conjunction to estimate fish growth and feeding rates. Although these models can individually be used to estimate feed intake based on a known growth curve, their combined use enables the estimation of both feed intake and growth. Therefore, they should be viewed as complementary rather than competing approaches.

In conclusion, the current model provides a practical framework for predicting feed intake in Atlantic salmon based on body weight and temperature. A promising direction for future research is the incorporation of additional environmental variables, such as dissolved oxygen and stress levels, which significantly influence feeding behavior and metabolic rates. By incorporating these often-overlooked factors, the model could offer more accurate and responsive feed intake predictions. Unlike commercial feeding tables, which are typically rely on generalized averages and lack transparency, this model uses clearly defined, measurable inputs, enabling the development of customized feeding strategies that better reflect real farms conditions. This will help farmers avoid both over- and underfeeding, thereby improving operational efficiency. However, it should be noted that the present model was developed using data from multiple and diverse contexts, so it's current estimates represent generalizations that may not fully capture the nuances of specific environments. Nevertheless, the modeling approach used is adaptable and the model can be recalibrated with site-specific data to enhance local accuracy.

CRediT authorship contribution statement

Ronnestad Ivar: Writing – review & editing, Supervision, Resources, Funding acquisition. **Soares Filipe:** Writing – review & editing, Project administration, Data curation. **Budaev Sergey:** Writing – review & editing, Supervision, Data curation. **Conceição Luis E.C.:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Azevedo Marina Linhares:** Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Formal analysis, Data curation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquaeng.2025.102562.

Data availability

Data will be made available on request.

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