



Modelling how the physical scale of experimental tanks affects salmon growth performance



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ABSTRACT

In this study, we explored the potential of using mathematical models for studying the effects of physical scale of production units on the growth performance of Atlantic salmon (*Salmo salar* L.). Atlantic salmon are typically produced in large sea cages, but for ethical, practical and economic reasons, most research experiments are performed in tanks or cages of comparatively small volumes, and it is therefore important to consider the representability of small-scale experiments with regard to growth performance. Based on an existing model, we developed a model for estimating the effects of changes in physical scale on salmon growth performance. The model was verified using experimental data obtained from a laboratory study featuring growth experiments in tanks of different sizes, and found able to predict the effects of increasing tank scale. We also used the model in a series of virtual experiment studying how sensitive the scaling effect is towards how (i.e. changing only radius, only depth or both) the volume is scaled. The results from the virtual studies indicate that larger production volumes lead to improved feed ingestion and growth, provided the increase in volume is achieved through horizontal or horizontal plus vertical expansion of the units, but also implies that the nature of the scaling effects depends on other factors such as tank cross section.

1. Introduction

The on-growing phase of modern finfish aquaculture is conducted in either sea-based fish farms or land-based facilities, and standard sea-cages used in the Norwegian salmon industry today typically measure 157 m circumference, and span depths down to 50 m. To sustain a profitable and ethical production, the industry depends on research efforts that contribute to maintaining production efficiency (e.g. Aas et al., 2006), reducing environmental impact (e.g. Bendiksen et al., 2011), and/or ensuring fish welfare (e.g. Oppedal et al., 2011b). This relationship between industry and research is likely to continue in the future, and will be particularly important as the industry expands into more exposed locations (Bjelland et al., 2015), and more extensive use of closed containment systems (e.g. Terjesen et al., 2013; Davidson et al., 2016).

However, the majority of the research efforts aimed at aquaculture are conducted in laboratory facilities that are of substantially smaller physical scales than their industrial counterparts. This raises the

question whether results from laboratory experiments will be directly relevant for industrial production of finfish, or if disparities in physical scale could lead to differences in fish performance (i.e. growth rate, mortality and behaviour). A recent experiment sought to test this for Atlantic salmon by comparing the fish performance observed in a set of different tanks with volumes ranging from 0.9 to 190 m³ (Espmark et al., 2017), using a parallel study conducted in full-scale marine sea-cages (120 m circumference, 30 m depth) as an industrial reference (Føre et al., 2016). To reduce any effects caused by differences in origin or life histories, all tanks and cages in the experiments were stocked with smolt from the same genetic strain and cohort. The experiments lasted 6 months, during which the production environment (i.e. temperature, light, feed type and feeding schedule) in the tanks was adjusted to match those applied and measured in the sea-cages to isolate the effects of scale as much as possible. The main findings in Espmark et al. (2017) indicated that there was a significant difference in fish performance between the different tank sizes, suggesting that scale effects are important to take into account in scientific studies aimed at

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Atlantic salmon farming. Although the growth performance observed in the industrial sea-cages (Føre et al., 2016) compared well with the growth observed in the 3 m³ tanks (Espmark et al., 2017), an outbreak of Pancreas Disease (PD) made a direct comparison between industrial and laboratory scales difficult.

A numerical model able to predict scaling effects in aquaculture would represent a useful supplementary tool to such experiments since numerical simulations allow the effects of scale to be entirely isolated from other factors, which is difficult to achieve in physical experiments. Such models could for instance be used to simulate a particular experiment at several different scales from laboratory to full scale, and thus identify how much it is possible to scale down that experiment and still provide outputs relevant for industrial production. Alternatively, outputs from such simulations could be used to assess how outputs acquired in laboratory scale need to be adjusted to be representative for full scale. Ultimately, this means that models capturing scaling effects on fish performance can contribute to achieving the aims of the 3Rs in animal experimentation by reducing the number of fish used in each experiment (Reduction), reducing the number of physical experiments required (Replacement) and providing better planning of the experiments (Refinement).

Føre et al. (2016) developed a numerical model simulating salmon growth and behaviour that was validated against data from the full-scale trials. This model represents a good foundation for modelling how scaling effects impact the growth performance of fish. However, Espmark et al. (2017) conducted their experiments in tanks, where changes in spatial dimensions may result in large changes in internal flow patterns (Davidson and Summerfelt, 2004). Such hydraulic variations will in turn impact how feed pellets are distributed within the volume, and will also affect the behaviours of the fish (Oppedal et al., 2011a; Espmark et al., 2017). To capture the scaling effects observed in this study, the model thus needs to be able to predict such variations in flow patterns, and their effects on the fish and the rearing environment.

This study represents a continuation of the work presented by Føre et al. (2016), where we have focused on predicting eventual differences in salmon growth performance between tanks of different physical scales. We used an expanded and improved version of the model from Føre et al. (2016), with the main modifications being the addition of an estimate of water velocity fields in indoor tanks, and the responses of the fish toward such velocity fields. The model was verified against the results from the scaling experiments reported by Espmark et al. (2017), thus assessing how well the model captured differences in performance between tanks of different scales. We then conducted a virtual scaling experiment, where the production parameters (i.e. fish density, temperature and individual feeding rate) were kept identical over several different physical scales. By reviewing the outputs of these virtual experiments, we then demonstrated how numerical models may be used as efficient tools in the planning and execution of scaling experiments.

2. Materials and methods

In the following, we will focus on the details on model modifications and new features introduced to enable predicting effects of physical scale. For details on the base model, refer to Føre et al. (2016).

2.1. Model overview

Our model is individual-based and includes sub-models for simulating the behavioural (movement, feeding) and energetic (feed conversion, growth) dynamics of Atlantic salmon (main state variables are given in Table 1).

The simulated fish respond to a virtual production environment that describes tank hydrodynamics in addition to the factors included in the original model (i.e. the cage/tank, temperature, feed pellets and light, Føre et al., 2016), all of which except tank geometry may vary in both time and space. Moreover, the fish respond to other individuals and

Table 1
Main state variables for fish. ‘-’ denotes dimensionless.

Description	Symbol	Unit
Position and orientation	\mathbf{r}	m, radians
Swimming velocity vector	$\dot{\mathbf{r}}$	m s^{-1}
Behavioural mode	mode	-
Body length	BL	m
Dry body weight	BW	g
Structural volume	V	cm^3
Reserves	E	J
Gut contents	G	g

have stochastic behavioural components to account for less deterministic behaviours (Føre et al., 2009, 2013). To simplify the interactions between fish and environment, spatial variations in environmental datasets are discretised using staggered 3D-grids of cubic cells. The value of a particular environmental variable at the position of an individual at a given time is then found by 3D-spatial interpolation and linear time interpolation, yielding a scalar value. This value, together with a measure of the local spatial gradient of the variable, is presented to the fish.

Fish energetics are represented by a DEB model (Kooijman, 2000) with the two basic states *structural volume* (cm^3) and *energy reserves* (J), augmented by a state representing gut contents (g). This model is presented in detail in Føre et al. (2016).

All simulations were run using a fixed timestep of 1 s for the integration of the behavioural model, as this was necessary to capture the behavioural dynamics, while energetics in being a slower process was possible to integrate using larger timesteps.

2.2. Model modifications

2.2.1. Tank hydrodynamics model

Flow patterns in tanks are radically different from those in sea-cages. While the netting material in cages allows water exchange, tank walls are non-permeable meaning that all water exchange in a tank must occur through tank inlets/outlets. Together with tank geometry, the inlet/outlet setup will therefore be a key factor in determining the internal flow patterns (Davidson and Summerfelt, 2004). Specific configurations such as placing inlets close to the tank wall with nozzles parallel to the wall and outlets at the bottom have been found to give sufficient water exchange throughout the entire volume (Summerfelt et al., 2016).

Although the presence and behaviour of the fish will also influence tank hydrodynamics (Plew et al., 2015; Masaló and Oca, 2016), our main focus was on how flow patterns affected the fish and not vice versa. Hence, we applied a simplified approach to modelling tank hydrodynamics rather than using specialised and computationally demanding methods such as Computational Fluid Dynamics (CFD) or Smoothed Particle Hydrodynamics (SPH).

Davidson and Summerfelt (2004) found that water velocity tends to vary radially in a tank, with the lowest speeds occurring near the centre axis of the tank and with higher speeds near the tank wall. Moreover, local flow directions were found to depend strongly on nozzle alignment. Based on these findings, we assumed that flow velocity increases linearly with distance from the centre axis, and that the flow direction is parallel with the wall under the assumption that the nozzles were thus aligned. For simplicity, vertical velocity components were assumed to be negligible and not represented in the model, while horizontal velocities were kept constant through the water depth. The first step in developing the hydrodynamic model was thus to calculate an initial velocity field that approximated the movement speed of water between the cells within a staggered 2D-grid of cells (indexed by i and j) discretising the horizontal tank cross-section.

For a given cell (i, j) in the staggered grid, $u(i, j)$ represents the water

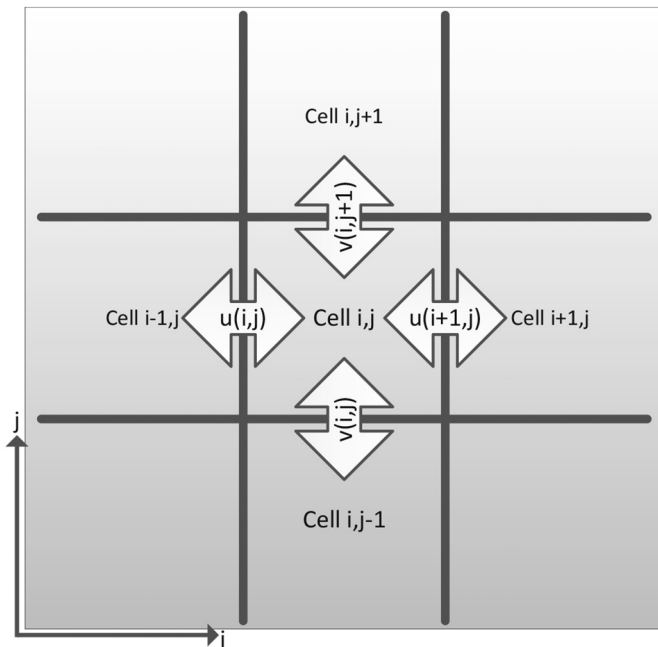


Fig. 1. Illustration of the water exchange between adjacent cells in the grid discretising the horizontal cross section of a tank. $u(i, j)$ and $v(i, j)$ represent water flow between cells along the i and j axes respectively.

velocity to or from cell $(i - 1, j)$, while $u(i + 1, j)$ represents the current to or from cell $(i + 1, j)$, and likewise along the j -axis for v (Fig. 1).

If a cell lies along the wall of the tank, all current components directed through the wall are set to zero to prevent unrealistic lateral water flow out of the tank. The balance for cell (i, j) is hence as follows for the unadjusted velocity field:

$$\Delta_{orig}(i, j) = u(i, j) - u(i + 1, j) + v(i, j) - v(i, j + 1) \tag{1}$$

The initial flow patterns set up using Davidson and Summerfelt (2004) did not inherently account for mass conservation in the sense that they do not guarantee that the sum of the water flow into and out from each model cell is zero. Since the hydrodynamic model is an

important driver for the pellet distribution model, the mass balance in the system needs to be correct to avoid inaccuracies in the transport of feed between cells. The expression in Eq. 1 was therefore expanded with adjustment terms $(\delta_u(i, j))$ and $(\delta_v(i, j))$ intended to correct any deviations causing mass imbalance in cells:

$$\begin{aligned} \Delta(i, j) = & (u(i, j) + \delta_u(i, j)) \\ & - (u(i + 1, j) + \delta_u(i + 1, j)) \\ & + (v(i, j) + \delta_v(i, j)) \\ & - (v(i, j + 1) + \delta_v(i, j + 1)) \end{aligned} \tag{2}$$

Numerical optimisation is a suitable method for finding $\delta_u(i, j)$ and $\delta_v(i, j)$ values that improve the mass conservation of the system. Optimisation algorithms are typically designed to minimise an object function that describes the system property that is sought optimised. Since we are seeking mass balance between the cells, the system property of interest in this case is the mass balance in all cells $(\Delta(i, j))$, leading to an object function consisting of the sum of squared cell balances for all cells:

$$\sum_{i,j} \Delta(i, j)^2 \tag{3}$$

This function will equal zero if all cells are in balance, and will conversely increase with increasing imbalances. By seeking the values of $\delta_u(i, j)$ and $\delta_v(i, j)$ that minimize the value of Eq. 3, we may therefore obtain an adjusted velocity field that approximately balances all cells. In this study, we subjected the object function (Eq. 3) to a commonly used method for optimising unconstrained multivariate functions (Lagarias et al., 1998), thus deriving adjusted current fields that were better at preserving mass flow to and from the cells (Fig. 2).

2.2.2. Pellet distribution

Since water current is an essential factor in the advection term in the feed distribution model (Alver et al., 2016), the discretisation grid of the pellet model was set to match the resolution of the velocity fields for the tank in all simulations. In being non-permeable for water, the walls of tanks represent boundaries over which particles such as feed pellets cannot be transported. Consequently, the pellet model was equipped with a feature which masked out all cells that are outside the tank boundaries. Together with the features in the hydrodynamic model prohibiting water flow through the wall, this prevented

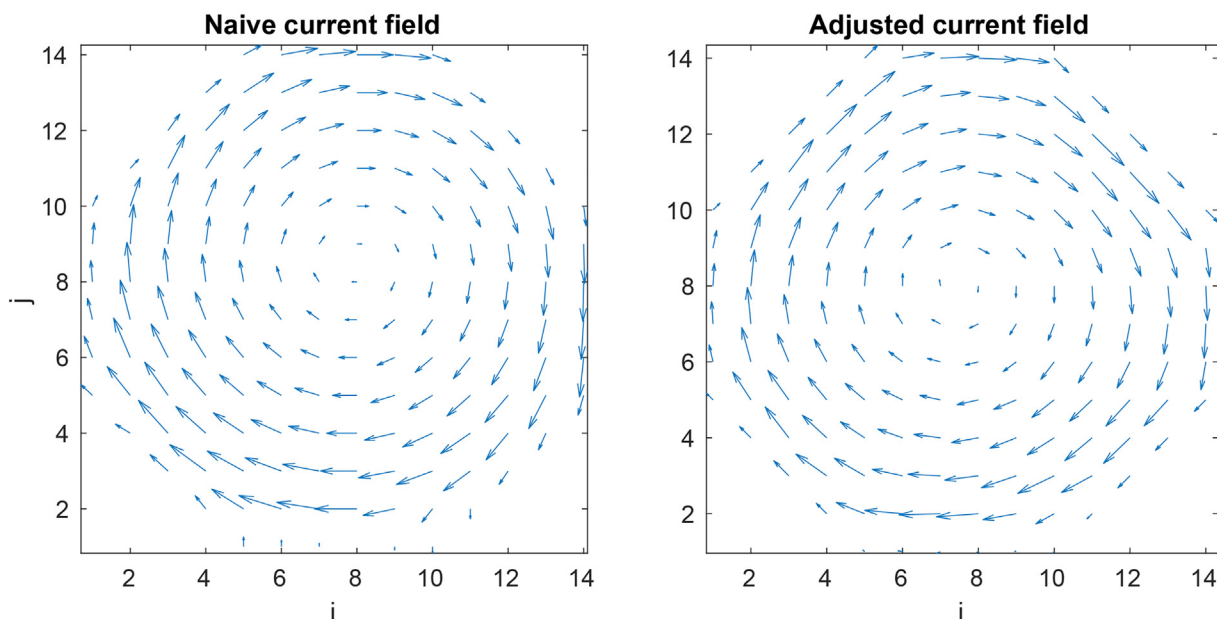


Fig. 2. Comparison between an unadjusted (“Naive” on the left) current field and a version of the same field that has been adjusted by optimisation (“Adjusted” on the right). The current field is here defined over a grid of 14 × 14 cells.

interchange of pellets with cells outside the tank, effectually keeping the feed inside the production volume. Atlantic salmon are believed to only attack moving particles and to ignore food lying still on the bottom (as demonstrated for juvenile salmon by Jørgensen and Jobling, 1992). For simplicity, pellets arriving at the tank bottom were therefore considered lost and represented feed waste in the model.

2.2.3. Fish behaviour

In general, little is known about how water velocity affects the behaviour of Atlantic salmon in a rearing unit. However, water velocities approaching the maximum swimming capacity of the fish are likely to have a strong effect on swimming speeds and directions, and may disrupt the schooling structures of the fish (Oppedal et al., 2011a). In the original version of the model (Føre et al., 2009, 2013), the desired movement vector of the fish (\mathbf{v}_{aggr}) used in computing the reference swimming velocity ($\dot{\mathbf{r}}_{ref}$) did not include a response toward water current. To introduce this, we expanded the expression for $\dot{\mathbf{r}}_{ref}$ to include a new specific response pattern, \mathbf{v}_{wc} (Eq. (4)).

$$\dot{\mathbf{r}}_{ref} = \tau \cdot \dot{\mathbf{r}}_{prev} + (1 - \tau) \cdot (\mathbf{v}_{aggr} + \mathbf{v}_{wc}) \quad (4)$$

The term $\dot{\mathbf{r}}_{prev}$ represents the swimming velocity vector in the previous timestep, whereas the parameter τ specifies how much the swimming speed of the fish is allowed to change between two timesteps. Unlike the specific response patterns included in \mathbf{v}_{aggr} (i.e. towards cage/tank, feed, temperature, light and other fish), \mathbf{v}_{wc} was not affected by the behavioural hierarchy outlined in Føre et al. (2009). This was done under the assumption that a fish will need to compensate for water velocity to maintain their desired positions in the cage/tank volume, irrespective of other behavioural decisions.

When travelling with the water current, a fish will not need to counter the effects of the current. \mathbf{v}_{wc} is therefore only provided a non-zero value when the angle (α) between the desired movement vector of the fish (\mathbf{v}_{aggr}) and the water current vector (\mathbf{V}_c) is larger than 90° (Eq. (5)).

$$\mathbf{v}_{wc} = -\frac{\mathbf{V}_c}{|\mathbf{V}_c|} \cdot M_{WC}, \text{ if } \alpha \geq 90^\circ, \text{ Otherwise} \quad (5)$$

When $\alpha \geq 90^\circ$, \mathbf{v}_{wc} will thus always directly oppose the water current encountering the fish. However, \mathbf{v}_{aggr} will often be a non-zero vector, and will if its direction opposes $|\mathbf{V}_c|$ counteract the effects of water current. To prevent "over-compensation" where \mathbf{v}_{wc} induces the fish to move against the current instead of just countering the effects of $|\mathbf{V}_c|$, M_{WC} is computed by subtracting the amplitude of the component of \mathbf{v}_{aggr} opposing \mathbf{V}_c from $|\mathbf{V}_c|$ (Eq. 6).

$$M_{WC} = |\mathbf{V}_c| - |\mathbf{v}_{aggr}|_{wc} \quad (6)$$

The reference swimming velocity of the fish ($\dot{\mathbf{r}}_{fish}$) is then subjected to limitations pertaining to the assumed movement capabilities of the fish (i.e. unable to move directly laterally and vertically, Sfakiotakis et al., 1999), and added to the current velocity to yield the final position derivative of the fish:

$$\dot{\mathbf{r}} = \dot{\mathbf{r}}_{fish} + \mathbf{V}_c \quad (7)$$

2.3. Model verification

We verified the model by comparing model output with experimental data obtained in the second phase (i.e. May 11, 2012 to October 6, 2012) of the experiments presented by Espmark et al. (2017), which featured fish reared in tanks with diameters of 0.9, 3 and 103 m³. The cross-section of the 0.9 m³ tanks was too small to allow a proper discretisation of the tank volume for the feed distribution and water velocity models without running into numerical difficulties. Hence, we only computed model output with data from the 3 and 103 m³ tanks. Two simulations featuring cylindrical tanks with diameters of 2 and

7 m, and depths of 0.96 and 2.68 m were set up to mimic the experiments in the 3 and 103 m³ tanks respectively. The current and feed models were initialised using a grid cell size of 0.25 m, resulting in resolutions of 8 × 8 and 28 × 28 cells for the cross section for the two tank sizes. The environmental conditions (i.e. temperature and light) in Espmark et al. (2017) were set to match those observed in the parallel full-scale study presented in Føre et al. (2016). Likewise, the feeding schedule from the full-scale study was adopted in the laboratory studies, with two meals (morning: startup between 05:00 and 08:00, afternoon: startup between 12:00 and 16:00) with a duration of between 3 and 7 h. Feed was delivered automatically using belt feeders (0.9 and 3 m³ tanks) or miniature rotary spreaders (103 m³ tanks) programmed to deliver feed at a constant rate during feeding, delivering sufficient feed per day to feed the fish to satiation.

All environmental settings and the feeding regime used in the experiments presented by Espmark et al. (2017) were applied as direct inputs in the model simulations, ensuring that the simulated fish were exposed to the exact same environment as the experimental fish. Feed delivery was simulated by applying the model for surface distribution outlined by Alver et al. (2016), using a feeder angle of 90°, and an airspeed of 2 ms⁻¹. Both simulations were set up with the same number of individual fish (115 for 3 m³, 3863 for 103 m³) as in the corresponding physical experiments by (Espmark et al., 2017), using the means and standard deviations in weight registered in the tanks at the start of the second experimental phase (mean = 84.56 g, stdev = 5.32 g for 3 m³; mean = 83.87 g, stdev = 0.58 g for 103 m³). We set the simulations up with a duration equal to the total length of the second experimental period, and stored results to disk every two simulated hours, producing a high-resolution dataset. After simulation, we compared the wet weight development as estimated by the model with the three samplings of wet weight made at the beginning (May 12, bulk sampling during transfer to new tanks), midway through (July 12, manual sampling of 100–200 individuals per tank) and at the end (October 10, bulk sampling) of the experiment.

2.4. Virtual experiment on scale effects

To further explore how scaling effects are manifested in the model, we did a series of simulation experiments using tanks with different scaling configurations. Six virtual experiments (Table 2) were derived as variations from a Base case (1 m radius, 1 m depth) by increasing only radius (R1: 1.75 m radius, R2: 3.5 m radius), only depth (D1: 2 m depth, D2: 3 m depth), and increasing both radius and depth (B1: R1 + D1, B2: R2 + D2). This enabled an evaluation of how the effects of changing only horizontal or vertical dimensions on fish growth performance compared with the situation when volume is scaled up without changing tank shape. The Base case contained 100 fish with mean weight of 80 g (stdev at 5 g), resulting in a biomass density of about 2.5 kg m⁻³ that was kept constant across all virtual experiments by scaling the number of fish with the volume. For simplicity, temperature and light values in the virtual experiments were set to those observed in the sea-cages on July 1 by Føre et al. (2016), while the feed amount per unit biomass in all cases was set to that applied in the 3 m³

Table 2

Simulation cases used for virtual study of effects of physical scale on fish performance.

Name	R (m)	D (m)	V (m ³)	N (number of fish)	Res (n _x × n _y × n _z)
Base	1.0	1.0	3.14	100	8 × 8 × 4
Radius 1 (R1)	1.75	1.0	9.62	306	14 × 14 × 4
Radius 2 (R2)	3.5	1.0	38.49	1225	28 × 28 × 4
Depth 1 (D1)	1.0	2.0	6.28	200	8 × 8 × 8
Depth 2 (D2)	1.0	3.0	9.43	300	8 × 8 × 12
Both 1 (B1)	1.75	2.0	19.24	613	14 × 14 × 8
Both 2 (B2)	3.5	3.0	115.45	3675	28 × 28 × 12

tanks by Espmark et al. (2017) on the same date.

The cell size used in the discretisation for the pellet and water flow models determines the volume in which a fish may try to capture feed at any given position in the tank. To prevent variations in this parameter from affecting the likelihood of capturing feed between the cases, the cell size and D_{max} were kept constant at 0.25 m at all scales. Since the model is driven by largely deterministic sub-processes, any scaling effects on fish growth performance would manifest in model output irrespective of simulation duration. We therefore limited the duration of the virtual experiments to 1 day for each case. If a longer simulation period was chosen for these studies, the different weight gains at different scales would entail that the feed delivered per individual fish in the tanks would have to be changed to maintain a constant ratio between feed delivered and biomass in the tanks. Moreover, as the fish grow larger, maintaining a similar feeding efficiency also requires that pellet size is increased. Such factors could add uncertainty to our ability in discerning the pure effects of varying physical scale, underlining the rationale of choosing a short simulation time.

3. Results

3.1. Model verification

Simulation output compared well with the experimental data for the 103 m³ tank, overestimating growth throughout the period, with higher estimated than observed end weights (Fig. 3). There was a reduction in the estimated growth around the time of the second observation in the experiment which coincided with a two day period in which feed delivery ceased.

The model underestimated growth in the 3 m³ tank, leading to a lower simulated end weight than in the observations (Fig. 3). However, the disparity between estimated and observed end weight was smaller than for the 103 m³ tank. Similarly to in the 103 m³ tank case, there was a drop in estimated weight around one third into the experimental period, coinciding with a three day period in which the fish were not fed.

The same trends were also seen when comparing estimated and observed Specific Growth Rate (SGR) values (Table 3).

3.2. Virtual experiment on scale effects

For R1 and R2, the simulation results featured an increase in weight gain (Fig. 4 a), gut fullness (Fig. 4 b), SGR (Fig. 4 c) and energy reserves (Fig. 4 d) with increased tank radius. In contrast, increased depth (D1 and D2) entailed a decrease in all these factors compared with the base

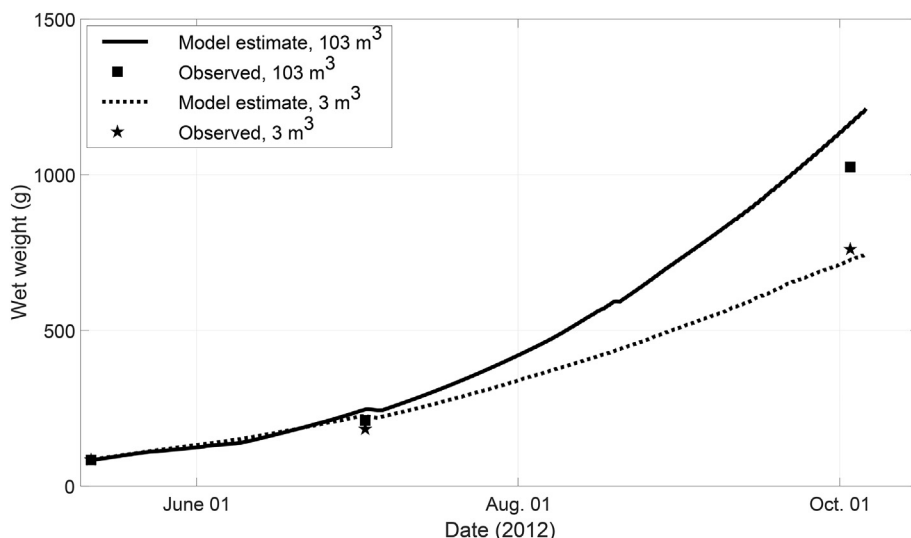


Fig. 3. Comparison between numerical model estimates and experimental results on wet weight. Results were obtained in the land-based facilities of Nofima, and includes data from a 103 m³ (solid line: model estimate, black squares: experimental results) and 3 m³ tank (dashed line: model estimate, black stars: experimental results).

Table 3

Estimated and observed SGR values for the experimental period.

Period	Tank size	Model estimate of SGR (%)	Observed SGR (%)
12.05–12.07	3 m ³	1.85	1.49
12.05–12.07	103 m ³	2.03	1.77
12.07–10.10	3 m ³	1.26	1.55
12.07–10.10	103 m ³	1.68	1.72
12.05–10.10	3 m ³	1.47	1.53
12.05–10.10	103 m ³	1.81	1.74

case (Fig. 4 a-d), suggesting that the trend for increasing depth was opposite of that of increasing radius. The increases in scale which included modifications of both radius and depth (B1 and B2) showed a similar tendency as that of R1 and R2, with increasing fish performance with increasing scale.

4. Discussion

4.1. Model verification

The model appeared able to simulate scaling effects in tank based salmon aquaculture since simulation results described a similar difference in fish growth performance between the 3 and 103 m³ cases as found in the experiments by Espmark et al. (2017). Although there were deviations between model predictions and experimental data in both cases, model outputs were more similar to experimental outputs for the 3 m³ tank, suggesting that it was better at capturing the dynamics in the smallest tank.

Nutrient assimilation is the primary factor behind fish growth in any fish farming operation, as seen in the experimental results from Espmark et al. (2017) where observed scaling differences were associated with a generally higher feed intake in larger tanks. This effect is also represented in the numerical model, and was the main factor behind all scaling effects predicted by the model during this study. Such scale dependent changes in feed intake could occur because an increase in tank volume enables better spatial dispersal of the feed, providing larger foraging volumes for the fish and higher pellet retention times. This may result in the fish being more exposed to available feed. Alternatively, it is possible that this effect is caused by the inter-individual behaviour of the fish (Niwa, 1994). A main component in the simulated inter-individual behaviour is that the fish will exhibit avoidance towards neighbouring fish getting too close (Førre et al., 2016). The magnitude of this response increases with the number of neighbouring fish considered, which again depends on local fish density. Since feed is

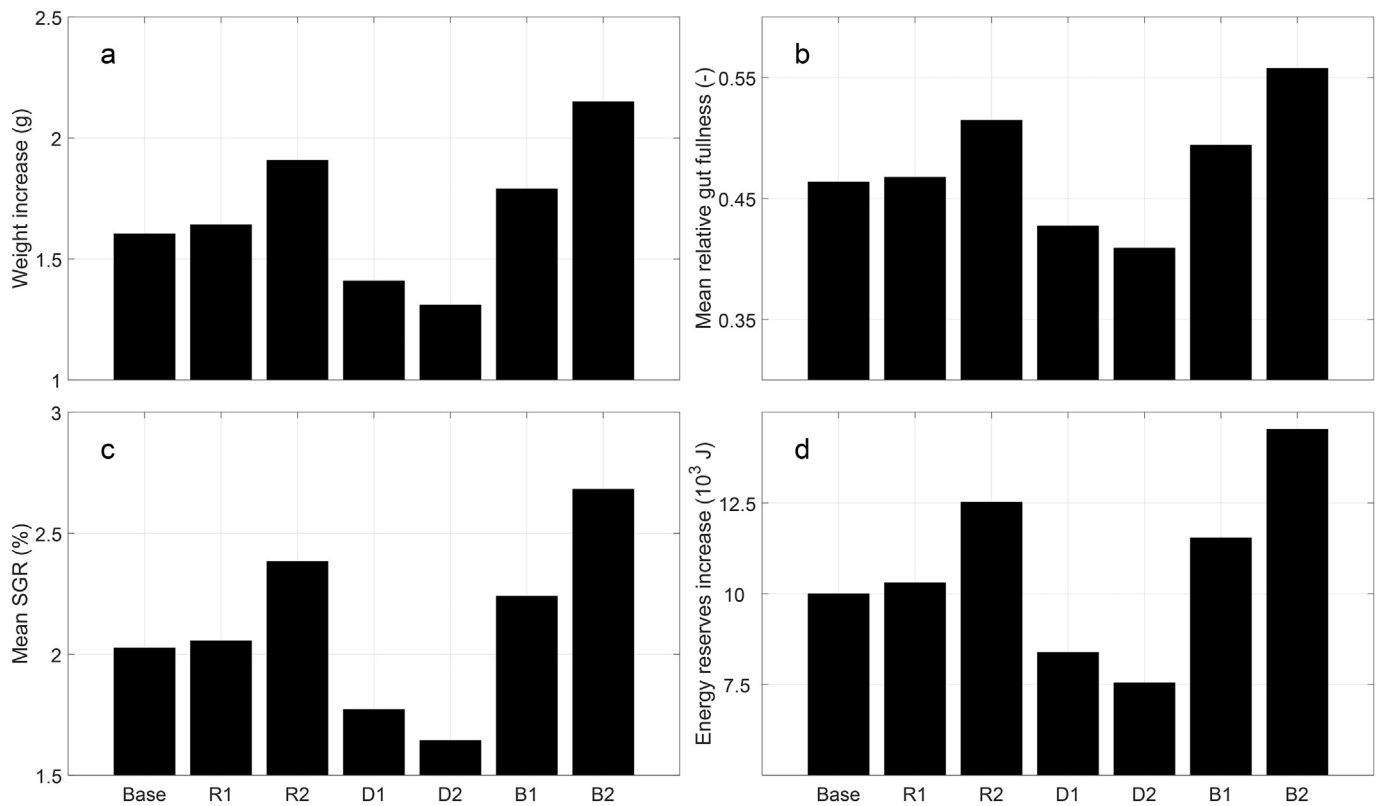


Fig. 4. Results from virtual experiment on scale effects using the model. Bars provide values representing the different scale cases, entitled “Base” (base case), R1 and R2 (varying radius), D1 and D2 (varying depth), and B1 and B2 (varying radius and depth). a) end wet weight in g, b) mean relative gut fullness (dimensionless), c) mean SGR in % d) end energy storage level.

a strong attractor for the simulated fish, feed delivery in a small volume will lead to higher fish concentrations than if feed is more dispersed in space. It is therefore likely that local fish densities during feeding were generally lower in the 103 m³ tanks compared with the 3 m³, and hence that the simulated fish had better opportunities to remain near the feed throughout a feeding period in those tanks than in the smaller tanks.

It is important to consider that the experimental design in Espmark et al. (2017) might also have inadvertently affected the simulation results, as observations of uneaten food were used to continually adjust the daily feed delivery to the tanks throughout the experimental period with the intent of feeding to satiation while minimising feed waste. As feed delivery numbers from Espmark et al. (2017) were used as inputs to the model, such variations could impact the simulated growth. Although Espmark et al. (2017) used different feed delivery methods in the 103 and 3 m³ tanks, both methods were designed to distribute feed as evenly over the water surface in the tank as possible. The feeding method used in our model simulations was similarly set up to distribute the feed evenly, hence we do not believe that differences in feed delivery had a notable impact on the outcomes of the study.

For both tank sizes, the model overestimated the growth rates of the salmon in the first half of the experimental period. This could be because the fish in the physical experiments had been transferred to the tank recently (Espmark et al., 2017), and could be acclimatising to their new rearing habitat. Acclimatisation is not accounted for in the numerical model, and could therefore cause overestimation in the simulation results. Espmark et al. (2017) found that the fish in both the 103 and 3 m³ tanks had increased mortality rates after the transfer to these tanks, and it is likely that increased mortality could be accompanied by reduced feeding motivation and feed intake. The model performed better at predicting fish growth over the latter part of the experiment (12.07–10.10), which is in line with this hypothesis.

4.2. Virtual experiment on scale effects

Increasing only radius (R1 and R2) and increasing radius and depth (B1 and B2) led to higher growth rates in the virtual experiments, implying that increases in tank volume entailed better growth performance for these cases. Gut fullness followed a similar trend across these scale transitions, meaning that the primary causes behind the simulated scale effect were improved feed availability and feed intake in the fish. These observations fit with those made in the verification study, and the higher growth performance in B1 and B2 than in R1 and R2 was probably because of the increased feed retention time achieved when increasing tank depth. In contrast, increasing only depth (D1 and D2) appeared to have the opposite effect, with lower growth rates than in the base for both scale increases. This suggests that not only the scaling relationship, but also the dimension (i.e. depth, radius or both) in which the scaling occurs has an impact on fish performance. A possible explanation for this is that even though feeding was scaled up to achieve the same feed vs. biomass relationship as in the Base case, the cross section area of the tank remains unchanged. This in turn means that feed delivery (except for the total amount of feed delivered) would be identical between the cases. Accordingly, the upscaling from the Base case to D1 and D2 resulted in a larger number of fish trying to consume a larger amount of feed within the same feeding volume as in the Base case. This then resulted in higher local fish densities, which could inhibit feed intake. Furthermore, the simulated fish seek towards the highest feed concentration (Føre et al., 2016), reducing the effect of longer feed retention time as the fish would prefer the upper part of the water column rather than fully utilise the tank volume. However, since this trend was not seen in the transitions between R1 and B1 (depth changed from 1 to 2 m), and R2 and B2 (depth changed from 1 to 3 m), this effect is probably also dependent on the absolute area of the cross section, with setups using larger cross sections being less sensitive.

In summary, the results imply that increased physical scale is generally beneficial for feed intake and growth. However, the effect when only depth was varied suggests that too small tank cross sections (e.g. radius < 1 m) could lead to worse growth performance than would be expected due to the scaling process alone. If this effect is also present in real experiments, it could partially explain why the fish kept in the smallest scales (i.e. 0.9 m³) in the studies of Espmark et al. (2017) exhibited severely worse growth performance than the fish kept in at larger scales. However, experimental validation will be necessary before a proper hypothesis can be formulated on this matter.

5. Conclusion

In this study, we have developed a numerical model that predicts differences in the growth performance of fish reared at different physical scales, and tested this model in a hypothetical scale experiment. Through verifications against experimental data, the model was found able to predict observed scaling effects between two different tank scales, although the model overestimated the magnitude of the difference in growth performance. Our findings illustrate how numerical models can be valuable tools for experiments within aquaculture research, either as a virtual experimental facility in the design phase prior to the setup of a physical experiment, or to assess the representability of small scale experiments in a large scale industrial setting. Such numerical models may also be used as tools for addressing the 3Rs (Replacement, Reduction and Refinement) of animal experimentation, as a model may be used to Replace fish experiments, Reduce the number of animals used in experiments, and Refine the experimental design.

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