Aquacultural Engineering 110 (2025) 102526

Contents lists available at ScienceDirect

Aquacultural Engineering

journal homepage: www.elsevier.com/locate/aque

Development and evaluation of reference feed intake models for meagre (*Argyrosomus regius*)

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ARTICLE INFO

Keywords:
Meagre
Feed intake model
Precision feeding
Nutritional modelling

ABSTRACT

The aim of the study was to identify a basic reference feed intake model to facilitate understanding of the impact of temperature as the key environmental factor, along with body weight and dietary composition. These basic models should provide the baseline for further research to advance precision farming practices and support efficient production for meagre (*Argyrosomus regius*). Several reference models, with different levels of complexity, were built using data from scientific publications and feeding tables, followed by evaluating 27 different models using various fitting methods. Each model's mean absolute percentage error was estimated through repeated 5-fold cross-validation (with n = 200 iterations). Models were divided into four categories based on the inclusion of temperature and diet composition parameters: simple feed-independent models, complex feed-independent models, simple feed-dependent models, and complex feed-dependent models. The best model from each category was identified, followed by an assessment of the overall best. Consistent with dynamic energy budget theory, models using a fixed body weight exponent of 2/3 demonstrated better fit. Feed-dependent models incorporating lipid levels outperformed feed-independent ones. Additionally, simpler models with temperature parameters effectively predicted feed intake at optimal temperatures, while more complex models predicted intake better above the thermal optimum. The reference models selected in this study can be applied to estimate feed requirements over time for production or experimental trials, benchmark feeding to isolate the effect of other variables, support growth models and alternative feeding tables, and provide decision support.

1. Introduction

Meagre (*Argyrosomus regius*) is a promising emerging species that can contribute to the diversification of Mediterranean aquaculture. Meagre stands out as an appealing species for aquaculture due to several enticing characteristics, including its rapid growth potential, flesh quality, economic value, adaptability to captivity, and resilience in diverse environmental conditions (Monfort, 2010; Pfalzgraff et al., 2023). The cultivation commenced in the 1990s in France and, since then, different aspects of cultivation technology have been developed: larval rearing, nutritional requirements, and production technology (Martìnez-Llorens et al., 2011; Pérez et al., 2014; Pfalzgraff et al., 2023; Ribeiro et al., 2015; Roo et al., 2010; Saavedra et al., 2018, Saavedra et al., 2022).

Over the last few years, there has been a growing interest in rearing meagre as a strategy to mitigate the potential risks associated with market saturation of the Mediterranean marine aquaculture, which is currently dominated by gilthead seabream (*Sparus aurata*) and European seabass (*Dicentrarchus labrax*) (Couto et al., 2016). To reach the full potential of meagre cultivation and to increase its production, fish farming companies seek to reduce the production costs of the species.

Efficient feed management is crucial for a successful and sustainable aquaculture production for all species, including meagre. Feed constitutes the primary fraction of production expenses and can exceed 50 % of total running costs (Buentello et al., 2000; Iversen et al., 2020). This underscores the importance of developing tools to support development of improved feeding management practices, aiming to improve economic performance and advancing precision farming. This is especially

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https://doi.org/10.1016/j.aquaeng.2025.102526
Received 11 November 2024; Received in revised form 20 January 2025; Accepted 21 February 2025
Available online 25 February 2025

important for species like meagre, where comprehensive information on feeding and nutrition is still lacking, including key information regarding biological, nutritional, and environmental factors that drive feed intake. Developing a reference feed intake model provides the simplest baseline equations that can be extended in further studies. This is a critical step to establish precision farming practices in meagre production.

Feeding fish in culture still relies on intuition and experience, leading to economic losses and environmental impact due to feed waste (Sun et al., 2016). Mathematical models can address these issues by using mathematical equations to represent biological and environmental processes to estimate daily feed intake and predict growth. By incorporating factors such as body weight, temperature, and dietary composition, mathematical models can help to refine feeding strategies, enhance efficiency, and support sustainable aquaculture.

Over the past few decades, numerous mathematical models have been developed in aquaculture to optimize feed administration. At the individual level, the most widely used approaches for modeling feed intake in fish include models for digestive tract content, and bioenergetics. Digestive tract content models estimate feed intake by analyzing the temporal changes in stomach or gastrointestinal contents, incorporating factors such as transit and evacuation rates to simulate the return of appetite and feed intake. For example, the MAXIMS model, developed by ICLARM (Sainsbury, 1986), has been applied to estimate the intake of various fish species, and Burton and Boisclair (2013) developed a model to predict consumption rates in juvenile Atlantic salmon (*Salmo salar*) based on stomach content analysis. On the other hand, the bioenergetic model is based on the principles of bioenergetics to predict feed intake. Bioenergetic models have been applied in many different studies and different species, such as rainbow trout (*Oncorhynchus mykiss*), gibel carp (*Carassius auratus gibelio*), gilthead seabream (*Sparus aurata*), and Barramundi (*Lates calcarifer*) (Bermudes et al., 2010; Libralato and Solidoro, 2008; Railsback and Rose, 1999; Serpa et al., 2012; Zhou et al., 2005).

The aim of this study was to establish one or more mathematical reference feed intake models to characterize the influence of three primary factors affecting feed intake: (i) temperature, representing the key environmental determinant, (ii) body weight and (iii) dietary composition. To achieve this, several models with different levels of complexity were tested by integrating existing published data with commercial feeding tables. The models evaluated and fitted to the data are widely utilized in aquaculture research, with the novelty of this study arising from their specific application to meagre (*Argyrosomus regius*), a species of increasing significance in aquaculture.

The selected reference models provide a basic framework for developing more advanced models of feed intake, metabolism, and growth in meagre. Additionally, they serve as a benchmark for evaluating and optimizing feeding management practices, contributing to more efficient and sustainable meagre farming. Furthermore, these models offer a platform for future research to incorporate the effects of additional environmental factors, such as oxygen levels, pH, and nitrate concentrations, on feed intake, thereby expanding its applicability in precision aquaculture.

2. Materials and methods

2.1. Data collection

The present study was performed based on published literature data and commercial feeding tables available online for meagre (*Argyrosomus regius*). Therefore, no experimental work was performed during this research. Data describing meagre feed intake rates was systematically gathered from 42 sources published between 2010 and 2022. A complete list of these publications is provided in the supplementary data. According to the description of each paper, the nutritional values of the experimental feeds were collected (protein, lipids, fiber, ash, moisture, digestible protein, gross energy, digestible energy) and experimental conditions (initial and final weight, number of days of the trial, temperature). It is important to note that while not all studies clearly distinguish between feed intake and feed offer, for this study, the data from these publications were assumed to reflect feed intake. Feed intake was calculated as the average feed consumption per day of trial divided by the geometric mean of the average body weights at the sampling dates. The body weight ranged from 2.6 to 1160 g and the water temperature ranged from 15.5 to 27.6 ºC (Fig. 1).

Due to the limited range of temperatures and fish sizes available in the literature for meagre, 16 commercial feeding tables covering different life stages (from fry to adult) of meagre were added as auxiliary feed intake data. These tables, with a body weight range of 0.05 g to 4000 g and a temperature range from 9 to 31 ºC, provided essential information on recommended feeding rates according to fish body weight, feeding rate or feed conversion ratio, water temperature, and feed nutritional composition. The indicative feeding guide from each feeding table, expressed as kilograms of feed per 100 kg of fish per day, was directly extracted from the commercial feeding tables (non-simulated data) and used as a proxy for feed intake during this study. It is important to note that the values collected from commercial feeding tables likely refer to "feed offer" rather than actual "feed intake". In total, the dataset consisted of 4359 entries, covering different life stages, with body weights ranging from 0.05 g to 4000 g and temperatures from 9 to 31 ºC. A summary of the data ranges can be found in Table 1.

2.2. Model design

Mathematically, all feed intake (FI) models followed the same generic form, where the effects of body weight (BW), temperature and diet properties are considered multiplicatively separable (Eq. 1).

$$FI\ (BW,\ temperature,\ diet) = f(BW) \times g(temperature) \times h(diet) \quad (1)$$

For all models, the f(BW) function follows a power-law relationship depending on two estimated parameters, α and β:

$$f(BW) = \alpha \times BW^{\beta}$$

Table 2 contains a detailed description of the 27 different models considered, categorized into 4 different groups of models that differ in terms of the structure of the $g(temperature)$ and $h(diet)$ functions:

1) Simple feed-independent models
   $g(temperature)$ is a simple one-parameter function;
   $h(diet) = 1$ (i.e., diet is assumed to not affect feed intake rates).
2) Complex feed-independent models
   $g(temperature)$ is a more complex function (2+ parameters);
   $h(diet) = 1$ (i.e., diet is assumed to not affect feed intake rates).

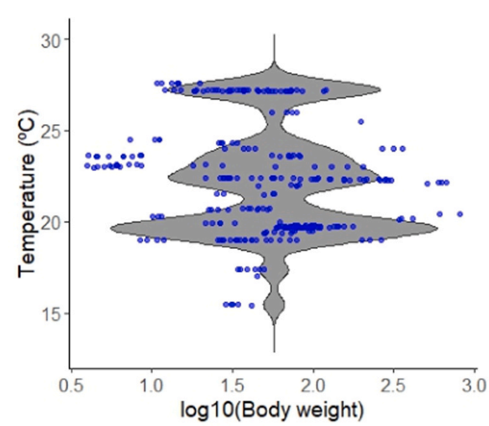

Fig. 1. Violine plot of the log10-transformed range of body weight (from 4.29 to 763.32 g) and temperature of the published data sources.

Table 1
Minimum and maximum values of the different variables collected from the published data sources and commercial feeding tables, for meagre.

Data source	Scientific publications		Commercial feeding tables	
Variable	**Minimum**	**Maximum**	**Minimum**	**Maximum**
Body weight (gram)	4.29	763.32	0.05	4000
Temperature (°C)	15.45	27.6	9	31
Feed crude protein (% diet)	40.50	63.75	40	64
Feed crude lipid (% diet)	10.24	26.66	9	20
Feed fiber (% diet)	0.73	7.70	0.4	3.2
Feed ash (% diet)	3.82	16.24	6.6	13
Feed moisture (% diet)	2.35	13.30	NA	NA
Feed gross energy (MJ/kg)	14.86	25.95	19.4	22.4
Feed digestible protein (% diet)	35.64	56.10	NA	NA
Feed digestible energy (MJ/kg)	11.89	20.76	15.8	19.6

3) Simple feed-dependent models
   $g(temperature)$ is a simple one-parameter function;
   $h(diet)$ does not have more than one parameter.
4) Complex feed-dependent models
   $g(temperature)$ and $h(diet)$ are too complex to fit any of the previous types.

The numbers following each model acronym (e.g., FI1, FI2, EI1, PI3) represent the number of parameters considered in the respective model. For both simple and complex feed-independent models, a version with an acronym containing the letter 'k' (e.g., 'FI1k') indicates that the model includes the inverse of thermodynamic temperature as a predictor.

The abbreviations used are as follows: *BW* (Body Weight), *temp* (Temperature), GE (Gross Energy) in feed, DE (Digestible Energy) in feed, CP (Crude Protein) in feed, DP (Digestible Protein) in feed, CL (Crude Lipids) in feed, NFE (Nitrogen-free extract), *z* (Correction Factor) for nutritional components, and *fra* (Fraction) of the nutritional component, *other* for addition nutritional components such as ash and moisture, *higher order effects* for interactions between the nutritional components. Fitted parameters: α, β, γ, δ, ε.

2.3. Model fitting

For each model, different fitting methods were implemented in R version 4.2.1. In most cases, the model was linearized (under the assumption of multiplicative error) and parameters were determined using either least squares regression ("simple" methods, using function stats::lm()), Huber loss minimization ("robust" methods, using function MASS::rlm()) or mixed-effect modelling ("mixed" methods, source being the random effect, using function lme4::lmer()). For Feed Intake Complex family models (FIC), the feed-dependent effect was assumed to follow a polynomial response defined over the simplex, which considers the sum of the feed composition variables equals to one (Cornell, 1984). The fitting for this family was performed using elastic net regularization (using function glmnet::glmnet()), either considering only first-order effects ("basic" variants) or first-order and higher-order effects ("cplx" variants).

In some cases, variants of the fitting methods were obtained by:

- Forcing the body weight exponent to a fixed value of 2/3 ("fixed23" variants) as assumed by the Dynamic Energy Budget theory (Kooijman, 1986);
- Excluding the auxiliary data from the commercial feeding table during fitting process ("i" variants), to assess how the model would perform using only the scientific publications data, therefore, minimizing potential biases or overfitting that could result from

Table 2
The list of the 27 models that were analyzed.

Name	Equation	Number of parameters
Simple feed-independent models		
FI1	$\alpha \times BW^{\beta} \times e^{(\gamma \times temp)}$	3
FI1k	$\alpha \times BW^{\beta} \times e^{\left(\gamma \times \frac{1}{temp}\right)}$	3
Complex feed-independent models		
FI2	$\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2)}$	4
FI2k	$\alpha \times BW^{\beta} \times e^{\left(\gamma \times \frac{1}{temp} + \delta \times \frac{1}{temp^2}\right)}$	4
FI3	$\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2 + \varepsilon \times temp^3)}$	5
FI3k	$\alpha \times BW^{\beta} \times e^{\left(\gamma \times \frac{1}{temp} + \delta \times \frac{1}{temp^2} + \varepsilon \times \frac{1}{temp^3}\right)}$	5
Simple feed-dependent models		
EI1	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp)}}{feed_{GE}}$	3
DEI1	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp)}}{feed_{DE}}$	3
PI1	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp)}}{\frac{feed_{CP}}{100}}$	3
DPI1	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp)}}{\frac{feed_{DP}}{100}}$	3
LI1	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp)}}{\frac{feed_{CL}}{100}}$	3
Complex feed-dependent models		
EI2	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2)}}{feed_{GE}}$	4
DEI2	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2)}}{feed_{DE}}$	4
PI2	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2)}}{\frac{feed_{CP}}{100}}$	4
DPI2	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2)}}{\frac{feed_{DP}}{100}}$	4
LI2	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2)}}{\frac{feed_{CL}}{100}}$	4
EI3	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2 + \varepsilon \times temp^3)}}{feed_{GE}}$	5
DEI3	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2 + \varepsilon \times temp^3)}}{feed_{DE}}$	5
PI3	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2 + \varepsilon \times temp^3)}}{\frac{feed_{P}}{100}}$	5
DPI3	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2 + \varepsilon \times temp^3)}}{\frac{feed_{DP}}{100}}$	5
LI3	$\frac{\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2 + \varepsilon \times temp^3)}}{\frac{feed_{CL}}{100}}$	5
FIC1a	$\alpha \times BW^{\beta} \times e^{(\gamma \times temp)} \times e^{\left(z_{CP} \times frac_{CP} + z_{CL} \times frac_{CL} + z_{NFE} \times frac_{NFE} + z_{other} \times frac_{other} + \text{higher order effects}\right)}$	14
FIC2a	$\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2)} \times e^{\left(z_{CP} \times frac_{CP} + z_{CL} \times frac_{CL} + z_{NFE} \times frac_{NFE} + z_{other} \times frac_{other} + \text{higher order effects}\right)}$	15
FIC3a	$\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2 + \varepsilon \times temp^3)} \times e^{\left(z_{CP} \times frac_{CP} + z_{CL} \times frac_{CL} + z_{NFE} \times frac_{NFE} + z_{other} \times frac_{other} + \text{higher order effects}\right)}$	16
FIC1b	$\alpha \times BW^{\beta} \times e^{(\gamma \times temp)} \times e^{\left(z_{CP} \times frac_{CP} + z_{CL} \times frac_{CL} + z_{starch} \times frac_{starch} + z_{fiber} \times frac_{fiber} + z\_ash \times frac\_ash + z\_moisture \times frac\_moisture + \text{higher order effects}\right)}$	25
FIC2b	$\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2)} \times e^{\left(z_{CP} \times frac_{CP} + z_{CL} \times frac_{CL} + z_{starch} \times frac_{starch} + z_{fiber} \times frac_{fiber} + z\_ash \times frac\_ash + z\_moisture \times frac\_moisture + \text{higher order effects}\right)}$	26

(*continued on next page*)

Table 2 (*continued*)

Name	Equation	Number of parameters
FIC3b	$\alpha \times BW^{\beta} \times e^{(\gamma \times temp + \delta \times temp^2 + \varepsilon \times temp^3)} \times e^{\left(\begin{array}{c} z_{CP} \times frac_{CP} + z_{CL} \times frac_{CL} + z_{starch} \times frac_{starch} + z_{fiber} \times frac_{fiber} + \\ z\_ash \times frac\_ash + z\_moisture \times frac\_moisture + higher\ order\ effects \end{array}\right)}$	27

incorporating commercial feeding data. The dataset size before and after exclusion is as follows: 4644 and 285, respectively. This approach allows an evaluation of how the inclusion of auxiliary data influences model fitting.

- Recalibrating the "α" parameter using only the data from scientific publications ("r" variants). For that, all available data (scientific publications and feeding tables) was used, followed by a correction step for data from scientific publications. The recalibration of the parameter "α" was based on the correction adjusted, based on the median deviation between predicted and observed feed intake values for the scientific population dataset. This approach ensured that the recalibrated "α" was more representative of the experimental data from scientific publications.

2.4. Model evaluation

To determine the best process to obtain reference models of the four described categories, it is important to obtain an estimate of the generalization error of the resulting models, that is an estimate of the prediction error of the model in future contexts. To do so, a series of repeated 5-fold cross-validations (with n = 200 iterations) were performed to estimate, for each model and fitting method combination, the expected mean absolute percentage error (MAPE; Eq. 2) for unseen samples. In each fold of cross-validation, 80 % of the dataset was used for training and 20 % for validation.

$$MAPE(\%) = \frac{100}{n} \sum_{i=1}^{n} \left| \frac{P_i - O_i}{O_i} \right| \tag{2}$$

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

Cross-validation is a popular model selection method focused on its predictive effectiveness to future observations. It involves splitting the data into a calibration sample that is used to fit the model parameters and validation sample applying the fitted equations to predict the model output. Then, the difference between the predictions generated using the first are checked on the second. 5-fold cross-validation then involved splitting the data into 5 equal subsamples, four of which are used for independent calibrations and one for validation. The cross-validation is conducted 5 times averaging for the final result (Hjorth, 2017).

Additionally, model selection was further supported by using Information Criteria using Akaike Information Criterion corrected for small sample sizes (AICc; Eq. 3) values to assess the relative quality of the models, considering both their predictive performance and complexity.

$$AICc = n\ln\left(\frac{SEE}{n}\right) + \frac{2k(k+1)}{n-k-1} \tag{3}$$

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

First, this was performed separately for each of the four model categories, to determine the best process (and model) within each category. The best models of each category were compared in a final cross-validation, to ensure that the test metrics are directly comparable (Fig. 2).

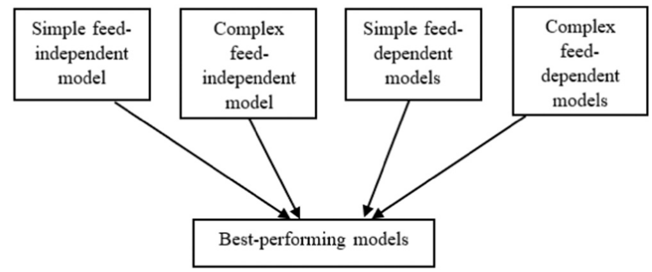

Fig. 2. Each box represents a cross-validation test that was performed to reach the model with the best performance.

2.5. Model analysis

After the final cross-validation, the models with the best performance were analyzed by extrapolation analysis, residual analysis and evaluating predicted performance with different factors; body weight and temperature. When performing the extrapolation analysis, each model was assessed in terms of how well it performed to predict feed intake beyond the range of data used for parameter estimation. For the residual analysis, the normality and homogeneity of residuals were tested. The evaluation of performance with different factors was used to determine if the model performance varies across different conditions (body weight and temperature).

3. Results and discussion

3.1. Model evaluation

Overall, our results point to rather large amount of unmodelled variation in feed intake rates (30 % < MAPE < 62 % in all cases, see Tables 3 to 5). The high value of MAPE can be explained by the high variability of the data obtained from the publications. The large dataset, which includes significant variation in unmodelled factors affecting feed intake, such as daily meals, feeding schedules, and dissolved oxygen, is a significant source of uncertainty. In addition, a higher level of prediction is hardly attainable because pronounced variability in feed intake is inherent to fish feeding, therefore it can justify the high values of MAPE

Table 3
Overall results of cross-validation and AICc for the simple feed-independent model.

Model/Fitting	Validation MAPE (%)	AICc
FI1/simple_fixed23	35.98	20311.65
FI1k/simple_fixed23	36.03	20262.90
FI1/robust_fixed23	36.08	20249.68
FI1k/robust_fixed23	36.15	20217.67
FI1/mixed_fixed23	37.68	20264.10
FI1/mixed_fixed23_r	38.05	20221.40
FI1k/robust_r	39.39	19034.20
FI1/robust_r	39.41	19068.85
FI1k/robust_fixed23_r	39.89	20648.18
FI1/robust_fixed23_r	39.98	20712.71
FI1k/simple_fixed23_r	40.41	20435.93
FI1/simple_fixed23_r	40.50	20557.81
FI1k/simple_r	40.88	18811.79
FI1/mixed_r	40.89	18857.10
FI1/mixed	40.92	19047.94
FI1k/mixed_r	40.94	19524.94
FI1/simple_r	40.97	19868.98
FI1k/mixed	41.03	18842.02
FI1/simple	41.49	18782.70
FI1k/simple	41.78	18705.54
FI1/robust	41.80	18830.88
FI1k/robust	42.07	18770.32
FI1k/robust_i	47.09	19267.74
FI1/robust_i	47.36	19316.57

Table 4
Overall results of cross-validation and AICc for the complex feed-independent model.

Model/Fitting	Validation MAPE (%)	AICc
FI2k/robust_fixed23	40.00	16828.29
FI2/robust_fixed23	40.23	16837.55
FI3/robust_fixed23	40.98	16928.58
FI3k/robust_fixed23	41.02	16945.46
FI2k/mixed	41.79	17742.32
FI2/mixed	41.95	17738.52
FI3k/mixed	42.77	17734.31
FI3/mixed	42.78	17905.37
FI2k/simple_fixed23	42.87	17421.78
FI2/simple_fixed23	43.23	17428.19
FI3/simple_fixed23	44.52	17559.79
FI3k/simple_fixed23	44.59	17565.66
FI2k/robust	48.75	15762.32
FI2/robust	48.93	15724.44
FI3/robust	49.60	15678.15
FI3k/robust	49.64	15678.32
FI2k/simple	53.22	15576.57
FI2/simple	53.68	15532.28
FI3/simple	55.18	15466.23
FI3k/simple	55.25	15469.23

Table 5
Overall results of cross-validation and AICc for the simple feed-dependent model.

Model/Fitting	Validation MAPE (%)	AICc
LI1/simple_fixed23	34.88	19619.82
LI1/robust_fixed23	35.11	19579.59
EI1/simple_fixed23	35.16	20139.45
EI1/robust_fixed23	35.28	20073.63
LI1/simple	35.64	19030.89
DEI1/simple_fixed23	37.17	19804.13
DEI1/robust_fixed23	37.21	19801.84
LI1/mixed	37.30	19039.10
DPI1/simple_fixed23	39.27	20716.55
DPI1/robust_fixed23	39.31	20641.35
PI1/simple_fixed23	39.51	20719.53
EI1/simple	39.54	18793.84
PI1/robust_fixed23	39.56	20645.34
EI1/mixed	39.87	20427.11
DEI1/mixed	42.40	18039.60
DEI1/simple	44.31	18514.34
DPI1/mixed	46.28	19824.14
PI1/mixed	46.57	19428.07

(Assan et al., 2021; Martins et al., 2011).

3.1.1. *Simple feed-independent models*

The overall results of the cross-validation and AICc for the simple feed-independent models (Table 3) indicate a relatively high amount of unmodelled variation in feed intake rates (MAPE < 48 %). Comparing the different models, we can see that model FI1 with fitting method simple_fixed23 displayed the best result, with a MAPE of about 36 %, with combinations "FI1/robust_fixed23", "FI1k/simple_fixed23" and "FI1k/robust_fixed23" presenting similar performance levels (again, with a MAPE on the order of 36 %). As a general pattern, we observe that forcing the body weight exponent to a fixed value of 2/3 (methods "_fixed23") has a clear positive effect on model prediction quality, which aligns with the principles from the Dynamic Energy Budget theory that the energy ingestion rate is proportional to the surface area of the organism $\{V^{2/3}\}$ (Kooijman, 1986). When analyzing AICc, "FI1/robust_fixed23_r" had the highest value (20,712.71), while "FI1k/simple" had the lowest value (18,705.54). Additionally, "FI1k/robust_r" showed a balanced performance with an AICc of 19,034.2 and a MAPE of about 39 %, demonstrating a good balance between model fit and complexity. On the other hand, models such as "FI1k/robust_fixed23_r" and "FI1/robust_fixed23_r", which have similar MAPE values around 39 %, show higher AICc values of 20,648.18 and 20,712.71, respectively, providing a good fit but are less efficient, as indicated by their higher AICc values.

Using mixed-effects modeling (methods "mixed") or applying rescaling of the "α" parameter (methods "_r") does not seem to bring clear benefits. Similar results were observed in the specific case of growth models tailored for salmon farming, in which the inclusion of random effects did not improve the model fit (Aunsmo et al., 2014). Although feed intake and growth are not the same, there is a strong relationship between both parameters, with both being influenced by various biotic and abiotic factors (Brett, 1979; Brett and Groves, 1979). However, feed intake and growth, while distinct, are related; for example, selection for increased growth rate in Atlantic salmon will increase feed intake and improve feed utilization (Thodesen et al., 1999).

Furthermore, we observe that excluding the auxiliary feeding table data (methods "_i") for fitting provides no benefits. Both MAPE and AICc values were higher, suggesting a worse model in terms of fit and complexity.

Finally, comparisons of the test error metrics for the "FI1" vs. "FI1k" models did not reveal any apparent advantage in using the inverse of the thermodynamic temperature as a predictor (instead of the temperature).

3.1.2. *Complex feed-independent models*

The results of the of the cross-validation and AICc of the complex feed-independent models (Table 4) show higher prediction errors (MAPE < 56 %) compared to the simple feed-independent models. Furthermore, the model with a log-quadratic temperature effect had a lower prediction error than the one with log-cubic temperature effect. This indicates that additional complexity on the temperature effect does not seem to improve the capacity of the models to predict meagre feed intake. This, at least in part, can be explained by the fact that the collected meagre data range between 15.5 and 27.6 ºC. This limited temperature range may not provide sufficient variability for the more complex models to capture meaningful patterns that improve the prediction of measured feed intake. Therefore, a simpler log-quadratic temperature effect is more appropriate for the available data. Additionally, studies assessing the thermal tolerance and metabolic scope of meagre have demonstrated that at 34 °C meagre exhibits a significantly reduced feed intake, compared to the optimal range of 24–29 °C. This suggests that the log-cubic temperature models could have a better performance in a data set with a broader temperature variability (Stavrakidis-Zachou et al., 2021). In this set of models, we observe that, besides being beneficial to fix the body weight exponent to 2/3, the use of robust fitting methods seems to be particularly useful. As in the simple feed-independent models, we do not observe a clear benefit in using mixed-effect modelling or inverse thermodynamic temperature as a predictor.

When analyzing AICc, " FI3/mixed" had the highest value (17,905.37), while " FI3/simple" had the lowest value (15,466.23). The models using the calibration method "robust_fixed23" show a balance between complexity and performance, with moderate AICc values in the range of 16,828.29–16,945.46.

3.1.3. *Simple feed-dependent models*

The results of the cross-validation of the simple feed-dependent models (Table 5) show a lower prediction error (MAPE < 47 %) compared to the simple feed-independent models. Comparing the different models, we can see that model LI1 generally had a lower error than model PI1, which indicates that the impact of the percentage of lipids (and energy) on feed intake is higher than the impact of the percentage of protein in the feed. Nevertheless, a study conducted with juvenile meagre, which investigated the impact of protein and lipid levels on growth, showed that the correlation between feed intake and protein is higher than that with lipid levels. Moreover, it demonstrated an increase in feed intake until lipid levels reached 14 %, followed by a subsequent decline as lipid percentages further increased (Chatzifotis et al., 2010). Again, the fitting methods fixing the body weight to 2/3 had better results calibrating the models. The least square "simple_fixed23" method showed a smaller error result than "robust_fixed23." On the other hand, the "mixed" method had the highest MAPE values for all feed-dependent model variables.

When analyzing AICc, "DPI1/simple_fixed23" had the highest value (20,716.55), while "DEI1/mixed" had the lowest value (18,039.60). The models using the calibration method "simple_fixed23" and "robust_fixed23" show a balance between complexity and performance, with moderate AICc values in the range of 19,579.59–20,645.34.

Table 6
Overall results of cross-validation and AICc for the complex feed-dependent model.

Model/Fitting	Validation MAPE (%)	AICc
LI2/robust_fixed23	33.41	16212.26
LI3/robust_fixed23	33.82	16214.29
FIC1a/simple_basic_fixed23	35.53	19836.28
FIC1a/robust_basic_fixed23	35.64	19883.36
FIC1a/simple_cplx_fixed23	35.88	19805.48
FIC1a/robust_cplx_fixed23	35.99	19852.89
LI2/simple_fixed23	36.25	16575.04
LI2/mixed	36.59	16532.01
EI2/robust_fixed23	36.87	16592.50
LI3/mixed	37.07	16325.10
LI3/simple_fixed23	37.12	16635.53
EI3/robust_fixed23	37.57	16673.91
EI2/simple_fixed23	39.74	17197.32
EI2/mixed	39.87	16426.96
LI2/simple	40.12	16046.51
EI3/mixed	40.71	16836.52
LI3/simple	40.99	16001.56
EI3/simple_fixed23	40.99	17322.92
DEI2/robust_fixed23	42.43	16069.85
DPI2/robust_fixed23	43.02	17449.46
PI2/robust_fixed23	43.19	17455.85
DEI3/robust_fixed23	43.25	16141.76
DEI2/mixed	43.33	17025.15
DPI3/robust_fixed23	44.16	17634.34
PI3/robust_fixed23	44.24	17642.18
DEI3/mixed	44.28	17525.10
FIC1a/simple_basic	44.44	18770.97
FIC1a/simple_cplx	44.78	18740.24
FIC1b/simple_basic	44.98	18809.89
FIC1b/simple_cplx	45.26	18785.12
DPI2/simple_fixed23	45.37	18036.46
PI2/simple_fixed23	45.49	18039.98
FIC1a/robust_basic	45.51	18830.07
FIC1a/robust_cplx	45.84	18800.42
DEI2/simple_fixed23	46.18	16664.06
DPI2/mixed	46.28	16968.71
PI2/mixed	46.28	167034.2
PI3/simple_fixed23	46.89	18209.86
DPI3/simple_fixed23	46.90	18205.44
PI3/mixed	47.30	17258.21
DPI3/mixed	47.38	17286.75
DEI3/simple_fixed23	47.58	16772.97
EI2/simple	48.73	15573.12
EI3/simple	50.21	15504.77
FIC2a/simple_cplx	53.82	15339.94
FIC2a/simple_basic	53.98	15389.53
FIC2b/simple_cplx	54.73	15384.08
FIC2b/simple_basic	54.76	15428.16
FIC3a/simple_cplx	55.12	15293.46
FIC3a/simple_basic	55.28	15343.13
FIC3b/simple_cplx	56.08	15336.79
FIC3b/simple_basic	56.10	15381.57
DEI2/simple	57.17	15093.01
DEI3/simple	58.60	15007.45
PI2/simple	59.97	15143.22
DPI2/simple	60.18	15144.03
PI3/simple	61.55	15050.02
DPI3/simple	61.76	15050.73

3.1.4. Complex feed-dependent models

The cross-validation results for the complex feed-dependent models (Table 6) overall showed a lower error compared to other model groups (MAPE $<$ 62 %). Consistent with the findings in simple feed-dependent models, those focusing on lipid feed intake demonstrate superior performance, underscoring the significance of lipid content in feed as a crucial variable in feed intake calculations. Notably, FIC1a, incorporating four components in feed intake calculation ("crude protein", "crude fat", "nitrogen-free extract", and "rest"), outperforms FIC1b, which employs six components ("crude protein", "crude fat", "starch", "fiber", "ash", and "moisture"). Again, this suggests that the lipid composition of the feed predominantly influences feed intake. This finding is relevant for the understanding of both feed intake and appetite control in this species. In addition, models from the more complex family (FIC) with only direct effects of nutrition (basic) had better results than models that also included the effect of the interaction between the nutritional composition (cplx). Thus, assuming linear effects provides better prediction capacity for complex FIC models. Models within the FIC1 category, utilizing temperature as an exponential function, exhibit superior results compared to models employing multiple parameters for temperature (FIC2 and FIC3). That implies that introducing additional complexity to the temperature effect did not enhance the models' capacity to predict meagre feed intake. Utilizing fixed body weight as 2/3 again improved model quality for complex feed-dependent models. Simple and mixed fitting methods resulted in higher prediction error than other model groups.

When analyzing AICc, "LI3/robust_fixed23" had the highest value (19,883.36), while "DEI3/simple" had the lowest value (15,007.45). The models using the calibration method "robust_fixed23" show a balance between complexity and performance, with moderate AICc values in the range of 16,046.51–18,209.86.

3.2. Model analysis

3.2.1. Fitting of best performing-models

Overall, the best-performing models with the lowest error validation (Table 7) were characterized by high amount of unmodelled variation in feed intake rates (MAPE $<$ 41 %). All the best performing models had the body weight exponent to a fixed value of 2/3, in accordance with the Dynamic Energy Budget principles (Kooijman, 1986). The Dynamic Energy Budget model has been successfully used to provide robust simulation of growth and feed intake in production units in the European sea bass (*Dicentrarchus labrax*) (Stavrakidis-Zachou et al., 2019). Lipid-dependent models exhibit better performance than feed-independent models in the present study. This contrasts with other studies reporting that the dietary lipid level did not affect the daily feed intake for meagre juveniles (Chatzifotis et al., 2010). Additionally, it is important to emphasize that the model "LI2/robust_fixed23" and "LI3/robust_fixed23" demonstrated a marginal difference in MAPE values. This indicates that the level of complexity of the temperature for this type of model has a relatively minor effect compared to models that are feed independent. Simple models calculating energy intake had a closer value of MAPE to the simple models calculating lipid intake, which shows that energy is also a relevant nutritional factor in the feed, and it conditions feeding intake. The complex models (FIC) with more than four nutritional parameters as predictors did not improve the quality of the model. Therefore, we conclude that the lipid parameter in feed intake is the most important. The feed complex independent model had the highest value of MAPE. Thus, the additional complexity on the temperature effect does not improve the model capacity to predict feed intake for meagre. In general, the "robust" fitting method did not show any significant advantage over the "simple" fitting. However, from a broader perspective, robust fitting models displayed slightly better fitting values, with an improvement of almost 2 %. The improvement in the use of the "robust" fitting method can be attributed to its approach, which is less sensitive to variability and atypical deviations in the feed

Table 7
Best performing-models, equation with value of variables, and overall results of cross-validation. The abbreviations used are as follows: *BW* (Body Weight), *temp* (Temperature), GE (Gross Energy) in feed, DE (Digestible Energy) in feed, CP (Crude Protein) in feed, DP (Digestible Protein) in feed, CL (Crude Lipids) in feed, NFE (Nitrogen-free extract) in feed, *z* (Correction Factor) for nutritional components, and *fra* (Fraction) of the nutritional component.

Model/Fitting	Equation with value of variables	Validation MAPE (%)
LI2/robust_fixed23	$\frac{(2.31 \times 10^{-5}) \times BW^{0.67} \times e^{(0.51 \times temp - 0.01 \times temp^2)}}{\frac{feed_{CL}}{100}}$	33.41
LI3/robust_fixed23	$\frac{(8.63 \times 10^{-5}) \times BW^{0.67} \times e^{(0.29 \times temp + 2.61 \times 10^{-4} \times temp^2 - 1.70 \times 10^{-4} \times temp^3)}}{\frac{feed_{CL}}{100}}$	33.82
LI1/simple_fixed23	$\frac{(1.85 \times 10^{-3}) \times BW^{0.67} \times e^{(0.07 \times temp)}}{\frac{feed_{CL}}{100}}$	34.93
LI1/robust_fixed23	$\frac{(1.76 \times 10^{-3}) \times BW^{0.67} \times e^{(0.07 \times temp)}}{\frac{feed_{CL}}{100}}$	35.12
EI1/simple_fixed23	$\frac{(2.52 \times 10^{-1}) \times BW^{0.67} \times e^{(0.06 \times temp)}}{feed_{GE}}$	35.15
EI1/robust_fixed23	$\frac{(2.45 \times 10^{-1}) \times BW^{0.67} \times e^{(0.06 \times temp)}}{feed_{GE}}$	35.26
FIC1a/simple_basic_fixed23	$(1.20 \times 10^{-2}) \times BW^{0.67} \times e^{(0.06 \times temp)} \times e^{(0.50_{CP} - 1.45_{CL} - 1.07_{NFE} + 1.20_{other})}$	35.53
FIC1a/robust_basic_fixed23	$(1.19 \times 10^{-2}) \times BW^{0.67} \times e^{(0.06 \times temp)} \times e^{(0.51_{CP} - 1.44_{CL} - 1.06_{NFE} + 1.21_{other})}$	35.64
FI1/simple_fixed23	$(1.20 \times 10^{-2}) \times BW^{0.67} \times e^{(0.06 \times temp)}$	35.95
FI1k/simple_fixed23	$(1.07 \times 10^{-2}) \times BW^{0.67} \times e^{\left(-5.76 \times \frac{1}{temp}\right)}$	36.00
FI1/robust_fixed23	$(1.16 \times 10^{-2}) \times BW^{0.67} \times e^{(0.06 \times temp)}$	36.03
FI1k/robust_fixed23	$(1.02 \times 10^{-2}) \times BW^{0.67} \times e^{\left(-5.86 \times \frac{1}{temp}\right)}$	36.09
FI2k/robust_fixed23	$(7.99 \times 10^{-5}) \times BW^{0.67} \times e^{\left(-46.1 \times \frac{1}{temp} - 78.1 \times \frac{1}{temp^2}\right)}$	39.85
FI2/robust_fixed23	$(1.45 \times 10^{-4}) \times BW^{0.67} \times e^{(0.52 \times temp - 0.01 \times temp^2)}$	40.07

intake data.

3.2.2. Evaluation of best performing models

The best models each category was selected for further performance evaluation: — "FI1/simple_fixed23" (simple feed-independent), "FI2k/robust_fixed23" (complex feed-independent), "LI2/robust_fixed23" (simple feed-dependent models), and "FIC1a/simple_ basic_fixed23" (complex feed-dependent). A set of three simulations using different temperatures was conducted to evaluate the selected models to assess the feed intake prediction accuracy. The temperature selection was based on the thermal tolerance of the species. In natural habitats meagre are exposed to temperatures ranging from 14 to 26°C (Duncan et al., 2013). In addition, meagre critical maximum thermal tolerance has been reported to be 37.5°C, with a significant decrease in feed intake with temperatures above 34°C (Kır et al., 2017). However, due to the data range of temperature of scientific publications and feeding tables it was decided to test 30°C instead of higher temperatures. Therefore, the temperatures selected were 15°C, 25°C, 30°C, with the feed variables being crude protein 47 %; crude lipids 16 %, gross energy 21 kJ/g; nitrogen-free extract 20 %, starch 18 %, fiber 2 %, ash 8.5 %, moisture 8.5 %; digestible protein 41 %; digestible energy 18 kJ/g.

Evaluating the predictive performance of the models under the temperature of 15°C, which is a low temperature for the species, it is possible to notice that all models had similar feed intake predictions (Fig. 3). However, it has been reported that broodstock would not consume feed below a temperature of 14°C. (Duncan et al., 2013). Therefore, none of the tested models would provide a realistic estimate of feed intake for fish weighing above 5.5 kg.

When comparing the predictive performance of the models at a temperature of 25 °C, which lies in the optimum temperature range of higher performance in meagre, similar patterns emerge (Fig. 4). The models "FI1/simple_fixed23" and "FIC1a/simple_basic_fixed23" exhibit overlap, as do the models "FI2k/robust_fixed23" and "LI2/robust_fixed23". Overall, all the models give good fit predictions compared to the data from scientific publications.

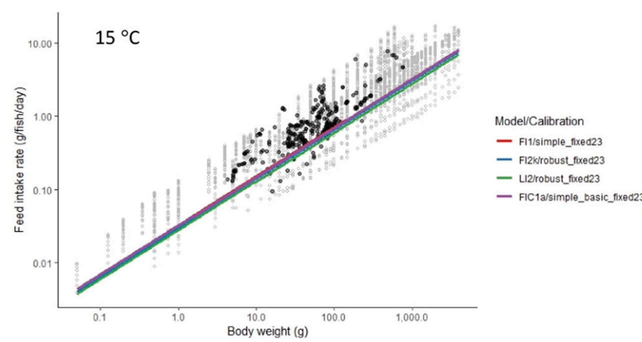

Fig. 3. Evaluation of best performing models for meagre at a temperature of 15 °C. The x-axis represents body weight (g), and the y-axis represents feed intake rate (g/fish/day), both variables are log-transformed. Black dots are data from scientific publications, and grey dots are auxiliary data from the feeding tables. The models "FI1/simple_fixed23" and "FIC1a/simple_basic_fixed23" overlap, followed by "FI2k/robust_fixed23" in blue and "LI2/robust_fixed23" in green.

At 30 °C, which is above the optimum for meagre cultivation (Fig. 5), both models with temperatures as a log-quadratic function (LI2 and FI2k) had a better performance, while "FI1/simple_fixed23" and "FIC1a/simple_basic_fixed23" tended to overestimate the feed intake. This indicates that the feed intake of meagre at high temperature is better predicted with models adding higher complexity terms for the temperature effect. This may, at least in part, be related to the lower water oxygen levels, combined with higher metabolic rates which typically occur at higher temperatures (Christensen et al., 2020; Stavrakidis-Zachou et al., 2021). Feed intake suppression at high temperatures due to low water oxygen levels has been described for meagre, salmon, and rainbow trout (Glencross, 2009; Remen et al., 2016; Stavrakidis-Zachou et al., 2021). Therefore, it may be advisable to extend feed intake prediction models with the effect of oxygen levels, for species where high temperatures are to be expected during part of the

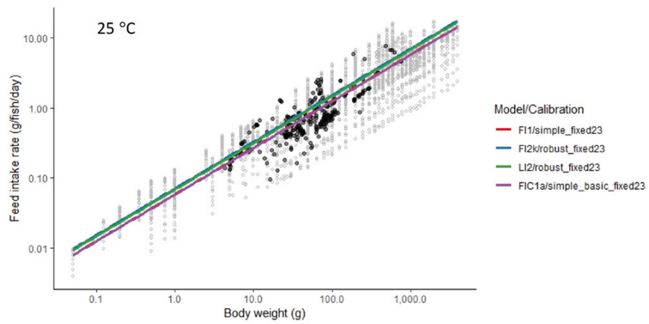

Fig. 4. Evaluation of best performing models for meagre at a temperature of 25 °C. The x-axis represents body weight (g), and the y-axis represents feed intake rate (g/fish/day), both variables are log-transformed. Black dots are data from scientific publications and grey dots are from the auxiliary data from the feeding tables. The models "FI1/simple_fixed23" and "FIC1a/simple_basic_fixed23" exhibit overlap, as do the models "FI2k/robust_fixed23" and "LI2/robust_fixed23".

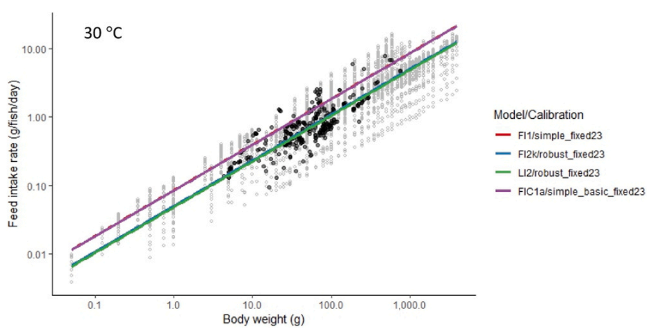

Fig. 5. Evaluation of best performing models for meagre at 30 °C. The x-axis represents body weight (g), and the y-axis represents feed intake rate (g/fish/day), both variables are log-transformed. Black dots are data from scientific publications and grey dots are from the auxiliary data from the feeding tables. The models "FI1/simple_fixed23" and "FIC1a/simple_basic_fixed23" exhibit overlap, as do the models "FI2k/robust_fixed23" and "LI2/robust_fixed23".

year. This is certainly the case of meagre farmed in the Mediterranean in a climate change scenario.

4. Guideline for practical use

Based on the performance evaluation, the flowchart provides a guideline for selecting the most appropriate feed intake model for meagre based on temperature conditions (Fig. 6). For temperatures below the optimal range, simpler models such as "FI1/simple_fixed23" and "FIC1a/simple_basic_fixed23" are recommended, as they use fewer parameters and offer efficient, reliable predictions. At optimal temperatures (24–29°C), these models continue to perform well, maintaining accurate predictions (Stavrakidis-Zachou et al., 2021). However, for temperatures above the optimal range, models with greater temperature complexity, like "FI2k/robust_fixed23" and "LI2/robust_fixed23," are advised. The latter models incorporate additional temperature-dependent terms to capture the reduced feed intake more effectively at high temperatures, offering improved predictive performance under such conditions.

5. Conclusion

The comprehensive analysis of various feed intake models for meagre reveals nuanced insights into their predictive capabilities. The evaluation of feed intake models for meagre shows that those with simpler temperature terms, such as "FI1/simple_fixed23" and "FIC1a/simple_basic_fixed23," perform well at lower and optimal cultivation temperatures (e.g., 15°C and 25°C), providing accurate feed intake predictions. However, under high-temperature conditions (e.g, 30°C), models with added temperature complexity, particularly those employing log-quadratic terms (e.g., "LI2/robust_fixed23" and "FI2k/robust_fixed23"), provide a more accurate feed intake prediction. These reference models offer many practical applications: they can estimate feed requirements over time for production or experimental trials; they can assist to differentiate the effects of key factors, like temperature and body weight, and evaluate impact of secondary factors such as diet composition and dissolved oxygen on feed intake. When integrated with feed-dependent growth models, they enhance the ability to assess fish growth under varying temperature conditions, which is especially valuable for precision farming and site selection studies. In addition, they provide a more robust and more sustainable alternative to feeding tables by using continuous functions instead of discrete values and can

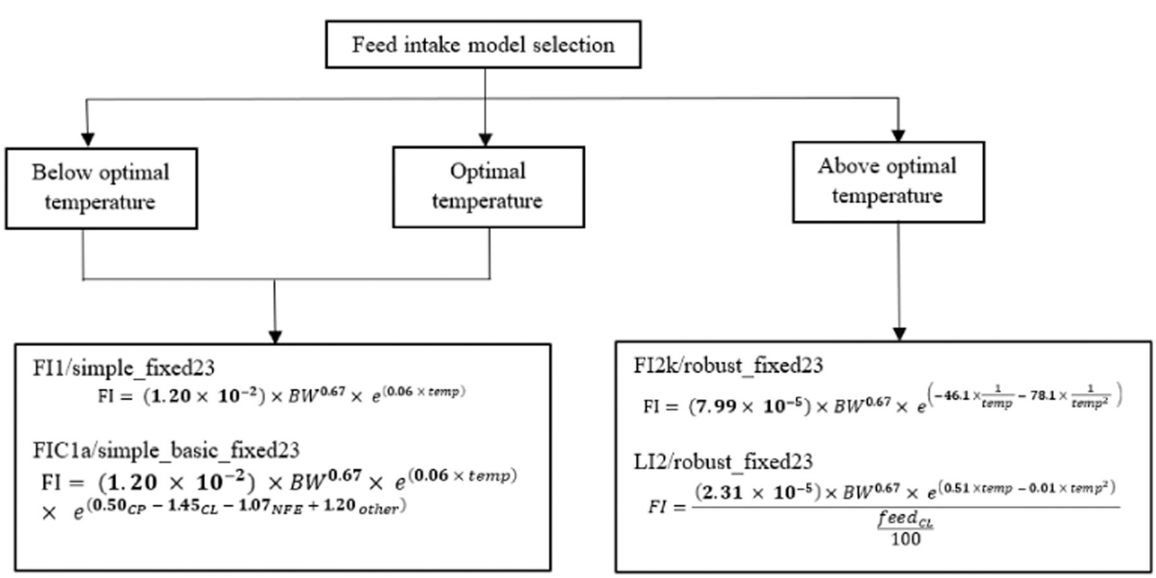

Fig. 6. Recommended feed intake model selection for meagre based on temperature condition. *BW* (Body Weight), *temp* (Temperature), CP (Crude Protein) in feed, DP (Digestible Protein) in feed, CL (Crude Lipids) in feed and NFE (Nitrogen-free extract) in feed.

help identify overfeeding or underfeeding situations. However, it is worth noting that the models developed in this study have the limitation of considering only temperature as the environmental factor influencing feed intake, which restricts the model's ability to capture the full range of environmental factors on feed intake. Expanding the model to include additional factors, such as pH, salinity, or dissolved oxygen, would enhance its applicability and provide a more comprehensive understanding of feed intake dynamics. Despite their simplicity, the models presented here effectively capture the impact of a key environmental factor (temperature) as well as other relevant nutritional factors on the feed intake of meagre. This provides a valuable tool for advancing precision aquaculture practices and supporting the efficient and sustainable production of meagre.

Funding

This work is part of the NoviFEED project, financed by Iceland, Liechtenstein and Norway, through EEA grants, in the scope of the program Blue Growth, operated by Directorate-General for Maritime Policy (DGPM), Portugal, under reference PT-INNOVATION-0099.

CRediT authorship contribution statement

Marina Azevedo and Tomé Silva wrote the main manuscript text, developed the conceptual framework, methodology, software implementation, and validation of the formal analysis. Tomé Silva, Sergey Budaev, Luis E.C. Conceição, and Ivar Rønnestad provided supervision and investigation support. Marina Azevedo, Tomé Silva, Sergey Budaev, and Filipe Soares managed data curation. Filipe Soares managed the project. Luis E.C. Conceição and Ivar Rønnestad secured funding. All authors reviewed the manuscript and approved the final version.

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.2025.102526.

Data availability

Data will be made available on request.

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