

FishMet: A digital twin framework for appetite, feeding decisions and growth in salmonid fish

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Abstract

Salmonids are important fish species in aquaculture in countries in the temperate zone. Optimisation of feeding in next generation precision fish farming requires developing models for decision support and process control. Black box ML and AI models are often very efficient but have drawbacks, such as requiring large amount of training data and reduced performance in novel situations where no data are available. Thus, developing realistic process models of fish appetite, feeding decisions (feed intake), energetics and growth is necessary. Such models are essential for predicting the fish performance (feed intake, waste from uneaten feed and faeces, growth) in novel “what if” scenario testing. We have built a conceptual model based on a review of major neurophysiological mechanisms and feedback loops controlling appetite and food intake in fish. Building on this, we have developed the FishMet model: a novel extensible stochastic simulation framework that represents the basic feedback loops controlling appetite, feeding decisions, energy budget and growth in salmonid fish. The model is supported by server-based components and open API for data assimilation and on-demand model execution that allows to use FishMet as a digital twin. We demonstrate relatively good prediction of stomach and gut digesta transit and food intake in the rainbow trout *Oncorhynchus mykiss*. The digital twin also demonstrated good prediction of growth and feeding efficiency in a pilot scale experiment on the Atlantic salmon *Salmo salar*. We discuss the concept of the digital twin and the directions of further development of the model as an applied predictive tool.

Keywords: appetite, feed intake, growth, model

Introduction

Atlantic salmon (*Salmo salar*) is the most important aquaculture species in Norway (Grefsrud et al., 2024) and recently rainbow trout (*Oncorhynchus mykiss*) also has a significant increase in production. Both species are reared in many other countries (FAO, 2024). Recent developments in salmon aquaculture aim at precision fish farming (Antonucci and Costa, 2020; Føre et al., 2018; Wang et al., 2021), that involves multiple diverse sensors to monitor the cage environment and the state of the fish, assess the level of appetite (hunger and satiation), feed anticipation, feed intake, welfare and stress. Then, the amount of feed provided can be optimized precisely to the actual fish condition, avoiding under-, over-feeding and feed waste, thereby increasing production, economic value and reducing environmental impacts. However, the industry currently remains quite far from such an ideal condition. In many cases, the feeding process is controlled manually by an experienced operator using underwater cameras to infer the cessation of the fish appetite from behaviour observation and sinking depth of uneaten feed pellets. The maximum feed amount calculation typically follows the guidelines that are based on fish size and environmental conditions (temperature) rather than the behaviour of the fish. The pellets are delivered through feed lines that run from silos to nets by a flow of tempered air or water. This type of feeding control has been developed and improved over the last decades with many innovations in the feeding infrastructure (Afewerki et al., 2023; Føre et al., 2022).

However, determining the level of appetite and the amount of feed to optimize intake for growth is a challenging task. There is no agreement about the best feeding control strategy in the industry. Feeding intensity, the number, the time distribution of meals, and what the fish farmer considers as “satiated fish,” have a strong influence on the amount of feed provided to the fish—in most cases overfeeding—and on the feed waste produced (O. Folkedal, IMR, Matre, Norway pers. comm). Fish appetite should be monitored for every meal. The difficulty to assess the internal hunger state of the fish, especially in a large tank or cage, is the major limitation for optimal feed management. An even more difficult task is to predict appetite and feed intake in various counterfactual scenarios. This requires integration of diverse knowledge about the fish feeding behaviour, neurobiology and physiology.

In this work we present a computational framework for a digital twin system for appetite, feed intake and growth of salmonid fish. We also present a prototype cloud server system that can run and integrate the digital twin with most fish farm management and decision support systems over standard web-based interface. We have implemented an initial model with a set of simplifying

assumptions, parametrised it based on published data and feed tracer experiments with the rainbow trout. We also re-parametrised the model for the Atlantic salmon and conducted a demonstration and testing experiment in the AquaBioTech Group research service facility using an aquaculture steering system.

Requirements for digital twin model of appetite and feed intake in salmonid fish

Theoretical models and trial-based feeding tables have been developed to calculate the daily food requirements and feed intake of salmonid fish in aquaculture (see Kaushik and Médale, 1994; Ricker, 1979; Sun et al., 2016 for reviews). Most of them involve estimates of fish energy requirement (e.g. Cho and Bureau, 1998; Cho, 1992; Dumas et al., 2010), growth rate (e.g. Austreng et al., 1987) and thermal-unit growth coefficient (Bureau et al., 2006; Lugert et al., 2016) based on common energy partitioning scheme (see Bureau et al., 2002). But most of the current models do not account how appetite vary dynamically as a function of the feeding protocol and other factors. This makes such models a rather rough tool for fine-grained feeding control. For example, the prominent Wisconsin model (see FB4, Deslauriers et al., 2017) includes two consumption parameters: the maximum daily consumption rate C_{max} and the proportionality factor P describing constraints on the feeding rate (also see Railsback et al., 2021; Railsback and Rose, 1999). This is adequate for ecological and life history models with time scale of many days (Kepler et al., 2014; Mangel and Satterthwaite, 2016; Satterthwaite et al., 2010) but not for predicting food intake in a single meal. Additionally, food intake is directly or indirectly a user input to most of these models rather than the output. For example, in FB4 and similar models, C_{max} is based on trials with *ad libitum* feeding at the optimal temperature. One of the few exceptions is the integrated model of feeding behaviour and growth by Føre and co-authors (Føre et al., 2016), which is an individual-based simulator predicting growth based on distribution of feed pellets, behaviour and dynamic energy budget.

Because appetite is a dynamic result of many internal and external factors (Delgado et al., 2017; Rønnestad et al., 2017; Volkoff et al., 2010), it can differ within and across days, bringing about the associated variation in food intake and instantaneous growth rate. Food intake in the Atlantic salmon depends on the time since previous meal, the meal size and other factors, suggesting that feeding should be adjusted dynamically (Gomes et al., 2023). Rainbow trout with free access to food with demand feeders can maximize growth rate, but not feed conversion, which could have minimized food waste (Alanärä, 1992). Similarly, feeding trout to satiation increases growth rate

but reduces efficiency (Azevedo et al., 1998). Significant feed losses may result from large discrepancy between the amount of food supplied and ingested, with peaks resulting in 40 to 60% higher food rations per day compared to the lowest values. This makes measuring and modelling appetite a key factor for feeding and growth optimization. But it is not an easy task because the level of appetite in fish is controlled by several physiological and neural mechanisms with complex feedback loops that respond to a variety of environmental factors, the level of stress etc. (Best et al., 2022; Conde-Sieira et al., 2018; Rønnestad et al., 2017; Soengas et al., 2018; Volkoff and Rønnestad, 2020). Fish growth is also a complex process that reflects aspects of metabolism, bioenergetics (Bureau et al., 2002), behavioural activity and other factors (Canosa and Bertucci, 2020; Sheridan, 2021).

Recent advances in machine vision, machine learning and convolutional neural networks make these methods increasingly popular in aquaculture research (Gladju et al., 2022; Iqbal et al., 2022; Li et al., 2022; Li and Du, 2022; Mandal and Ghosh, 2023; Rowan, 2023; Yang et al., 2021; Zhao et al., 2021) including food intake control, feeding optimization and growth modelling (Adegboye et al., 2020; Chahid et al., 2022; Chen et al., 2020; Georgopoulou et al., 2024; Kong et al., 2022; Li et al., 2020; Son and Jeong, 2024; Ubina et al., 2021; Zhang et al., 2023; Zhou et al., 2019). This makes it possible to estimate when the fish reach satiety—and the automatic feeder should be switched off—based on patterns of fish locomotion and behaviour recorded by underwater cameras or echo-sounder. In absence of detailed causal understanding and the high complexity, black-box machine learning and optimisation methods may look most promising (Gladju et al., 2022; Zhao et al., 2021).

However, these methods have a serious drawback: they require large amount of data—often manually labelled—continuously input for model training and recalibration (Marcus and Davis, 2019; Pearl, 2019). This has been identified as one of the major obstacles for AI in aquaculture (e.g. Yang et al., 2021). Such detailed data are currently rarely available in most commercial fish farm systems. While tightly controlled and sensor-rich land-based RAS systems may be better adapted to at least some aspects of data-intensive control, it is more difficult for sea cages. In sea cages—especially offshore, cameras, sensors and other advanced equipment operate in a harsh subsea or moist environment 24/7 throughout the year, sometimes adverse weather conditions. This increases the risks of technical issues and failures, requiring very high reliability and not permitting to exclude human involvement. All this further increases the high cost of the equipment, IT support and specific experience required to run the data-intensive systems.

Furthermore, while the current machine learning methods can be fascinatingly effective in approximating patterns from the large body of existing data, they have difficulties in novel cases for which no data are yet available (Marcus and Davis, 2019; Pearl, 2019). This is not just a transient limitation that can be mitigated with further technology development, but links with fundamental problems like the bias-variance dilemma (Belkin et al., 2019; Bishop, 2006) and universal induction that are in a general case unsolvable (Rathmanner and Hutter, 2011; Solomonoff, 2009). While black-box methods can be used for ongoing control of the feeding process, they are very limited for most types of “what-if” novel scenario modelling. What is the predicted feed intake and growth if the number and/or time distribution of meals is changed? How will the fish respond if one increases or reduces the pellet input rate or pellet size? What if this is done differently for the different meals? What will occur if water temperature suddenly rises? Currently, such alterations are assessed subjectively based on the expert experience or field tests that are often difficult to evaluate correctly, especially because it is hard to ensure strict control of the major factors in most sea cage production environments because of logistical restrictions and natural environmental variability. Performing controlled factorial experiments, however, is very expensive and may be untenable in production environments. What is needed, in addition to models of ongoing control, is a predictive decision support tool for various what-if scenarios (Føre et al., 2016).

We believe that developing a model that integrates the major causal mechanisms and feedback loops affecting the fish appetite and individual feeding decisions would be a more fruitful path. A similar approach has been started in the past (Olsen and Balchen, 1992), but encountered difficulties due to lack of good theories for devising equations and of empirical data for parametrisation. Earlier models (Føre et al., 2016; Olsen and Balchen, 1992) assumed a simple link between gut fullness and appetite or consider any contact between the simulated fish and feed particle as “intake” (Takahashi and Komeyama, 2023). Now we have empirical data and the quality theories that will help develop, parametrise and calibrate more physiologically realistic models. Multiple signalling feedback mechanisms—beyond simple gut fullness—need to be considered into the process simulation model of appetite, reflecting more intricate details of physiological and neural control.

Simulation involves decomposing a system into its most principal parts, putting them together in a running computer code and then reproducing a complete causal trajectory of the system in a computational experiment (Schwartz, 2008; Wolfram, 2002). This can be especially efficient when we are interested in the complete dynamics of the process rather than a single output value. A theory-based simulation model therefore will not only give a predicted numerical estimate (e.g. feed

intake, growth rate), but also provide hints on how and why it went there, increasing transparency and explainability (Hagras, 2018). Furthermore, an applied model should follow the “digital twin” methodology (Budaev et al., 2024; Føre et al., 2024; National Academies of Sciences, Engineering, and Medicine, 2024; Purcell and Neubauer, 2023; Singh et al., 2022; Thelen et al., 2022a; Ubina et al., 2023; Wright and Davidson, 2020), namely mimic the structure, context and behaviour of the fish feeding decisions machinery with bidirectional assimilation of data from the physical fish farm. That is, a causal process simulation model should represent the basic mechanisms responsible for feed intake, chime transport through stomach and gut, nutrient absorption, main physiological feedback loops controlling appetite, general behavioural activity, energy balance and finally growth. Then, specific decisions to consume individual feed pellets should naturally follow from the modelled level of appetite. Feeding decisions—to consume or ignore the pellet—provide the input for stomach and gut. Thus, the model will represent long simulation cycles with feed pellets input and the overall feed consumption and growth as the main outputs. Implementing individual decisions for each feed pellet results in a computation intensive model, but modern computer hardware is sufficiently fast. As an advantage, such a fine-grained level allows modelling and prediction of virtually any arbitrary feed input pattern with any number and distribution of meals. This potentially provides for an advanced tool best suited for prediction in a wide range of novel “what-if” scenarios.

Control of appetite in salmonid fish: an outline of mechanisms

Appetite in a wider sense covers a range of processes and phenomena directly associated with food intake, food selection, sensation, motivation and food preference (Blundell et al., 2010). But more specifically, it is defined as an affective state: the desire to eat food. Appetite is related to hunger: a sensation evoked by depletion of nutrients in the body (Grossman, 1955) and the subjective drive to eat (Blundell et al., 2010). Thus, control of appetite includes a tonic component that represents a drive arising from the basic biological need for energy (Blundell et al., 2020). Appetite can therefore be thought as an ancient and conservative evolutionary adaptation that ensures that the organism obtains energy for all its various fitness-related needs. Fish follow a common pattern typical of most vertebrates. Appetite, feeding behaviour, and feed intake are controlled by the hypothalamus through complex integration of peripheral and central signals (Rønnestad et al., 2017; Soengas et al., 2018; Volkoff, 2016). The hypothalamus receives a range of afferent neuronal and humoral signals originating in the digestive tract, liver, adipose tissue, and other organs. Along with nutrient and energy related sensory systems within the brain (Soengas, 2021; Soengas et al., 2024),

this provides a dynamic input of the current nutrient and energy status, including gut filling and fat reserves, that modulates food seeking and adaptive decision-making.

The central regulation of appetite and energy expenditure in teleosts is localised in a complex neuronal network of the lateral tuberal nucleus of the hypothalamus (Cerdá-Reverter et al., 2003; Cerdá-Reverter and Peter, 2003; Norland et al., 2023; Rønnestad et al., 2023). In this region, two main neuronal population play opposing roles on feed intake control. The appetite stimulating neurons express neuropeptide Y and agouti-related peptide: NPY and AgRP. Their receptor antagonists include the appetite suppressing neurons expressing proopiomelanocortin (POMC), along with Cocaine- and amphetamine-regulated transcript CART. When activated, the anorexigenic POMC and CART neurons decrease feed intake whereas their antagonist, the orexigenic NPY and AgRP neurons, increase food intake. These neurons communicate within each other and project to higher order neurons within and outside the hypothalamus to yield the final appetite drive as a motivator to decisions and behaviour. Bidirectional interactions between caudal and lateral hypothalamic loci have been implicated in appetite, food search and ingestion decision larval zebrafish (Wee et al., 2019). Hunger is linked with increased neural activity in the caudal hypothalamus. Once the fish locates the feed and starts consumption, activity in this area sharply declines, remaining low until it becomes satiated. Then, the activity of the caudal hypothalamus returns to normal levels. But concurrent with the activity of the caudal area, the activity in the lateral hypothalamus displays a pattern opposite to the caudal area. In hungry fish larvae this activity is lower, but it increases when food becomes available and the larvae starts to feed. When the larvae approaches satiety and reduces its ingestion rate, the activity of lateral hypothalamus neurons declines. Thus, reciprocal inhibition of caudal and lateral hypothalamic nuclei works as two separate switches regulating food search and food intake when it is available.

Once the food is ingested, it is transferred through the multi-compartment digestive tract where it is degraded and slowly assimilated. Valves secure strictly one-way flow between its separate compartments, facilitating special processing of the chyme (a viscous mass of partially digested food) in each compartment. Assimilation of a meal requires many enzymatic and transport pathways taking part in the different compartments. The luminal conditions are normally optimized to maximise the digestive process in each segment.

The first compartment that receives the ingested food in salmonids, as in most mono gastric vertebrates is the stomach which serves an important role as a short-term reservoir (Stevens and Hume, 2004). The stomach is one of the main contributors to short-term regulation of food intake

(Grove et al., 1978). No absorption of nutrients normally occurs in the stomach: only food intake (input) and gastric evacuations (output) need to be considered for the mass balance (Jobling, 1981). Afferent signals convey sensory information via hormones and neural pathways to the brain that food is secured (Bromley, 1994; Holmgren et al., 1982) even before nutrients are absorbed. The stomach generates muscular contractions contributing to mechanical degradation of the food and providing for a steady supply of chyme to the anterior midgut (Jobling, 1996). It also produces and releases hormones (e.g. ghrelin) and generates neural signals that dynamically affect gastric digestion and modulate appetite based on filling and content (Holmgren and Olsson, 2009; Olsson and Holmgren, 2011). Stomach volume varies significantly during food deprivation and ingestion cycles (Lai et al., UiB pers. comm). An empty stomach sends stretch information to the brain stem that then contributes to the generation of hunger. Filling with food brings about distension that is recorded by stretch receptors, signalling the brain stem of satiety. Once food is ingested, there is a receptive relaxation that enables the stomach to accommodate more food (Grove and Holmgren, 1992). The increased volume of the stomach and the decrease in muscle tone continues for a considerable period after the volumetric stimulus is removed. Gastric response allows further slow relaxation of the stomach up to the maximum volume V_{max} (Grove, 1986). Once distension has occurred, the stomach starts the digestive process. The food items are broken down through a combination of muscular contractions of the stomach wall and enzymatic action in the acid medium. However, it will take some time before these process starts, since they rely on reflexive activation of secretions from the gastric glands (Bromley, 1994; Darnell and Meierotto, 1962). Harder dry pellets remain solid for much of the gastric digestion phase while soft pellets rapidly degrade into boluses. Big meal causes a “saturation” because the gastric epithelium secretion rate is limited (Grove, 1986).

Partly degraded feed (chyme) is gradually expelled into the small intestine in the gastric evacuation process (Jobling, 1996). It occurs in small pulses and holds dietary components that are sufficiently degraded and dissolved to pass as a fluid bolus into the anterior midgut. The gastric evacuation rate and time have been subject of many studies because they were postulated to predict food intake, assuming that the amount of food expelled from stomach equals the amount eaten (Andersen, 2022; Bromley, 1994; Jobling, 1986). However, for most fish, this is not as simple because the passage of food out of the stomach is controlled by several nervous and hormonal mechanisms and feedbacks (Jobling, 1981), for example, the energy flow into the hindgut (Jobling, 1986). Data obtained in studies of higher vertebrates indicated that gastric emptying is largely controlled from the midgut (Boron and Boulpaep, 2017) and functionally, these mechanisms tend to regulate the load to match

the digestive capacity in this compartment and maximize digestion. The hormone Cholecystokinin (CCK) is believed to have an important role in this control (Murashita et al., 2008; Rønnestad et al., 2007). Therefore, additional terms for negative feedback should be included into equation-based models of gastric evacuation in fish (Jobling, 1981). For example, the stomach would transfer decreasing volumes of identical nutrient concentration as emptying proceeds, or constant volumes of decreasing nutrient concentration. Or it might even release varying volumes and concentrations in a time sequence such that when a pulse is released, the intestine receives a constant mass of nutrient, dry weight or energy (Grove, 1986).

Once the midgut receives the chyme, a range of processes continues to degrade, digest and finally absorb the dietary nutrients. Midgut processes involve secretion of bile and pancreatic enzymes along with the final digestion at the epithelia as the absorption process assimilates the nutrients into the enterocytes and further into the circulation (Jobling, 1996). The digesta is evaluated by stretch receptors, osmoreceptors and chemical/nutrient-receptors that provide sensory signals for digestion control, including release of secretions and the rate of gut passage. These sensors also send direct or indirect satiation signals to the brain. There are several gut peptide hormones released from the midgut, of which CCK and PYY are the most prominent (Murashita et al., 2008), but GLP-1 also emerge as a potential important hormone in fish (Volkoff, 2016). As in mammals these hormones are believed to act anorexigenically on the hypothalamus. None of the hormones released in the midgut stimulate appetite. As long as there is significant nutrient content (qualitative and quantitative) in the midgut as part of the post-prandial processing of a meal, these signals will suppress appetite (Blundell et al., 2020). Consistent with these mammalian data, in the Atlantic halibut—a species whose appetite is notoriously difficult to stimulate in aquaculture—feed intake was not stimulated by an empty stomach, but rather correlated to the midgut filling (E. Lygre, UiB, pers. comm). It looks like low filling or nutrient influx blocks anorexigenic pathways and stimulate appetite. Thus, midgut plays a critical role in the control of appetite, presumably implicating the digesta passage rate so that satiation signals respond to the presence of digesta in the lumen. The time course of digestion in midgut can be well modelled as a tubular plug-flow chemical reactor. Then, in catalytic (i.e., enzymatic) digestive reactions, the reaction rate is well described by the Michaelis-Menten function of substrate concentration (Penry and Jumars, 1987, 1986). Integrated analysis of digestive strategy using reactor models has been usefully applied in a few studies of fish (Horn and Messer, 1992) and intestinal hydrolysis following Michaelis-Menten kinetics has been employed in simulation models of human intestinal absorption (Moxon et al., 2016).

The hindgut in salmonid fish is a separated region from the midgut. It is involved in water and ion uptake and enterohepatic circulation and plays an important immunological role (Wallace et al., 2005). The hindgut does not appear to play a significant role in appetite control, even though abundant microbiota might exert indirect effects on appetite and food intake via health and cognitive functions (Butt and Volkoff, 2019).

Post-absorptive and post-prandial processes, which occur during and after nutrients are absorbed into the bloodstream, will also significantly influence appetite and feed intake. These processes regulate energy homeostasis, with the overall aim to ensure that intake of energy aligns with the body's metabolic demands and is therefore also linked to allocation of the dynamic energy budget including growth (Sheridan, 2021). The key mechanisms involved include hormonal signalling, neural pathways (mainly via the vagus nerve), and nutrient sensing. The gut derived hormones, Ghrelin, CCK, PYY, GLP-1 are believed to be released dynamically as part of the regulation of the digestive process (Volkoff, 2019). In addition, insulin is secreted in response to blood levels of glucose while the role of leptin is less clear in fish than in mammals it is believed to be released in response to available energy in the liver or adipose tissue, but both hormones seem to suppress appetite in fish (Volkoff, 2019). In the post-absorptive state, the mechanisms mentioned above collectively function to inhibit appetite and reduce feed intake.

Direct sensing of nutrients is also an important modulator of appetite. There are described sensory mechanisms for glucose, amino acids and fatty acids that activate different pathways that affects the hypothalamic neurons involved in appetite control (Soengas et al., 2024). Within the neurons themselves, there are also cellular mechanisms that sense the energy state at the molecular level (Soengas, 2021). This occurs via AMP-activated protein kinase (AMPK) that is activated when cellular energy (ATP) levels are low and stimulates AgRP NPY neurons, promoting food intake. mTOR (mechanistic target of rapamycin) is a nutrient sensor activated by amino acids and glucose. In hypothalamic POMC neurons, activation of mTOR signals energy sufficiency and suppresses food intake.

The FishMet model

Model overview

FishMet is a mechanistic, process-based simulation model aimed at predicting appetite, feed intake and growth in salmonid fish. Its computational part follows the principles of process simulations

(Birta and Arbez, 2013; Gould et al., 2007) and agent-based modelling (Railsback and Grimm, 2019). FishMet is a discrete time model running over a predefined number of time steps with the resolution (time step) equivalent to 1s. The model works at the fine-grained level of individual feed pellets and individual fish decisions. This will potentially allow for complex simulations with variable feed, complex schedules and stochastic environment. Currently the model represents a single individual viewed as an equivalent of a group average. This has been done to reduce the computational complexity and facilitate easier parametrisation and interpretation. However, it would be possible to extend the model to simulate a population of fish with individual variation of parameter values. Then, the outputs are both statistical distributions of the population values.

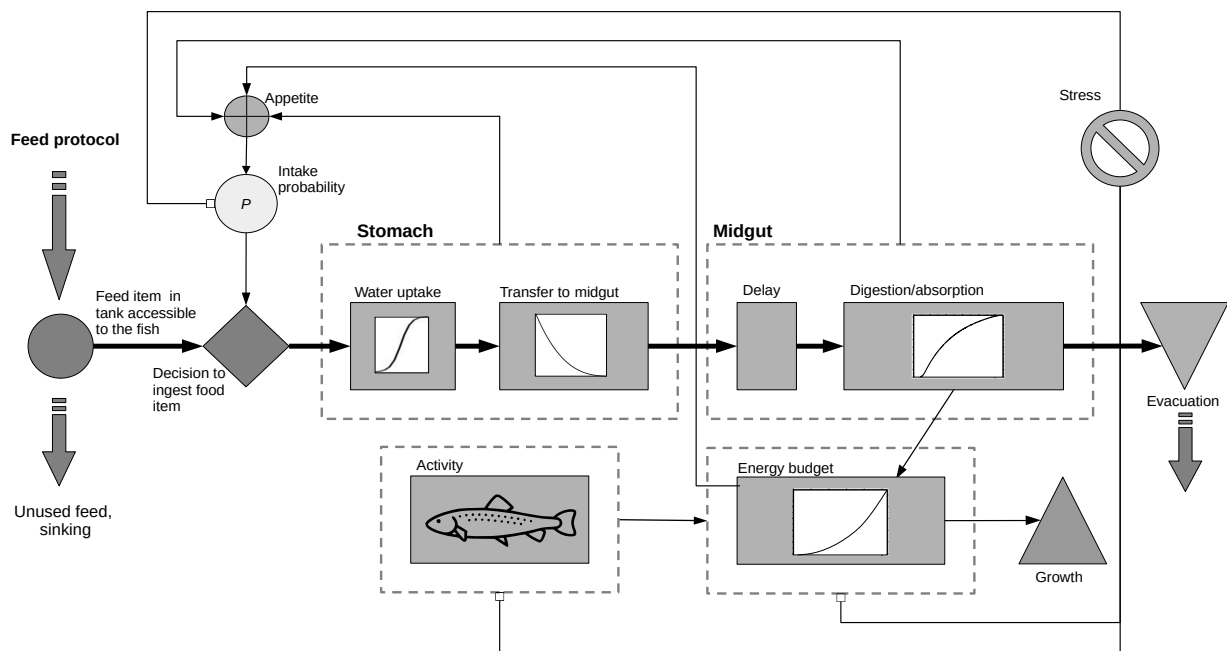


Figure 1: An overview of FishMet. Arrows indicate the various causal effects and their direction. Thick arrows depict food and digesta mass transfer; thin arrows, feedback loops and energy to growth link. For stress, all effects involve suppression, depicted by squared-tip arrows. Rectangles are used for components of processing, circles depict possible effects and events, crossed circle is used for ‘either or’ selection, diamond indicates decision, triangles are major outputs. See Model overview for explanation.

An overview of the model is presented in Figure 1. A simulation starts with the input of the first feed item (pellet). Because the model treats every item individually, any feeding schedule can be accepted. But in the simplest cases feed pellet input is defined by meal times when feed is provided as well as the feed input rate: the number of pellets administered per minute. The fish then makes the decision to eat or ignore each food item depending on the appetite level. In absence of a good theory of how subjective appetite is represented in the “mind” of the salmonid fish, we define appetite as a simple stochastic probability of consuming the pellet. Each pellet that has been

consumed by the fish is transferred to the stomach. Here it undergoes water uptake, increasing its mass without altering energy content. The ingested feed pellets accumulate in the stomach and slowly transfer to midgut once they are sufficiently disintegrated. Once feed item occurs in the midgut, it, after a delay due to time for digestion, is subjected to absorption following the Michaelis-Menten mass dynamics. Feed digestibility is limited, depending on digestibility of ingredients and all non-digested mass is evacuated from the organism. The flux of energy that is incoming to the organism as a result of absorption is added into the simplified dynamic energy budget, with the baseline metabolic costs, costs of digestion and processing (standard dynamic action) and locomotion subtracted. Any energy surplus contributes to the fish growth. The level and pattern of fish locomotor activity comes as input into the model and normally follows the diurnal cycle (lower at night, higher during the day). An increase in locomotion as a consequence of feed anticipation and active feeding or other factors can also be modelled. Signals from stomach fullness, midgut fullness and the body energy level (= rate of energy input – rate of energy used) combine to determine the level of appetite using a “winner takes all” mechanism, implicating competition between the three neural circuits (but at stomach component has priority and wins at high stomach fullness, avoiding stomach overflow). The effects of stomach and midgut are anorexigenic, acting to suppress the appetite at high levels of fullness. The last, but strong, suppressive feedback to the appetite comes from stress, which has a prolonged anorexigenic effect, adds to the energetic costs (allostatic load) and can reduce locomotor activity. Finally, the level of appetite determines if the next food item (pellet) is consumed at the next time step cycle. The model works as a loop over the predefined maximum number time steps with possible dynamic adjustment of the parameters (e.g. feed input) that provides data assimilation option.

In absence of good quantitative theory, it may be difficult to develop reasonable equations for some subprocesses described by the model. In such cases, we used a nonparametric, data-driven approach: instead of a mathematical equation, we used interpolation over an empirically defined grid points using cubic splines (Knott, 2000; Schwartz, 2008). Cubic splines then provide a smooth line drawn over the (small number of) grid points so all intermediate values are easy to calculate. This allows encoding any empirical pattern even in absence of a specific theory or mathematical model. The grid for interpolation could be based on either literature data (e.g. decoding a published plot) or data from experimental trials.

This makes the model significantly dependent on the accuracy of the empirical data: if the data are imprecise or biased, the model credibility is compromised. However, there seem to be no feasible

alternative in absence of good theory with rigorous mathematical equations. One can use a regression-based empirical equation, but it is also limited by the data quality. Furthermore, parametric regression has an additional issue: the process is described by an equation and this equation is correctly specified. This may be a challenging task for non-linear processes affected by many complex feedback loops. Nonparametric regression such as local kernel-based smoothing (Eubank, 1999; Härdle, 1990) is a feasible statistical alternative that can help in inferring the interpolation grid (conditional expectation of Y given X , rather than formula fitting). Another simpler method is to base the grid on average values that come from a factorial experiment. In either case, interpolation-based parametrization for an empirical pattern seems to be a simple and practical approach that requires only an array of data points (with confidence area indicating uncertainty). Optimization then can use interpolation-based (Brent, 1973) or other derivative-free (Audet and Hare, 2017) methods. Such a locally black-box approach still holds the advantages over the global black-box methods like ML because it represents causal mechanisms and pathways that control the feeding and digestion process. Therefore, integrating empirical model components into mechanistic models may provide a solution to the “mechanistic versus empirical” dilemma (Poppi, 2008): mechanistic models advance our understanding while empirical provide for more precise prediction within the limits of their calibration data. We can hope for more sufficient prediction through better understanding, especially in absence of formal account and outside of the available data.

Details of the model

In the following test, we provide a description of the model components following the sequence of processes and units as in the above *Model overview* section. The input parameters of the model are given in Table 1.

Table 1. Main input parameters of the FishMet model

Environment:

- Temperature, °C

Fish characteristics:

- Fish body mass at the start of the simulation, g
- Stomach mass equivalent of filling capacity, g
- Midgut mass equivalent of filling capacity, g

Stomach:

- Ingestion delay (time to complete the water uptake), s
- Interpolation grid for food chyme, stomach transit pattern
- Stomach emptying grid matrix (fish body mass x temperature)

Midgut:

- Digestion delay: time to the start of the absorption process in the midgut, min
- Michaelis-Menten food absorption parameters for midgut (r and K)
- Maximum residence time of a chyme particle in midgut, min

Appetite:

- Parameters of the logistic functions describing appetite components in stomach and midgut.
- Parameters of the logistic function describing energy component of appetite

Energy budget:

- Interpolation grid setting how basal (standard) metabolic rate (SMR) depends on the temperature
- Branchial and urinary nitrogen excretion rate, $\mu\text{mol g}^{-1} \text{h}^{-1}$
- Parameters defining the specific dynamic action (SDA), maximum absorption rate and SMR scaling factor
- Average locomotor activity (day, night, hunger-related increment, standard length per (SL) per s)

Food characteristics

- Dry mass of the feed item (pellet), g
- Gross energy content of the feed, MJ/kg
- Digestibility: maximum absorption ratio in the mid-gut, relative to the dry mass of food
- Water uptake relative to the initial dry food item mass
- Water uptake in stomach, logistic function parameters

Food scheduling

- Food input rate during a meal s^{-1}
 - Feeding schedule (time-based Boolean vector)
-

Feed protocol. The feeding protocol is defined by a boolean vector that describes whether the food is provided during a specific time step (“True”) or not provided (“False”). Therefore, any arbitrary vector can be defined by loading data from a file or generating data based on a static rule.

Decision to eat. The fish is assumed to perceive every feed item and makes decision to eat it with the probability corresponding to its appetite. All ignored food items are lost and contribute to the food waste. The part of the model describing the decision to eat is based on a significant oversimplification: we assume that the fish easily locates all pellets. This could occur because the visibility conditions are perfect, the fish have learned the feeding location and signals associated with feed dispenser while and competition and social interference is low. A more complex implementation will be needed in the future, e.g. including spatial distribution of the feeder and pellets (e.g. Alver et al., 2016; Takahashi and Komeyama, 2023), visual perception range and light characteristics of the environment (e.g. Aksnes and Utne, 1997) as well as social effects.

Processing food items in the stomach. The fate of each food item (pellet) i consumed by the fish is followed throughout the whole digestion process. The time elapsed since the food item i was consumed (food item residence time) is denoted as T_i . The period that a food item i is processed in the stomach can be divided into two unequal parts: (a) water uptake and (b) subsequent slow

transfer to midgut. Thus, the part of the mass of the i th food (chyme) item in the stomach c_i depends on its residence time T_i and is calculated as follows. First, during water uptake period $T_i < \delta_i$, c_i increases (without changing the energetic value) up to the maximum value c_{max} following the logistic equation (1) where a and r are the input logistic function parameters:

$$c_i = c_0 + \frac{c_{max} - c_0}{1 + a \times e^{-r \times T_i}} \quad (1)$$

Second, following the food item residence time $T_i \geq \delta_i$, the feed chyme particle mass c_i slowly transitions to midgut as defined by (2). Letting $I(T_n, R_n, T)$ denote the proportion of c_{max} remaining in the stomach at the time T defined by a cubic spline interpolation (the interpolant I monotonously and nearly asymptotically decreases as a function of time and is based on a parameter grid (T_n, R_n)), the portion of the mass c_i still residing in the stomach at $T_i - \delta_i$ reduces from the largest value c_{max} as

$$c_i = c_{max} \times I(T_n, R_n, T_i - \delta_i) \quad (2)$$

Thus, the resulting pattern of food mass change in the stomach has the form illustrated by Figure 2.

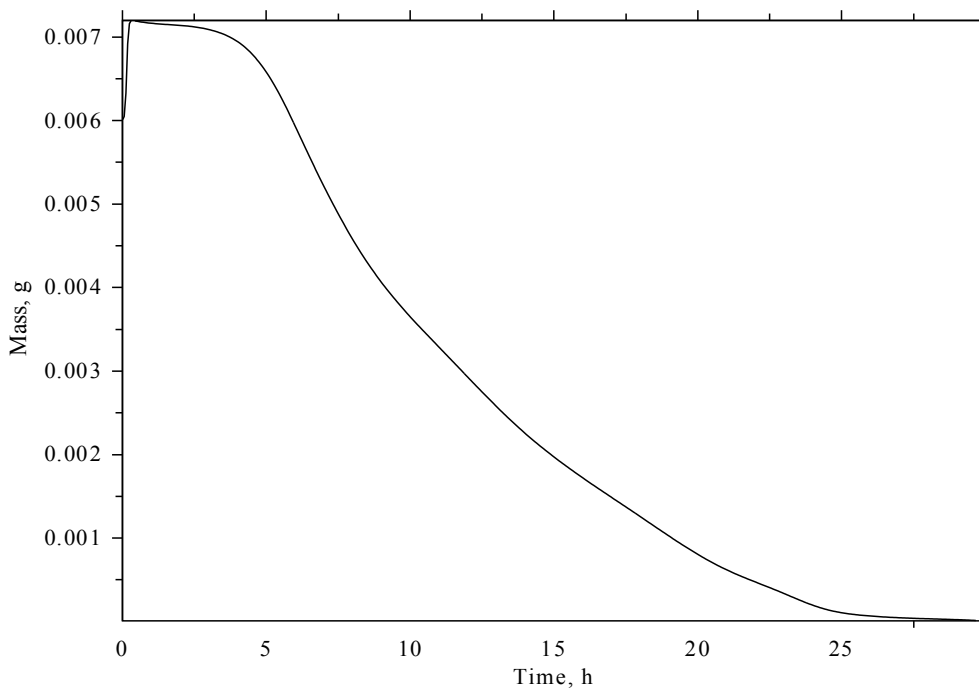


Figure 2: An example of stomach transport pattern based on cubic spline approximation with empirically recorded data grid. The mass scaling corresponds to a single food pellet. Note that the initial increase of the food item mass represents the water uptake.

The overall pattern of food transport within the stomach defined by the grid vectors T_n and R_n is further adjusted for the fish body mass and temperature. This adjustment is nonparametric. It is defined by spline interpolation over two dimensions based on the stomach emptying grid matrix $T_{S=0}$ that reflects experimental (or published) data on stomach emptying. The $T_{S=0}$ matrix determines the empirical values of time needed to empty stomach of fish for combinations of n levels of temperature and m levels of body mass:

$$T_{S=0} = \begin{bmatrix} T_{S=0}(1, 1) & \cdots & T_{S=0}(1, n) \\ \vdots & \ddots & \vdots \\ T_{S=0}(m, 1) & \cdots & T_{S=0}(m, n) \end{bmatrix}$$

The adjustment is based on linear rescaling via spline interpolation over the two dimensions (m and n) using the emptying time as the reference. This effectively “stretches” or “shrinks” the time dimension of the adjusted stomach pattern for the given fish mass and temperature. A drawback of this method is that the same isometric pattern, determined by $I(T_n, R_n, T)$, is assumed for all temperatures and fish body sizes, which is unrealistic. But it is based completely on empirical values and can be used in absence of any theoretical assumptions underlying the various complex effects of temperature or body mass on stomach retention, chyme transport and emptying time.

There can be many factors that can affect the transition of the food chyme through the stomach, including not only temperature, but also oxygen, nutritional content, pellet size and other physical characteristics e.g hardness (Bogevik et al., 2021). There is no general theory that can provide equations accounting for these multiple factors and their interactions. However, parametrization based on empirically obtained interpolation data array seem to provide a simple, flexible and practical solution because it can be easily adjusted based on experimental data. If more resources are available, a tracer-based recalibration experiment can be conducted to obtain the whole stomach transit pattern data with the best available precision. Alternatively, a simpler trial can be conducted to determine only the stomach emptying time; then the interpolation array can then be adjusted proportionally to fit this updated emptying duration.

Digestion in the midgut. As the pellets transition from the stomach, respective proportion of their mass appears and then increases in the midgut by a value of Δc_i . Then, the digestion process starts. There is a digestion delay δ_d between the moment a food item occurs in the midgut and its absorption process commences. In the absorption process, a proportion of the mass of each food item in the mid-gut is subtracted at each time step following the equation (3), letting r_{max} and K

denote the Michaelis-Menten equation parameters: the maximum rate and the half-rate constant (Srinivasan, 2022). $\sum c_i$ is the total mass of food chyme in the midgut.

$$c_{i+1} = c_i - c_i \frac{r_{max} \sum c_i}{K + \sum c_i} \quad (3)$$

This models an overall mass-dependent digestive reaction process assuming that accumulation of food chyme stimulates the release of enzymes that in turn facilitate absorption rate until the asymptotic maximum K is achieved. Temperature effect is introduced through an adjustment of the r_{max} parameter through spline approximation over a predefined interpolation grid matrix of adjustment factor for a set of specific temperatures (based on empirical data). We therefore assume that temperature affects the maximum absorption rate. The absorbed amount of the food mass contributes to the energy balance and growth of the fish. There is an upper limit on how much mass can be absorbed using this mechanism, defined by digestibility A . Also, there is a maximum time limit M_{max} for a food item staying in the midgut.

Evacuation. Finally, food items that has reached the maximum absorption degree and residing in the midgut for more then M_{max} are evacuated.

Energy budget. In the model, we follow the standard energy partitioning scheme (Bureau et al., 2002; Bureau and Hua, 2008) where overall intake of energy (IE) is divided into digestible energy (DE) and recovered energy (RE), and further to basal metabolism (HeE), voluntary activity (HjE), heat increment of feeding (HiE), branchial and urine energy ($ZE+UE$), and fecal energy (FE) expenditures. FE in the model was accounted for by the digestibility coefficient (maximum absorption ratio relative to dry mass of the feed, A), so digestible energy $DE = IE - FE$ was assumed to be $DE = IE \times A$ ($A < 1.0$). Then recovered energy RE is defined by the equation (4):

$$RE = DE - (ZE + UE) - HiE - HeE - HjE \quad (4)$$

We assume that all the recovered energy directly contributes to the fish growth that may include deposition in adipose tissue, which seems a sensible approximation for intensely growing and non-reproducing juveniles.

The energy budget of the fish is recalculated at each time step i based on the energy intake from absorption $F_i(\Delta a)$. The feed gross energy content was set to E_G (set to 23.0 kJ/g), but this will obviously depend on the diet. The energy content (kJ) of the feed mass Δa (g) given digestibility A can be calculated as

$$F(\Delta a) = A \times E_G \Delta a$$

The overall energy balance of the fish is then updated according to equation (5), based on the general partitioning given in (4). We denote E_i the energy balance of the fish at step i , $F_i(\Delta a)$ the energy intake from food absorption Δa at step i , E_{UE+ZE} the rate of branchial and urine (ZE+UE) energy loss (s^{-1}), E_{SDA} the specific dynamic action equivalent to HiE , E_{SMR} the energetic equivalent of the basal metabolism HeE (standard metabolic rate, SMR, s^{-1}) and E_{AMR} the energetic equivalent of the voluntary activity HjE (active metabolic rate AMR, s^{-1}).

$$E_i = E_{i-1} + F_i(\Delta a) - E_{UE+ZE} - E_{SDA} - E_{SMR} - E_{AMR} \quad (5)$$

For model parametrisation, E_{UE+ZE} is calculated from the rate of branchial and urinary nitrogen excretion (rescaled to s^{-1}) as a fixed input parameter. This is usually determined experimentally from the difference between digestible nitrogen intake and its branchial and urinary loss (Bureau et al., 2002; Saravanan et al., 2012). We assume that one gram of excreted nitrogen is equivalent to 24.85 kJ of energy expenditure (Saravanan et al., 2012).

The specific dynamic action SDA (energy equivalent of HiE) represents the extra metabolic cost associated with ingestion and digestion of the food that is reflected in a postprandial increase of oxygen consumption (Chabot et al., 2016; McCue, 2006; Secor, 2009). We assume that digestion (absorption and immediate post-absorption metabolic effects) is far the largest determinant, so E_{SDA} is defined by linear scaling of the basal metabolic rate E_{SMR} as a function of the absorption rate $(a_t - a_{t-1})/\Delta t$:

$$E_{SDA} = E_{SMR} \times k \frac{a_t - a_{t-1}}{\Delta t}$$

The scaling coefficient k is back calculated from the input parameters that define the expected peak absorption rate and the associated increment factor for E_{SMR} . (e.g. 2.0 if E_{SDA} is equal to double of E_{SMR} at the peak absorption rate). We believe that such parametrization is sufficiently simple and practical first approximation in view of lacking mathematical theory and the existing uncertainties and debates regarding the mechanisms and measurement of SDA (Goodrich et al., 2024; Secor, 2009). Our definition of peak SDA in terms of SMR scaling agrees with the pattern (close match between the increases of peak SDA and SMR) observed in the rainbow trout (Adams et al., 2022). Nonetheless, the model is a significant simplification: accounting for the major bioenergetic effect, it lacks anticipatory, cognitive, ingestion-related effects and delayed post-absorption effects (e.g. protein synthesis taking time). Yet, it results in a peak magnitude and a time course (see Figure 3)

similar to the commonly observed pattern (Chabot et al., 2016; McCue, 2006; Secor, 2009). The largest difference is that our model includes only the strongest factor linked with nutrient absorption. Hence, it does not represent slow continuous build-up of oxygen uptake starting much earlier with the onset of eating and decaying exponentially during a longer time post-absorption.

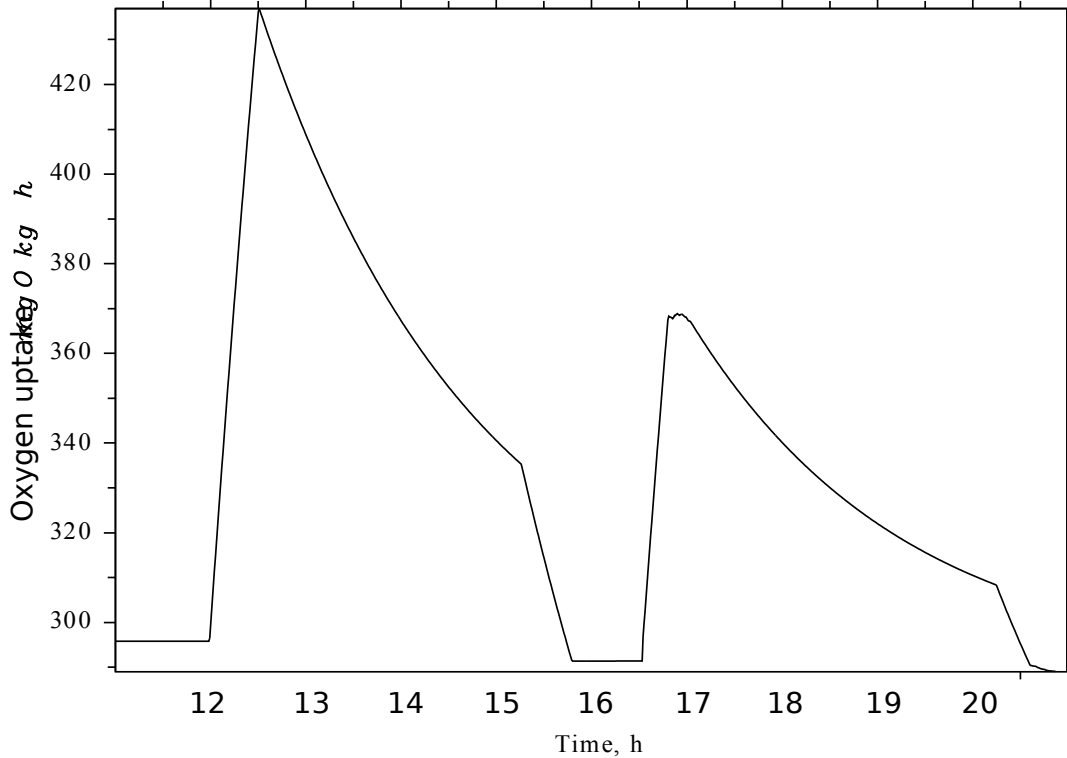


Figure 3: An example of SDA pattern based on simulation of the digestion of two meals given to a rainbow trout with mass 100 g at 16°C. The time is in hours after the first meal.

The basal metabolism, SMR, in the rainbow trout is based on the plot data from Evans (Evans, 1990, Figure 9), that were deciphered to produce the grid arrays for cubic spline interpolation to allow recalculation of intermediate values for the model.

It is assumed that fish locomotion has two major components: baseline activity U_b dependent on the diurnal cycle and an increased activity during feeding U_a . We also assumed that appetite tends to linearly increase activity. The active metabolic rate (AMR) for the Atlantic salmon is defined by the equation (6) based on (Grøttum and Sigholt, 1998), letting M the fish mass, t temperature and U average swimming speed:

$$E_{AMR} = 61.6 \times M^{-0.33} \times 1.03^t \times 1.79^U \quad (6)$$

The values calculated using this equation numerically agree with those presented for rainbow trout by (Evans, 1990). As a first approximation we used the equation (6) for both species.

Appetite. The level of appetite (A) determines the probability that the modelled fish makes the decision to consume specific feed item. In the current model version, there are three factors determining the fish appetite: (a) stomach fullness, (b) midgut fullness and (c) overall energy balance increment/decrement. Respectively, there are three appetite components: the stomach appetite component α_s , energy balance component, α_E and the midgut component, α_m . The stomach and midgut appetite components are calculated based on the logistic equation (7) denoting m the relative stomach (or midgut) filling and a and r logistic parameters:

$$1 - \frac{1}{1 + a \cdot e^{-r \cdot m}} \quad (7)$$

The energy appetite component is defined similarly, using this equation (8), letting Δ_E the difference between the two consecutive average energy budget values in units of the SMR depicting the direction and value of energy accumulation, while r and b logistic parameters:

$$\frac{1}{1 + e^{-r_E \cdot (-\Delta_E - b_E)}} \quad (8)$$

Then, the overall appetite is determined in such a way that the stomach component α_s exclusively determines it at high stomach fullness (i.e. stomach appetite component below parameter threshold $\alpha_s < \alpha_{min}$) to avoid stomach overfilling:

$$A = \begin{cases} \alpha_s, \alpha_s < \alpha_{min} \\ \max(\alpha_s, \alpha_m, \alpha_E) \end{cases}$$

This mimics a “winner takes all” mechanism that could occur on the basis of lateral inhibition of the α_s , α_E and α_m neural signals. We tried a few alternative mechanisms (e.g. additive and multiplicative) but the “winner takes all” showed the most stable appetite control without significant splashes. There is currently no definite theory on how the various signalling feedback components of appetite combine to produce its final subjective value in fish. But recent neurobiological research points to the importance of mutually inhibitory interactions between discrete circuits (Wee et al., 2019).

Stress. In absence of good quantitative theory, we do not implement any specific mechanism or mathematical equations describing the effect of everyday (or chronic) stress. But acute stress comes to the model as a singular interruption defined by a set of external parameters. We assume that stress exerts three effects: (a) significantly suppresses fish appetite (contributing to reduced growth); (b) adds allostatic energetic cost and (c) can also suppress background locomotor activity

(e.g. Espe et al., 2021; Folkedal et al., 2012; Höglund et al., 2022; Pankhurst et al., 2008). These effects are implemented as weighting function σ_t (stress factor) that depends on the time t elapsed since the stress event occurred. We assume that the stress interruption creates a sudden change and then the respective value slowly returns to the normal over time, up to several days. The stress effect on appetite assumes its complete suppression and is described by

$$A_{stress} = A - A\sigma_t$$

while stress-related increase of the resting metabolic rate is given by equation (9), where μ_{max} defines the maximum allostatic load (e.g. when $\mu_{max} = 0.5$, stress raises the resting metabolic rate by 50% at maximum).

$$E_{stress} = E_{SMR} + E_{SMR} \times \mu_{max}\sigma_t \quad (9)$$

Finally, the suppressing effect of stress on the baseline locomotion, assuming the maximum extent of suppression is bounded to u_{max} , is defined as

$$U_{stress} = U_b - U_b \times u_{max}\sigma_t$$

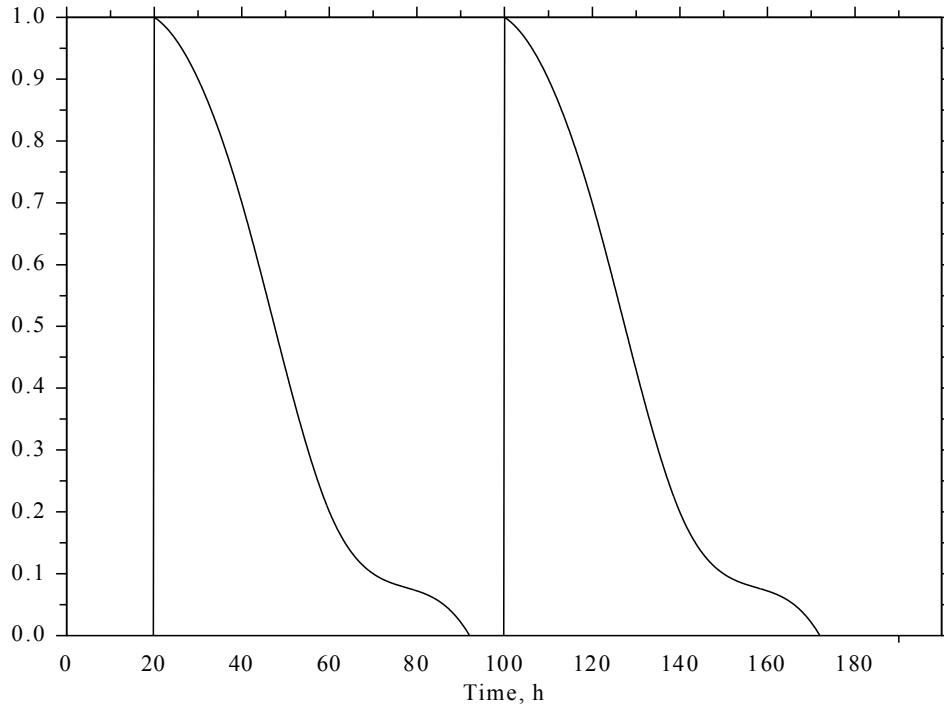


Figure 4: An example of the stress factor σ_t with two stress events at 20 and 100 hours of simulation.

Our implementation of σ_t is based on cubic spline interpolation over a time grid that provides flexibility but requires empirical data for parametrisation. Figure 4 shows an example pattern of the stress factor σ_t for two stressful events.

Overall, this allows to model a variety of stress effects, strong and mild. However, parametrisation should be done separately in each case or at least for major classes of stress (e.g. delousing, cage cleaning etc.). The experimental data that need to be collected in such cases are the peak extent and the time-dependent pattern. For example, the largest relative change of oxygen consumption in a respirometer will provide the μ_{max} parameter while the maximum reduction of locomotion, u_{max} . Given the generic description in the model, it is difficult to provide general values applicable to all cases in advance. For a very preliminary orientation, a mild stressor such as bare environment without shelter can increase the resting metabolic rate to 30% giving $\mu_{max} = 0.3$ in the Atlantic salmon (Millidine et al., 2006).

Software design and implementation

Software architecture and implementation. We developed FishMet as a software program using the following design principles: (1) A computation intensive stochastic simulation program that

should be programmed using a high-performance compiled language, preferably also implementing parallel execution. (2) It should have minimum software dependencies for both the developer and user (e.g. not require installing a proprietary calculation platform, language interpreter or third-party libraries). (3) The resulting program should be portable across computing platforms, operating systems and environments. (4) It should use open standards tools and open-source components, not depend on a single proprietary technology, avoiding vendor lock-in. (5) The modelling program should include an easy to use graphical interface, facilitating its potential use by non-programmers on a typical PC. (6) But it must nonetheless be itself programmable, enabling to run various batch scenarios, both on a PC and server. (7) As a complex software, FishMet should be thoroughly documented.

To meet these design requirements, we programmed FishMet in modular, object-oriented style in Fortran 2003-2008 (Adams et al., 2009; Brainerd, 2015). Fortran is portable, works on nearly any platform and operating system, there are several alternative high-quality compilers, both free and commercial. Fortran compilers produce highly optimized machine instructions that ensures very fast computation; it also natively support several parallel programming paradigms. This makes Fortran the preferred language for high performance scientific computing (Loh, 2010; Ray, 2020; it was recently gaining higher popularity, see TIOBE language popularity index for June 2024, <https://www.tiobe.com/tiobe-index/>). The system includes several modules for the computational core, input, output, user interface and graphics. Program execution is controlled through two different interface modules: the graphical user interface and console interface, implementing a simple command processor. The default parameters of the model are obtained from a plain-text configuration file that uses the same notation as the command processor. A portable graphic library can be optionally linked to both interface modules. The source code follows the literate programming paradigm (Knuth, 1992) and includes embedded developer documentation in Doxygen (<https://www.doxygen.nl>) format. The build system automatically generates a set of developer documents in pdf and html.

Verification and validation. *Verification* ensures that the conceptual model is correctly implemented in the software code and runs as intended while *validation* involves model assumptions—that they are correct with reference to the real world system being modelled (Oberkampf and Roy, 2010). For FishMet, verification is conducted by build-time debug mode that outputs much additional information and the use of software tests with pFUnit testing framework (Rilee and Clune, 2014), <https://github.com/Goddard-Fortran-Ecosystem/pFUnit>). Validation of the

model is based on comparison of simulated results with fish trials (see Testing the FishMet model). At this stage of the model development, we were largely concerned in reproducing overall patterns rather than precise numerical fit, which will require more experimental trials under a range of conditions. This amounts to pattern-oriented corroboration approach (Railsback and Harvey, 2020).

Prototype digital twin server system. Developing a simulation model alone is not sufficient for a digital twin usable in the industry settings. Proper digital twin requires a dedicated and scalable server-based infrastructure with interfaces for automatic data acquisition, assimilation, model control, execution and export of modelling outputs (National Academies of Sciences, Engineering, and Medicine, 2024; Thelen et al., 2022a). This should ensure on-demand invocation of the digital twin simulation with constant data access over a standard application programming interface (API). Then, the cloud-based farm steering and decision support system will trigger the digital twin simulator whenever model-based prediction is required, providing all the necessary data and control variables (Figure 5).

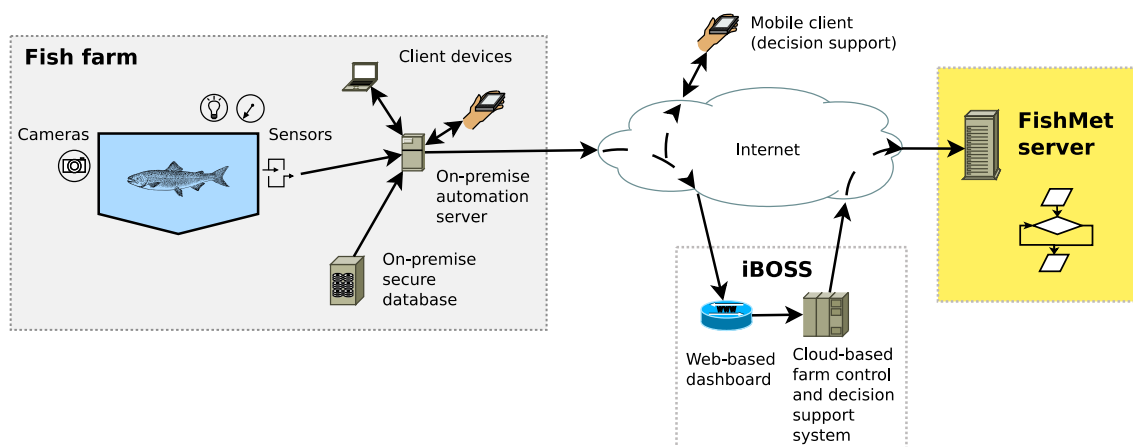


Figure 5: An overview of a possible cloud-based decision support system for a fish farm. The diagram uses iBOSS as an example decision-support system and dashboard, which connects to the FishMet server over a network-based interface.

We have developed a prototype server-based system that works in this way. This system has been integrated and tested with the Biology Online Steering System (iBOSS, see Lafont et al., 2020). The system includes a cloud-based virtual server running Debian Linux on an IaaS¹ provider. It includes a web server and a set of components ensuring secure authentication, generation of FishMet batch control script, model execution triggering, data access etc. We have also developed an application programming interface (API) based on open standards for model control and data exchange. The API is based on JSON data (<https://www.json.org>) over the https protocol.

1 Infrastructure as a Server is a cloud computing model centred around on-demand scalable access to virtualised server resources, including CPU, storage, networking etc.

The system works as follows. First, feeding schedule data for use as input to the FishMet model can be obtained directly from the feeder (raw data as timestamps when the feeder is turned on and off for retrospective analysis or ongoing feeding control) or produced by the steering system (e.g. automatically generated to a schedule being modelled) and then pushed to the FishMet server over the https protocol. Second, the parameters of the model (that differ from the default values, defaults are kept on server) are pushed to the FishMet server in the same way. Sending the JSON model parameter data triggers model execution via the inotify mechanism of the Linux kernel, that initiates data conversion to the FishMet format, auto-generation of the execution script, running the model job and saving data to the server storage. Finally, the farm steering system retrieves the model results in CSV format to be utilized for end-user decision support. The interactions between the farm steering system and the FishMet server are shown in Figure 6.

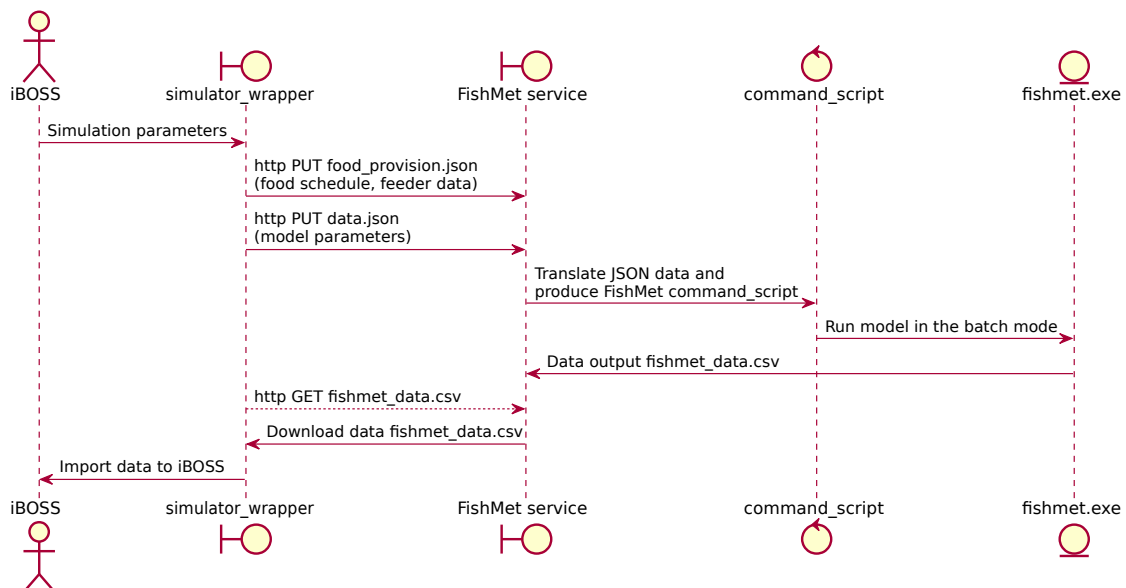


Figure 6: Interaction diagram depicting the interaction between the fish farm steering control server and the FishMet server. iBOSS system is used as the steering system.

Source code. The Fortran source code for the basic model algorithm is published as open source at <https://git.app.uib.no/Sergey.Budaev/fishmet.git>.

Testing the FishMet model

Stomach and gut filling in rainbow trout

Methods. To provide a preliminary parametrisation and testing of the model, we used the data available from a gut transit experiment with rainbow trout at three different temperatures ($16\pm 1^\circ\text{C}$, $18\pm 1^\circ\text{C}$ and $20\pm 1^\circ\text{C}$) conducted at the AquaBioTech Group facility (Rønnestad et al.,

unpublished). Due to the nature of the available data, we focus on the stomach and gut filling and passage patterns. The experiment was conducted as follows. First, a total of 200 fish with the average mass 127.9 g (range 76-194 g) were placed in a 650L cultivation tank and acclimated for one week to the test temperature and hand-fed at apparent satiation with a control diet. Two experimental diets (YtOX and CTRL) were formulated, to be isonitrogenous, isolipidic and isoenergetic. Second, on the sampling day, fish were fed twice until apparent satiation with YtOX at 9:00 a.m. and with CTRL at 2:00 p.m. The YtOX diet was formulated with a 0.2% inclusion of Yttrium oxide, an inert marker that can be detected in faeces and often used for digestibility trials (Sørensen et al., 2002). The sampling was performed at three different time frames: 20 min, 1 h and 2h after feeding. A total of 6 fish at each sampling point were netted and killed with an overdose of tricaine methanesulfonate (MS-222), followed by biometrics measurement (weight, total and fork length) and dissection. The gut was split in 3 compartments: (a) stomach; (b) anterior plus medium intestine (midgut) and (c) posterior intestine, with a surgical ligature to avoid any loss or migration of material. Each region was gently squeezed to remove the content, subsequently weighed and stored in a separate container. Third, 24h after the feeding and sampling, 6 fish were euthanised with overdose of MS-222 before feeding following the same procedure. Samples were stored at -20 degree until further analysis. At the end of each experiment fish were replaced in the cultivation tank, re-establishing the original number and the new temperature set to start the acclimation period of one week. Each sample was dried for 24h in an oven at 60 °C and weighed.

Parameters of the model were based on the published data for stomach size (Pirhonen and Koskela, 2005; Salgado et al., 2018), stomach emptying, (Grove et al., 1978) and energetics (Evans, 1990; Grøttum and Sigholt, 1998; Ohlberger et al., 2005) that were then adjusted based on the trial data at 16°C to minimize average squared differences between the observed means and the simulated values. Then, we tested how well these parameters can represent the trial data at 18°C and 20°C. However, uncontrolled feeding history prior to the trials, cross-sectional design, small number of sampling points, small sample sizes and high variability among the fish made it difficult to test the pattern at different temperatures formally. Hence, these results are considered as a first approximation, waiting for more detailed experiments.

Results and discussion. The model fitted rather well the stomach filling data observed at 16°C (Figure 7). Linear models of the form $M = E + T$, where M is the simulation-based stomach or gut fullness, E is the stomach or midgut data from the experiment and T is temperature (16, 18 or 20°C), were fitted to check the agreement between the simulation and experiment. There was significant

effects for both stomach ($t_{106}=4.2$, $p<0.001$, Cohen $d=0.38$) and midgut ($t_{115}=3.5$, $p<0.001$, Cohen $d=0.32$), but no significant effects of the temperature in either case ($p>0.1$). Some discrepancies between model and the trial data were visible at 18°C and 20°C, especially at the first meal (9:00). Midgut filling had a concordant pattern, but trial data reveal a higher rate of initial gut transfer not accounted for by the model, especially at the highest temperature (hence effect size d is lower). The experimental data show that the average mass of the chyme rises simultaneously both in stomach and midgut which is difficult to explain assuming digestion is a slow sequential process. This might be an artefact of some chyme possibly remaining from pre-trial meals. However, rainbow trout is also known to be a voracious feeder and will often feed aggressively when food is plentiful. It may therefore be possible that some individuals have continued to ingest feed despite that stomach have been filled to max capacity and that transfer to midgut have started early. But we believe that the major factor is the cross-sectional design in our study where each data point represented an individual fish with different size and mass, as well as stomach and midgut filling used to calculate the transfer rate. Hence the stomach and gut data likely include several confounding factors. A longitudinal experiment recording the stomach and gut contents in the same individuals over time would be a more appropriate but is technically hardly possible, particularly due to the stress effects of repeated sampling. Given the design limitation, it is difficult to ensure sufficient precision of the individual data. Overall, however, the pattern of stomach filling seems to show a good agreement with the trial data (see Figure 7). Importantly, a model calibrated at 16°C predicts stomach emptying rather well at 18°C and 20°C. In spite of this, further work may be required to adjust the midgut passage and absorption part of model. To do this, an experiment with more sampling points to cover the digestion process more evenly over time would be helpful.

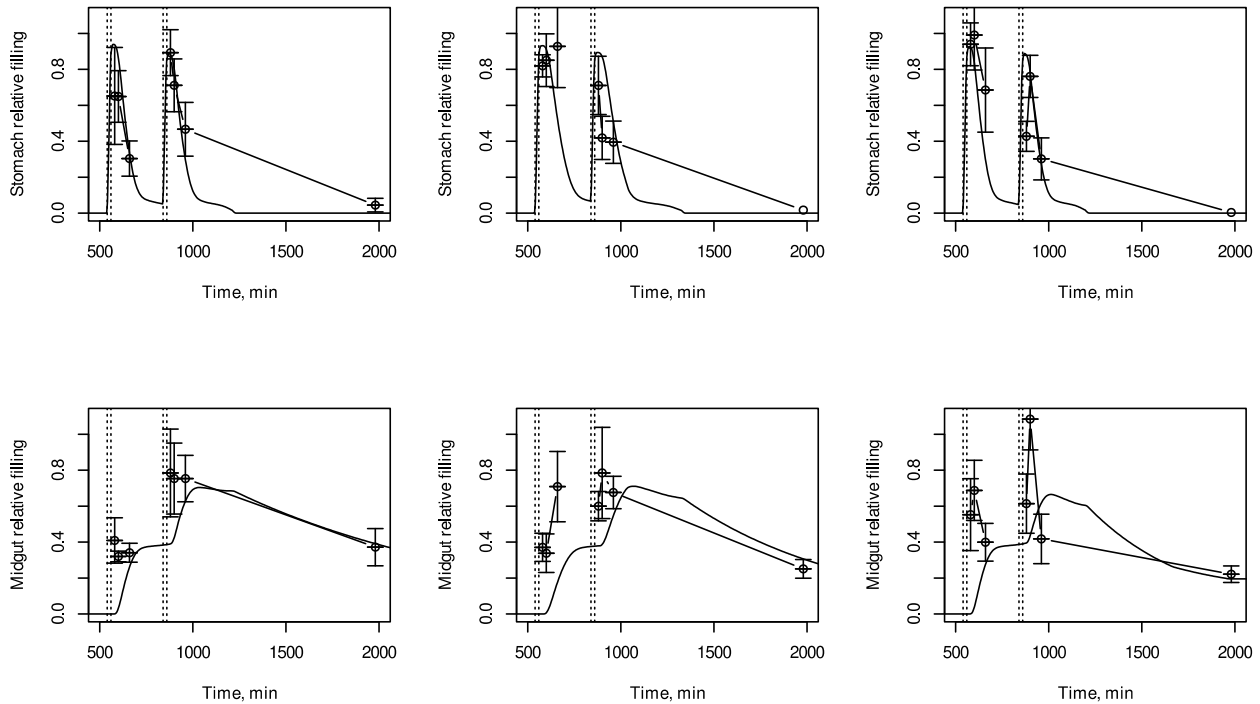


Figure 7: Comparison of the FishMet-based simulation of stomach and midgut filling with trial data. Vertical dotted lines depict meals. Trial data include mean \pm std.error. To compare model-based relative filling with the dry weight of the fish gut contents having dissimilar scaling, the plotting values were rescaled as ratios to the average of the maximum observed values (e.g. for an i th point $\frac{c_i}{(1/n) \sum \max(c_1, c_2, \dots, c_i, \dots, c_n)}$) for each temperature group. This assumes that the maximum values observed in trial correspond to the maximum filling (that is reasonable given the unrestricted meals) and diminished the effect of body mass variability across the samples. Vertical dotted lines show start and end of meals.

Feed intake over multiple meals in the rainbow trout

Methods. To test how the FishMet model predict the feed intake in the rainbow trout in a complex feeding schedule over several meals, we used the data set generated in trials investigating the relationships between the time course of stomach fullness and feeding behaviour (Panasiak, 2021). The trials were conducted in the RAS at the AquaBioTech testing facility (see Panasiak, 2021; Rønnestad et al., 2022 for details). In a series of three experiments, the fish were scheduled from one to three distinct meals consisting of custom diets. In one of the meals in each test the diet was labelled with inert but X-ray opaque soda lime glass Ballotini beads (0.4-0.6 mm diameter). This allowed to estimate the exact amount of food consumed during a particular meal by taking radiographic images of the fish and counting the beads. There is a strong linear relationship ($r^2 > 0.9$) between the mass of the feed assessed from the bead count and that recovered from the fish digestive system (Panasiak, 2021). In trial 1, the fish were given only one labelled meal until

apparent satiation (20 min) and radiographed 45 min after feeding. In trial 2, the fish were administered an unlabelled diet in the first meal of the day (meal 1). After 6h 45min, they were given the second meal with labelled diet and radiographed 45 min later. In trial 3, the fish were fed an unlabelled meal 1, 3h later unlabelled meal 2 and finally the meal 3 labelled with Ballotini beads 3h 45 min after the meal 2. The fish were radiographed 45 min after the last feeding. All experiments were conducted at 16°C and the fish were never reused. The average body mass of the fish sampled and radiographed in the three experiments was respectively 689.8 g (440-939 g), 838.0 g (614-1038 g) and 797.7 g (516-1028 g). Each sample included 20 individuals; each radiography included two X-ray images. The fish were anaesthetised with MS-222 prior to radiography.

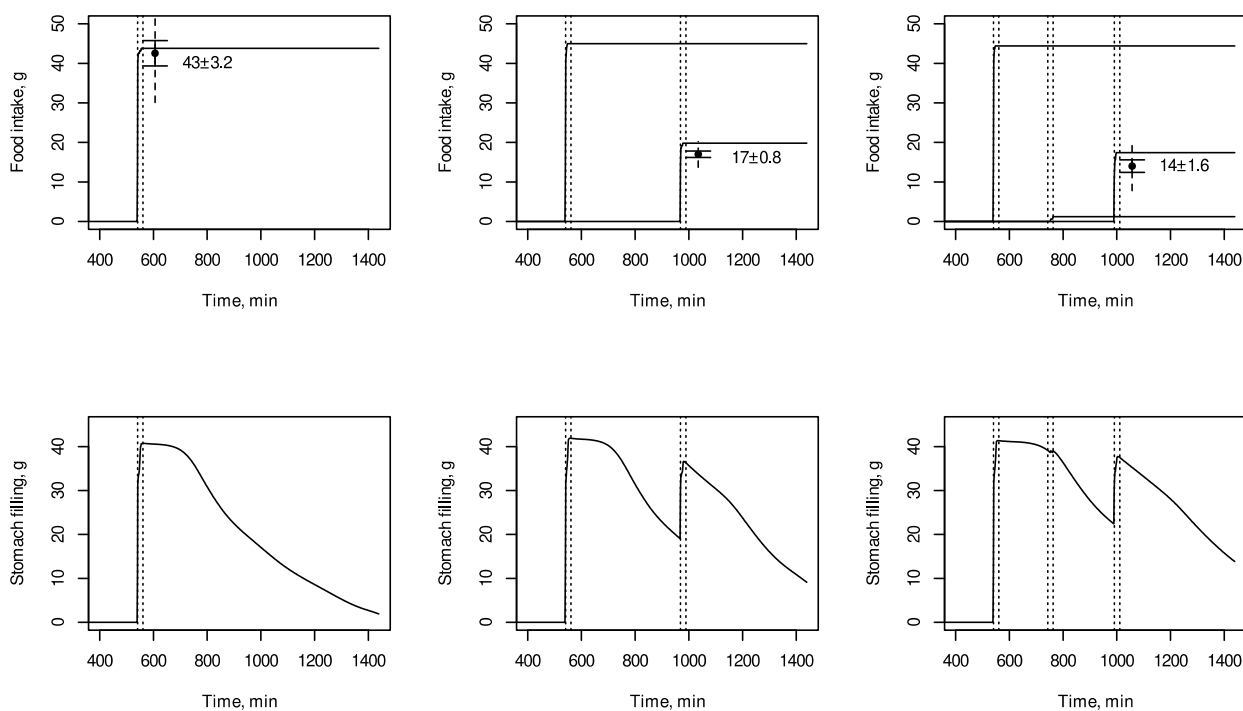


Figure 8: Upper row: cumulative feed intake calculated for each of the three meals in simulations corresponding to the trials 1 to 3. Vertical dotted lines depict meals. The average feed intake assessed from the labelled meal is presented as average \pm and std. error. Dashed whiskers are 99.9% confidence interval. Lower row: the time-based pattern of stomach filling in the simulation experiments.

Three simulation experiments were conducted with the FishMet model using identical temperature, body mass and feeding schedule as in the above three experiments. Then, we calculated the cumulative feed intake in each of the meals. The average mass of the food corresponding to the last labelled meal (calculated from the radiographic data) was then compared with that obtained in the simulation. Additionally, the stomach contents data were plotted for all the meals.

Results. The FishMet model provided realistic estimates—within the 99.9% confidence interval—of the feed intake in the meals corresponding to the labelled food (Figure 8). Furthermore, the stomach filling visualization gives some additional information for understanding of the feed intake and digestion pattern. For example, the small amount of feed ingested in the second meal of the three-meal trial is well accounted for by the still high stomach fullness at this time point.

Pilot scale demonstration of the digital twin prototype in salmon RAS

Methods. The functionality of the prototype digital twin system was tested in a pilot scale demonstration in RAS conducted at the AquaBioTech Group testing facility. Fish were kept in two 650l circular tanks equipped with cameras, software-controlled automatic feeder, water filters, disinfection, protein skimmer under continuous monitoring and data exchange with the iBOSS cloud system (see Cusimano et al., 2024 for more details). A total of 400 fish (initial weight of $13.58 \pm 0.01\text{g}$) were randomly placed in two tanks and fed at 2.22% of live biomass per day with commercial feed (Start alevin, 2mm, Alltech Coppens). The feed was delivered four times per day (09:00, 11:30, 14:00 and 16:00) by automatic feeder in the first tank and by hand in the second. Each feeding event lasted for 15 minutes. Fish were sampled in bulk (100%) every week until the end of the trial; they were not fed 24h before sampling. The data from the feeder were retrieved to the iBOSS cloud and then to the FishMet simulation server. Starting from week 16 (April) 2023, daily simulations were conducted using the actual feeding schedule (timestamps from the feeder and pellet input rate), initial fish mass, and temperature in the tanks. Parametrization of the FishMet were based on the published data for the Atlantic salmon (Aas et al., 2017; Hvas et al., 2020; Mock et al., 2022), with adjustments for the actual RAS environment during the first week (week 15) of the demonstration (average diurnal pattern of swimming speed based on video analysis). Then the FishMet model produced predictions for feed intake and fish growth. Each week, the predictions were compared with the actual fish measurements using the average mass across the two tanks. At the end of the trial period, a single global simulation was conducted using the archived feeder and temperature data along with the starting fish weight. In absence of gut transition data, here we focused on the fish growth, that helped to check the bioenergetic part of the model.

Results. The predictions of the fish growth by the FishMet simulations over the seven weeks of the demonstration were in a good agreement with the fish data (see Figure 9). In particular, the mean absolute percentage error ($MAPE = 1/n \sum |O_i - P_i| / |O_i|$, where O_i is the i s observed and P_i , predicted values) did not exceed 10%. More information is available in (Cusimano et al., 2024).

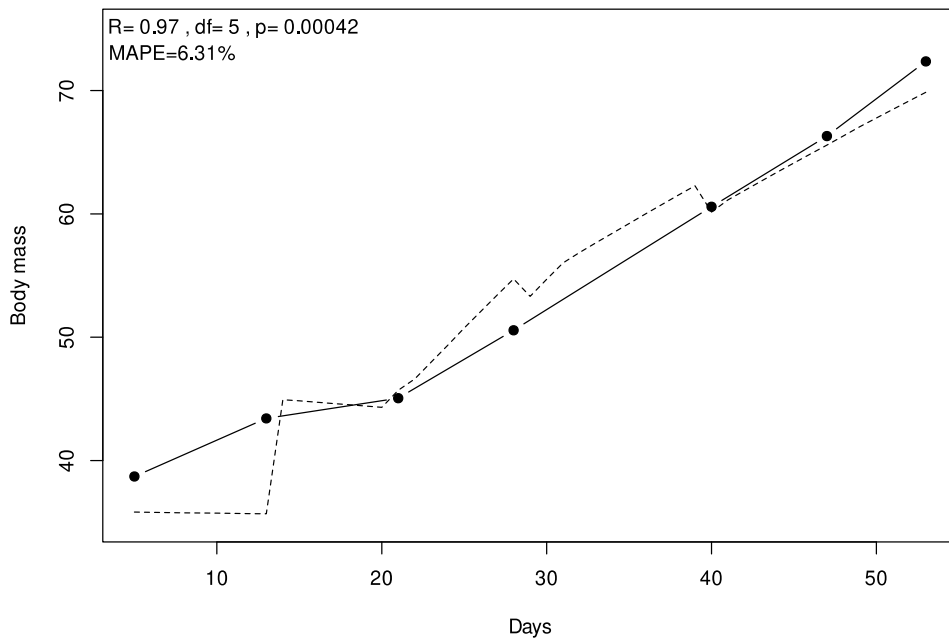


Figure 9: Predicted (dashed line) and observed (average body mass, solid line) body mass of the Atlantic salmon in pilot demonstration trial. Solid line depicts the observed data, dashed line predicted values.

General Discussion

A digital twin model includes representation of the whole process using the currently available general theory. Unlike the standard experimental approach—to split and isolate the organism’s “machinery” into separate components—it works by re-creating, putting elements together, to make the artificial system “run.” We assembled a very schematic simulation of a multicomponent fish and were able to demonstrate that it can run with qualitatively realistic behaviour. This essentially follows the bequeath left by Richard Feynman, a theoretical physicist and Nobel laureate: “What I cannot create, I do not understand” (this was written on the blackboard at the time of his death) (Lupas, 2014; Way, 2017). This “reverse engineering” process relies on the mechanisms and, where possible, equations describing separate subprocesses. Many of them are based on the experimental data. However, some elements of the theoretical puzzle are lacking for a range of reasons. It may be difficult to obtain empirical data, for example. Sometimes we are just overlooking certain questions that emerge only when we try to combine the known elements together. Thus, one benefit of building the holistic digital twin is in identifying the unknowns that we do not yet know, thereby

turning them into “knows unknowns” (Budaev et al., 2024). This results in a better integrative theory.

Furthermore, a digital twin model could make it possible to assess aspects that are difficult or impossible to measure. Experiments to establish the rate and pattern of gut transit have been an important area in aquaculture research due to their crucial role for optimizing feeding (Bogevik et al., 2021; Mock et al., 2022; Volkoff and Rønnestad, 2020). However, establishing the mass transit of the digesta within the gastrointestinal system is difficult. Several experimental methods have been developed, such as tracers and Ballotini glass beads, but the information that can be obtained is nevertheless limited. A longitudinal design with real-time *in vivo* recording at high resolution is hardly possible. But cross-sectional data are often difficult to analyse because of variability in the fish body size and multiple factors affecting the food intake. The simulation experiments (Figures 7 and 8) provide a high resolution “window” into the fish gut over a potentially unlimited time scale. Furthermore, modelling the feedback loops that control the fish appetite and food intake, even with a simple bioenergetic model, would make it possible to predict feed intake, growth and feed waste in a variable industrial setting. Unlike the existing feeding tables and static equation-based models, such prediction is possible for any arbitrary feeding schedule, even if it dynamically changes over time (pellet input rate, pellet size, number and timing of meals, temperature and other factors). Then, one can conduct various “what-if” experiments to optimize feeding for higher efficiency and to develop the best mitigation scenarios for a range of disruptions. Combined with a model of the stress effects on the appetite, this would potentially provide a valuable applied tool.

Even though we have been able to demonstrate the high potential for the digital twin prototype, it remains only the initial step with limited scope and applicability. Further work needs to be done over several directions. First, an extended calibration is needed under a wider range of conditions, especially temperature and a wider range of fish size. Second, while the effect of temperature is included in the model, other important environmental factors are still missing. The most crucial candidate for implementation is the oxygen saturation that is known to affect feed intake and many other physiological characteristics (Magnoni et al., 2018; Remen et al., 2016; Saravanan et al., 2013, 2011). The model predicts oxygen uptake, but still requires extensive testing and calibration. When this is done, oxygen saturation in the environment will be added as an input parameter. The current model is based on the food mass and ignores the macronutrient composition (e.g. protein, lipids, amino acids, fibre) that are also important (Bendiksen et al., 2002; Conde-Sieira and Soengas, 2017; Figueiredo-Silva et al., 2012; Gélineau et al., 2001) as well as the metabolic post-

absorptive handling of nutrients (Soares et al., 2023). Both appetite regulation and bioenergetics include no modulation by the life history stage, including smoltification and reproduction. The appetite is represented as simple probability of feeding decision and considers neither anticipation nor competition with other responses such as fear, exploration or social interactions. There is currently also no account of hedonic regulation of appetite (Campos et al., 2022) and subjective gustatory preferences that are highly characteristics and stable in fish (Kasumyan, 2019; Kasumyan and Døving, 2003). The effect of stress is an extremely simplistic appetite-suppression input to the model. A more advanced model including competition and trade-offs between different motivations and emotions (Budaev et al., 2020; Del Giudice et al., 2018; Taborsky et al., 2022) using the concepts of allostasis (Korte et al., 2007; Sterling, 2012; Tschantz et al., 2022) and predictive regulation (Kristiansen and Fernø, 2020) would make it possible to represent the level of stress as an output of the model. This could further allow to predict the welfare status of the fish (Budaev et al., 2024, 2020).

Individual differences in physiological and behavioural traits are other important factor that needs to be considered (Castanheira et al., 2015; Huntingford and Adams, 2005; Rosenfeld et al., 2020; Takahashi and Komeyama, 2023). The current digital twin models a single fish which is assumed to represent the average for the population. Modelling a population characterised by a statistical distribution of the parameters would provide for more realistic predictions, especially if the social relationships between the fish, dominance relations, interference competition and density-dependent effects are represented. Spatially explicit movement of individually different model agents within the tank or cage is another important area that has attracted interesting studies (Takahashi and Komeyama, 2023). The computational complexity of such multiagent models can be drastically reduced through data-driven surrogate or degradation approaches with machine learning (Thelen et al., 2022a, 2022b). Precise calibration of complex simulation models with unidentifiable parameters can be done using sequential Bayesian designs (Kennedy and O'Hagan, 2001; Sung and Tuo, 2024; Sürer et al., 2024).

Developing larger and more complex digital twin and simulation models, especially if they are scaled up to the level of the whole fish farm (Lan et al., 2022; Peladarinos et al., 2023; Ubina et al., 2023) is a far too complex task for a single team, developer or designer. A monolithic model would simply not scale up (level of whole farm) and down (to more intricate physiological details). Therefore, the concept of distributed simulation and model federation has gained attention in several industries (Topçu et al., 2016) and the military (Tolk, 2012). It involves developing

component-based reusable and interoperable modelling systems that can be freely combined with and plugged into other models using standardised input-output interfaces, software wrappers and libraries. There exist several model federation frameworks, such as the High Level Architecture (HLA) (standardised by IEEE, 2010; Topçu and Oğuztüzün, 2017) and Functional Mock-Up Interface (FMI) (<https://fmi-standard.org/>, maintained by a consortium of companies). The HLA has a long history (particularly in the US Department of Defence, see Tolk, 2012) and is more prominent (Topçu and Oğuztüzün, 2017). The modular object-oriented architecture of the FishMet model fits well with the HLA. For example, the server components have functionality similar to the HLA runtime infrastructure (RTI) providing a mediator that ensures coupling with other components strictly without data storage, as required by the HLA rules (IEEE, 2010). The object model template (OMT) that specifies the data model is part of the FishMet documentation and implemented in the JSON API. If the FishMet is intended to be interoperable with a specific federated application set, it can be adapted to the common federated object model (FOM). The basic management object model (MOM) is described by the interaction diagram (Figure 6). The FMI approach is more tightly linked with software implementation and depends on FMI wrappers. There is no publicly available FMI wrapper for Fortran, but the language is interoperable with C, so an implementation is possible. Alternatively, FishMet can be repackaged as a library callable from Python and then Python FMI tools may be used. Thus, the FishMet model can be integrated into common federated simulation environments with relatively little effort.

The digital twin models are computation-intensive and requires high performance approach to computations, e.g. parallel hardware architectures (especially if a population is modelled). This implicates the requirement to use parallel computing techniques, such as Fortran coarrays (Ray, 2020). Furthermore, possible industrial application of the digital twin should consider the need to temporarily increase the computational resources in situations of higher demand. This can be solved using cloud server systems with dynamic virtual machine scaling. Further, the data assimilation mechanism for the digital twin requires integration with the software controlled automatic feeders by different vendors, a variety of the sensor and IoT systems that are used by the diverse aquaculture industry. Finally, the simulation system should be integrated with the existing and newly developed farm steering and decision support systems. Thus, in addition to further development of the biological models with additional validation and calibration experiments, substantial work must be conducted to develop the simulation infrastructure and especially user interfaces providing simple and efficient user experience for the aquaculture industry. The FishMet

model is just one of the first steps on this exciting avenue towards the next generation digitized precision aquaculture.

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