Integral projection model reveals differences in individual growth performance and body mass distributions in response to three different rations in a large aquaculture experiment

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Summary

Fed aquaculture is one of the fastest growing and most valuable food production industries. The efficiency with which farmed fish convert feed into biomass influences both environmental impact and economic revenue. Salmonid species, such as king salmon (*Oncorhynchus tshawytscha*), exhibit high levels of plasticity in vital rates such as feed intake and growth rates. Accurate estimations of individual variability in vital rates are important for production management. The use of mean trait values to evaluate feeding and growth performance can mask individual-level differences that potentially contribute to inefficiencies. Here, we apply an integral projection model (IPM) to investigate individual variation in growth performance of 1625 individually tagged king salmon fed one of three distinct rations and tracked over 276 days. To capture the observed sigmoidal growth, we compared a non-linear mixed-effects (logistic) model to a linear regression model used within the IPM framework. Ration significantly influenced several aspects of growth. Mean final body mass and mean growth rate increased with ration, however, variance in body mass and feed intake also increased significantly over time. Trends in body mass mean and variance were captured by both logistic and linear models, suggesting the linear model to be suitable for use in the IPM. Higher rations resulted in a decreasing proportion of individuals reaching the cohort's mean size or larger by the end of the experiment. This suggests that, in our trial, feeding to satiation did not produce the desired effects of efficient and uniform growth in juvenile king salmon. While monitoring individuals through time is challenging in commercial aquaculture settings, recent technological advances combined with an IPM approach could provide new scope for tracking growth performance in experimental and farmed populations. The IPM framework also allows the exploration of other size-dependent processes affecting vital rate functions, such as competition and mortality.

Keywords:
Chinook salmon, demography, feed efficiency, feeding hierarchy, feeding regime, sustainable seafood production, individual performance variability, structured population models

1. Introduction

Over the past three decades, the aquaculture sector has been one of the fastest growing food production sectors by annual growth rate (FAO, 2018). Among the multitude of finfish species cultured worldwide, salmonids are some of the most valuable (FAO, 2016). Salmonid production is projected to continue to grow, but meeting the nutrient requirements of salmonids and consumer expectations regarding the nutrient profile of salmon products has become more challenging due to marine resource limitations (FAO, 2020). Sustainable industry growth requires further improvements in feed innovation and management, to successfully balance fish growth performance, environmental impacts, and the nutrient composition of salmon products (Froehlich et al., 2018; Shepherd & Jackson, 2013).

For commercial aquaculture to be successful, fish cohorts are required to grow rapidly and uniformly to what is considered a usable size at the minimum cost of resources and capital (Timmons et al., 2002). A well-informed feeding regimen can increase the likelihood of optimum growth, reduce costs, and decrease environmental impacts from waste outputs (Davidson et al., 2016). Despite extensive monitoring and control opportunities, estimating cohort properties such as growth rates, fish size distributions, and total biomass in experimental or commercial fish populations poses challenges. Particularly in commercial farms, true cohort values are often impossible to obtain due to the extensive sampling effort

involved and the negative effects of stress on the fish (Nilsson & Folkedal, 2019; Shieh & Petrell, 1998). These are key inputs for many important decisions in the production process, such as feed ration assignment, feed cost calculations, harvest planning, and estimation of production yield (Føre et al., 2018; Lugert et al., 2016). Similarly, aquaculture experiments continue to use mean body size as the primary currency by which studies measure the success of experimental treatments in growth trials. The use of mean trait values, however, potentially masks the meaningful effects of individual variation on cohort-level processes (Fritschie & Olden, 2016). Furthermore, small biases in size distribution or biomass estimates may produce significant deviations in scientific, management and economic outcomes (Nilsson & Folkedal, 2019). Size-structured population models highlight the importance of investigating growth variability and might be able to provide new insights into the mechanisms that determine size variability of cohorts in aquaculture research.

Size-structured population models that incorporate individual-level variation are useful for the exploration of population dynamics and ecosystem feedbacks (e.g. Filipe & Kyriazakis, 2019; Griffiths et al., 2020; Vincenzi et al., 2014). The common denominator is the understanding of body size as the fundamental functional trait that influences organismal vital rates such as metabolism, uptake, mortality, and reproduction rates. Individual vital rates are then integrated and scaled up to the population, community or ecosystem level (Andersen et al., 2016; Blanchard et al., 2017). Both the mean body size and the individual variation around the mean, i.e. the frequency distribution of body size, are impacted by variation in internal and external factors. Following Jensen's inequality, the aggregate sum of any function that scales allometrically will be altered at the population level should either the mean or the size distribution around the mean change (Fritschie & Olden, 2016). Therefore, it is necessary to select a size-structured model approach which allows the projection of both

mean and variance of changes in individual body size. One such model is the integral projection model.

Integral projection models (IPMs) are size-structured models that describe how populations structured by continuous individual-level state variables change in discrete time (Easterling et al., 2000). These models perform well with body size as the state variable. Deterministic IPMs are data-driven and parameterised with simple regressions that relate an individual's state to its vital rates, such as growth, survival and reproduction (Coulson, 2012; Merow et al., 2014). The core of the IPM is the kernel which is the function that predicts how the body size distribution of a population changes from one time step to the next. In addition to the mean change in the state variable at the population level, the IPM allows the flexible modelling of the changes in variance. The level of complexity of the biological processes included in the model is determined by the extent and quality of the available data. One exceptional feature of IPMs is that they provide insights into mechanistic population-level processes from individual-level observations that cannot easily be inferred from statistical models of vital rates alone, while remaining computationally simple. So far, IPMs have been employed in ecological studies to estimate population growth rates under variable environmental conditions (Coulson, 2012; Ellner & Rees, 2006; Heather et al., 2018). This type of growth modelling has been shown to accurately capture growth trajectories in many plant and animal species, including fishes (e.g. Heather et al., 2018; White et al., 2016). To the authors' knowledge, the present study will be the first application of an IPM in aquaculture.

To adapt the IPM framework for application in aquaculture it is necessary to identify the relevant biological processes and select a state variable that allows inferences about said

processes. The present study uses body mass as the state variable, measured in grams of wet weight, because body mass is a key determinant of fish performance in aquaculture. Since grow-out and reproduction are isolated operations in commercial aquaculture, and because the experimental animals were pre-reproductive juveniles, with negligible mortality rates, only growth rates are considered. We use the IPM to assess the effects of ration on individual growth performance in New Zealand King or Chinook salmon (*Oncorhynchus tshawytscha*) reared in a freshwater recirculation aquaculture system (RAS). The advantage of using data from RAS is that the majority of biotic and abiotic factors are kept stable and can hence be excluded from the analysis. This case study is ideal because the experimental fish had not undergone extensive selective breeding and their performance with respect to growth and feed efficiency remains highly variable (Araujo et al., 2021; Semeniuk et al., 2019).

2. Materials and methods

The current project made retrospective use of data and did not require Animal Ethics approval. The experimental setup has previously been described in detail by Esmaeili et al. (2021) and Zhao et al. (2021). Below we focus only on the aspects of the experiment vital to this study.

2.1 King salmon growth trial dataset

A single cohort of all-female king salmon juveniles were sourced from a local hatchery (Clearwater Hatchery, Mt Cook Alpine Salmon, Twizel, New Zealand), where the fish were individually implanted with a passive integrated transponder (PIT) tag (HID Global, EM4305 684,230, 12 mm glass tags). The growth trial was conducted over a period

of 276 days in the Finfish Research Centre (FRC) at the Cawthron Aquaculture Park (CAP), New Zealand. After a 21-to-24-day acclimation period to tank conditions at 15°C, 1625 fish (average wet weight ± SD: 40.67 ± 8.13 g, wet weight range: 21.14g – 63.75 g) were haphazardly distributed amongst nine 8000 L circular freshwater tanks. The initial stocking was 176 to 187 fish per tank with a coefficient of variation for wet weight between 16% and 21%. Throughout the experiment, water temperature was maintained at 17 ± 0.5°C and photoperiod was set to 24 h continuous light to prevent early maturation.

2.2 Feeding regimes and sampling

The experiment tested the effects of three feed rations, 60%, 80%, or 100% satiation (n=3) on growth performance. One extruded feed with pellet sizes of 4 mm and 6 mm was used throughout the experiment (Tasman Freshwater experimental diet, Ridley, Australia). Fish were handfed one meal per day. The 100% satiation ration was determined by hand feeding until apparent satiation, defined as the time when the feeding response of all individuals within a tank had ceased. The respective feed amounts for the 60% and 80% feed ration treatment groups were calculated using a feed model based on daily observations of feed amount consumed by the 100% satiation treatment group and adjusted for predicted average weight and tank biomass. For simplicity, the rations of 60%, 80% and 100% satiation will be referred to as treatments 60S, 80S, and 100S, respectively. Fish were removed if they ceased feeding or lost weight, or for biomass reduction at the later stages of the experiment. Tank feed intake was measured daily: uneaten pellets were collected, counted, and subtracted from the weight of feed delivered. In addition to repeated measurements of individual wet weight and fork length under anaesthesia (65 ppm tricaine methane sulfonate (Syndel, Canada)) on six occasions (days 0, 91, 124, 173, 221 and 276), individual daily feed intake

(DFI) was quantified using the x-ray "ballotini" bead method (McCarthy et al., 1993; Talbot & Higgins, 1983; Walker et al., 2012) on days 124, 173, 221 and 276.

2.3 Integral projection model of the king salmon experiment

An IPM describes the probability density distribution of the body mass $w_i = w(t_i)$ of a population at a sequence of discrete times $t_1, t_2, \ldots, t_n$ (Coulson, 2012). An IPM assumes that the body mass w_{i+1} of an individual at time t_{i+1}, conditional on its body mass w_i at time t_i, is given by the growth kernel $G(w_{i+1}|w_i, t_i)$. If the probability density distribution of body masses at time t_i is $n(w_i, t_i)$, it follows that (Rees et al., 2014) the probability density distribution of body masses at time t_{i+1} is

$$n(w_{i+1}, t_{i+1}) = \int_0^{w_{i+1max}} G(w_{i+1}|w_i, t_i) n(w_i, t_i) dw_i \qquad \text{eqn 1.}$$

The growth kernel can relate the body mass at each time to the body mass at the previous time through a linear model. If conditional on w_i, the body mass w_{i+1} is normally distributed with mean $\beta_{0i} + \beta_{1i} w_i$ and variance ς_i^2,

$$w_{i+1} \sim N(\beta_{0i} + \beta_{1i} w_i, \varsigma_i^2) \qquad \text{eqn 2,}$$

and the body masses at time i are also normal with mean μ_i and variance σ_i^2

$$w_i \sim N(\mu_i, \sigma_i^2) \quad \text{eqn 3,}$$

192

193 then $w_{i+1}$is also normally distributed, with mean

194

$$\mu_{i+1} = \beta_{0i} + \beta_{1i}\mu_i \quad \text{eqn 4}$$

195

196 and variance

197

$$\sigma_{i+1}^2 = \beta_{1i}^2\, \sigma_i^2 + \quad \varsigma_i^2 \quad \text{eqn 5.}$$

198

199 The model parameters β_{0i}, β_{0i}, and ς_i^2 can be estimated by regressing the body mass w_{i+1} of
200 each individual against their body mass w_i at the previous time t_i. Fitting data across all time
201 increments at once led to the violation of at least two of the underlying assumptions of linear
202 regression models, namely normality, and homoscedasticity, making the linear regression
203 model invalid (Zuur et al., 2009). Linear regressions fitted to the data time increment by time
204 increment, however, presented with normally distributed and homogenous residuals. To
205 create one growth kernel for each of the ration treatment groups that covers the entire
206 experimental period, individual growth kernels were calculated for the relevant body mass
207 ranges of each of the time increments and then added together.

208

209 To demonstrate the legitimacy of this approach for logistic growth, we also fitted a
210 logistic non-linear-mixed effects model (Pinheiro & Bates, 2000) to model body mass over

time (see Supplementary material for a more detailed description of the logistic model). The logistic model can be expressed in terms of the weight $w_i = w(t_i)$ at time t_i

$$\mathrm{w}(t) = \frac{w_{max}}{1 + (\mathrm{w_{max}} - \mathrm{w_i})/\mathrm{w_i}\ \exp(-K(t - t_i))} \qquad \text{eqn 6.}$$

Expanding this expression in a Taylor Series in w_i yields

$$w(t) = e^{-k\,(t-t_i)} w_i + O(w_i^2) \qquad \text{eqn 7.}$$

This relation approximates the growth kernel of the IPM, and suggests the coefficients of the linear regressions for the IPM should be approximately $\beta_{0i} = 0$ and $\beta_{1i} = e^{-k(t_{i+1}-t_i)}$. All calculations were performed using the open-source software R (R Core Team, 2020).

3. Results

The linear regressions fitted to the time increment subsets of each ration agreed closely with the predicted body size means from the logistic model as well as the data (Figs 1–2). The main difference between the model predictions of the two approaches was that the linear regressions did not include predictions for low-performance individuals that had been removed during a previous sampling interval while the logistic model did.

[Figure 1]

The goodness of fit of the linear regressions and the logistic model was assessed by calculating the percentage error (PE) between the predicted mean body size and the observed mean body size for each ration treatment group at each time point or time interval. Interestingly, the highest deviation between observed mean body size and predicted mean body size for the logistic model was found at the initial time point (i.e. w_0) for the 80S (18% PE) and 100S (36% PE). Similarly, the linear regression predictions deviated most from the observations during the first time increment (60S: 1.42%; 80S: 1.49%, 100S: 1.50%). Predicted mean final body size, w_{max}, in the logistic model deviated less from the observed values for all ration sizes, and the PE decreased with increasing ration size (60S: 5.37%; 80S: 3.04%; 100S: 2.97%). This trend for the last time interval was partially mirrored by the linear regressions (60S: 0.31%; 80S: 0.24%; 100S: 0.46%). Mean percentage error (MPE) was calculated as the mean of all PEs for each ration treatment over the entire experimental period. For the logistic model, MPE was lowest for the 60S treatment at 3.97%, followed by the 80S treatment at 5.7% and 9.12% for the 100S treatment. The higher MPEs of the 80S and 100S treatments were significantly influenced by the deviation between observed and predicted mean initial sizes (w_0, cf. Table 1 Supplementary Material). For the linear regressions, the MPEs for all treatments were significantly lower than those of the logistic model and the differences in MPE between the treatments was negligible at 0.57% for the 60S treatment, followed by the 80S treatment at 0.54% and the 100S treatment at 0.53%.

[Figure 2]

In addition to the growth trajectories, we visually compared the probability density distributions of observed vs. predicted body mass (Fig. 3). Again, we found the predictions to mirror the observations, capturing details such as a slight right-skew in the distributions of the final time increments for the 60S and 80S treatments as well as the right-skew in the penultimate time increment and the bimodality that is indicated in the last time increment of the 100S treatment group (see Fig. 3, column five for the 60S and 80S treatment groups, and columns four and five for the 100S treatment group).

[Figure 3]

Overall, ration size significantly influenced several aspects of growth, both at the individual and at the cohort level. Mean final size as well as mean growth rate were considerably augmented by increased ration size (see Fig. 1). Variance also significantly increased with ration size through time (cf. Figs 1, 3). The initial coefficients of variation (CVs) were found to be similar for all treatment groups, 19.9% in the 60S treatment group, 18.9% and 21.05% in the 80S and 100S treatments, respectively. While the variance remained relatively constant in the 60S treatment group (final CV = 20.65%), the CVs of the 80S and 100S treatments were substantially elevated at 23% and 30.6%, respectively, by the end of the experiment. This became especially evident when comparing the widths of the growth kernels for each ration treatment (Supplementary Material, Fig. 2). While the 60S treatment resulted in a relatively narrow, almost linear band of transition probabilities across all sizes w_t, we observed an increased fanning effect at the higher rations which indicated a higher variability of achieved sizes w_{t+1} from the same value w_t. The trends in the individual daily feed intake (DFI) data mirror the trends in growth in response to ration size and

individual body size: both mean and variance of individual DFI increased with increasing ration and body size (Fig. 4).

[Figure 4]

Additionally, we examined the proportion of the experimental cohorts that grew to the respective mean size or larger by the last time point to illustrate potential management implications of the respective ration treatments. In the 60S treatment, the largest proportion, 63.4% or 196 of 309 individuals, grew to the cohort's mean size or larger (642 – 989g), followed by the 80S cohort where 58.09% or 176 of 303 individuals reached the mean size or larger (791 – 1343g). In the 100S treatment, less than half of the cohort, namely 48.44% or 124 of 256 individuals, grew to the cohort mean size or larger (873 – 1497g).

4. Discussion

Overall, our study demonstrates that feeding to satiation achieved the highest mean and maximum growth rates but resulted in highly variable final body masses. Our results thus question whether the common aquaculture practice of feeding to satiation produces the desired effects of efficient, fast, and uniform growth in king salmon. They also highlight the potential shortcomings of approaches that report growth in terms of mean and standard deviation and demonstrate the importance of exploring the size structure of a fish cohort and the processes that yield certain body mass distributions. One of the strengths of the IPM framework that makes it very suitable to this kind of investigation is the mechanistic projections of deterministic vital rate functions, such as growth rate, which allows insights into cohort-level processes.

Improving fish growth performance while reducing the environmental footprint and maintaining economic viability has been the main goal of empirical aquaculture research for decades. Because aquaculture feed formulations rely on limiting resources and are the single largest expense in fed aquaculture enterprises, with a share in production costs of over 50% (Iversen et al., 2020), the sustainability of the sector depends on the continuous improvement of feed formulations and feeding practices (e.g. Carter & Houlihan, 2001; Hasan & Soto, 2017).

Ration size is one of the most influential feeding regime factors and is readily manipulated to enhance the likelihood of optimum growth as well as lower costs and environmental impact from uneaten pellets or waste outputs (Davidson et al., 2016). Our study on the growth performance of a cohort of all-female, juvenile king salmon fed three rations of 60% (60S), 80% (80S) and 100% satiation (100S) for 276 days demonstrates that there are large differences in mean and individual-level growth performance under different feeding regimes. In accordance with earlier studies in salmonids, the data of the present study showed that mean growth in the high ration group (100S) significantly exceeded mean growth of the intermediate (80S) and the low ration groups (60S) (e.g. Kiessling et al., 2005; Mazur et al., 1993; Shearer et al., 1997). The proportion of fish, however, that reached a body size equal to the treatment group mean or larger decreased with increasing ration size, raising questions about the efficiency of feeding to satiation. In contrast to previous findings, the variance in growth performance as approximated by variance in body mass increased significantly with ration size and over time. Davis and Olla (1987) as well as McCarthy et al. (1992) had reported that reduced rations resulted in higher variability in growth rate than medium or high ration sizes due to presumably higher competition under resource limitation.

Disproportionate growth and an increase in the variance in body mass or feed intake have previously been attributed to the preferential acquisition of feed by dominant individuals and interpreted as indicators of interference competition for resources, also called a feeding hierarchy (Jobling, 1995). Within a strong feeding hierarchy, a small number of dominant fish monopolise feed which may result in faster growth and larger body sizes. Meanwhile, the feeding activity of subordinate fish is supressed, as they consume smaller meals (Metcalfe, 1986; Ryer & Olla, 1996). The trends in individual daily feed intake and the right-skewed or bimodal probability density distributions of body mass might indicate the establishment of such feeding hierarchies as a source of the increased growth variability in the treatment groups 80S and 100S towards the end of the experiment. During hand feeding, the 60S and 80S fish exhibited a strong feeding response and completed their meals quickly, whereas the feeding response was more variable in the 100S fish, with slower feeding. This could have allowed more dominant fish to eat larger meals (Ryer & Olla, 1991; Thorpe et al., 1990). Although the directionality of the relationship between individual body mass and dominance status is contested, generally larger fish have been found to be more dominant in husbandry conditions (Huntingford et al., 1990; Metcalfe et al., 1992).

Individual variation is increasingly recognised by ecologists and fisheries scientists as important parameter for understanding and predicting the dynamics of wild populations and their interactions with the surrounding ecosystem (e.g. Fritschie & Olden, 2016). Because morphological and physiological functions scale allometrically with body mass, focussing solely on the mean body mass will potentially bias predictions at the population level, when there is high variance (Fritschie & Olden, 2016). Environmental variables, such as temperature, affect physiological rates and how they scale with body mass, and hence have

353 varying effects on individuals of different sizes (Leblanc et al., 2019). One of the advantages
354 of the IPM is that it allows the modeller to mathematically model mean and variance of vital
355 rates, and hence allow a more detailed picture of the variability in vital rates and
356 consequently the body size composition of fish cohorts. In aquaculture research, however,
357 mean trait values continue to be the primary currency by which studies measure and compare
358 growth performance and treatment effects. Even mechanistic frameworks simulating
359 aquaculture operations appear to preferentially report parameter and variable means only (e.g.
360 Føre et al., 2016; Zhou et al., 2018).
361
362 Commonly used growth functions in aquaculture research, such as the absolute
363 (AGR) or specific growth rates (SGR), are also often calculated based on the stocking and
364 harvest data only, leaving intermediate data unconsidered (Hopkins, 1992). Both growth
365 models used here, however, allow for trends in the data over the entire experimental period.
366 This is reflected in the mean percentage error (MPE). Lugert et al. (2016) reported MPE
367 values of 11.27% and 13.37% for AGR and SGR, respectively, for an aquaculture experiment
368 of comparable duration with RAS-raised salmonids of similar initial and final sizes. At MPE
369 values of 0.57% and 3.9% (60S), 0.54% and 5.7% (80S), and 0.53% and 9.1% (100S), both
370 the linear regressions and the logistic model, respectively, perform better. The logistic model
371 overestimated the body mass range at the low end of the growth performance scale. This is
372 likely due to observations for under-performing individuals being included at earlier
373 sampling points, but then removed from the dataset. Additional processes may have also
374 contributed to the extent of divergence between models and data. King salmon have highly
375 variable life cycles, and the underlying processes are not well understood. Considerable
376 plasticity in metabolic efficiency, resource use, associated foraging behaviour, and the timing
377 of life cycle events has been documented between different strains and regions of occurrence

(Higgs et al., 1995; Leblanc et al., 2019; Salin et al., 2019). Despite king salmon being a commonly farmed species in New Zealand, not all the farmed stocks are selectively bred and commercially important traits such as feed consumption, feed efficiency and growth remains highly variable (Araujo et al., 2021; Esmaeili et al., 2021; Semeniuk et al., 2019; Walker et al., 2012). The absence of systematic control of intraspecific genotypic variation and the resulting phenotypic differences are likely to lead to divergent individual growth trajectories in a controlled environment and under different resource availability treatments (Leblanc et al., 2019; Semeniuk et al., 2019). Future applications of IPMs in aquaculture might consider the inclusion of terms that allow the representation of phenotypic variability in factors that contribute to growth variability and have been shown to affect dominance status, such as standard metabolic rate (Cutts et al., 1998; Metcalfe et al., 1995).

Our study shows that deterministic IPMs are powerful tools to investigate processes that shape a population's demography from the individual level. The employment of phenomenological methods such as regression models makes this approach flexible and accessible to practitioners. The deterministic core of the approach, however, means that results can only be interpreted for the exact conditions of the underlying experiment. For the prediction of aquaculture cohort responses to a changing environment, the incorporation of fully mechanistic model formulations such as the dynamic energy budget into an IPM could be instructive (e.g. Smallegange et al., 2017). Additionally, extending the IPM using Markov chain theory (Tuljapurkar, 1990) might allow the model to represent stochastic processes, such as variation in environmental factors or interactions between individual fish, which may increase the approach's explanatory power and aid with capturing the observed variance. To explore feeding hierarchies and their effects on growth (and survival) in more detail, quantification of the strength of competitive interactions among individuals could be captured

within the IPM framework (Griffiths et al., 2020). Future work on the use of IPMs in aquaculture research that focuses on both the incorporation of size-based mechanisms for growth depensation as well as mortality would be promising extensions.

Authors' contributions:
A.S.J., J.L.B., C.G.C. and S.H. conceived the original ideas for the investigation and methodology; J.E.S. and S.P.W. collected the data as well as providing critical comments at the different stages of the manuscript; A.S.J., J.L.B. and S.W. performed the statistical analysis. A.S.J. led the writing of the manuscript under supervision of J.L.B., C.G.C. and S.H. All authors contributed critically to the drafts and gave final approval for publication.

Statement of inclusion:
Our study brings together authors from a number of different countries, including scientists based in the country where the study was carried out. This study made use of existing data collected for industry research and development. The outcomes of this study were shared with local stakeholders. Whenever relevant, literature published by scientists from the region was cited.

Conflict of interest:
The authors have no conflicts of interest to declare.

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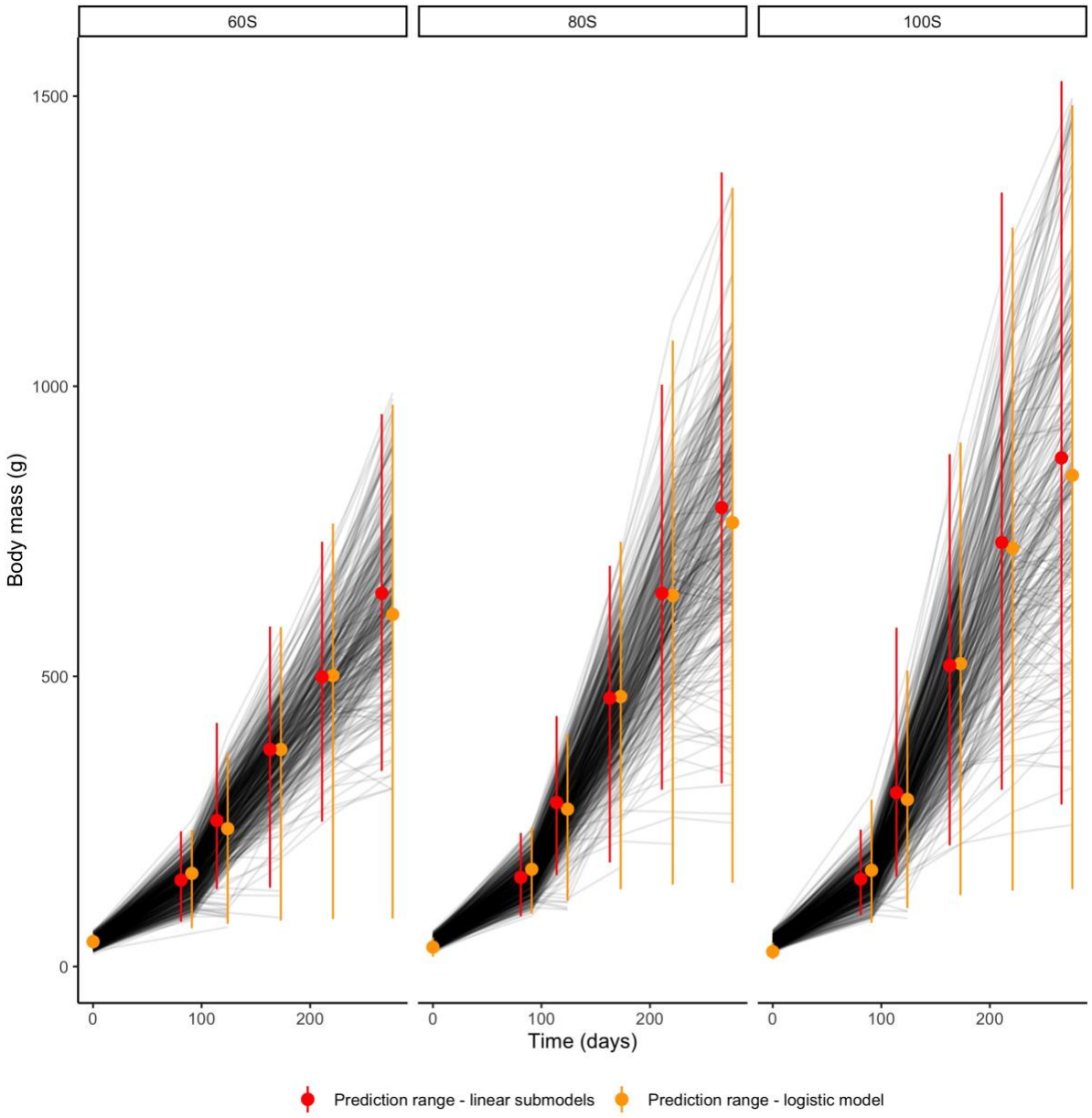

639
640 Figure 1. The predictions of the non-linear mixed-effects (logistic) model (orange) and the
641 linear regression models fitted to the time increment subsets (red – offset by -10 days on the
642 x-axis) of the observed individual growth trajectories (grey lines).

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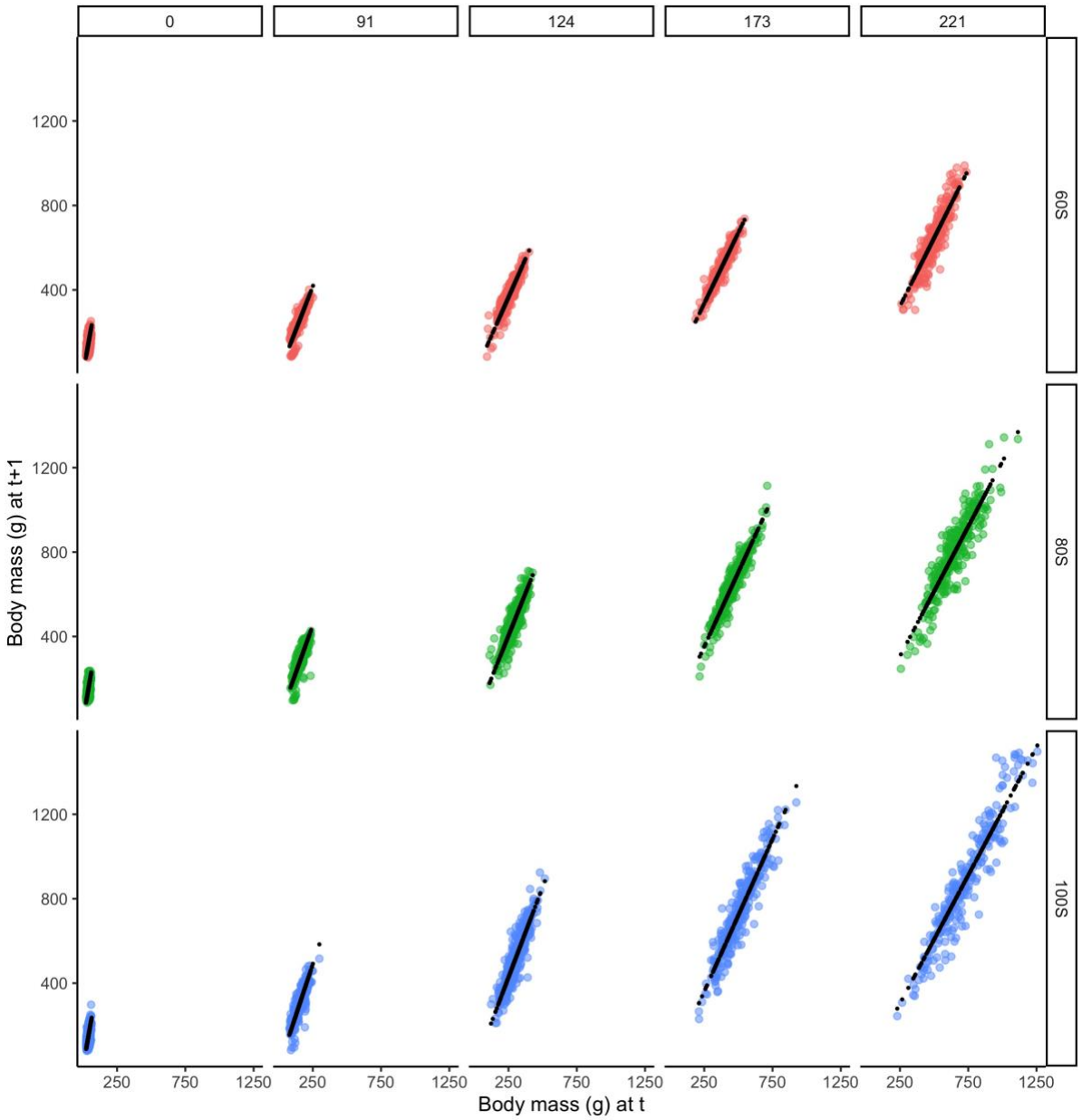

644

645 Figure 2. Linear model predictions over data for body mass (g) at time *t* against body mass at

646 *t+1*. Each column represents one of five time increments (time t to time t+1), named after the

647 number of days representing time t (i.e. day 0, day 91, day 124, etc.), and each row represents

648 one of the three ration treatments 60S, 80S and 100S. Each panel shows the experimental

649 observations (coloured points) as well as the fitted mean of the growth regressions $E(w_{t+1})$

650 (black points).

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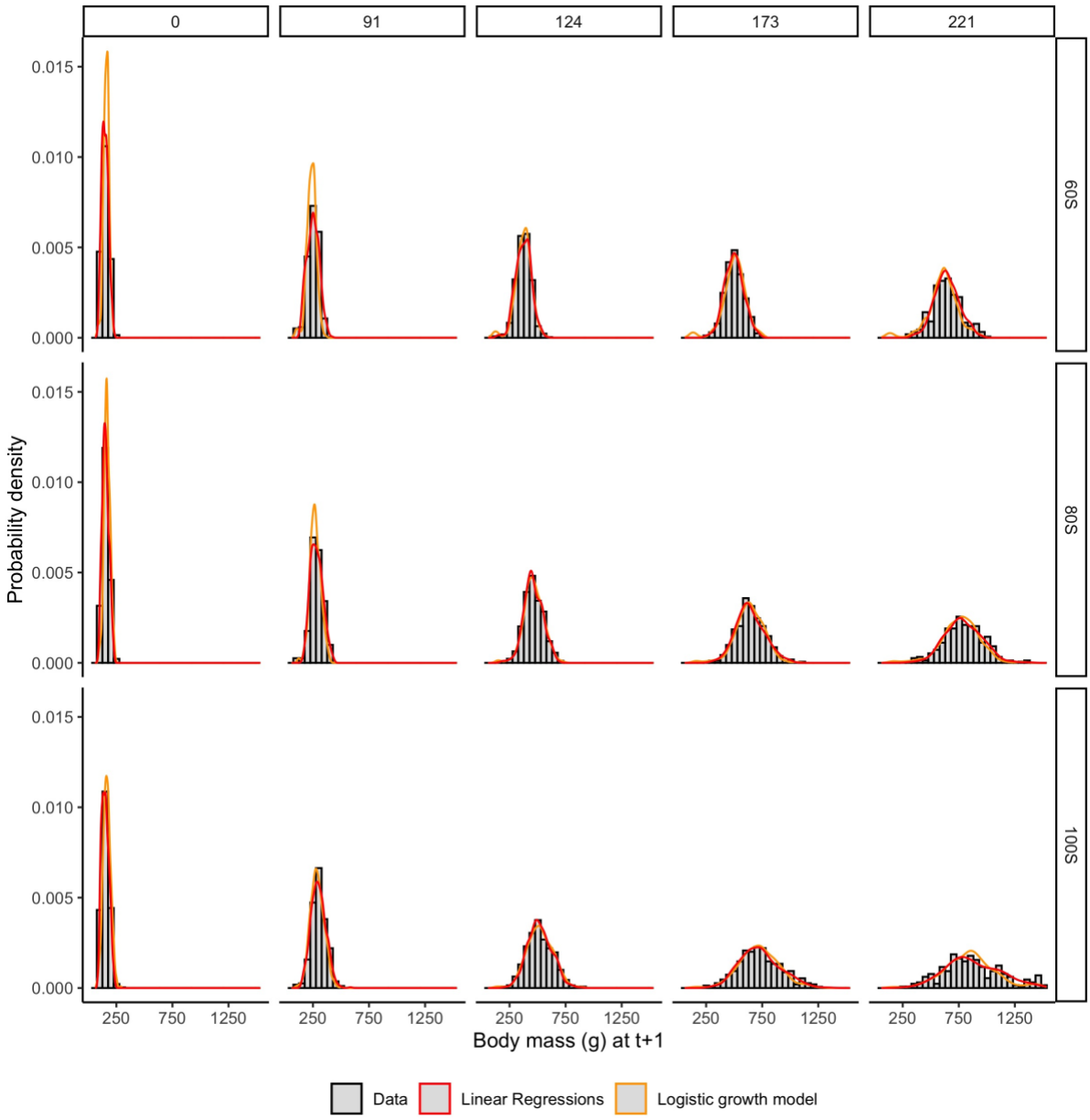

652

653 Figure 3. The black histograms depict the probability density distributions of observed body
654 mass w_{t+1} while the overlaid red (linear regressions) and orange (logistic model) lines
655 represent the probability densities of predicted body mass w_{t+1} from the growth models. Each
656 column represents one of five time increments (time t to time t+1), named after the number of
657 days representing time t (i.e. day 0, day 91, day 124, etc.), and each row represents one of the
658 three ration treatments 60S, 80S and 100S.

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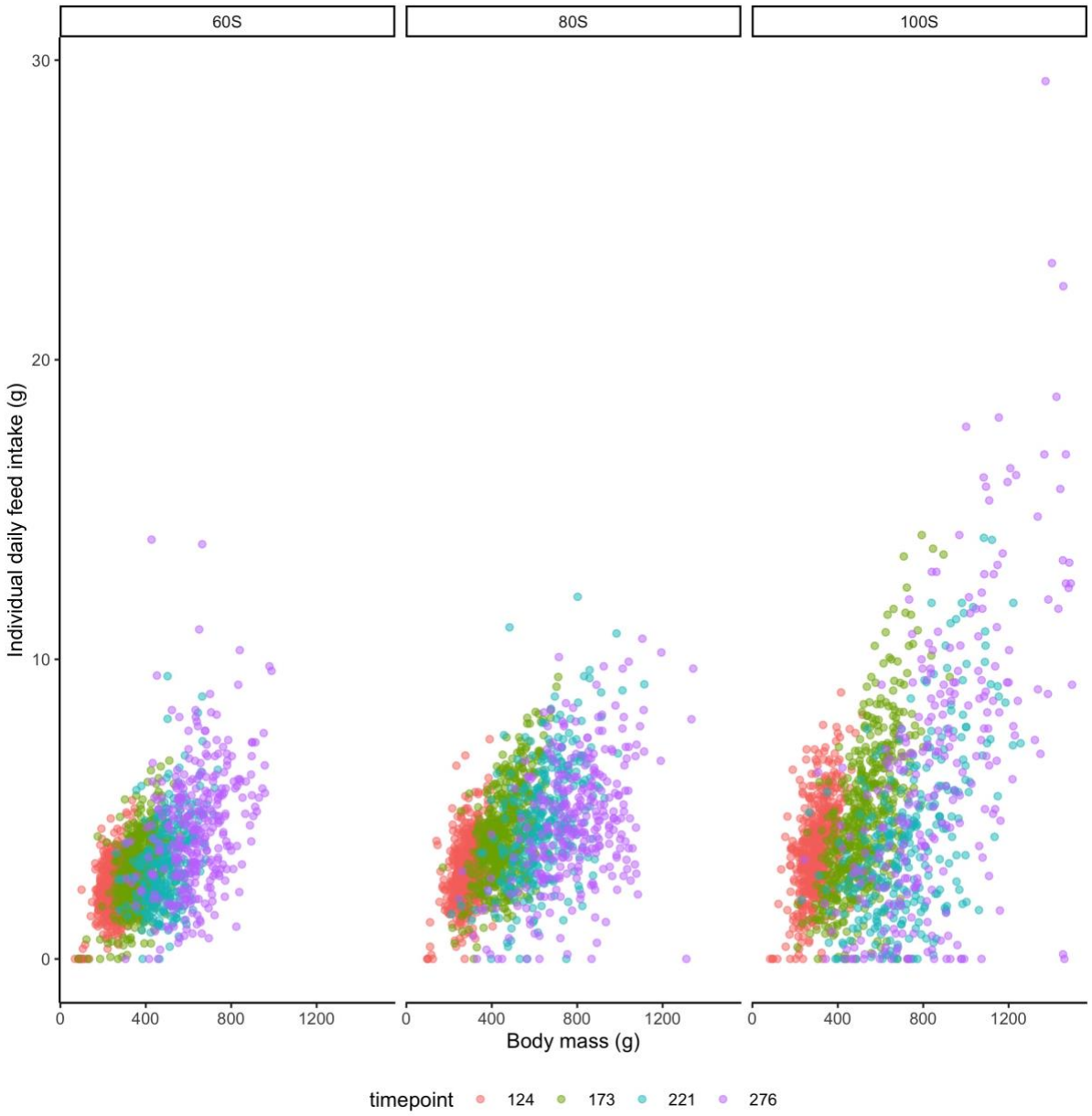

661

662 Figure 4. Individual daily feed intake (g) measured using the x-ray “ballotini” bead method at
663 four different timepoints (days 124, 173, 221, 276) and plotted against individual wet weight
664 (g). Mean and standard deviation of individual feed intake increase with body size and ration
665 level. It appears that the 60S and 80S rations result in less variable daily feed intake
666 compared to the 100S ration.

667