

A biometrical traits-to-feed model integrating fish nutrition and genetic improvement of feed utilisation traits: Predicting changes in optimal feed phosphorus levels for selectively bred rainbow trout

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ABSTRACT

Feed whose composition matches nutritional requirements of farmed animals is fundamental for sustainable food production. Selective breeding of fish changes growth, body composition and feed utilisation of fish and hence also nutritional requirements. We derived equations that directly estimate the required changes in feed formulation from measured trait changes, bypassing the traditional estimation by experimental dose-response trials. We applied the model to determine changes in optimal feed phosphorus (P) levels in rainbow trout that has been improved across decades by a breeding programme. The equations show that the effect of changes in body composition (body P%, fillet%, viscera%) on digestible phosphorus inclusion level is modest and linear. The effects of FCR (feed conversion ratio) and phosphorus retention efficiency are strong and highly non-linear, implying that the available phosphorus levels for rainbow trout need to be increased due to their improved FCR, and less so due to their increased fillet% and reduced viscera%. Despite the complex non-linear relationships on the observed raw scale (i.e., additive effects), the multiplicative effects of the traits on a log-log scale are actually simple and intuitive. During the last decades, dietary phosphorus has been reduced to limit nutritional loading to environment. Forecasting showed that the required feed phosphorus levels for rainbow trout under selective breeding are expected to be further increased, and a care must be taken not to reduce the dietary levels too much. The equations integrate quantitative genetics and fish nutrition under one united predictive framework, and they are applicable to other fish species.

1. Introduction

Aquaculture, the farming of *fish, shellfish, algae and other aquatic organisms*, is one of the fastest growing food production industries, and global farmed fish production has exceeded beef production in 2011 (FAO, 2022). For decades, feed development and progress in the understanding of fish nutrition have advanced aquaculture practices and fish performance. For each fish species, specific nutritional requirements that fulfil their physiological and developmental needs have been set, and aquafeeds are developed to reflect these requirements (NRC, National Research Council, 2011).

Nutritional requirements of fish are generally estimated through an analysis of dose-response studies in which fish are fed with multiple

feeds that have different amounts of a nutrient, and fish performance is evaluated to determine the optimal requirement while avoiding deficiency or toxicity (Shearer, 2000). Due to the complexity of testing simultaneously dozens of nutrients, and the high cost of undertaking such studies, they are often performed under simplifying assumptions (e.g., the effects of essential nutrients on growth are marginally independent as long as all other essential nutrients are provided in excess) and the implicit notion that nutritional requirements are essentially static. Once the requirement of a specific nutrient has been estimated for a specific species based on one or more studies (NRC, National Research Council, 2011), typically at a limited range of fish sizes and under a narrow range of environmental conditions, the value is often accepted as being universally valid, despite different studies showing a significant

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variation (e.g., Oliva-Teles et al., 2020).

Dietary phosphorus has been a focus of research for decades due to its essential role in fish physiology and environmental impact of aquaculture (reviewed by Lall, 2002; Bouwman et al., 2013; Prabhu et al., 2013; Lemos and Tacon, 2017; Sugiura, 2018, 2025a, 2025b; Huang et al., 2020; Luo, 2023). In fish, phosphorus (P) is essential for the development of bone structure and cells. Phosphorus deficiency can cause reduced growth, decreased feed efficiency, reduced bone mineralization and increased frequency of skeletal abnormalities (Lall, 2002). Dietary phosphorus supplies most of the phosphate fish requires, and only a limited part of it absorbed from water. The retained phosphorus accumulates in skeletal tissue as well as in soft tissues such as heart, liver, kidney, muscle and blood. Moreover, production licences of fish farms in some countries, such as in Finland and Denmark, are based on the amount of phosphorus in the feed used at a farm (e.g. Kossman, 1989; Dalsgaard et al., 2023). This is because an extensive amount of phosphorus in aquatic environment leads to eutrophication which needs to be avoided (Bouwman et al., 2013; Sugiura, 2018; 2025a, 2025b; Luo, 2023). Hence, the phosphorus content in aquafeeds must be carefully balanced to provide an adequate amount for fish physiology while minimizing environmental phosphorus discharge. To address this, phosphorus levels in feeds have been significantly reduced over recent decades (Bouwman et al., 2013; Dalsgaard et al., 2023), while digestibility has been improved through nutritional innovations (Lemos and Tacon, 2017), and technologies to reduce phosphorus in waste have been developed (Luo, 2023).

Selective breeding programmes are applied in aquaculture species to improve fish traits such as feed conversion ratio (FCR, feed intake / weight gain), fillet percentage, amount of slaughter waste, fasting maintenance costs, and protein and energy retention efficiencies (Kause et al., 2016, 2022; Gjerdem and Rye, 2018; Vandeputte et al., 2022; Kajbaf et al., 2024), which may directly modify nutritional requirements. A match between feed composition and genetic potential of fish would be critical to improve resource efficiency, product quality and fish health and welfare. Consequently, it seems relevant to be able to quantitatively predict the impact of such changes in fish traits on optimal feed formulation targets, including digestible phosphorus inclusion levels.

As an alternative to empirical dose-response studies, factorial models have been developed to determine dietary requirements of fish and shrimp based on simple processes that describe energy and nutrient balance, such as feed intake, metabolic loss, and new tissue growth (e.g., Lupatsch et al., 1998, 2001; Glencross, 2008, 2021), and this approach has been used also for dietary phosphorus (Pfeffer and Pieper, 1979; Nakashima and Leggett, 1980; Shearer, 1995; for a review and criticism see Prabhu et al., 2013 and Sugiura, 2025a). In addition, there have been approaches to reduce phosphorus emissions (and hence P in feed) from farming of large rainbow trout by matching the dietary bioavailable P concentrations to fish requirements using whole-body P concentration and expected individual raw material digestibility as criteria (Dalsgaard et al., 2023). These studies have some similarities to our study - the models include some fish traits that are applicable to selective breeding. However, the current knowledge gap is that there is a need for a multi-trait model to link the specific traits changed by selective breeding to predict the way the trait changes impact optimal diet composition (Graphical summary in Appendix A). Such an approach is the first step to integrate selective breeding and fish nutrition.

In this study, we derived a set of mathematical traits-to-feed models that directly estimate the required changes in feed formulation from measured trait changes. We apply these models to the decades-long data from the Finnish national breeding programme for rainbow trout that have been used previously to estimate the genetic changes in fish trait related to feed utilisation, growth and body composition (Kause et al., 2022). In the current study, the objectives were 1) to establish formal biometrical equations that link changes in fish traits to the required changes in optimal dietary nutrient inclusion levels. 2) To apply the

equations to the genetic changes in fish traits in the Finnish national breeding programme of rainbow trout to estimate the changes in the required dietary phosphorus inclusion levels across decades, and finally, 3) to forecast the required phosphorus inclusion levels up to year 2050, assuming the breeding programme would continue as previously demonstrated. Though this study focuses on the phosphorus requirements of rainbow trout, the underlying concept and derived equations are generic and can be applied to most essential nutrients and fish species.

2. Material and methods

In our traits-to-feed framework, the required changes in feed formulation are directly calculated from measured or assumed trait changes. To establish general formulas, we start by assuming energy and mass conservation to define a budget for any nutrient or energy (i.e., gain = intake - losses). Then we consider a series of assumptions with increasing levels of complexity (and realism). Expanding the budgets under each of these sets of assumptions leads to different closed-form formulas that directly relate relevant fish traits to the optimal feed inclusion levels of a nutrient or energy. The specific effect of each fish trait on optimal inclusion levels was then obtained and analysed both through an analytical sensitivity analysis and plots of the marginal effects of each trait (under varying parameters). We developed two models, one simple and one advanced, with the target of presenting nutrient inclusion levels in a feed on a digestible (as fed) basis. In our calculations, feed intake is as fed on wet feed weight basis, growth is wet weight gain, and body composition is on live weight basis. To develop the models we collected data from published papers, and when values were reported on dry basis, we converted them to wet weight based values.

2.1. Development of a simple traits-to-feed model

2.1.1. Simple model 1: Optimal feed formulation depends on feed efficiency, nutrient retention efficiency and the abundance of the nutrient in whole body

Assumptions:

Phosphorus gain (e.g., in g/day) can be estimated by:

$$\text{gain}_p = \frac{d(P_w)}{dt} = FI \times \text{diet}_p \times RE_p \quad (1)$$

where P_w represents the rate of increase of mass of phosphorus in fish body (usually in g/day), FI represents feed intake rate (usually in wet weight g/day), diet_p represents the fraction of the diet that constitutes total phosphorus (i.e., number between 0 and 1), and RE_p represents the efficiency of phosphorus retention (i.e., number between 0 and 1, in g P gained / g P intake).

Nutrient amount in fish whole body generally follows an allometric pattern:

$$P_w = a \times BW^b \quad (2)$$

where BW represents wet weight of fish body, while a and b are species-dependent (or strain-dependent) parameters or constants. Thus:

$$\frac{d(P_w)}{d(BW)} = a \times b \times BW^{b-1} \quad (3)$$

If nutrient gain remains a fixed proportion of wet weight growth, i.e. the isometric case of $b = 1$, this expression simplifies further to:

$$\frac{d(P_w)}{d(BW)} = a = \text{body}_p \quad (4)$$

This means that for a fish with isometric whole body composition, the amount of phosphorus, body_p , is always a fixed fraction of the total wet weight (value between 0 and 1). For phosphorus, after circa 2 g wet

body weight, whole-body P content (per wet weight) tends to remain stable (Shearer, 1994; Fontagné et al., 2009).

Calculations:

Then we derive $diet_p$ using the following calculations.

$$\frac{d(P_w)}{dt} = \frac{d(BW)}{dt} \times \frac{d(P_w)}{d(BW)} \text{ (true by definition, chain rule)} \quad (5)$$

$$retention_p = growth \times \frac{d(P_w)}{d(BW)} \text{ (same as the line above)} \quad (6)$$

$$FI \times diet_p \times RE_p = growth \times \frac{d(P_w)}{d(BW)} \text{ (using assumption eq.1)} \quad (7)$$

$$diet_p = \frac{growth}{FI} \times \frac{1}{RE_p} \times \frac{d(P_w)}{d(BW)} \text{ (rearrange previous equation)} \quad (8)$$

$$diet_p = \frac{1}{FCR} \times \frac{1}{RE_p} \times \frac{d(P_w)}{d(BW)} \text{ (simplify)} \quad (9)$$

$$\begin{aligned} diet_p &= \frac{FE}{RE_p} \times \frac{d(P_w)}{d(BW)} \text{ (make substitution feed efficiency on a 'as fed' basis)} \\ &= FE = \text{wet weight gain/feed intake} = 1/FCR \end{aligned} \quad (10)$$

Next, we estimate the partial (additive) effects that feed efficiency and phosphorus retention efficiency have on the required phosphorus levels in the diet, by taking the partial derivatives of Eq. (10) with respect to these relevant factors:

$$\frac{\partial(diet_p)}{\partial(FE)} = \frac{1}{RE_p} \times \frac{d(P_w)}{d(BW)} \text{ and } \frac{\partial(diet_p)}{\partial(RE_p)} = -\frac{FE}{RE_p^2} \times \frac{d(P_w)}{d(BW)} \quad (11)$$

Using assumption Eq. (2), we obtain:

$$\frac{\partial(diet_p)}{\partial(FE)} = \frac{1}{RE_p} \times a \times b \times BW^{b-1} \text{ and } \frac{\partial(diet_p)}{\partial(RE_p)} = -\frac{FE}{RE_p^2} \times a \times b \times BW^{b-1} \quad (12)$$

If we further assume approximate isometry (see assumption Eq. (2)), we can simplify these to:

$$\frac{\partial(diet_p)}{\partial(FE)} = \frac{1}{RE_p} \times body_p \text{ and } \frac{\partial(diet_p)}{\partial(RE_p)} = -\frac{FE}{RE_p^2} \times body_p \quad (13)$$

Under this assumption, we can additionally calculate the (additive) effect that a change in $body_p$ would have on the required phosphorus levels in the diet (assuming everything else is kept constant):

$$\frac{\partial(diet_p)}{\partial(body_p)} = \frac{FE}{RE_p} \quad (14)$$

On the other hand, if we assume multiplicative effects over $diet_p$, we will have:

$$\log(diet_p) = \log\left(\frac{FE}{RE_p} \times \frac{d(P_w)}{d(BW)}\right) \text{ (applying 'log' to both sides of Eq.10)} \quad (15)$$

Taking the approximate isometry approximation and simplifying:

$$\begin{aligned} \log(diet_p) &= \log(FE) + \log\left(\frac{d(P_w)}{d(BW)}\right) - \log(RE_p) \\ &= \log(FE) + \log(body_p) - \log(RE_p) \end{aligned} \quad (16)$$

Thus, the estimated multiplicative effects are:

$$\begin{aligned} \frac{\partial(\log(diet_p))}{\partial(\log(FE))} &= \frac{\partial(\log(diet_p))}{\partial(\log(body_p))} = 1 \text{ and } \frac{\partial(\log(diet_p))}{\partial(\log(RE_p))} = \frac{\partial(\log(diet_p))}{\partial(\log(FCR))} \\ &= -1 \end{aligned} \quad (17)$$

The calculations derived above are generic, and similar relationships can be established for gross energy, protein, minerals or other essential nutrients, mutatis mutandis.

2.1.2. Simple model 2: Optimal feed formulation depends on feed efficiency, nutrient retention efficiency, fillet yield and viscerosomatic index

Whole body phosphorus%, or any other nutrient, is challenging to record in thousands of large fish but it can be modelled to be influenced by fillet yield and viscerosomatic index. These two traits can be recorded in breeding programmes (Kause et al., 2007, 2022), generating a link between selective breeding and fish nutrition.

Assumptions:

Body phosphorus, $body_p$, (value between 0 and 1), in fish whole body depends on fillet yield (YLD = fillet weight / body weight) and viscerosomatic index (VSI = viscera weight / body weight) as:

$$body_p = fillet_p \times YLD + viscera_p \times VSI + other_p \times (1 - YLD - VSI) \quad (18)$$

$$body_p = other_p + YLD \times (fillet_p - other_p) + VSI \times (viscera_p - other_p) \quad (19)$$

where YLD represents fillet yield, VSI represents viscerosomatic index, $fillet_p$ represents the amount of phosphorus in the fillet (as a fraction of fillet weight), $viscera_p$ represents the amount of phosphorus in the viscera (as a fraction of viscera weight), and $other_p$ represents the amount of phosphorus in the remaining fraction (i.e., skin, eviscerated and filleted carcass including skeleton and head).

To simplify, tissue-level compositional isometry is assumed. Thus:

$$\frac{d(P_w)}{d(BW)} = other_p + YLD \times (fillet_p - other_p) + VSI \times (viscera_p - other_p) \quad (20)$$

Calculations:

$$diet_p = \frac{FE}{RE_p} \times \frac{d(P_w)}{d(BW)} \text{ (starting from Eq.10)} \quad (21)$$

$$diet_p = \frac{FE}{RE_p} \times (other_p + YLD \times (fillet_p - other_p) + VSI \times (viscera_p - other_p)) \quad (22)$$

We now estimate the partial (additive) effects that relevant traits have on the required phosphorus levels in the diet, by taking the partial derivatives of Eq. (20) with respect to these relevant factors:

Partial effect of feed efficiency (as before):

$$\frac{\partial(diet_p)}{\partial(FE)} = \frac{1}{RE_p} \times body_p \quad (23)$$

Partial effect of phosphorus retention efficiency (as before):

$$\frac{\partial(diet_p)}{\partial(RE_p)} = -\frac{FE}{RE_p^2} \times body_p \quad (24)$$

Partial effect of fillet yield:

$$\frac{\partial(diet_p)}{\partial(YLD)} = \frac{FE}{RE_p} \times (fillet_p - other_p) \quad (25)$$

Partial effect of viscerosomatic index:

$$\frac{\partial(diet_p)}{\partial(VSI)} = \frac{FE}{RE_p} \times (viscera_p - other_p) \quad (26)$$

Combining the partial effects to obtain a linear approximation of the

overall effect, we obtain:

$$d(\text{diet}_p) = \frac{\partial(\text{diet}_p)}{\partial(\text{FE})} \times d(\text{FE}) + \frac{\partial(\text{diet}_p)}{\partial(\text{RE}_p)} \times d(\text{RE}_p) + \frac{\partial(\text{diet}_p)}{\partial(\text{YLD})} \times d(\text{YLD}) + \frac{\partial(\text{diet}_p)}{\partial(\text{VSI})} \times d(\text{VSI}) \quad (27)$$

$$d(\text{diet}_p) = \frac{1}{\text{RE}_p} \times \text{body}_p \times d(\text{FE}) - \frac{\text{FE}}{\text{RE}_p^2} \times \text{body}_p \times d(\text{RE}_p) + \frac{\text{FE}}{\text{RE}_p} \times (\text{fillet}_p - \text{other}_p) \times d(\text{YLD}) + \frac{\text{FE}}{\text{RE}_p} \times (\text{viscera}_p - \text{other}_p) \times d(\text{VSI}) \quad (28)$$

$$d(\text{diet}_p) = \frac{1}{\text{RE}_p} \times \left((\text{other}_p + \text{YLD} \times (\text{fillet}_p - \text{other}_p) + \text{VSI} \times (\text{viscera}_p - \text{other}_p)) \times d(\text{FE}) - \frac{\text{FE}}{\text{RE}_p} \times (\text{other}_p + \text{YLD} \times (\text{fillet}_p - \text{other}_p) + \text{VSI} \times (\text{viscera}_p - \text{other}_p)) \times d(\text{RE}_p) + \text{FE} \times (\text{fillet}_p - \text{other}_p) \times d(\text{YLD}) + \text{FE} \times (\text{viscera}_p - \text{other}_p) \times d(\text{VSI}) \right) \quad (29)$$

Furthermore, we calculate the same overall effect, but in a multiplicative way:

$$d(\log \text{diet}_p) = \frac{1}{\frac{\text{FE}}{\text{RE}_p} \times (\text{other}_p + \text{YLD} \times (\text{fillet}_p - \text{other}_p) + \text{VSI} \times (\text{viscera}_p - \text{other}_p))} \times \frac{1}{\text{RE}_p} \times \left((\text{other}_p + \text{YLD} \times (\text{fillet}_p - \text{other}_p) + \text{VSI} \times (\text{viscera}_p - \text{other}_p)) \times d(\text{FE}) - \frac{\text{FE}}{\text{RE}_p} \times (\text{other}_p + \text{YLD} \times (\text{fillet}_p - \text{other}_p) + \text{VSI} \times (\text{viscera}_p - \text{other}_p)) \times d(\text{RE}_p) + \text{FE} \times (\text{fillet}_p - \text{other}_p) \times d(\text{YLD}) + \text{FE} \times (\text{viscera}_p - \text{other}_p) \times d(\text{VSI}) \right) \quad (30)$$

Simplifying, we obtain:

$$d(\log \text{diet}_p) = \frac{d(\text{FE})}{\text{FE}} - \frac{d(\text{RE}_p)}{\text{RE}_p} + \frac{d(\text{YLD}) \times (\text{fillet}_p - \text{other}_p) + d(\text{VSI}) \times (\text{viscera}_p - \text{other}_p)}{\text{other}_p + \text{YLD} \times (\text{fillet}_p - \text{other}_p) + \text{VSI} \times (\text{viscera}_p - \text{other}_p)} \quad (31)$$

or

$$d(\log \text{diet}_p) = d(\log \text{FE}) - d(\log \text{RE}_p) + \frac{d(\text{YLD}) \times (\text{fillet}_p - \text{other}_p) + d(\text{VSI}) \times (\text{viscera}_p - \text{other}_p)}{\text{body}_p} \quad (32)$$

or

$$d(\log \text{diet}_p) = d(\log \text{FE}) - d(\log \text{RE}_p) + \frac{\text{YLD} \times (\text{fillet}_p - \text{other}_p)}{\text{body}_p} \times d(\log \text{YLD}) + \frac{\text{VSI} \times (\text{viscera}_p - \text{other}_p)}{\text{body}_p} \times d(\log \text{VSI}) \quad (33)$$

The calculations derived above are also generic, and similar relationships can be established for gross energy, protein, minerals or other essential nutrients, *mutatis mutandis*.

When the absolute values of traits can be directly measured (rather than just the changes or trends in traits), it is possible to go further and obtain formulas that estimate in closed-form the optimal feed formulations for the specific trait values considered. In the case of total phosphorus in a feed, the obtained formula (for the simplest model considered) is:

$$\text{diet}_p = \frac{1}{\text{FCR}} \times \frac{1}{\text{RE}_p} \times \text{body}_p \quad (34)$$

Finally, diet_p can be converted to be optimal dietary inclusion level that is based on digestible phosphorus:

$$\text{diet}_{\text{DP}} = \frac{1}{\text{FCR}} \times \frac{\text{ADC}_p}{\text{RE}_p} \times \text{body}_p \quad (35)$$

where ADC_p is the apparent digestibility coefficient of phosphorus which represents the fraction of feed phosphorus that is digestible with a

value ranging between 0 and 1 (digestible P / total P in feed). In all our calculations, an ADC_p value of 0.7 was assumed. In practice, the value can be higher when feeds with high proportion of fish meal are used (or

when other highly digestible forms of phosphorus are added to feeds), or lower when feeds with higher proportion of plant-based ingredients are

used (Hua and Bureau, 2006).

2.1.3. Simple model: Optimal feed phosphorus levels as a function of fish traits

Using the Eq. (35), we performed a series of demonstrations to illustrate how optimal digestible phosphorus level in a feed, diet_{DP} ,

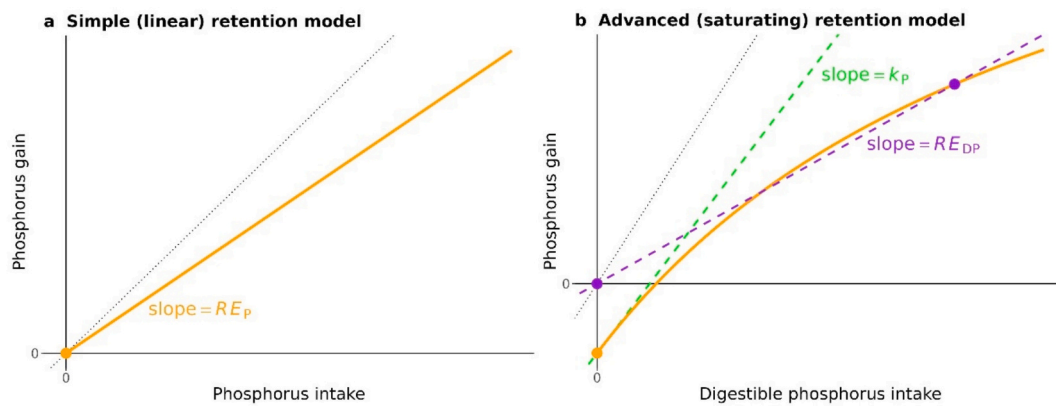


Fig. 1. Plot showing the intake-gain relationships assumed by a) the simple and b) the advanced model. In the simple model a), the slope of the intake-gain relationship (orange line) corresponds to retention efficiency of phosphorus (RE_p). In the advance model b), the intake-gain relationship is curved (orange line), and the value of retention efficiency of digestible phosphorus (RE_{DP}) corresponds to the slope of the line joining the origin and the response at the current intake (two dots on the purple dashed line), and thus, RE_{DP} depends on intake. The value of k_p (maximum marginal retention efficiency) corresponds to the slope of the line (green dashed) that is tangent to the response at zero intake and, thus, k_p does not depend on intake. For both plots, three thin dotted black line corresponds to $y = x$ line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

changes when values for fish traits are changed.

First, the impact of a change in FCR from 0.5 to 3 on digestible phosphorus inclusion level was calculated. Three levels of phosphorus retention efficiencies were assumed: 20 % (low), 40 % (assumed current), and 60 % (high). These levels simulate hypothetical differences in fish genetics and/or in feed formulation. In modern rainbow trout feeds, retention efficiency of phosphorus is near 40 % (Prabhu, 2015; Dalsgaard et al., 2023). RE_p of 20 % would be achieved with a very poor diet and it is an underestimation for modern diets, but it is a useful value to test the functioning of our model. For body phosphorus%, the standard assumption has been that $body_p$ is 0.4 % (Lall, 2002) from which the value was changed upwards and downwards.

The impact of changes in fillet YLD and VSI on $diet_{DP}$ was assessed by replacing $body_p$ in Eq. (35) with the $body_p$ calculated with Eq. (19) that has the individual body parts included. Phosphorus contents used were 0.299 % for the fillet, 0.079 % for the viscera, and 0.827 % for the rest of the body. These parameters had original values of 0.340 %, 0.090 %, and 0.940 %, which were extracted from the literature (Shearer, 1994; Rasmussen and Ostfeld, 2000; Kause et al., 2002; Dumas et al., 2007; Toppe et al., 2007; Souza et al., 2015; Li et al., 2019). These values are based on the reported ash percentages of body parts multiplied by the expected proportion of phosphorus from ash (0.1794). However, when these and YLD of 0.648 and VSI of 0.114 from the Finnish rainbow trout (Kause et al., 2022) were implemented in Eq. (19), the resulting $body_p$ was 0.450 %. To adjust the expected $body_p$ from Eq. (19) to be 0.4 %, the relative proportions of $fillet_p$, $viscera_p$ and $other_p$ values were held unchanged but their sum was lowered.

2.1.4. Simple model: Effect of phenotypic trend in FCR on optimal feed phosphorus levels

Phenotypic trend in FCR between 1980 and 2016 at commercial fish farms in the mainland Finland has been published by Kause et al. (Kause et al., 2022; and its Fig. 1). The data include annual means of farm-level economic FCR calculated as the ratio of fish feed used and fish biomass grown at a farm in a given year. To match the years with the breeding programme data, the average farm-FCR from 1993 to 2016 were used here as input (the original data of Fig. 1 from Kause et al., 2022 is reproduced in Appendix B).

In scenario 1a) the expected change in $diet_{DP}$ in relation to the phenotypic change across years in farm-FCR was calculated using Eq. (35), with the $body_p$ parameter being fixed to 0.4 % and RE_p set to either 20 %, 40 % or 60 %. The phenotypic trend in farm-FCR is influenced by farm management, feed development, environmental conditions and genetic improvement, all combined (Kause et al., 2022). The annual

averages of fillet YLD and VSI from these farms are unknown but the genetic trends from the breeding programme are known (Kause et al., 2022), and hence, in scenario 1b), the phenotypic trend of farm-FCR was included along with the genetic trends of YLD and VSI (section 2.1.5), and RE_p was set again to either 20 %, 40 % or 60 %.

2.1.5. Simple model: Effect of genetic trends in FCR, fillet% and viscera% on optimal feed phosphorus levels

The impact of genetic changes in rainbow trout traits across years in the Finnish national breeding programme on $diet_{DP}$ was calculated. The method used is a genetic trend analysis in which phenotypic records of individual fish with pedigree information across generations are analysed. The change in fish traits across generations can be partitioned into genetic improvement (i.e., due to selection) and the remaining environmental and residual effects (e.g., management, feeds, environmental changes) (Lynch and Walsh, 1998). The key is to use the pedigree and phenotypes of individuals and their relatives to estimate an individual's breeding value for a particular trait (EBV) (see e.g., Kause et al., 2005, 2022). Breeding value is an individual's genetic worth for a particular trait and it estimates the expected performance level of its offspring. Genetic trend analysis is a standard, well established method in animal breeding to estimate progress of breeding programmes (Lynch and Walsh, 1998).

The data used as input on the genetic trends in FCR, YLD, VSI and body weight at 2 years of age (BW) in rainbow trout are available as graphs in Kause et al. (2022; its Supplementary Data). The data include average estimated breeding values for a total of 23 year-classes born between 1992 and 2015 with an average generation interval of 3 years. The EBVs were estimated based on 547,246 individuals with a known pedigree (Kause et al., 2022). FCR and fillet YLD do not have records from all year-classes, instead FCR has been recorded in 1 and YLD in 2 year-classes, and their genetic (co)variances with the other traits recorded and selected in the breeding programme (BW, VSI, survival, maturity age, muscle lipid%) are known, which allows the estimation of genetic trends for all of these traits (Kause et al., 2022). To transform the genetic trends of Kause et al. (2022) (that are deviations from the trait mean) to the observed scale, the trait means when the (co)variance components were estimated were fixed to be the trait mean level for that year, and the genetic trend was subtracted or added to the years before or after it, respectively. These means are FCR = 1.260 (year 2001), 0.6475 YLD (2003), and VSI 0.1148 (2004) (from Kause et al., 2022).

These genetic trends are reproduced in Appendix C. Note that the fish born 1992 are in on-growing production one year later, in 1993, and hence there is a one-year difference between birth year and the

production year when farm-FCR is recorded. The relationships between FCR, YLD, VSI and BW have been discussed in detail by Kause et al. (2007, 2008, 2016).

In the breeding programme, the parents for each generation have been selected based on their estimated breeding values for growth (since 1992), maturity age (since 2001), external appearance (since 2001), skeletal deformations (since 2002), fillet colour (since 2003), VSI (since 2005), cataract caused by *Diplostomum* parasite (since 2003) and survival (since 2010), and the optimal genetic contributions method has been used to control the rate of inbreeding (Kause et al., 2005, 2022).

Three scenarios were calculated using Eq. (35) in which $body_P$ was calculated with Eq. (19) from fish traits. Base scenario 2: no genetic change (the year 1992 genetic values of FCR, YLD and VSI were used for all year-classes); Scenario 2a: FCR genetic trend (the genetic trend of FCR across years was used whereas YLD and VSI were fixed to the genetic values of year 1992); and Scenario 2b: All genetic trends (the genetic trends of all three traits were included). Base scenario is the benchmark trend, and scenarios 2a and 2b are expressed as deviations, induced by selective breeding, from the benchmark. All three scenarios were calculated for RE_P of 20 %, 40 %, and 60 %. There is no information on the genetic changes in RE_P values, and hence alternative scenarios were used.

2.1.6. Simple model: Forecasting optimal feed phosphorus levels

The optimal feed phosphorus levels were forecasted from production year 2016 onwards until year 2050. The year 2050 is an arbitrary future year to forecast likely trends in feed formulation of rainbow trout. Specific results are given also for year 2024, so that the currently used feed composition can be compared to the predicted $diet_{DP}$ of the genetically improved fish.

For this purpose, the data of the average annual EBVs of FCR, YLD and VSI in the breeding programme (Appendix C) were used to calculate the annual genetic changes in the average EBVs of each trait. A regression model was used in which the natural log-transformed average EBVs of a trait (on y-axis) were regressed against the birth year (on x-axis). The regression slope is equivalent to a multiplicative effect, and its exponent is the annual change in the average EBV. For example, for FCR the slope is -0.00634 , and $\exp(-0.00634)$ equals 0.99368 , which implies that FCR has been improved (reduced) every year by 0.6320 % [i. e., $100 \times (1 - 0.99368)$]. Then the levels of all traits at each year until 2050 were calculated. Selection for VSI (which is highly negatively genetically correlated with YLD) was initiated in year-class 2005 and hence the genetic trends of these two traits are highly curvilinear (Kause et al., 2022). To calculate the linear slope of the genetic trend for these two traits, the annual EBV means starting from year 2002 (one generation backwards to set 2002 as the starting level) were used. To predict $diet_{DP}$, three scenarios were calculated. In scenario 3a, RE_P was maintained stable at 40 % and the genetic trends of all traits were included. In an optimistic scenario 3b, RE_P was initially 40 % and then improved by 0.5 % per year while including all the genetic trends. In an optimistic scenario 3c, RE_P was initially 40 %, and RE_P was improved annually by 0.71 % while including all the genetic trends, which maintained inclusion level more or less stable. The $diet_{DP}$ value of year 2016 calculated using scenario 1b was used as the starting value of the forecasting scenarios.

2.2. Development of advanced traits-to-feed model

Due to some limitations of the simple model, we have developed a more advanced model that has additional components to more accurately describe feed utilisation of fish, and that more clearly separates strict genetic-bound fish traits from farm management and feed-related factors. For the justification and full derivation of the model, see Appendix D and Fig. 1.

2.2.1. Advanced traits-to-feed model

The advanced model is:

$$diet_{DP} = \frac{1}{FCR} \times \frac{1}{k_P} \times (scalebody_P \times exp_P \times BW^{exp_P-1}) \times \left(\frac{growth_{\%} + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - growth_{\%})}{1 - \left(growth_{\%} + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - growth_{\%}) \right)} \right) \left(\frac{1}{growth_{\%}} \right) \left(\frac{1}{1 - \left(\frac{BW}{BW_{\infty}} \right)^{1/3}} \right) \quad (36)$$

and $diet_{DP}$ can be converted to be dietary inclusion level that is based on total phosphorus:

$$diet_P = \frac{1}{FCR} \times \frac{1}{k_P} \times \frac{1}{ADC_P} (scalebody_P \times exp_P \times BW^{exp_P-1}) \times \left(\frac{growth_{\%} + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - growth_{\%})}{1 - \left(growth_{\%} + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - growth_{\%}) \right)} \right) \left(\frac{1}{growth_{\%}} \right) \left(\frac{1}{1 - \left(\frac{BW}{BW_{\infty}} \right)^{1/3}} \right) \quad (37)$$

in which k_P is maximum marginal retention efficiency, $scalebody_P$ is the scaling factor in the allometric phosphorus-BW relationship, exp_P is the exponent of the allometric phosphorus-BW relationship, BW_{∞} is an asymptotic maximum body weight that a fish can potentially achieve, $growth_{\%}$ is the target growth rate relative to the maximum growth rate capacity of a species. In this way, the term $\frac{1}{FCR}$ quantifies the efficiency of conversion of feed intake into growth, the $(scalebody_P \times exp_P \times BW^{exp_P-1})$ part quantifies how this growth translates into phosphorus gain, and the term $\frac{1}{k_P}$ quantifies how this phosphorus gain is related to phosphorus intake, the term $\frac{1}{ADC_P}$ converts phosphorus from a digestible to a total basis, and the last two parts penalize situations of very high or very low growth rate, as well as high body weights. The advanced model considers that 1) body composition may depend on body weight (exp_P may be different from unity), 2) retention efficiencies tend to saturate with increased feed intake and growth, 3) nutrient gain should be negative when intake is zero (Prabhu et al., 2013), and 4) fish cannot grow and retain nutrients arbitrarily fast ($growth_{\%} < 1$), nor grow to arbitrarily large sizes ($BW < BW_{\infty}$) (Appendix D, Fig. 1).

Specifically, k_P is the slope of the phosphorus gain against digestible phosphorus intake when the digestible intake is zero, or mathematically, $\frac{\partial gained_P}{\partial intake_{DP}} (intake_{DP} = 0)$, which corresponds to the maximum marginal efficiency of digestible phosphorus retention (under the assumption of a saturating relationship) (Fig. 1). In the simple model, relation of intake and gain remains linear, with the (constant) slope corresponding to the RE_P parameter (Fig. 1a). In the advanced model, the (marginal) retention efficiency goes down as the intake increases and, as gain reaches the upper bound of the saturation relationship, this (marginal) retention efficiency tends to zero (Fig. 1b).

For body phosphorus, the weight-dependent body composition may not be essential because it remains rather constant especially during on-growing phase (around 0.35–0.40 %) with exp_P close to 1 and, thus, an isometric relationship of the simple model is a reasonable approximation, but it clearly applies to feed components such as (digestible) energy (where the exponent is close to 1.2) (Shearer, 1994; Lall, 2002; Dumas et al., 2007).

The motivation of including $growth_{\%}$ is that if fish are feeding too little and growth is consequently slow, then the basal and maintenance costs dominate over the costs of growth (and retention efficiency is low). If fish are feeding too much, then fish enter the saturated part of the dose-response relationship (i.e., the slope of retention efficiency also

goes down) (Fig. 1b), which also leads to increased dietary inclusion levels. The parameter BW_{∞} is included because fish become very inefficient at retaining nutrients as they approach their maximum (asymptotic) size (see Appendix D for the detailed derivation of effects of BW_{∞}).

2.2.2. Advanced model: Optimal feed phosphorus levels as a function of fish traits

To illustrate the properties of the advanced model, the impact of a change in FCR (range: 0.5–3), BW (range: 100 g – 2000 g), exp_P (range 0.9–1.1), $scalebody_P$ (two different values) and k_P (two different values) on $diet_{DP}$ level was calculated using Eq. (36). These results were plotted on the same graph as the results from the simple model with $body_P = 0.4$ % and RE_P of 20 %, 40 %, and 60 % of section 2.1.3, to compare the two models.

The values of $scalebody_P$ (0.005159) and exp_P (0.9405) were first derived from the body weight and phosphorus percentage values collected from the literature (Azevedo et al., 1998; Bureau and Cho, 1999; Vielma et al., 2000; Cheng et al., 2003a, 2003b; Satoh et al., 2003; Hernandez et al., 2004; Bureau et al., 2006; Zhang et al., 2012; Rema et al., 2019). Note that exp_P below unity means phosphorus% is decreasing when BW is increasing. As presented in Fig. 1b, the value for k_P (0.4853) was first estimated from the literature by taking the first derivative (slope) of the saturating relationship between phosphorus gain and digestible intake when $intake_{DP} = 0$ ($n = 342$ values for gain-intake pairs) (Azevedo et al., 1998; Bureau and Cho, 1999; Bureau et al., 2006; Vielma et al., 2000; Hernandez et al., 2004; Glencross et al., 2008; Zhang et al., 2012; Vale Pereira et al., 2023; Four unpublished trials of F. Soares at Sparos Ltd). Although some of these papers do not

explicitly present data on P retention, it can be estimated based on the data made available in each publication (such as, feed intake, dietary P content, initial and final whole-body P content and body weight). Thereafter, values of $scalebody_P$, exp_P and k_P were manually changed to simulate alternative scenarios. In rainbow trout, BW_{∞} is not known but it was assumed to be 45,000 g. The largest rainbow trout observed has been 24,500 g (Froese and Pauly, 2024), and using that value would have produced higher $diet_{DP}$ values especially for large fish. The second k_P value used was 0.80 that produced results that resemble the $diet_{DP}$ values of the simple model with RE_P values around 20 % (section 2.1.3). The k_P value of 0.8 is simulating a more up-to-date value for the current rainbow trout farming in Finland (feeds and genetic material).

For all alternatives, $growth\%$ of 0.5 was used because it produces close-to-minimal FCR in large fish, and hence closely follows the commercial practice at farms.

2.2.3. Advanced model: Effect of genetic trends in FCR, BW , k_P on optimal feed phosphorus levels

The expected changes in $diet_{DP}$ in relation to the genetic trends of FCR and BW were calculated using Eq. (36). Similar to the approach used for the simple model, different scenarios were first calculated and their difference to the benchmark with no genetic trend was calculated. Three scenarios were calculated. Base scenario 4: no genetic change (the year 1992 genetic values for FCR and BW were used for all the following year-classes). Scenario 4a: FCR genetic trend (the genetic trend of FCR across years was used whereas BW was fixed to the year 1992 value). Scenario 4b: all genetic trends (the genetic trends of both FCR and BW were used). The scenarios were calculated with k_P of 0.4853 (literature)

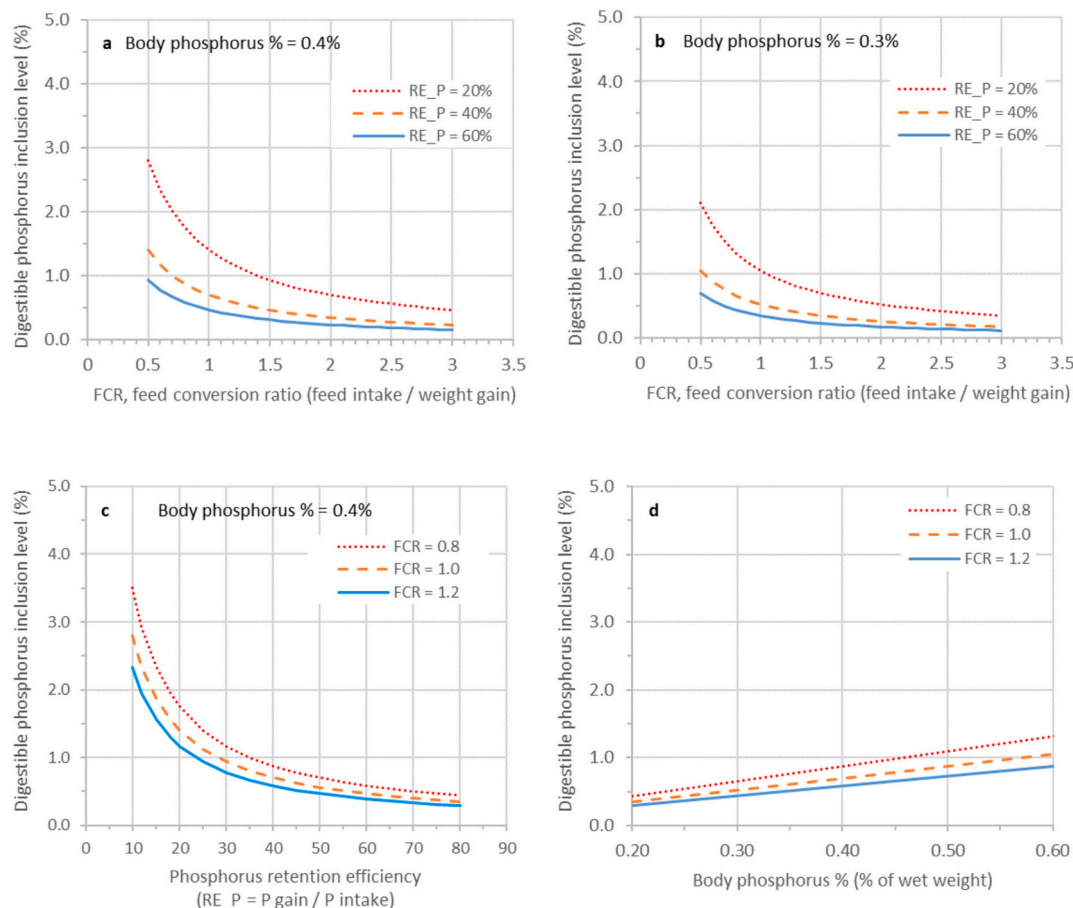


Fig. 2. Effect of different traits on optimal feed phosphorus levels, under different feed conversion ratios (FCR) and whole body phosphorus levels of a) 0.4 % and b) 0.3 %, and different c) phosphorus retention efficiency (RE_P) and d) body phosphorus percentage values, based on the simple model 1.

and 0.80 (simulating present day), and *growth%* of 0.5 was always assumed.

3. Results

3.1. Simple model 1: Optimal feed formulation depends on feed efficiency, nutrient retention efficiency and the abundance of the nutrient in whole body

3.1.1. Additive effects

The obtained expressions show that the (additive) effect of FCR on digestible phosphorus inclusion levels is strictly negative, i.e., if FCR decreases and is hence improved, the optimal inclusion levels increase, and, if FCR increases the inclusion levels decrease (Fig. 2a). The strength of this trend depends on both the phosphorus content of fish (higher phosphorus content implies stronger effect) (Fig. 2ab) and on phosphorus retention efficiency (higher phosphorus retention efficiency implies weaker effect) (Fig. 2c). The effect of feed efficiency (on a 'as fed' basis), $FE = \text{weight gain} / \text{feed intake}$, would be the opposite to the trend of FCR, given that FE equals $1/FCR$.

The (additive) effect of phosphorus retention efficiency on $diet_{DP}$ is strictly negative, i.e., if RE_p increases and hence is improved, the inclusion levels decrease, and if RE_p decreases, the inclusion levels increase. The strength of this trend depends on the phosphorus content of fish (higher levels imply a stronger effect) (Fig. 2ab) and on FCR (Fig. 2c), and inversely on the square of the phosphorus retention efficiency itself (higher levels imply a weaker effect) (Fig. 2c).

Finally, the (additive) effect of the phosphorus content of fish on $diet_{DP}$ is strictly positive, i.e., if it increases, so do $diet_{DP}$ (Fig. 2d). If phosphorus content of fish decreases, so do the optimal inclusion levels, and its strength depends on both FCR (lower FCR implies a stronger effect) and on phosphorus retention efficiency (higher phosphorus retention efficiency implies weaker effect), as shown in Fig. 2a and b.

3.1.2. Multiplicative effects

The partial effects of the relevant factors on $diet_{DP}$, when expressed in a multiplicative (i.e., scale-invariant) form, lead to extremely simple (linear with unit slope) partial effects that are straightforward to interpret (Eqs. (30–33)). A decrease (increase) in FCR by X% leads to an increase (decrease) of X% in optimal inclusion levels, if everything else is fixed. A decrease (increase) in phosphorus retention efficiency by X% leads to an increase (decrease) of X% in optimal inclusion levels, if everything else is fixed. An increase (decrease) in the phosphorus content of fish by X% leads to an increase (decrease) of X% in optimal inclusion levels, if everything else is fixed (Eqs. (30–33)).

Furthermore, assuming independence between factors, the overall

multiplicative effect when changing several factors simultaneously can also be directly estimated:

$$\Delta \log(diet_{DP}) = \Delta \log(body_p) - \Delta \log(FCR) - \Delta \log(RE_p) + \Delta \log(ADC_p)$$

Thus, for example, if the phosphorus content of fish increases by X% and phosphorus retention efficiency increases by Y%, then a reduction in FCR of Z% is only possible if we increase the phosphorus content in the diet by approximately $(Z + X \cdot Y)\%$. For example, if phosphorus content stays the same and phosphorus retention efficiency increases by 0.1 %, a decrease in FCR of 0.5 % would require an increase in $diet_p$ of approximately $(0.5 - 0.1)\% = 0.4 \%$. Or, a decrease of X% in FCR along with an increase of Y% in phosphorus retention efficiency would imply a necessity to increase $diet_p$ by about $(X - Y)\%$, if everything else is unchanged.

3.2. Simple model 2: Optimal feed formulation depends on feed efficiency, nutrient retention efficiency, fillet yield and viscerosomatic index

3.2.1. Additive effects

When whole body phosphorus content is replaced by different body parts and their phosphorus content (Eq. (19)), the effects of FCR and phosphorus retention efficiency on $diet_{DP}$ are the same as for the simple model 1, both in additive and multiplicative terms (result not shown).

The effects of fillet YLD (Fig. 3a) and VSI (Fig. 3b) on $diet_{DP}$ are linear and very weak. Their partial effects are proportional to the differences in the phosphorus content of different tissues. Given this, the effect of YLD will be positive if the phosphorus content of fillet is higher than the phosphorus content of the gutted and filleted carcass (and negative otherwise), while the effect of VSI will be positive if the phosphorus content of the viscera is higher than the phosphorus content of the gutted and filleted carcass (and negative otherwise) (Eqs. (18) and (19)).

3.2.2. Multiplicative effects

The multiplicative effect of changes in YLD and VSI are independent of FCR and phosphorus retention efficiency levels but depend on the current YLD level and on the current VSI level (since the amount of phosphorus in the body depends on both) (Section 2.1.2). Similarly to what is seen with additive effects, the strength and direction of this effect is directly dependent on the difference between fillet phosphorus content and the phosphorus content in the gutted and filleted carcass.

3.3. Simple model: Effect of phenotypic trend in FCR on optimal feed phosphorus levels

The phenotypic values of farm-FCR recorded at commercial farms between 1993 and 2016 were improved from 1.65 to 1.06 (Fig. 4a).

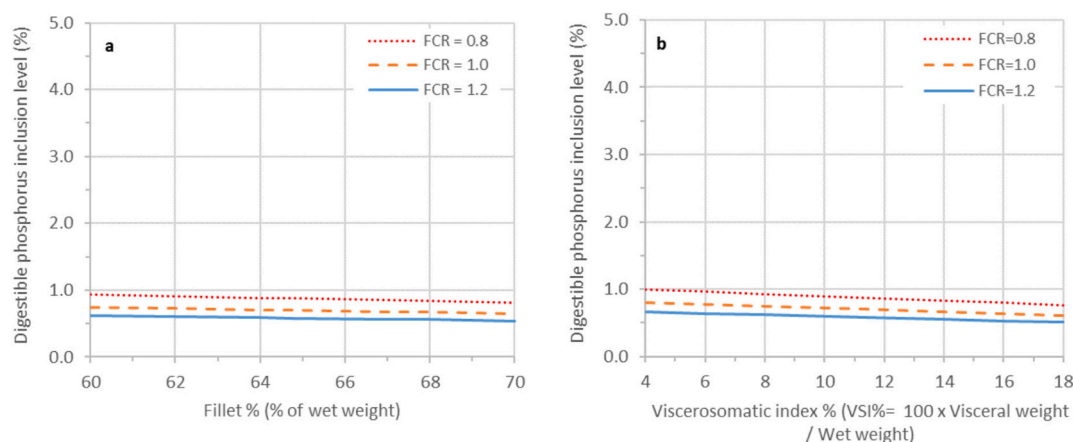


Fig. 3. Effects of a) fillet yield percentage and b) viscerosomatic index percentage on optimal feed phosphorus levels at different feed conversion ratios (FCR) based on the simple model 2, under different FCR values. In 2a, viscerosomatic index% is fixed to 11.4 %, and in 2b) fillet% is fixed to 64.75 %.

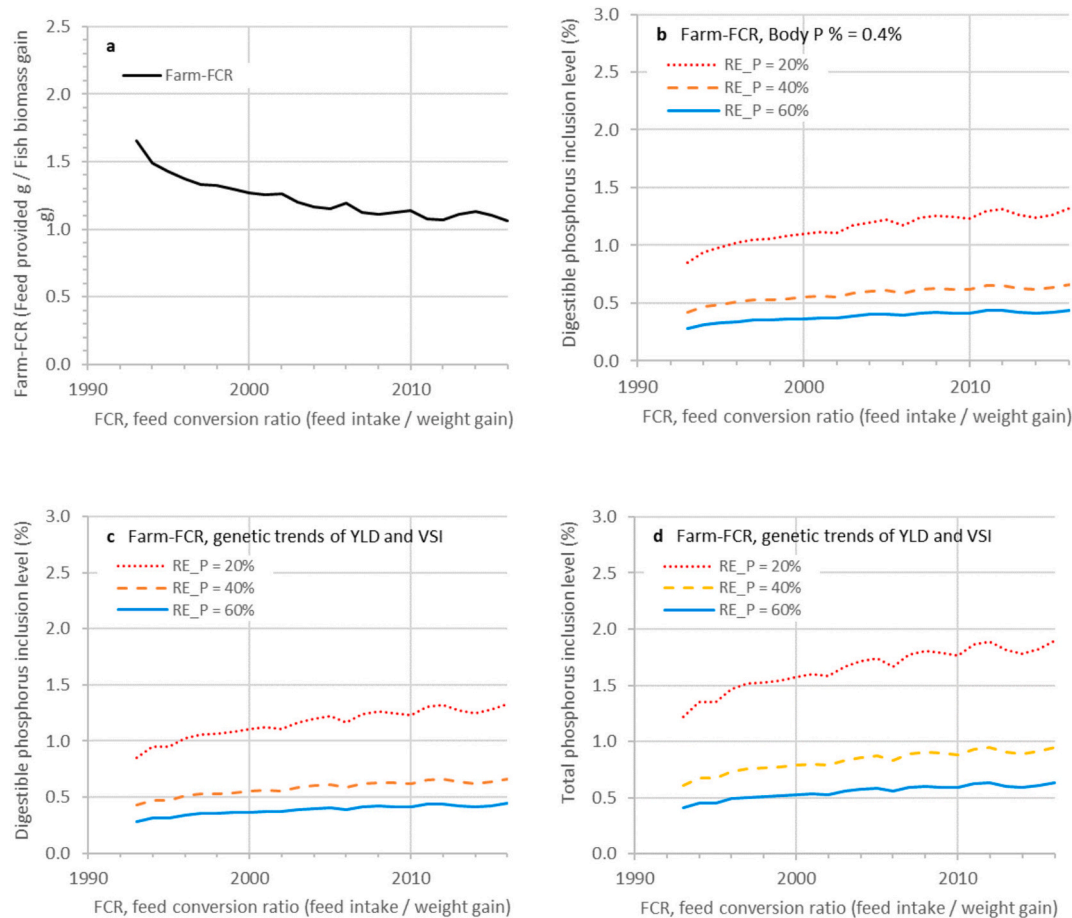


Fig. 4. a) Economic feed conversion ratio at commercial fish farms (farm-FCR) in Finland between 1993 and 2016, b) Effect of trend in farm-FCR on digestible phosphorus inclusion levels ($diet_{DP}$), when body phosphorus% is 0.4 %, calculated using the simple model 1, c) Effect of farm-FCR and genetic trends in fillet yield (YLD) and viscerosomatic index (VSI) on $diet_{DP}$, calculated using the simple model 2, and d) Effect of farm-FCR and genetic trends in fillet yield (YLD) and viscerosomatic index (VSI) on total phosphorus inclusion levels ($diet_P$), based on the simple model 2, under different phosphorus retention efficiency levels (RE_P).

Table 1

Estimated genetic trends in fish traits across years expressed as % change per year.

Trait	b	$\exp(b)$	% genetic change per year	R^2 , %
FCR, feed conversion ratio	-0.00634	0.99368	-0.6320	89.8
YLD%, Fillet%	0.0008236	1.0008	0.0824	76.3
VSI%, Viscera%	-0.00752	0.9925	-0.7492	80.1
Body weight, g	0.01617	1.0163	1.6301	89.0

b - slope of natural log-transformed trait regressed against birth year. R^2 , % - Percentage of variation explained by the regression model.

Assuming that only FCR was changed, $diet_{DP}$ increased from 0.4239 % to 0.6598 % if RE_P was assumed to be 40 % (Fig. 4b; scenario 1a). That is a 55.7 % increase, and an annual rate of 1.94 %. When including also the estimated genetic changes in fillet YLD and VSI, $diet_{DP}$ showed very similar level and pattern, increasing from 0.4271 % to 0.6634 % if RE_P was assumed to be 40 % (Fig. 4c; scenario 1b). This implies a major effect of FCR rather than body composition on phosphorus inclusion level. When the scenario 1b is expressed on total P basis, there was a change in $diet_P$ from 0.6101 % to 0.9478 % (Fig. 4d). Alternative RE_P

values had a major impact on $diet_{DP}$ and $diet_P$ (Fig. 4bcd), as expected based on the model characteristics (Fig. 2ab).

3.4. Simple model: Effect of genetic trends in FCR, fillet% and viscera% on optimal feed phosphorus levels

Table 1 shows the estimates of the genetic trends in four key traits which may affect the required diet composition. The optimal average annual genetic improvement (in %) was estimated to be -0.632 % for FCR, +0.082 % for fillet YLD, -0.749 % for VSI, and 1.63 % for body weight (Table 1). These trends are consistent with the breeding objectives (Kause et al., 2022), and imply that the traits are expected to be genetically changed by selection, and hence also optimal nutrition levels of feeds will also change.

Assuming that only FCR was genetically improved across birth years from 1992 to 2015 (scenario 2a), $diet_{DP}$ was cumulatively increased by 0.17747 %-points, 0.08873 %-points, and 0.05916 %-points, if RE_P was assumed to be 20 %, 40 % or 60 %, respectively (Fig. 5a). When simultaneously including the estimated genetic changes in FCR, fillet YLD and VSI, the induced cumulative changes in $diet_{DP}$ showed very similar increases, 0.17503 %-points, 0.087517 %-points, and 0.058344 %-points, respectively (Fig. 5b; scenario 2b). This implies a major effect of FCR, rather than body composition, on $diet_{DP}$. Alternative RE_P values

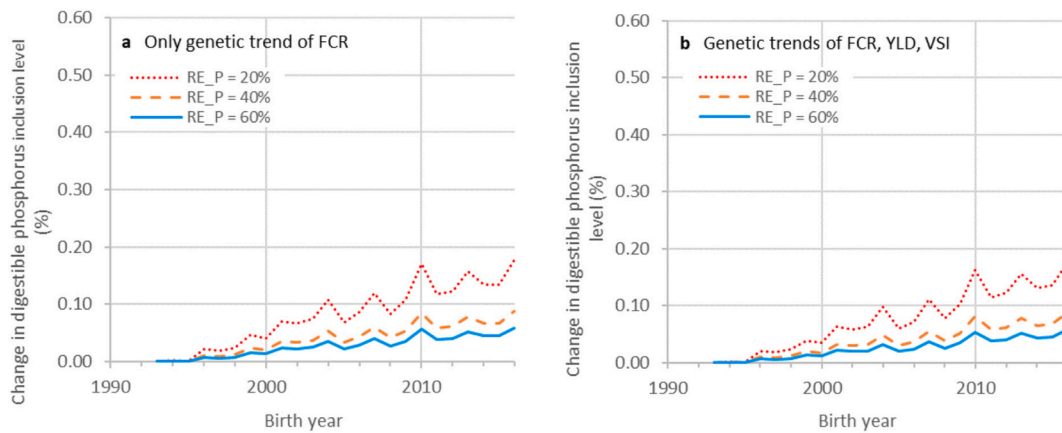


Fig. 5. Effect of genetic trends in a) feed conversion ratio (FCR), and b) FCR, fillet yield % (YLD) and viscerosomatic index % (VSI) on optimal feed phosphorus levels, under different phosphorus retention efficiency levels (RE_P), estimated using the simple model 2.

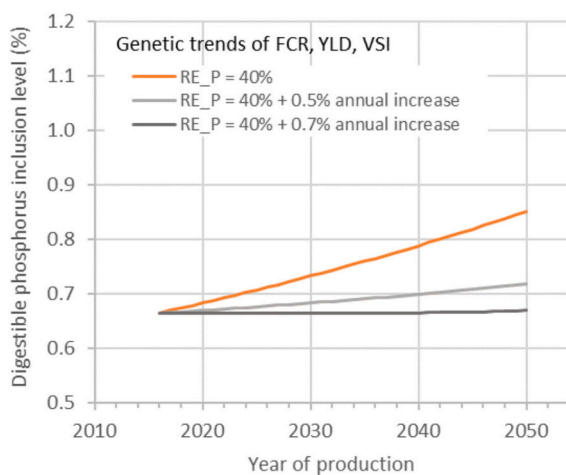


Fig. 6. Estimated optimal feed phosphorus levels in rainbow trout feeds as a function of time (production years 2016–2050) when feed conversion ratio (FCR), fillet yield (YLD) and viscerosomatic index (VSI) evolve due to breeding, based on three different scenarios 3a–c calculated using the simple model 2. Orange line: pessimistic, assuming constant phosphorus retention efficiency of 40 %; Light grey: Optimistic, assuming a 0.5 % yearly improvement in phosphorus retention efficiency; Dark grey: Optimistic, assuming 0.71 % yearly improvement in phosphorus retention efficiency.

Table 2

Estimated genetic levels of fish traits and optimal phosphorus levels ($diet_{DP}$) in rainbow trout feeds in production years 2016, 2024 and 2050, calculated using the simple model 2.

Year	FCR	YLD, %	VSI, %	body _P , %	$diet_{DP}$, %	$diet_{DP}$, %	$diet_{DP}$, %
					$RE_P = 40\%$	$RE_P = 40\%$	$RE_P = 40\%$
						% + 0.5 % annual increase	% + 0.7 % annual increase
2016	1.061	65.2	10.6	0.4033	0.6652	0.6652	0.6652
2024	1.010	65.7	10.0	0.4056	0.7027	0.6752	0.6640
2050	0.845	67.1	8.22	0.4114	0.8517	0.7188	0.6696

FCR – Feed conversion ratio; YLD – Fillet yield, %; VSI – viscerosomatic index, %; body_P – phosphorus content of body, %; $diet_{DP}$ – Optimum digestible phosphorus level in a feed (%); RE_P – Retention efficiency of phosphorus.

had a major impact on $diet_{DP}$ (Fig. 5ab), as expected based on the model characteristics (Fig. 2ab).

3.5. Simple model: Forecasting optimal feed phosphorus levels

When the estimated genetic trends (Table 1) were extended into the future, the predicted $diet_{DP}$ is expected to continue to increase if phosphorus retention efficiency is maintained stable at the level of 40 %, and in 2050, $diet_{DP}$ is expected to be 0.8517 %. This is a 28.0 % increase from year 2016, and an annual rate of increase of 0.73 % (scenario 3a) (Fig. 6). For year 2024, the predicted estimates for the optimum digestible values were 0.66–0.70 % on wet feed basis which is total P of 0.94–1.0 % assuming ADC_P of 70 % (Table 2). The adequateness of the current phosphorus feed levels in the future will depend a lot on the bioavailability of phosphorus in a feed. If RE_P is improved, e.g. around 0.5 % - 0.7 % per year (scenarios 3bc), the optimal $diet_{DP}$ remains steady or is only slightly increased (Fig. 6).

3.6. Advanced model: Optimal feed formulation

When using $growth\%$ of 0.5 with k_P , $scalebody_P$ and exp_P values extracted from the literature, the $diet_{DP}$ values predicted by the advanced model for all body weights were higher than $diet_{DP}$ predicted by the simple model (Fig. 7a). Fixing $body_P$ to be independent of body weight at a value of 0.4 % increased $diet_{DP}$ slightly (Fig. 7b) because 0.4 % is higher than the $body_P$ values (0.33–0.39) predicted for 100 g – 2000 g fish by the parameter values from the literature. When k_P was elevated from 0.49 to 0.80, a scenario reflecting improved phosphorus retention efficiency, $diet_{DP}$ values were reduced and, for small fish sizes, partly overlapped with the results of the simple model (Fig. 7cd).

It is important to note that a rainbow trout with high body weight has higher FCR compared to a fish with low body weight. Hence, $diet_{DP}$ for a large fish with a consequent high FCR can be lower than $diet_{DP}$ of a lighter fish. For instance, assuming k_P of 0.80 and size-dependent $body_P$, and comparing small fish with FCR of 0.9 and BW = 100 g against larger fish with FCR = 1.2 and BW = 500 g, leads to $diet_{DP}$ values of 1.53 and 1.41, respectively (Fig. 7c).

When growth rate is expressed as a proportion of maximum growth rate ($growth\%$) and all other parameters remain fixed, the lowest levels of $diet_{DP}$ occur at intermediate $growth\%$ values, especially in larger fish (Fig. 7e). This is because the points of highest growth efficiency occur at intermediate $growth\%$ values (Eq. (36)). If $growth\%$ is close to 1, then the retention efficiency of phosphorus becomes very low. Note that, under a saturating model, when retention efficiency is close to the maximum, the

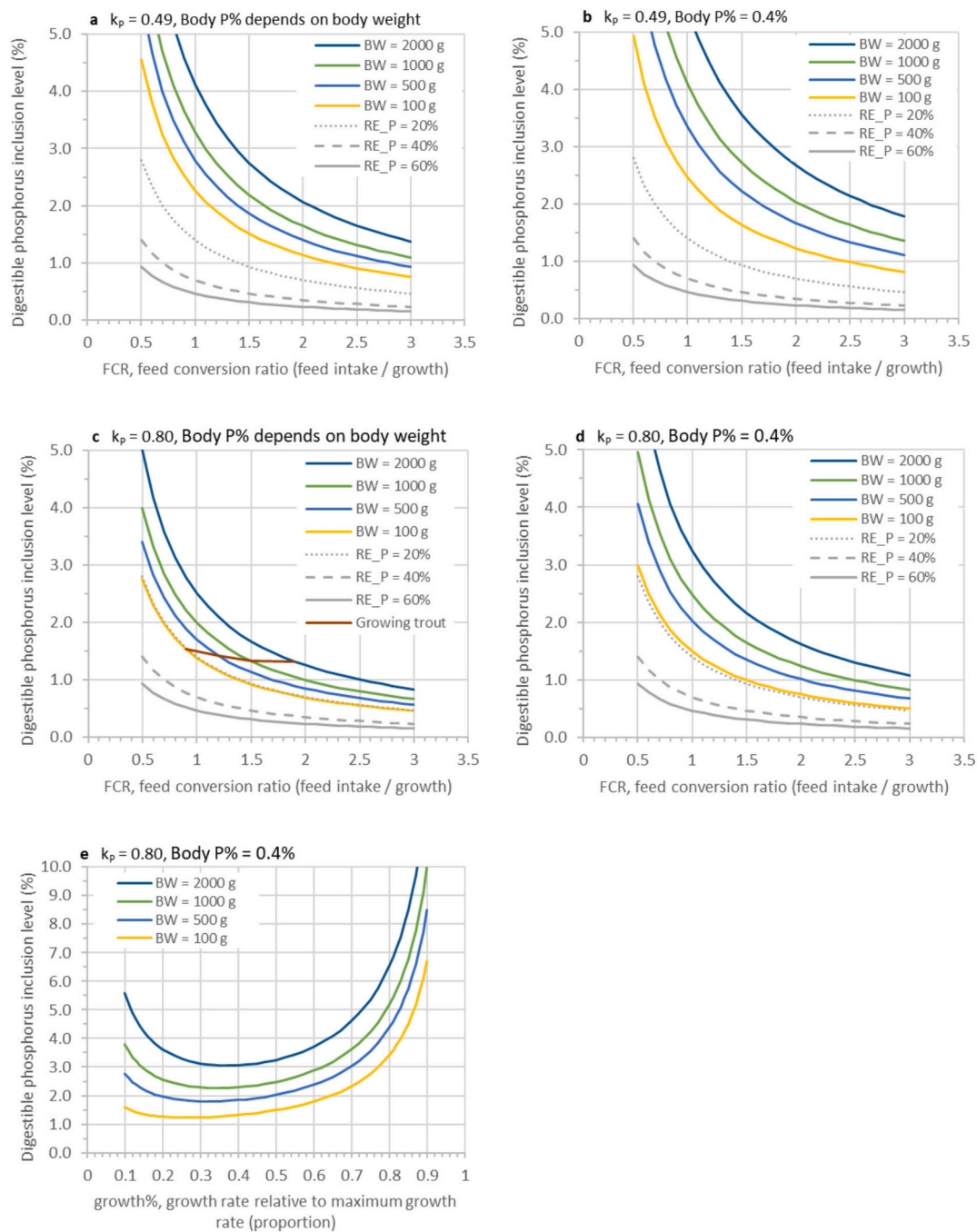


Fig. 7. The effect of parameters of the advanced model on optimal feed phosphorus levels when a) model parameters are based on the literature, $k_p = 0.4853$, $scalebody_p = 0.005159$, $exp_p = 0.9405$, b) parameters are set to maintain body phosphorus fixed and independent of body weight, $k_p = 0.4853$ but $scalebody_p = 0.004$, $exp_p = 1.0$, c) Phosphorus retention efficiency coefficient is increased and body phosphorus is body weight dependent, $k_p = 0.80$, $scalebody_p = 0.005159$, $exp_p = 0.9405$, d) Phosphorus retention efficiency coefficient is increased and body phosphorus held stable, $k_p = 0.80$ but $scalebody_p = 0.004$, $exp_p = 1.0$. In a-d) growth% is set to 0.5, while in e) Growth% is varied, $k_p = 0.80$ and body phosphorus is held stable at $scalebody_p = 0.004$ and $exp_p = 1.0$. The 'growing trout' line in c) is a fish with FCR of 0.9 at 100 g BW and 1.2 and 1.5 FCR at 500 g and 1000 g, respectively.

slope of gain on intake will be close to zero (Fig. 1b), and the optimal $diet_{DP}$ will shoot up (Fig. 7e).

3.7. Advanced model: Effect of genetic trends in FCR, BW, k_p on optimal feed phosphorus levels

Assuming that only FCR was genetically improved across years by a selection programme, $diet_{DP}$ was increased cumulatively by 0.4112 %-points or 0.2491 %-points, when k_p was either 0.49 or 0.80 (Fig. 8a; scenario 4a). When simultaneously including the estimated genetic

changes across years in FCR and BW, the cumulative changes in $diet_{DP}$ were increased to 0.7587 %-points and 0.4599 %-points, when k_p was either 0.49 or 0.80 (Fig. 8b; scenario 4b). The advanced model that penalizes efficiency by the saturation of gain at high feed intake levels and by high BW, gave higher expected genetic changes in $diet_{DP}$ compared to the simple model. By fixing $body_p$ to be stable 0.4 %, the trends were slightly increased (results not shown), in line with the pattern in Fig. 7ab.

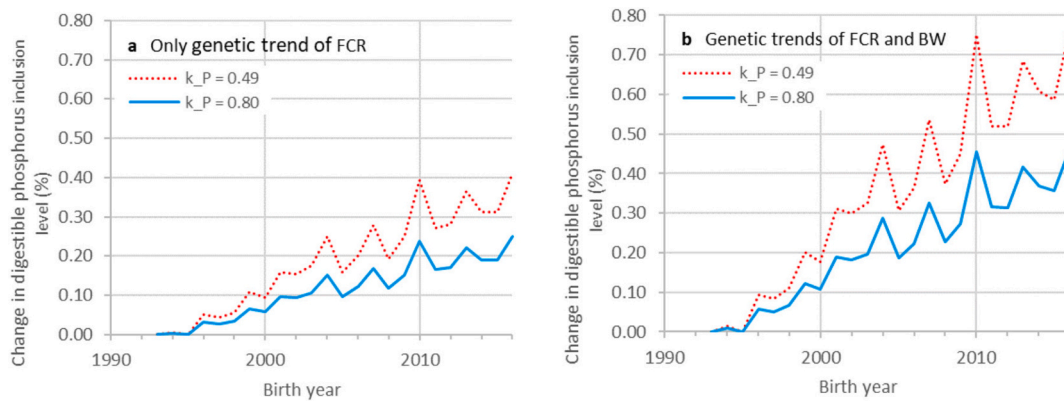


Fig. 8. Effect of genetic trends in a) feed conversion ratio (FCR), and b) FCR and body weight (BW) on optimal feed phosphorus levels, under different phosphorus retention coefficients (k_P), estimated using the advanced model.

4. Discussion

We developed and demonstrated the use of the biometrical traits-to-feed model to determine the expected changes in the optimal dietary inclusion levels of nutrients when traits related to growth, body composition and feed utilisation change. The change can be due to any factor (fish management, genetics, environmental effects) and here we analysed the changes induced by selective breeding. Models typically used to define the nutritional requirements of fish rely on factorial approaches, bioenergetic or nutrient-based models that integrate growth, nutrient retention, maintenance, and metabolic needs under varying environmental and physiological conditions (e.g., Jobling, 1994; Shearer, 1995; Cho and Bureau, 1998; Bureau et al., 2002; Glencross, 2008, 2021; NRC, National Research Council, 2011; Soares et al., 2023; Sugiura, 2025a). The models are refined using empirical data from feeding trials and are increasingly incorporating dynamic and mechanistic elements to better simulate nutrient utilisation and environmental interactions. The choice for a suitable approach depend on the purpose, availability of the data, and the required level of complexity. The originality of the current study is that the derived equations are initial steps to unite fish nutrition and quantitative genetics of fish traits used in selective breeding programmes. Both quantitative genetics and fish nutrition are mathematical and predictive in nature, and the traits-to-feed equations merge these two fields that have been typically treated separately.

During the past decades, aquaculture has been the fastest growing food production sector with an annual growth rate of 6.7 % (FAO, 2022), and selective breeding programmes have been recently implemented in several new aquaculture species (Houston et al., 2020). Due to the expanding aquaculture, there is a growing demand of feed ingredients for carnivorous fish including salmonids, and hence also for alternative ingredients that may originate from novel sources of plants, algae or side streams from production of other farmed animals, whose nutritional composition and digestibility are less well understood. Accordingly, both genetics of farmed species and the use of feed raw materials are evolving. The here proposed traits-to-feed model combines breeding and fish nutrition to provide a tool to develop more sustainable aquaculture feeds in the long term.

4.1. Simple and advanced model

The predictions of the traits-to-feed model show that the effect of changes in FCR and retention efficiency on optimal dietary inclusion levels are strong and highly non-linear (Eq. (35), Fig. 1). For FCR,

optimal inclusion levels are elevated especially for the fish with low FCR. In other words, all else being fixed, a fish that extracts more wet weight growth from a fixed amount of feed fed (i.e., has low FCR) needs a feed that is more dense in nutrients, otherwise nutritional requirements are not met and the body will be diluted in the content of the nutrient. For phosphorus, the increase in optimal nutrition inclusion level in a feed ($diet_{DP}$) is especially strong when FCR is low and approaching 1.0 that is a typical current level in rainbow trout farming (Fig. 4a; Kause et al., 2022).

In contrast to FCR, the results show that the effect of changes in body composition (content of a nutrient in the whole body, fillet%, and viscera%) on nutrient inclusion level is linear and modest, 1 % higher phosphorus percentage in the body implies 1 % higher phosphorus inclusion level in a feed (Eq. (35), Figs. 2 and 3). Naturally, when the content of a nutrient in the whole body is partitioned to be determined by the content in different body parts (Eq. (19)), that is fillet, viscera and the rest of the carcass, the change in $diet_{DP}$ depends on the relative changes in body parts and on the relative contents of the nutrient in each body part.

In the context of our study, nutritional requirements are defined as the minimum nutrient levels required to sustain optimal or near-optimal zootechnical performance of the traits analysed. Traditionally nutritional requirements of fish have been estimated through laborious and costly dose-response experiments in which fish are fed with multiple feeds with a different content of a nutrient, and the results are specific to the tested nutrient, focal species and life stages, and they do not produce forecasts (Shearer, 2000). Our traits-to-feed model bypasses the estimation of nutritional requirements which depend on factors such as temperature, and estimates directly what the composition of the feed should be which, apparently, does not depend on factors like temperature. The equations we derived are generic and also predictive - they can be applied to many fish species or genetically different populations. Our models do not replace the dose-response experiments. Rather, our models are one additional predictive tool to resolve the optimal match between feed composition and genetic characteristics of fish strains, and this match is expected to enhance fish health and welfare, resource efficiency and product quality in aquaculture. We applied the model to phosphorus in rainbow trout, but the model is general and can be applied to most essential nutrients or energy.

The formulas of the simple model, obtained under a simplistic assumption of a linear relationship between intake and gain of a feed ingredient, provide a useful first-order approximation to the effect of changes in fish traits on optimal feed formulation targets. The digestible amount of a certain nutrient (or energy) required in diet is proportional

to the relative amount of that nutrient (or energy) in the body of fish, and inversely proportional to FCR and to the retention efficiency of that nutrient (or energy). This implies that the effect of relevant fish traits on optimal feed formulation targets is, in this case, straightforward, since each trait multiplicatively and independently affects the optimal target in the same way.

The advanced model was developed to include body weight and growth rate as well as the saturation effect between intake and gain. The advanced model produced higher optimal dietary inclusion levels than the simple model. This is mostly because the advanced model includes realistic physiological factors that penalizes the situations of very high or very low growth rate, as well as of high body weights, that lead to reduced retention efficiency (Eq. (36)). The reduced retention efficiency subsequently leads to increased optimal levels of digestible nutrients in a feed (Fig. 7). The advanced model has more realistic biological assumptions (Appendix D) and hence has potential to be more useful than the simple model. We expect that, for dietary protein and energy, the advanced model will be especially more suitable than the simple model, and even the relative changes in protein-to-energy ratio in feed can be determined for differently sized fish. Dietary protein content is typically determined in relation to digestible energy (DE) content, to avoid that fish would not use protein, one of the most feed expensive ingredients, as an energy source (Grayton and Beamish, 1977). More generally, the reasoning used for defining the correct nutrient level relative to DE is that fish may consume feed to fulfil their energy needs and cease eating once their energy demands are met (e.g., NRC, National Research Council, 1987; Cho and Bureau, 2001). The same reasoning may apply to phosphorus (Rodehutsord, 1996; Sugiura, 2025a). The Eq. (36) can be further modified to directly estimate such a ratio (Appendix E), and for instance, the estimated protein inclusion levels can then be expressed as 'g of digestible protein required in the feed per kJ of DE in the feed'. On the other hand, lipid and hence energy content of a fish body is strongly impacted by body weight (Shearer, 1994; Lall, 2002; Dumas et al., 2007) and accounting this using the advanced model will be useful.

Not all the values of the parameters of the advanced model are accurately known, which influences the results we have presented. One benefit of using mathematic calculations such as ours is that it is possible to identify parameters that need better documentation in the future. In our study, we are not restricted to the data what exists now but are able to identify needs for future data collection and analysis. Specifically, the value of an asymptotic body weight that a fish can achieve (BW_{∞}) is currently unknown. The value is difficult to observe in reality but could be predicted using growth curve data which include also observations on very large fish. A key value representing maximum marginal retention efficiency, k_p , is also unknown for modern selectively bred fish. Both BW_{∞} and k_p greatly impact the outcomes of the model. In reality, k_p may well be above the value 0.80 used here which would bring down the predicted $diet_{DP}$ values. The presented predictions of the advanced model are likely overestimates, and they can be brought down by increasing BW_{∞} (and/or possibly k_p), or assuming higher FCR in real practical farming. Hence, the predictions of the advanced model presented here are speculative and provisional, and more of a demonstration of the model's characteristics.

The predictive formulas developed here within the traits-to-feed framework supplement the previous approaches and seek to help aquaculture stakeholders to make more informed decisions. For fish nutritionists and aquafeed formulators, these formulas can guide the formulation of diets that are adapted to specific fish strains and under specific conditions and growth targets. For fish farmers, these formulas can be used to adjust feeding rates to achieve specific growth rates (as a

function of fish size, diet composition and environmental conditions). For fish breeders, these formulas can inform them on the relative importance of different fish traits to be improved by selection.

4.2. Selective breeding and optimal feed phosphorus levels

FCR is one key trait influencing profitability of fish farming (Kankainen et al., 2016), and farmers and breeders aim to improve it (Kause et al., 2022). In rainbow trout farming in Finland, the farm-level FCR has dropped from 1.65 in 1993 to 1.06 by 2016 (Fig. 4a). Assuming phosphorus retention efficiency of 40 % and FCR of 1.06, the simple model predicts the optimal digestible phosphorus inclusion level to be around 0.66 % in 2016 (i.e., 0.94 % on total P basis). Prabhu (2015) estimated that digestible phosphorus inclusion levels of small rainbow trout should be on the order of 0.5 %, but like for any study, such estimates depend on FCR, body weight and the energy density of the feeds. In our study, the phenotypic improvement in FCR is associated with around 0.2359 %-unit increase in $diet_{DP}$ across years (when RE_p was assumed to be 40 %), and any further improvement in FCR will strongly increase the optimal inclusions level.

The results of the breeding programme data show that selective breeding has increased the required phosphorus content in rainbow trout feeds, especially due to the genetically improved FCR, and less so due to the increase in fillet percentage and the reduction in viscera percentage. Based on the predictions of the simple model and assuming phosphorus retention efficiency of 40 %, there has been a 0.08752 %-point increase in the required digestible phosphorus inclusion levels from production year 1993 to 2016 (Fig. 5).

Total dietary P levels in rainbow trout feeds have declined during the last decades to the current level of around 0.8 % (of dry matter, DM), and assuming moisture of 6–10 % in feed, that is 0.72–0.75 % of total P (Dalsgaard et al., 2023). These total P values are below the values (0.94 %) predicted by the simple model for a selectively bred fish with FCR of 1.06. A care must be taken not to reduce the dietary P levels too much, for instance to limit nutritional loading to environment. Low dietary P levels can result in weak bone, skeletal and cranial mineralization and ultimately to bone deformations (Lall, 2002; Fontagné et al., 2009). This is especially important because the dietary P requirements for maximum bone strength can be higher than those for maximum weight gain (Ogino and Takeda, 1976; Rodehutsord, 1996; Bureau and Cho, 1999; Prabhu et al., 2013) but the latter is not necessarily a criteria when formulating feeds (Sugiura, 2025a). When the estimated genetic trends (Table 2) were extended into the future, up to year 2050, the predicted optimal phosphorus feed levels are expected to still increase, if phosphorus retention efficiency is maintained stable at around 40 % (Fig. 6). Forecasting showed that, in this case, the optimal phosphorus inclusion level is expected to be increased by further 0.186 %-points, from 0.665 % to 0.852 % (at an annual rate of 0.73 %). In their scenario analysis of the development of nutrition loading to the environment, Bouwman et al. (2013) assumed that P content of rainbow trout feed would remain constant between 2010 and 2025. One reason for this was assumed to be the current high efficiency of salmonids and the high digestibility of nutrients in their feeds that have been improved already so much during last decades. This contrast again stresses the potential challenge in developing modern feeds that account for both environmental impacts and the needs of fish.

The adequateness of current phosphorus inclusion level depends a lot on the future bioavailability of phosphorus in a feed and on the level of FCR that a feed provides. Our model clearly shows that retention efficiency of phosphorus (RE_p) is a fundamental trait to be improved to satisfy nutrition needs in the future. Sugiura (2018) and more recently

Nathanailides et al. (2023) reviewed the potential ways to improve phosphorus retention and to reduce phosphorus pollution. To improve retention, several intestinal enzymes, transporters, and regulating factors have been implicated in aquafeeds. For example, alkaline phosphatase and other transporters aid in the absorption of phosphorus, and pH, calcium, and vitamin D influence the efficiency of these enzymes and transporters. These processes may also be influenced by gut morphology and its microbiome (Nathanailides et al., 2023). For instance, to convert phosphorus in plant-based raw materials to be better utilised by fish, phytase enzyme has been added into aquafeeds (Lemos and Tacon, 2017), and the incubation of sour dough consisting of plant materials with phytase and acidulant (Sugiura et al., 2001) and technology to facilitate the digestion of lignocellulose fibers (Castillo and Gatlin, 2015) could be implemented. Phosphorus retention efficiency likely exhibits low genetic variation in fish (Thodesen et al., 2001), and hence selective breeding is likely not an effective way to increase retention efficiency of phosphorus. The analysis of 41 parental half-sib and 82 full-sib families of Atlantic salmon (*Salmo salar*) by Thodesen et al. (2001) indicated non-significant genetic variation for apparent absorption coefficient (AAC) of phosphorus, and similarly, retention efficiencies of protein and energy show smaller among-family variation compared to FCR and growth in salmonids (Kause et al., 2009, 2016).

If the retention efficiency is improved in the future, e.g., around 0.5–0.7 % per year, due to improved phosphorus digestibility or a reduction in phosphorus losses from a body, the required phosphorus feed levels remain steady or only slightly increased, and the current inclusion levels might be adequate (Fig. 6). Otherwise, the inclusion levels may be insufficient to support growth and welfare of rainbow trout at the prescribed FCR. In that case, an alternative strategy to match diet composition and the dietary requirements is to reduce FCR by producing less palatable feeds which return $diet_{DP}$ back to the lower values.

To calculate the phenotypic and genetic trends as well as future projections in $diet_{DP}$ we have assumed a fixed ADC_P value, fixed yet alternative RE_P and K_P values, and the absence of genetic trend in RE_P and K_P . Across the decades, ADC_P , RE_P and K_P have likely gone up when high quality feeds (due to ingredients and additives) have been used and gone down when low quality feeds have been used (e.g. plant-based ingredients). Thus, the exact levels of $diet_{DP}$ across decades cannot be calculated, but are likely within the range of our simulated RE_P values of around 40 % (Prabhu, 2015; Dalsgaard et al., 2023). We assumed an absence of genetic change in RE_P across decades which may be realistic due to its very low genetic variation (Thodesen et al., 2001). Assuming too low efficiency and digestibility would mean that the presented levels of optimal dietary across decades would be too low.

Our model can be both validated and further refined by experimental tests. A useful approach would be to compare nutritional requirements of a wild strain to a selectively bred strain in a traditional dose-response experiment, and also to estimate genetic variation in the key parameters such as k of the advanced model, for which there is no information on genetically distinct fish strains or families. It is expected that aquaculture species with a long history of domestication and selective breeding, such as Atlantic salmon and rainbow trout, have gone through moderate changes in the nutritional requirements across years, whereas Mediterranean aquaculture species such as gilthead seabream (*Sparus aurata*) and European seabass (*Dicentrarchus labrax*), with a shorter history under selective breeding, are expected to show smaller changes in

nutritional requirements. A comparison of non-selected and selectively bred European seabass (Montero et al., 2023a) and gilthead seabream (Montero et al., 2023b) show improved growth and feed utilisation due to selection, so it is realistic to assume changes also in nutritional requirements of these species.

It is common practice, e.g. in pig and poultry production, that different breeds have different feed and feeding guidelines, so that the diet matches the genetic characteristics of the strain and the targeted end-product qualities, such as lean pork meat production or piglet production, but to our knowledge, there are no mathematical models that would combine genetics and nutrition in other farm animals.

5. Conclusions

This study developed and demonstrated a concept that integrates quantitative genetics and fish nutrition to determine the expected changes in the optimal nutritional inclusion levels in feeds when fish traits relevant to diet composition change. When applied to animal breeding and quantitative genetics, the model can be used to define optimal feeds for genetically different fish stocks, and to predict the expected future changes in optimal feed composition for stocks under selective breeding. Due to the general nature of this approach, the model can be applied to other fish species and breeding programmes, or to extend it to encompass different or larger sets of relevant nutrients or dietary energy.

CRedit authorship contribution statement

Antti Kause: Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis, Conceptualization. **Filipe Soares:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Tomé S. Silva:** Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization.

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Declaration of competing interest

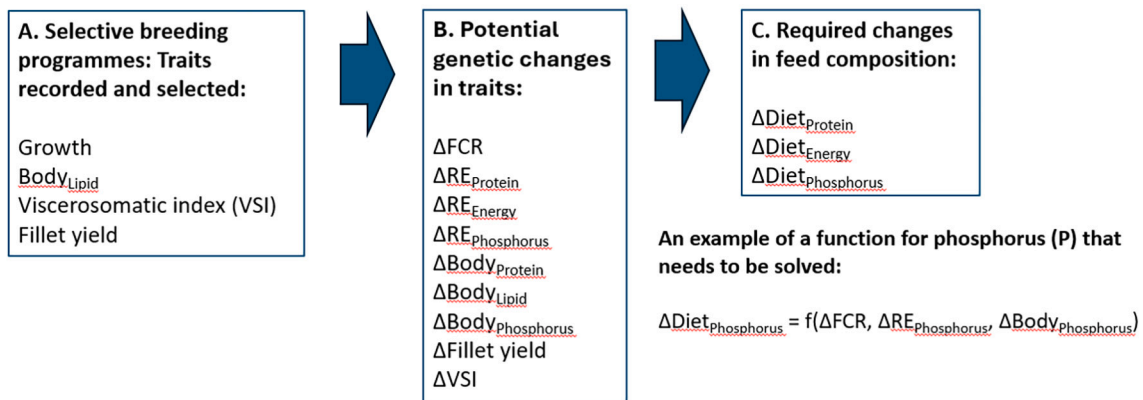
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Appendix A. The concept of the traits-to-feed model

The concept of the traits-to-feed model integrating fish nutrition and genetic improvement



Selective breeding programmes select for a set of traits (A) that potentially change multiple fish including the selected traits but also other correlated traits (B). Traits related to retention efficiency and nutrient compositions can change because they are correlated with the selected traits (Kause et al., 2002, 2007, 2008, 2016, 2022). The trait changes modify the dietary needs of the fish and a new type of diet composition is hence needed (C). Body - Body composition; FCR - Feed conversion ratio; RE - Retention efficiency; Diet - Nutrient inclusion levels in a feed.

Appendix B. Economic farm-level FCR at mainland fish farms in Finland across years

The average farm-FCR from 1993 to 2016 from Fig. 1 of Kause et al. (2022).

Year recorded	Respective birth year of fish	Economic farm-FCR
1993	1992	1.6515
1994	1993	1.4876
1995	1994	1.4271
1996	1995	1.3712
1997	1996	1.3302
1998	1997	1.3219
1999	1998	1.2972
2000	1999	1.2720
2001	2000	1.2524
2002	2001	1.2642
2003	2002	1.1968
2004	2003	1.1650
2005	2004	1.1483
2006	2005	1.1912
2007	2006	1.1264
2008	2007	1.1118
2009	2008	1.1235
2010	2009	1.1356
2011	2010	1.0772
2012	2011	1.0676
2013	2012	1.1102
2014	2013	1.1301
2015	2014	1.1067
2016	2015	1.0610

Appendix C. Genetic trends in fish traits across years

Average estimated breeding values of body weight at age 2 (BW, g), feed conversion ratio (FCR), viscerosomatic index (VSI, proportion) and fillet yield (YLD, proportion) based on the graphs in Kause et al. (2022, Supplementary Data).

Birth year	BW	VSI	FCR	YLD
1992	979.9	0.1107	1.3403	0.6465
1993	993.1	0.1109	1.3369	0.6464
1995	1041.5	0.1121	1.3126	0.6463
1996	1038.3	0.1110	1.3160	0.6468
1997	1058.4	0.1116	1.3100	0.6463
1998	1114.9	0.1151	1.2835	0.6455
1999	1098.4	0.1142	1.2903	0.6456
2000	1194.3	0.1129	1.2576	0.6471
2001	1183.2	0.1148	1.2600	0.6462
2002	1192.1	0.1179	1.2505	0.6449
2003	1291.7	0.1148	1.2158	0.6475
2004	1189.8	0.1148	1.2582	0.6462
2005	1208.9	0.1188	1.2379	0.6451
2006	1334.1	0.1142	1.2029	0.6477
2007	1234.7	0.1133	1.2419	0.6468
2008	1254.2	0.1104	1.2154	0.6498
2009	1456.0	0.1119	1.1540	0.6496
2010	1319.3	0.1098	1.2056	0.6495
2011	1303.2	0.1073	1.2011	0.6512
2012	1407.5	0.1083	1.1654	0.6515
2013	1383.0	0.1111	1.1879	0.6486
2014	1354.0	0.1066	1.1884	0.6512
2015	1437.9	0.1069	1.1469	0.6534

Appendix D. Justification and derivation of the advanced model

A more realistic model of fish growth (and, thus, of nutrient gain in fish) should account not just for energy and mass conservation, but also:

- a) the fact that fish lose mass (and, thus, nutrients) when feed intake is zero (i.e., fish should display fasting maintenance costs);
- b) the fact that fish growth rate is bounded (i.e., as nutrient intake tends to infinity, that rate of nutrient's gain should tend to a finite value);
- c) the fact that fish size is bounded (i.e., as time tends to infinity, fish mass should tend to a finite value, even if feed/food is not limited).

To ensure these properties, the advanced model was derived assuming a specific (and more realistic) type of growth. More specifically, it assumes the following differential equation (under the assumption that there are no nutritional limitations):

$$\text{growth} = \frac{d}{dt}BW = a f(T) BW^{2/3} - b f(T) BW$$

where a is the maximum specific anabolic rate, b is the maximum specific catabolic rate, and $f(T)$ is an arbitrary function of temperature that controls how anabolism and catabolism depend on temperature (and which must be bounded between 0 and 1).

This can be reparametrized to a form where the maximum body weight ($BW_{\infty} = \left(\frac{a}{b}\right)^3$) appears explicitly, and the maximum specific catabolic rate parameter (b) disappears:

$$\frac{d}{dt}BW = a f(T) BW^{2/3} \left(1 - \left(\frac{BW}{BW_{\infty}}\right)^{1/3}\right)$$

Under a realistic situation, where there are nutritional limitations, we have to assume that anabolism explicitly depends on feed (and nutrient and energy intake). If we specifically assume a saturating (Michaelis-Menten/Monod type) relationship (Srinivasan, 2022), we obtain the following expression:

$$\frac{d}{dt}BW = a f(T) BW^{2/3} \left(\frac{k_{\text{feed}} \times \text{intake}_{\text{feed}}}{k_{\text{feed}} \times \text{intake}_{\text{feed}} + a f(T) BW^{2/3}} - \left(\frac{BW}{BW_{\infty}}\right)^{1/3} \right)$$

where k_{feed} represents a feed-dependent feed efficiency parameter, which represents the efficiency of conversion of feed mass into fish biomass.

Under the assumption that, e.g., phosphorus is the limiting essential nutrient, we can directly equate anabolism with digestible phosphorus intake:

$$\frac{d}{dt}BW = a f(T) BW^{2/3} \left(\frac{\frac{dBW}{dP} \times k_p \times \text{intake}_{DP}}{\frac{dBW}{dP} \times k_p \times \text{intake}_{DP} + a f(T) BW^{2/3}} - \left(\frac{BW}{BW_{\infty}}\right)^{1/3} \right)$$

After expressing digestible phosphorus intake as a function of feed intake, we obtain the following:

$$\frac{d}{dt}BW = a f(T) BW^{2/3} \left(\frac{\frac{dBW}{dP} \times k_p \times \text{diet}_p \times ADC_p \times \text{intake}_{\text{feed}}}{\frac{dBW}{dP} \times k_p \times \text{diet}_p \times ADC_p \times \text{intake}_{\text{feed}} + a f(T) BW^{2/3}} - \left(\frac{BW}{BW_{\infty}}\right)^{1/3} \right)$$

Expressing $\frac{d}{dt}BW$ as 'growth(t)', we obtain:

$$growth(t) = a f(T) BW^{2/3} \left(\frac{\frac{dBW}{dP} \times k_p \times diet_p \times ADC_p \times intake_{feed}}{\frac{dBW}{dP} \times k_p \times diet_p \times ADC_p \times intake_{feed} + a f(T) BW^{2/3}} - \left(\frac{BW}{BW_{\infty}} \right)^{1/3} \right)$$

After rearranging the expression to isolate feed intake, we obtain:

$$intake_{feed} = \left(\frac{1}{\frac{dBW}{dP} \times k_p \times diet_p \times ADC_p} \right) \left(\frac{1}{1 - \left(\frac{growth(t)}{a f(T) BW^{2/3}} + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} \right)} \right) \left(growth(t) + a f(T) \left(\frac{1}{BW_{\infty}} \right)^{1/3} BW \right)$$

We now parametrize growth as a fraction of maximum growth:

$$growth(t) = \varphi(t) growth_{max}(t) = \varphi(t) a f(T) \left(BW^{2/3} - \frac{1}{BW_{\infty}^{1/3}} BW \right)$$

where $\varphi(t)$ represents growth as a fraction of the maximum possible growth (i.e., growth% in Eqs. (36) and (37)).

Using this as a replacement for every instance of 'growth(t)' in the $intake_{feed}$ expression above and simplifying, we obtain:

$$intake_{feed} = a f(T) BW^{2/3} \left(\frac{1}{\frac{dBW}{dP} \times k_p \times diet_p \times ADC_p} \right) \left(\frac{\varphi(t) + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - \varphi(t))}{1 - \left(\varphi(t) + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - \varphi(t)) \right)} \right)$$

Expressing feed intake as the product of FCR and growth, we obtain:

$$FCR \times growth(t) = a f(T) BW^{2/3} \left(\frac{1}{\frac{dBW}{dP} \times k_p \times diet_p \times ADC_p} \right) \left(\frac{\varphi(t) + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - \varphi(t))}{1 - \left(\varphi(t) + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - \varphi(t)) \right)} \right)$$

Replacing 'growth(t)' again by the above definition and isolating $diet_p$, we obtain:

$$diet_p = \left(\frac{1}{\frac{dBW}{dP} \times k_p \times ADC_p} \right) \left(\frac{a f(T) BW^{2/3}}{FCR \times \varphi(t) a f(T) \left(BW^{2/3} - \frac{1}{M_{\infty}^{1/3}} BW \right)} \right) \left(\frac{\varphi(t) + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - \varphi(t))}{1 - \left(\varphi(t) + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - \varphi(t)) \right)} \right)$$

Simplifying, we obtain:

$$diet_p = \left(\frac{1}{\frac{dBW}{dP} \times k_p \times ADC_p} \right) \left(\frac{BW^{2/3}}{FCR \times \varphi(t) \left(BW^{2/3} - \frac{1}{M_{\infty}^{1/3}} BW \right)} \right) \left(\frac{\varphi(t) + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - \varphi(t))}{1 - \left(\varphi(t) + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - \varphi(t)) \right)} \right)$$

Further simplification finally leads to:

$$diet_p = \frac{1}{FCR} \times \frac{1}{k_p} \times \frac{1}{ADC_p} \times \frac{dP}{dBW} \times \left(\frac{\varphi(t) + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - \varphi(t))}{1 - \left(\varphi(t) + \left(\frac{BW}{BW_{\infty}} \right)^{1/3} (1 - \varphi(t)) \right)} \right) \left(\frac{1}{\varphi(t)} \right) \left(\frac{1}{1 - \left(\frac{BW}{BW_{\infty}} \right)^{1/3}} \right)$$

where $\frac{dP}{dBW}$ should be defined based on a suitable body composition model, and calculated e.g. as $(scalebody_p \times exp_p \times BW^{exp_p-1})$, while $\varphi(t)$ represents growth as a fraction of the maximum possible growth (i.e., growth% in Eqs. (36) and (37)).

Appendix E. Optimal inclusion level of a nutrient relative to energy feed level

Through a small modification, it is possible to simultaneously make the models simpler (i.e., reduce their dependence on fish management parameters and difficult to estimate biological parameters) and to express the predictions in a way that is closer to fish requirements than to optimal feed formulation.

This can be done by expressing the required inclusion of all nutrients (protein, phosphorus, energy) in relation to the required amount of digestible energy in a feed (i.e., phosphorus inclusion levels would be expressed as 'g of digestible phosphorus required in the feed per kJ of digestible energy in the feed'). For example, in the case of the advanced model, if we take the ratio of optimal digestible phosphorus level ($diet_{DP}$) and optimal digestible energy level in a feed ($diet_{DE}$), we obtain:

$$\frac{\text{diet}_{DP}}{\text{diet}_{DE}} = \frac{\frac{1}{k_P} \times (\text{scalebody}_P \times \exp_P \times BW^{\exp_P-1})}{\frac{1}{k_E} \times (\text{scalebody}_E \times \exp_E \times BW^{\exp_E-1})}$$

$$\frac{\text{diet}_{DP}}{\text{diet}_{DE}} = \frac{k_E}{k_P} \times \frac{\text{scalebody}_P}{\text{scalebody}_E} \times \frac{\exp_P}{\exp_E} \times BW^{\exp_P - \exp_E}$$

note the lack of dependence on either FCR, BW_{∞} or growth%.

A direct consequence of this is that (in this case) the relationship between the optimal (digestible) phosphorus-to-energy content of feeds and fish body weight only depends on the body composition parameters $\exp_P$ (i.e., how fish size affects the phosphorus content of fish biomass) and $\exp_E$ (i.e., how fish size affects the energy content of fish biomass).

Given that the $\exp_E$ tends to be higher than 1 (usually on the order of 1.2), while the exponent for phosphorus and other nutrients is usually close to 1, this generally implies that the optimal digestible nutrient-to-energy ratios in fish feeds decrease as BW increases (i.e., $\exp_{\text{nutrient}} - \exp_{\text{energy}} < 0$), regardless of the values of the other parameters.

Data availability

The data of phenotypic and genetic trends are presented in the Appendices. All other data are confidential.

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