Aquacultural Engineering 112 (2026) 102635

Contents lists available at ScienceDirect

Aquacultural Engineering

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

Improving feed intake predictions in aquaculture: Integrating dissolved oxygen, body weight, and temperature for Atlantic salmon and meagre

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ARTICLE INFO

Keywords:
Salmo salar
Argyrosomus regius
Mathematical models
Feed intake prediction
Temperature and body weight
Dissolved oxygen

ABSTRACT

Mathematical models serve as essential tools to optimize feeding strategies, enhance feed efficiency and promote more sustainable aquaculture production. While previous studies primarily aimed to develop feed intake (FI) models based on body weight and temperature, the effect of dissolved oxygen (DO) — a critical environmental factor influencing FI—has often been overlooked. This work aimed to develop FI models for Atlantic salmon and meagre incorporating three main factors (i) body weight, (ii) temperature and (iii) dissolved oxygen. Oxygen-independent models were developed using data sourced from the literature, while Oxygen-dependent models utilized experimental trial data. The Akaike Information Criterion was used to assess and compare the relative quality of the Oxygen-dependent models. To evaluate the models' performance, an initial analysis was conducted by plotting the model predictions with DO levels from 0 to 10 mg/L. In addition, an independent dataset for each species was used to evaluate the developed models' performance, and model accuracy for each FI model was assessed via the mean absolute percentage error (MAPE). Results show that DO levels influence FI and growth in both species. For Atlantic salmon, Oxygen-dependent models significantly improved FI predictions, whereas for meagre, the Oxygen-independent model provided the most accurate FI predictions. These findings emphasize the importance of incorporating DO into FI models for species where it plays a significant role, while further research is needed to clarify the putative role of DO in meagre FI.

1. Introduction

Feeding in aquaculture demands careful attention from fish farmers since feed is one of the main expenses in intensive fish farming. Feed waste, besides representing an unnecessary cost, is the main factor underlying the environmental impact of aquaculture. Traditionally, feeding practices in aquaculture have relied on intuition and experience, employing approaches such as feeding to near apparent satiety or by a percent of body weight feed per day (Sun et al., 2016). However, these methods often bring inaccurate ration allowances, leading to overfeeding or underfeeding (Gomes et al., 2023). Overfeeding fish can cause environmental and economic issues, such as causing poor feed efficiency, water quality degradation, and increased production cost (Sun et al., 2016; Yogev et al., 2019). Underfeeding restricts fish growth, reduces feed efficiency, and may increase stress and aggression (Jobling et al., 2012; Martins et al., 2011). Therefore, optimizing feed intake is critical for enhancing growth, enhancing body composition, improving feed conversion efficiency, and minimizing nutrient losses.

Feed intake (FI) in fish is a complex process influenced by physiological and environmental factors. Fish adjust their voluntary intake based on their physiological state and prevailing water conditions (Fletcher, 1984; Kestemont and Baras, 2001). Various physiological

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https://doi.org/10.1016/j.aquaeng.2025.102635
Received 13 July 2025; Received in revised form 29 August 2025; Accepted 4 September 2025
Available online 5 September 2025

factors regulate FI in fish through a complex neural network in the brain that also receives peripheral neural and humoral signals (Bernier and Peter, 2001; Rønnestad et al., 2017; Yu et al., 2023). Body weight reflects the mass of metabolically active tissues, with metabolism known to scale with body size (Van Der Meer, 2006). As a result, it serves as a proxy for various physiological factors and is highly correlated with FI. Additionally, body weight influences stomach capacity, which ultimately determines the maximum volume of feed a fish can ingest (Pirhonen and Koskela, 2005).

The environmental factors that affect FI can be classified into (1) determining factors, including temperature, salinity, and photoperiod, and (2) limiting factors, such as dissolved oxygen (DO) (Sun et al., 2016). DO is particularly critical in aquaculture, as insufficient levels of oxygen (hypoxia) restrict oxygen-dependent metabolic processes essential for growth and feed utilization (Abdel-Tawwab et al., 2019). Temperature is the primary determining factor, significantly affecting metabolic rates, leading fish to adjust their feed intake to meet the changing energy demands. Additionally, temperature can affect digestive enzyme activity and overall digestion efficiency, thereby influencing feed intake (Handeland et al., 2008; Volkoff and Rønnestad, 2020), while also affecting the solubility of oxygen in water.

Predicting FI is essential for optimizing feeding strategies in aquaculture, improving feed efficiency, and promoting more sustainable production. Mathematical models provide a powerful tool in this context, allowing for estimation and forecast of FI and growth. However, most of the FI models available in the scientific literature focus on the effect of body weight and temperature, as applied to different species, for example turbot (*Scophthalmus maximus*), seabream (*Sparus aurata*), rainbow trout (*Oncorhynchus mykiss*) and Atlantic salmon (*Salmo salar*) (Árnason et al., 2009; Azevedo et al., 2025; Handeland, et al., 2008; Libralato and Solidoro, 2008; Railsback and Rose, 1999). Nevertheless, despite the pronounced influence of DO on FI rate, it is relatively rarely incorporated into these models, thereby limiting their accuracy and practical applicability (Remen et al., 2012, 2016).

The aim of this study was to improve the prediction of FI in Atlantic salmon (*Salmo salar*) and meagre (*Argyrosomus regius*) through mathematical modeling by incorporating DO as a key variable alongside body weight and water temperature. Atlantic salmon is a well-established aquaculture species, whereas meagre is an emerging species. This study considers not only their different biological characteristics but also the contrast in data availability for model development. Our objective is to capture the relationship between physiological and environmental factors influencing feeding behavior. First, an Oxygen-independent model was developed using data from the literature. Second, an Oxygen-dependent model was developed based on data from experimental trials. Finally, these models were integrated into a comprehensive FI model that accounts for DO, temperature, and body weight.

2. Material and methods

2.1. Feed intake models

The flowchart (Fig. 1) outlines the general process for developing the feed intake models for Atlantic salmon and meagre. Initially, an Oxygen-independent model was created using data sourced from the scientific literature. This was followed by the development of an Oxygen-dependent model, which utilized data generated from *in vivo* trials. Finally, both models were integrated to produce the combined model.

2.1.1. Oxygen-independent model

An Oxygen-independent model was developed for each species based on peer-reviewed published data (described on 2.2.1 Published data). The Oxygen-independent model considers the effects of temperature and body weight (BW) as multiplicatively separable (Eq. 1), where α represents a scaling factor that adjusts the baseline feed intake, β is an exponent that captures the allometric relationship between BW and FI, reflecting how metabolic demand changes with body size and γ quantifies the sensitivity of feed intake to changes in temperature, accounting for its impact on metabolic processes and overall energy requirements. This model equation was developed based on feed intake models from several fish species (eg. Clarke and Johnston, 1999; Jobling, 1993; Lupatsch, 2004; Lupatsch, 2009).

$$FI(BW, temperature) = \boldsymbol{\alpha} \times BW^{\beta} \times e^{(\gamma \times temperature)} \tag{1}$$

To evaluate the quality of the Oxygen-independent model, the distribution of residual error was evaluated and the prediction accuracy for each FI model tested was assessed by the mean absolute percentage error (MAPE) (Eq. 2).

$$MAPE = \frac{1}{n}\sum_{i=n}^{n}\left|\frac{y_i - \hat{y}_i}{y_i}\right| \times 100 \tag{2}$$

Where n is the number of observations, y_i represents the observed values, $\hat{y}_i$ the predicted values.

2.1.2. Oxygen-dependent model

To develop the Oxygen-dependent model, we assumed that the effect of DO is multiplicatively independent of the effects of body weight and temperature (Eqs. 3 and 4). Based on this, the Oxygen-independent model was applied to normalize the FI data obtained during the trials and estimate the effect of DO. By normalizing the trial data for body

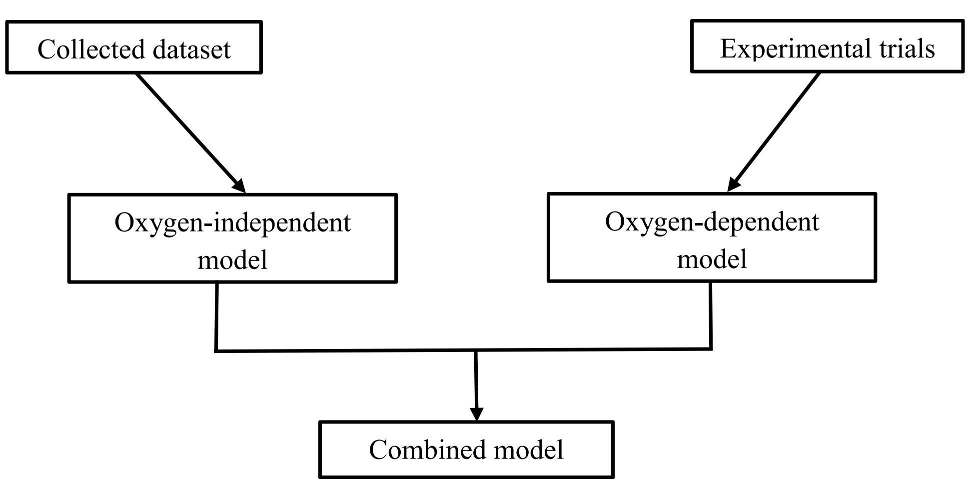

Fig. 1. Flowchart summarizing the development process of the feed intake (FI) model for each species.

weight and temperature, we removed their effects, allowing for a standardized comparison of dissolved oxygen's impact in subsequent analyses. The normalization of the data from the trial was performed separately using Oxygen-independent models for meagre and Atlantic salmon to account for species-specific differences.

$$FI_{predicted}(BW, temperature) = \alpha \times BW^{\beta} \times e^{\gamma \times temperature} \tag{3}$$

$$h(DO) \approx \frac{FI_{measured}(BW, temperature, DO)}{FI_{predicted}(BW, temperature)} \tag{4}$$

Where $FI_{measured}$ represents the FI data obtained during the trials, and $FI_{predicted}$ represents the predicted feed intake obtained with the Oxygen-independent model.

After isolating the effect of DO over feed intake, different equations were considered to model the $h(DO)$, as outlined in (Eqs. 5 to 8). The equations used to describe $h(DO)$ were selected based on previous studies investigating the effects of oxygen on feed intake (Remen et al., 2016; Subramaniam, 2013). Therefore, in these studies, dissolved oxygen was considered a limiting factor, and $h(DO)$ function was assumed to follow approximately a sigmoidal shape. All the models tested were saturating, meaning that as DO increases, the value of $h(DO)$ approaches 1. The following models were fitted using R with the *nls* function.

$$h(DO) = \frac{\log\left(1 + e^{1 - e^{\frac{\delta - DO}{\varepsilon}}}\right)}{\log(1 + e^{1})} \text{Softplus} - \text{exponential model} \tag{5}$$

$$h(DO) = \frac{1}{1 + e^{\frac{(\zeta - DO)}{\eta}}} \text{Sigmoid model} \tag{6}$$

$$h(DO) = \frac{DO^{\theta}}{K_{DO\_hill}{}^{\theta} + DO^{\theta}} \text{Hill model} \tag{7}$$

$$h(DO) = \frac{DO}{K_{DO\_monod} + DO} \text{Monod model} \tag{8}$$

To assess and compare the relative quality of the models, the second-order Akaike Information Criterion (AICc) was calculated for each $h(DO)$ equation using the *AICc()* function from the *MuMIn* package in R version 4.2.1. In addition, each model's residuals were evaluated to further inspect their performance.

AICc is defined by Eq. 9:

$$AIC_c = (2k - 2\ln(L)) + \frac{\{2k(k+1)\}}{\{n - k - 1\}} \tag{9}$$

where k represents the number of parameters in the model, n is the sample size, and L is the likelihood of observed data according to the model.

2.1.3. Combined model

After isolating the effects of DO using the Oxygen-independent normalization process and evaluating potential functional forms for $h(DO)$, a suite of combined models was developed to integrate the effects of body weight, temperature, and DO on feed intake. These combined models retained the parameters α, β, and γ from the Oxygen-independent model. The general structure of the combined models is expressed in Eq. 10.

$$FI(BW, temperature, DO) \approx \alpha \times BW^{\beta} \times e^{(\gamma \times temperature)} \times h(DO) \tag{10}$$

To evaluate the model's performance for both species, an initial analysis was conducted by plotting their predictions with DO levels ranging from 0 to 10 mg/L, considering a temperature of 15°C for Atlantic salmon and 25°C for meagre, and a body weight of 250 g for both species. This allowed to assess the predicted FI under hypothetical conditions. Afterwards, an independent dataset was used for each species to evaluate the developed models' performance. For Atlantic salmon, the dataset was extracted from Remen et al. (2016), providing additional data on feed intake under varying DO conditions at a temperature of 11 °C. For meagre, the evaluation dataset was derived from a separate trial conducted at IMPA (unpublished). This trial involved fish weighing 1094.76 ± 18.19 g, monitored over 104 days, under DO levels of 2.86 ± 0.12 mg/L and 6.46 ± 0.09 mg/L.

The prediction accuracy for each FI model tested was assessed by MAPE (Eq. 2).

2.2. Calibration and evaluation data

2.2.1. Published data

Peer-reviews scientific publications detailing feed intake rates for Atlantic salmon and meagre were utilized to calibrate the Oxygen-independent model for each species (see Supplementary material). Each publication provided a description of the experimental conditions and outcome variables (cumulative feed intake, temperature, number of trial days, initial and final weight). 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. Daily body weight was estimated through exponential interpolation between measured body weights at the sampling points.

2.2.2. Novel data: salmon

2.2.2.1. Experiment 1. Atlantic salmon were reared at the IMR's Matre Research Station (Matre, Norway) under experimental conditions from November 7, 2023, to March 6, 2024 (121 days). The trial tested three DO treatments in triplicate (Low, Medium and High; Table 1). Nine indoor tanks (5 m^3 each) maintained under 24-hour light regime, were stocked with 133 individuals per tank, each having an average initial body weight of 1034.73 ± 11.81 g. During the initial two weeks (November 7–20, 2023), DO was maintained at 7.31 ± 0.04 mg/L (85.10 ± 0.38 % saturation) across all tanks. From November 21, 2023, to March 6, 2024, DO levels were adjusted based on target ranges for each treatment. DO adjustments were made by controlling water flow rates and adding hyper-oxygenated water through an automatic oxygen control system. Water quality parameters were monitored, with temperature maintained at 11.87 ± 0.26 °C and salinity at 23.82 ± 0.58 ‰.

Throughout the experiment, a commercial diet (43.0 % crude protein, 28.0 % crude lipids, 22.1 MJ/kg gross energy; 7 mm pellet size; Protec, Skretting) was used to feed fish in all the tanks. Fish were fed two meals a day with automatic feeders. Daily feed intake was calculated as the difference between the feed administered to each tank and the uneaten feed recovered from sieves attached to the water outlet. The collected wet feed waste was converted to dry weight using a wet-to-dry conversion factor, which was established from five batches of spilled feed dried to constant weight under identical conditions and with the same collection system. On weekends, feed waste was not measured due to logistical constraints. Instead, it was estimated as the average of the measurements taken on Friday and Monday.

Statistical analysis revealed significant differences in weight and feed intake among the treatments. Welch's ANOVA was used for weight and feed intake, while a classical (linear model) ANOVA was applied for

Table 1
Dissolved oxygen (DO) levels used for each treatment applied to Atlantic salmon in experiment 1, expressed in mg/L and as a percentage of saturation (mean ± SD).

Treatment	Description	Dissolved oxygen (DO) levels
Low	Low oxygen level	4.91 ± 0.01 mg/L (54.21 ± 0.09 %)
Medium	Medium oxygen level	5.78 ± 0.02 mg/L (63.31 ± 0.07 %)
High	High oxygen level	8.31 ± 0.13 mg/L (89.59 ± 1.10 %)

FCR. Fish in the high dissolved oxygen group exhibited the highest final weight (3064.91 ± 190.68 g) and feed intake (2173.78 ± 87.49 g/fish), significantly outperforming medium oxygen group (body weight: 2529.75 ± 129.69 g 1590.70 ± 141.77 g/fish) and low oxygen group (final weight: 2294.57 ± 72.67 g; feed intake 1358.91 ± 65.69 g/fish). However, feed conversion ratio (FCR) did not differ significantly among the treatments.

The full experimental results are presented at Liland et al., (2025), while only the primary data necessary for modeling included in this study.

2.2.3. Novel data: meagre

2.2.3.1. Experiment 2. Meagre from an in-house bred population were reared at IPMA-EPPO facilities (Olhão, Portugal) under experimental conditions from April 12 to June 20, 2023 (69 days). The trial tested three DO treatments in triplicate (Low, Medium and High; Table 2). Nine outdoor tanks (3 m^3 each), maintained under natural light regime, were stocked with 43 individuals per tank, each having an average initial body weight of 691.26 ± 79.83 g. Prior to the trail, from March 31, 2023, to May 12, 2023, DO levels were adjusted based on target ranges for each treatment. DO levels were controlled using an automatic oxygen control system by adjusting water flow rates and injecting atmospheric air and/or pure oxygen, maintaining thresholds defined for each treatment. Water parameters were monitored throughout the trial, with temperature at 22.84 ± 1.42 °C and salinity at 37 ‰.

Throughout the experiment, fish were fed a single diet containing 49.2 % crude protein, 15.2 % crude lipids and 21.7 MJ/kg gross energy, with an 8 mm pellet size. The diet, formulated to resemble a commercial feed, was produced by Sparos Lda. (Olhão, Portugal). Fish were offered three meals per day to apparent satiation to minimize feed waste. Feeding occurred at regular intervals, and the total ration provided to each tank was meticulously recorded daily. Feed adjustments were made based on the observed intake to ensure sufficient availability without excessive surplus. After each feeding session, waste feed was collected and weighed to estimate feed intake.

Statistical analysis revealed significant differences in weight and feed intake among the treatments. ANOVA was used for weight and feed intake, while Tukey's HSD test was applied for FCR. Fish in the high dissolved oxygen level group exhibited the highest final weight (1143.47 ± 28.08 g) and feed intake (491.99 ± 25.58 g/fish), significantly outperforming low oxygen level (960.10 ± 45.18 g and 380.71 ± 15.05 g/fish, respectively) but showing no significant difference compared to medium oxygen level. Feed conversion ratio (FCR) was significantly lower in the high group (1.09 ± 0.02) compared to low (1.38 ± 0.14) and medium (1.16 ± 0.04).

2.2.3.2. Experiment 3. Meagre from an in-house bred population were reared at IPMA-EPPO facilities (Olhão, Portugal) under experimental conditions from August 18 to November 29, 2023 (104 days). The trial followed a 2 × 2 factorial design, tested in triplicate, in which fish were exposed to one of two dissolved oxygen levels (Low and High) and fed one of two diets (Diet A: 20.6 DP/DE; Diet B: 23.9 DP/DE) (Table 3). The experiment utilized 12 outdoor tanks (3 m^3 each) under natural light conditions, with 27 fish per tank and an average initial body weight of 1094.76 ± 18.19 g. Prior the trail, from November 16, 2023, to November 18, 2023, DO levels were adjusted based on target ranges for each treatment. DO levels were controlled using an automatic oxygen control system by adjusting water flow rates and injecting atmospheric air and/or pure oxygen, maintaining thresholds defined for each treatment. Water parameters were monitored throughout the trial, with temperature at 21.88 ± 3.12 °C and salinity at 37 ‰.

Throughout the experiment, fish were one of two diets, with an 8 mm pellet size (Diet A: 47.9 % crude protein, 20.7 % crude lipids, 21.8 MJ/kg gross energy, and 20.6 DP/DE; Diet B: 50.3 % crude protein, 15.9 % crude lipids, 21.2 MJ/kg gross energy, and 23.9 DP/DE). The diets, formulated to include practical ingredients used in commercial feeds, were produced by Sparos Lda. (Olhão, Portugal). Fish were offered three meals per day to apparent satiation to minimize feed waste. Feeding occurred at regular intervals, and the total ration provided to each tank was meticulously recorded daily. Feed adjustments were made based on the observed intake to ensure sufficient availability without excessive surplus. After each feeding session, waste feed was collected and weighed to estimate feed intake.

Statistical analysis revealed significant differences in weight and feed intake among the treatments. ANOVA was used for weight and feed intake, while Tukey's HSD test was applied for FCR. Fish in the high_A group exhibited the highest final weight (1766.90 ± 41.37 g), significantly outperforming low_A (1606.99 ± 47.71 g) and low_B (1518.21 ± 68.90 g). However, no significant difference was observed between high_A and high_B (1737.53 ± 21.22 g). Fish in the high_B group exhibited the highest feed intake (852.06 ± 33.04 g/fish), significantly higher than low_A (768.89 ± 14.80 g). However, no significant difference was observed between high_B, low_A (830.36 ± 19.68 g), and high_B (789.81 ± 33.25 g). Fish in the high_A group exhibited the lowest FCR (1.23 ± 0.02), significantly better than low_B (1.86 ± 0.29). However, no significant difference was observed between low_B, high_B (1.32 ± 0.03), and high_A (1.54 ± 0.10).

Similar to the trial on Atlantic salmon, the results of the meagre experiments are not part of this work, as they are being prepared to be independently published (Reference, unpublished).

3. Results

3.1. Oxygen-independent model

The collection of dataset results in a total of 64 peer-reviewed scientific publications were sourced for Atlantic salmon, covering a range of temperatures from 6.0 to 19.1 °C and body weights from 0.92 to 4075.84 g. For meagre, 42 scientific publications were sourced, with body weights ranging from 2.6 to 1160 g and temperatures from 15.5 to

Table 2
Dissolved oxygen (DO) levels used for each treatment applied to meagre in Experiment 2, expressed in mg/L and as a percentage of saturation (mean ± SD).

Treatment	Description	Dissolved oxygen (DO) levels
Low	Low oxygen level	2.95 ± 0.02 mg/L (41.98 ± 7.05 %)
Medium	Medium oxygen level	4.66 ± 0.02 mg/L (66.50 ± 5.46 %)
High	High oxygen level	6.60 ± 0.04 mg/L (93.35 ± 6.84 %)

Table 3
Dissolved oxygen (DO) levels used for each treatment applied to meagre in Experiment 3, expressed in mg/L and as a percentage of saturation (mean ± SD).

Treatment	Description	Diet	Dissolved oxygen (DO) levels
Low_A	Low oxygen level and Diet A	A	2.79 ± 0.04 mg/L (40.31 ± 1.28 %)
High_A	High oxygen level and Diet A	A	6.45 ± 0.07 mg/L (92.50 ± 3.28 %)
Low_B	Low oxygen level and Diet B	B	2.93 ± 0.15 mg/L (43.98 ± 3.28 %)
High_B	High oxygen level and Diet B	B	6.45 ± 0.12 mg/L (91.90 ± 1.12 %)

Table 4
Estimated parameters (± standard error), per species, for the Oxygen-independent model (Eq. 1), α, β, γ.

Species	Atlantic Salmon	Meagre
α	0.0149 ± 0.003	0.0113 ± 0.004
β	0.8299 ± 0.221	0.8131 ± 0.029
γ	0.0420 ± 0.006	0.0426 ± 0.013

27.6 ºC. The estimated parameters are presented in Table 4, and the complete list of peer-reviewed publications used in the analysis is provided in the Supplementary Material.

The model's Oxygen-independent performance was also evaluated for both species (Figs. 2A and 2B). A strong positive relationship was observed between body weight and daily feed intake (DFI) in both species. The MAPE for the Oxygen-independent model was 31.4 % for Atlantic salmon and 40.7 % for meagre, indicating a moderate level of predictive error in both cases. To assess the residual distribution, the Shapiro-Wilk test ($p \leq 0.05$) showed that the residuals were not normally distributed, suggesting that the model may systematically overestimate or underestimate FI in specific weight ranges. For Atlantic salmon (Fig. 2A), the scatter plot indicates both underestimation and overestimation around 2000 g, with a tendency to overestimate FI for larger fish (~4000 g). For meagre (Fig. 2B), the model overestimates DFI for smaller fish (< 200 g), as observed in the scatter plot.

3.2. Oxygen-dependent model

The complete Oxygen-dependent models and estimated parameters are presented in Table 5, for both Atlantic salmon and meagre.

The AICc values of each species model are presented in Table 6. The model comparison based on AICc values shows distinct patterns in predicting Atlantic salmon and meagre feed intake. For Atlantic salmon, the Sigmoid model achieved the lowest AICc value (-20.89), indicating the best fit among the tested models. The Softplus-exponential model followed closely (-19.63), while the Monod model (-7.24) had the worst performance. For meagre, the Hill model demonstrated the best fit, with the lowest AICc value (-26.63), followed by the Softplus-exponential model (-25.56) and the Sigmoid model (-25.31), while the Monod model (-24.09) had the worst performance.

Residual boxplots were assessed to evaluate the models' predictive performance for each species (Fig. 3). In general, the residuals of all models for both species are closely centered around zero, indicating that none of the models exhibit systematic bias in their predictions. However, the models for Atlantic salmon tend to have residuals slightly below zero, while the models for meagre show a slight tendency for residuals to be above zero. In addition, the residuals for the Monod model in Atlantic salmon exhibit a positive skew, suggesting that this model might underestimate FI prediction at high levels of DO.

Table 5
Estimated parameters (± standard error), per species, for Oxygen-dependent equations (Eqs. 6–9), δ, ε, ζ, η, K_{DO_hill}, θ, K_{DO_monod}.

Species		Atlantic Salmon	Meagre
δ	*Softplus-exponential model*	4.628 ± 0.173	0.995 ± 0.598
ε		1.795 ± 0.341	2.039 ± 0.488
ζ	*Sigmoid model*	4.402 ± 0.210	1.859 ± 0.446
η		1.445 ± 0.256	0.385 ± 0.758
K_{DO_hill}	*Hill model*	4.537 ± 0.171	1.585 ± 0.260
θ		4.186 ± 0.771	2.199 ± 0.464
K_{DO_monod}	*Monod model*	2.140 ± 0.458	0.582 ± 0.087

Table 6
AICc values for different Oxygen-dependent models used to predict feed intake in Atlantic salmon and meagre.

Model	AICc value	
	Atlantic salmon	Meagre
Softplus-exponential model	−19.64	−25.56
Sigmoid model	−20.89	−25.31
Hill model	−18.80	−26.63
Monod model	−7.24	−24.09

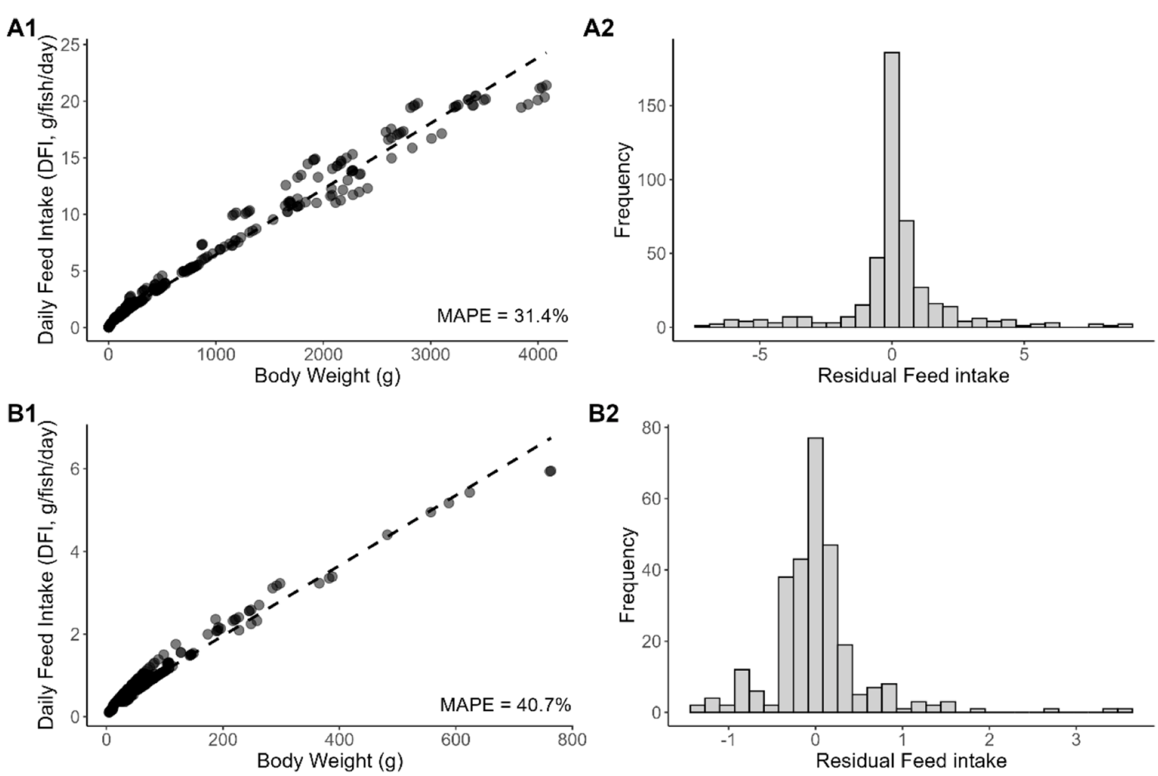

Fig. 2. Oxygen-independent model's performance for predicting Daily Feed Intake (DFI) in (A) Atlantic salmon and (B) meagre. A1 and B1 show the relationship between body weight (g) and daily feed intake (DFI, g fish/day), with the dashed line representing the model's predictions. The MAPE values indicate the mean model's predictive error: 31.4 % for Atlantic salmon and 40.7 % for meagre. A2 and B2 display the distribution of residuals, highlighting deviations from the model's predictions.

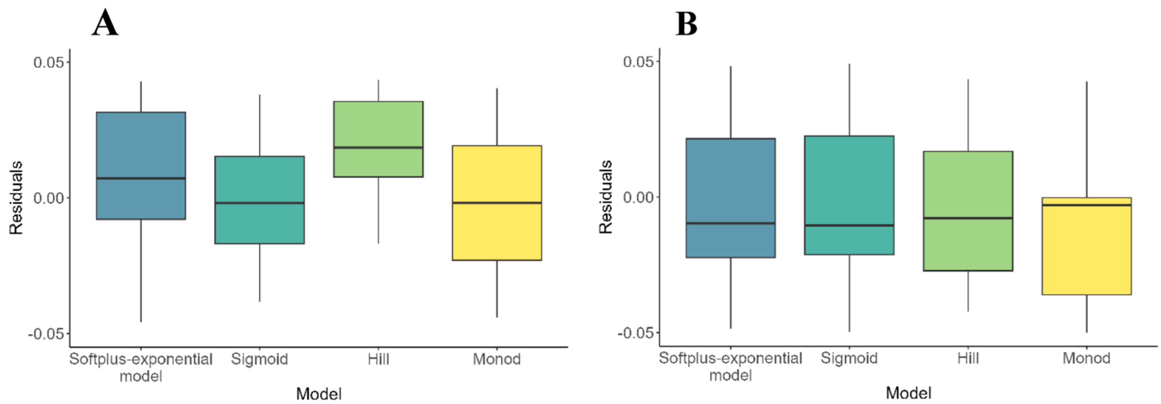

Fig. 3. Boxplots of residuals for the different models applied to (A) Atlantic salmon and (B) meagre. The boxplots display the distribution of residuals, with the error bars representing the 95 % confidence interval.

3.3. Combined models

3.3.1. Atlantic salmon

The models fitted to the Atlantic salmon data exhibit different curves, which illustrate the assumptions of how DO constrains feed intake (Fig. 4). The Monod model displays a concave curve, the K_{DO_monod} value indicates a low half-saturation point (2.140 ± 0.458), suggesting that feeding reaches half-maximum at low DO concentrations and plateaus early around 5–7.5 mg/L dissolved oxygen. The Sigmoid, Softplus-exponential, and Hill models exhibit S-shaped curves that start with a convex behavior at low DO, followed by a sharp increase and then by a plateau at higher DO.

When evaluating the models' performance under hypothetical conditions for Atlantic salmon, the Monod model showed a limited FI prediction, as it exhibited a steep growth from 0 mg/L to 5 mg/L. Similarly, the Softplus-exponential model failed to predict zero FI when DO was 0 mg/L. However, Sigmoid Model and Hill Model provided predictions that are closely aligned with expected FI patterns across the range of DO. Both models predicted near-zero FI at DO levels below 2.5 mg/L, followed by a rapid increase in FI between 2.5 and 7.5 mg/L, reaching a plateau at DO levels above 7.5 mg/L.

The models' predictive performance over the Remen et al. (2016) dataset (fixed temperature of 11°C) was evaluated focusing on the relationship between Daily Feed Intake (DFI) and dissolved oxygen levels (Fig. 5). For the S-shaped models (i.e., Softplus-exponential, Sigmoid and Hill), the error variance has larger residual at low DO (3–4 mg/L) compared to high DO levels. This heteroscedasticity indicates that these models underestimate feed intake at low dissolved oxygen concentrations, where observed feeding rates show much higher variability than predicted. On the other hand, the Monod model and the model proposed by Remen et al. (2016), appear to better describe feed intake at low DO levels. However, while the Monod model tends to underestimate feed intake at higher DO levels, the model of Remen et al. (2016) shows a more uniform variance distribution across the entire DO range. The Sigmoid and Hill models produced S-shaped curves, effectively capturing the increase in DFI with DO levels. These models showed an initial slow DFI increase at lower DO levels, which then accelerated at intermediate DO concentrations before stabilizing at higher DO levels. This behavior reflects the typical biological response, where feed intake increases with oxygen availability but eventually reaches a plateau. Monod model did not perform as well at low DO levels, giving underestimation of DFI at higher DO concentrations and overestimation at lower DO levels. The Monod model, showed limited sensitivity to the variation in DFI at low DO levels, failing to capture the gradual increase in feed intake seen in the data. The Softplus-exponential model showed a consistent increase in DFI as DO levels rose, but lacked the saturation effect observed in the Sigmoid and Hill models. As a result, the Softplus-exponential model overestimated

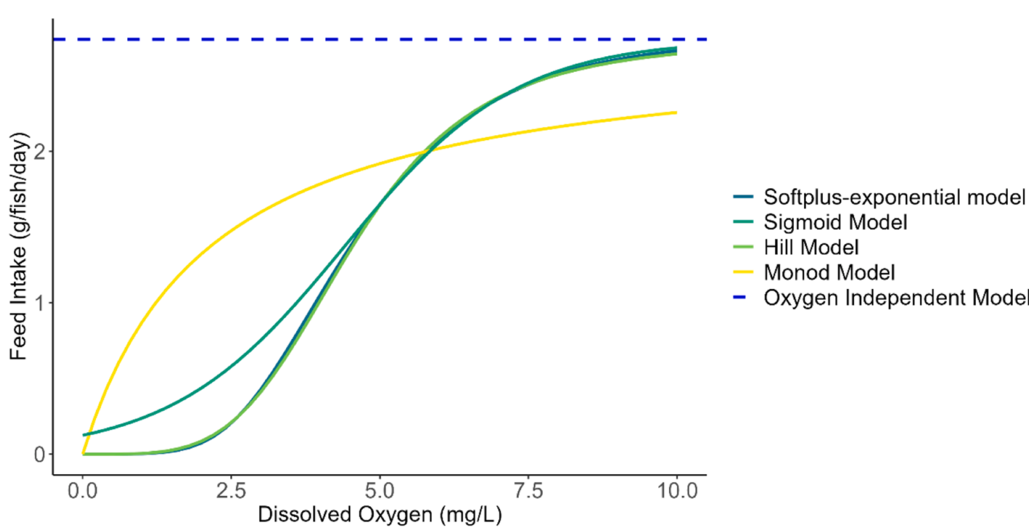

Fig. 4. Model predictions of feed intake under hypothetical DO conditions for Atlantic salmon. The curves represent the predictions from different models: Softplus-exponential model, Sigmoid model, Hill model, and Monod model. The dashed blue line represents the Oxygen-Independent model, which assumes no dependency on DO levels.

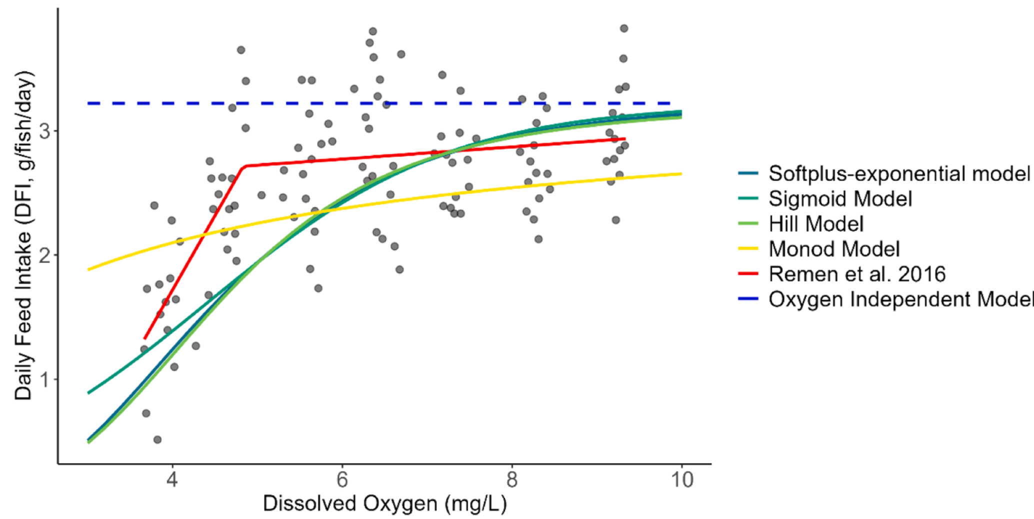

Fig. 5. Model comparison of Daily Feed Intake (DFI, g/fish/day) for Atlantic salmon as a function of dissolved oxygen (DO, mg/L) based on the Remen et al. (2016) dataset. The data points (gray dots) represent the observed DFI values across varying DO concentrations. The curves represent the predictions from different models: Softplus-exponential model, Sigmoid model, Hill model, and Monod model. The dashed blue line represents the Oxygen-Independent model, which assumes no dependency on DO levels. The red curve corresponds to the model proposed by Remen et al. (2016).

DFI at higher DO concentrations, especially when compared to the observed biological trend where feed intake stabilizes at elevated oxygen levels.

In general, for Atlantic salmon, the Oxygen-dependent models provided better predictions of DFI than the Oxygen-independent model (Table 7). The Softplus-exponential and Hill models exhibited the lowest MAPE values, 24.45 % and 24.47 %, respectively, indicating the best performance in predicting DFI based on dissolved oxygen levels. Given the MAPE values, it can be inferred that these two models outperformed the Remen et al. model, which had a higher MAPE value of 28.70 %. Additionally, the Oxygen-independent model demonstrated the highest MAPE (64.14 %), highlighting its poor predictive accuracy.

3.3.2. Meagre

The models fitted to the meagre data exhibit different curves, which illustrate the assumptions of how DO constrains feed intake (Fig. 6). The Monod model displays a concave curve, the K_{DO_monod} value indicates a low half-saturation point (0.582 ± 0.087), suggesting that feeding reaches half-maximum at low DO concentrations and plateaus early around 2–3 mg/L dissolved oxygen. The Sigmoid, Softplus-exponential, and Hill models exhibit S-shaped curves that start with a convex behavior at low DO, followed by a sharp increase and then by a plateau at higher DO. The Hill model shows the steepest transition, the Sigmoid model suggests a more gradual S-curve, while the Softplus-exponential model provides an intermediate response curve.

When evaluating the models' performance under hypothetical conditions for meagre, the Softplus-exponential model and Sigmoid model failed to predict zero FI at 0 mg/L DO. Instead, they predicted FI values of approximately 2.3 and 1.8 g/fish/day, respectively, when FI should be zero under such conditions. Although predicting zero FI at 0 mg/L DO, the Monod model exhibits a steep increase in FI at low oxygen levels, which would not be the expected feeding behavior under hypoxic conditions. Finally, the Hill model gives a more realistic representation of the FI curve that closely represents the expected feeding behavior as DO levels increase.

Table 7
Mean Absolute Percentage Error (MAPE) for each Atlantic salmon model applied to the Remen et al. (2016) dataset. The table shows the MAPE values for the Oxygen-Independent model, Softplus-exponential model, Hill model, Sigmoid model, and Monod model, which were evaluated based on their predictive accuracy of Daily Feed Intake (DFI).

Model	MAPE value (%)
Softplus-exponential model	24.45
Sigmoid model	25.00
Hill model	24.47
Monod model	25.64
Oxygen-Independent model	64.14
Remen et al.	28.7

To evaluate the predictive performance of the models results from experiment 3 were used (Fig. 7). The Softplus-exponential, Sigmoid, and Hill models provide similar predictions, particularly at DO levels above 4 mg/L. However, all three models show an underestimation of FI under both low and high DO levels. In contrast, the Monod model predicts higher FI values under low DO conditions compared to the other models but also underestimates FI compared to observed data. Therefore, for meagre FI prediction, the Oxygen-Independent model offers the most accurate predictions for both low and high DO levels.

Unlike the salmon results, the Oxygen-Independent model provided the best predictions of DFI for meagre, with the lowest MAPE, of 4.22 % (Table 8). In general, the Oxygen-dependent models showed higher MAPE values, with the Softplus-exponential model having the lowest value (12.06 %), followed closely by the Sigmoid (11.97 %), Hill (12.44 %), and Monod (12.38 %) models.

4. Discussion

The trials performed with Atlantic salmon and meagre highlight the importance of oxygen availability in supporting growth and feed intake. Atlantic salmon exposed to the higher (close to normal farming situation) DO levels (8.31 ± 0.13 mg/L) exhibited higher final weight and feed intake than at medium (5.78 ± 0.02 mg/L) and low (4.91 ± 0.01 mg/L) levels. Similarly, meagre raised under high DO levels (6.60 ± 0.04 mg/L) displayed higher final weight and feed intake at the end of the experimental period, compared to fish raised under medium and low DO levels (4.66 ± 0.02 mg/L and 2.95 ± 0.02 mg/L, respectively). These results are consistent with the other studies on Atlantic salmon suggesting that, when faced with a limited aerobic scope, fish tend to deprioritize growth, potentially reducing feed intake as a strategy to conserve available aerobic capacity (Jutfelt et al., 2021). Thus, hypoxia is a limiting factor to the energy budget and maximum growth potential.

Despite these differences in feed intake and weight for the trial

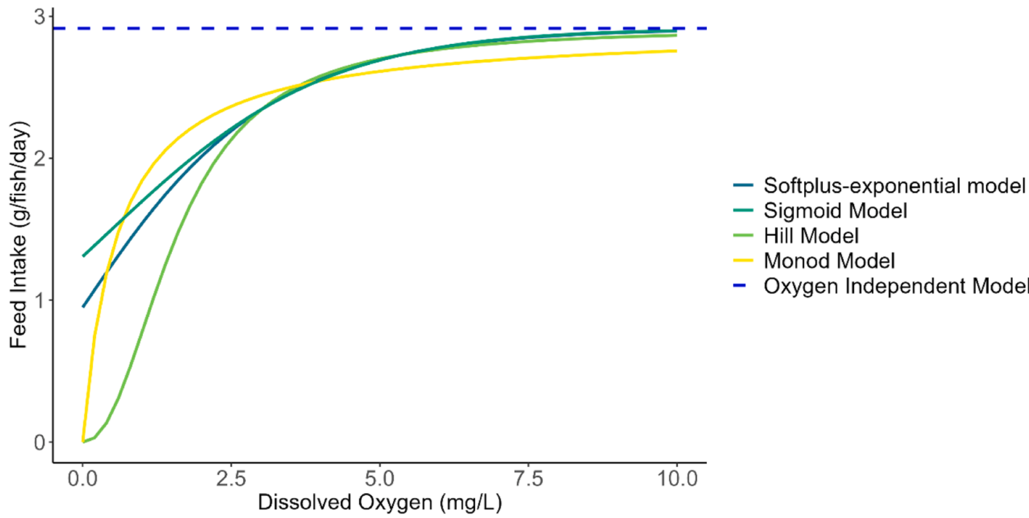

Fig. 6. Model predictions of feed intake under hypothetical DO conditions for meagre. The curves represent the predictions from different models: Softplus-exponential model, Sigmoid model, Hill model, and Monod model. The dashed blue line represents the Oxygen-Independent model, which assumes no dependency on DO levels.

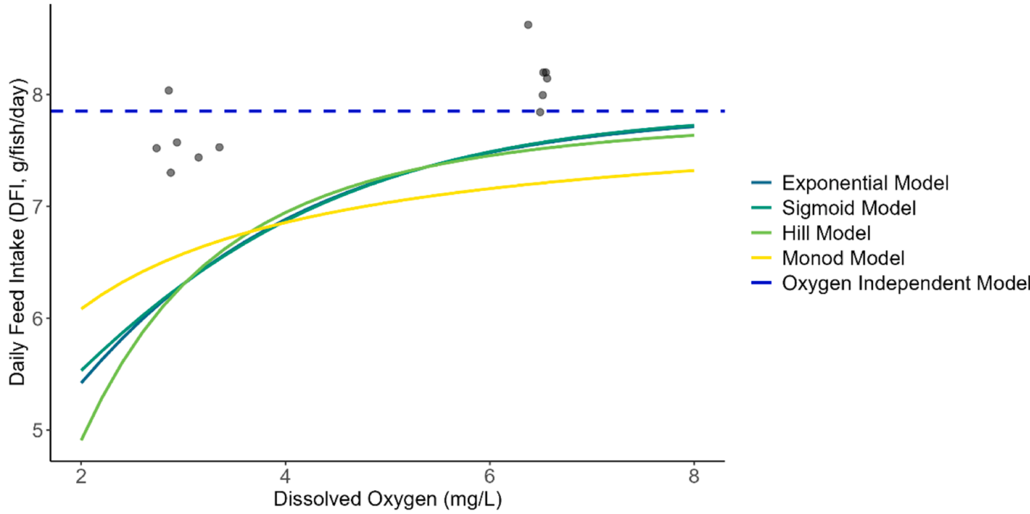

Fig. 7. Model comparison of Daily Feed Intake (DFI, g/fish/day) as a function of dissolved oxygen (DO, mg/L) based on trial 3 performed with meagre. The data points (gray dots) represent the observed DFI values across varying DO concentrations. The curves represent the predictions from different models: Softplus-exponential model, Sigmoid model, Hill model, and Monod model. The dashed blue line represents the Oxygen-Independent model, which assumes no dependency on DO levels.

Table 8
Mean Absolute Percentage Error (MAPE) for each model applied to an independent trial dataset. The table shows the MAPE values for the Softplus-exponential model, Sigmoid model, Hill model, Monod model and Oxygen-Independent model which were evaluated based on their predictive accuracy of Daily Feed Intake (DFI).

Model	MAPE value (%)
Softplus-exponential Model	12.06
Sigmoid Model	11.97
Hill Model	12.43
Monod Model	12.38
Oxygen Independent Model	4.22

performed with Atlantic salmon, FCR values remained consistent across treatments for both species, indicating that oxygen levels influenced intake volume rather than feed utilization efficiency. This agrees with other studies, such as Herrmann et al. (1962) on coho salmon, Stewart et al. (1967) on largemouth bass, and Tran-Duy et al. (2011) on Nile tilapia (*Oreochromis niloticus*). The consistent FCR values across treatments implies that, while dissolved oxygen levels influenced feed intake and growth, the fish maintained similar metabolic efficiency in converting consumed feed into biomass under all oxygen conditions. This could be due to compensatory physiological mechanisms or adaptations allowing efficient energy utilization regardless of oxygen availability.

When analyzing the models' predictions for Atlantic salmon, the Oxygen-dependent feed intake models demonstrated improved accuracy in predicting feed intake. Based on both hypothetical conditions and the predictive performance over the Remen et al. (2016) dataset, the Hill and Sigmoid models provided the best prediction behavior, effectively capturing the relationship between DO levels and DFI. In addition, it is possible to highlight the differences between the calibration method used for the developed models in this study and the method used by Remen et al. (2016), who employed broken-line regression. For example, in the hypothetical simulation conducted in this study at a temperature of 15°C and for fish weighing 250 g (Fig. 5), the estimated breakpoint for maximal feed intake (i.e., the minimum DO require for optimal feed intake) was 7.5 mg/L, whereas Remen et al. (2016) reported a lower value of 5.4 mg/L. However, when evaluating the predictive performance of the models over the Remen et al. (2016) dataset (Fig. 6) the Softplus-exponential and Hill models exhibited a lower MAPE value providing better predictions than the Remen et al. (2016) model.

In addition, it is relevant to note that Remen et al. (2016) suggest that the incipient dissolved oxygen level (i.e., the threshold below which feed intake is affected by DO) is temperature-dependent. In contrast, the Oxygen-dependent models developed in our work do not account for this temperature effect. Instead, they assume that the impact of dissolved oxygen on feed intake depends solely on the DO concentration, regardless of water temperature. Therefore, in future work, it would be important to further examine a wider range of temperatures and corresponding oxygen concentrations to fully understand the interaction effect between temperature and dissolved oxygen levels on feed intake, with the goal of generating a robust dataset for model calibration. This would allow for incorporating the specific temperature-oxygen interaction effect into the Oxygen-dependent model, ultimately improving its accuracy.

In contrast to the findings for salmon, the Oxygen-dependent model did not seem to improve the feed intake prediction for meagre. The Oxygen-independent model provided the most accurate predictions of feed intake for meagre, with the lowest MAPE. Still, the experimental trial showed a lower FI at low DO (DO1; 2.95 ± 0.02 mg/L). This contrast may be due to meagre's relatively low sensitivity to lowered DO levels at higher body weight, as fish had ~1 Kg at the validation trial, while it was ~0.7 Kg for the model calibration trial. More studies on the effect of DO on FI at different meagre sizes are necessary to clarify this. However, it might not be essential to include the DO effect in a FI model for meagre when working with scenarios of DO not going below a certain level (2.95 ± 0.02 mg/L).

The model developed in this study provides a practical tool for predicting feed intake in Atlantic salmon and meagre farming using simple variables; body weight, temperature, and dissolved oxygen. These models can be readily applied by farmers and researchers, as all parameter estimates and data sources are fully documented, making our results reproducible. Furthermore, the models can be adapted and tailored to site-specific conditions and operational requirements, given their design simplicity. The inclusion of dissolved oxygen as a parameter is particularly valuable for predicting feed intake in sea cages, which are exposed to fluctuating oxygen concentrations. It is important to note a limitation of this approach: literature data were incorporated under the assumption that DO have no measurable effect on feed intake, as DO was not reported or treated as an experimental variable in those studies. Although the selected trials were generally conducted under high oxygen availability, it cannot be guaranteed that DO effects were entirely absent. Future studies should aim to incorporate datasets where DO is explicitly reported, apply correction factors when oxygen levels are available but not standardized, or design experiments that systematically assess feed intake responses across different DO conditions to refine model calibration and reduce this source of uncertainty.

5. Conclusion

Dissolved oxygen is a significant factor that modulates FI, impacting fish growth and metabolic efficiency, although the sensitivity varies between species and possibly across fish sizes. In this study, we have developed models of FI that explicitly incorporate not only fish body weight and temperature but also DO levels, enhancing the predictive accuracy. For Atlantic salmon, Oxygen-dependent models effectively captured the relationship between DO and FI, with the Hill and Sigmoid models (represented by Eqs. 11 and 12, respectively) providing the overall best predictions.

$$FI(BW, temperature, DO) = \mathbf{0.01} \times BW^{\mathbf{0.83}} \times e^{(\mathbf{0.04} \times temperature)} \times \frac{DO^{\mathbf{4.186}}}{\mathbf{4.537}^{\mathbf{4.186}} + DO^{\mathbf{4.186}}} \quad (11)$$

$$FI(BW, temperature, DO) = \mathbf{0.01} \times BW^{\mathbf{0.83}} \times e^{(\mathbf{0.04} \times temperature)} \times \frac{1}{1 + e^{\frac{(\mathbf{4.402} - DO)}{\mathbf{1.445}}}} \quad (12)$$

However, for meagre, Oxygen-independent models performed better (Eq. 13), suggesting that meagre may be less sensitive to low DO levels, at least for larger fish sizes.

$$FI(BW, temperature) = \mathbf{0.01} \times BW^{\mathbf{0.81}} \times e^{(\mathbf{0.04} \times temperature)} \quad (13)$$

Further research is needed to better understand the specific oxygen requirements of meagre.

Authors contribution

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 Conceição, and Ivar Rønnestad provided supervision and investigation support. Marina Azevedo, Tomé Silva, Sergey Budaev, and Filipe Soares managed data curation. Filipe Soares, Nina Liland, Pousão-Ferreira managed the project. Luis Conceição and Ivar Rønnestad secured funding. All authors reviewed the manuscript.

CRediT authorship contribution statement

Luis E.C. Conceição: Writing – review & editing, Supervision, Funding acquisition. **Sergey Budaev:** Writing – review & editing, Supervision, Data curation. **Filipe Soares:** Writing – review & editing, Project administration, Data curation. **Tomé Silva:** Writing – review & editing, Supervision, Software, Data curation. **Marina Linhares Azevedo:** Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Rønnestad Ivar:** Writing – review & editing, Supervision, Project administration. **Pedro Pousão-Ferreira:** Writing – review & editing, Project administration. **Nina Liland:** Writing – review & editing, Project administration.

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.

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.2025.102635.

Data availability

Data will be made available on request.

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