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

Alexandra Johne[1], Chris Carter[1], Simon Wotherspoon[2], Scott Hadley[1], Jane Symonds[3], Seumas Walker[3], and Julia Blanchard[1]

[1]University of Tasmania Institute for Marine and Antarctic Studies
[2]Australian Antarctic Division
[3]Cawthron Institute

July 26, 2022

## Abstract

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.

1

1  **Integral projection model reveals differences in individual growth performance and**

2  **body mass distributions in response to three different rations in a large aquaculture**

3  **experiment**

4

5

6  Alexandra S. Johne[1]

7  Chris G. Carter[1]

8  Simon Wotherspoon[2]

9  Scott Hadley[1]

10  Jane E. Symonds[1,3]

11  Seumas P. Walker[3]

12  Julia L. Blanchard[1]

13

14  [1] Institute for Marine and Antarctic Studies, University of Tasmania, 20 Castray Esplanade,

15  Hobart, Tasmania, Australia

16  [2] Australian Antarctic Division, Kingston, Tasmania, Australia

17  [3] Cawthron Institute, Nelson, 7010, New Zealand

18

19  Corresponding author:

20  Alexandra Johne

21  Email: alexandra.johne@utas.edu.au

22    Summary

23

24    Fed aquaculture is one of the fastest growing and most valuable food production industries.

25    The efficiency with which farmed fish convert feed into biomass influences both

26    environmental impact and economic revenue. Salmonid species, such as king salmon

27    (*Oncorhynchus tshawytscha*), exhibit high levels of plasticity in vital rates such as feed intake

28    and growth rates. Accurate estimations of individual variability in vital rates are important for

29    production management. The use of mean trait values to evaluate feeding and growth

30    performance can mask individual-level differences that potentially contribute to

31    inefficiencies. Here, we apply an integral projection model (IPM) to investigate individual

32    variation in growth performance of 1625 individually tagged king salmon fed one of three

33    distinct rations and tracked over 276 days. To capture the observed sigmoidal growth, we

34    compared a non-linear mixed-effects (logistic) model to a linear regression model used

35    within the IPM framework. Ration significantly influenced several aspects of growth. Mean

36    final body mass and mean growth rate increased with ration, however, variance in body mass

37    and feed intake also increased significantly over time. Trends in body mass mean and

38    variance were captured by both logistic and linear models, suggesting the linear model to be

39    suitable for use in the IPM. Higher rations resulted in a decreasing proportion of individuals

40    reaching the cohort's mean size or larger by the end of the experiment. This suggests that, in

41    our trial, feeding to satiation did not produce the desired effects of efficient and uniform

42    growth in juvenile king salmon. While monitoring individuals through time is challenging in

43    commercial aquaculture settings, recent technological advances combined with an IPM

44    approach could provide new scope for tracking growth performance in experimental and

45    farmed populations. The IPM framework also allows the exploration of other size-dependent

46    processes affecting vital rate functions, such as competition and mortality.

2

51

## 1. Introduction

53

54         Over the past three decades, the aquaculture sector has been one of the fastest

55    growing food production sectors by annual growth rate (FAO, 2018). Among the multitude of

56    finfish species cultured worldwide, salmonids are some of the most valuable  (FAO, 2016).

57    Salmonid production is projected to continue to grow, but meeting the nutrient requirements

58    of salmonids and consumer expectations regarding the nutrient profile of salmon products has

59    become more challenging due to marine resource limitations (FAO, 2020). Sustainable

60    industry growth requires further improvements in feed innovation and management, to

61    successfully balance fish growth performance, environmental impacts, and the nutrient

62    composition of salmon products (Froehlich et al., 2018; Shepherd & Jackson, 2013).

63

64         For commercial aquaculture to be successful, fish cohorts are required to grow rapidly

65    and uniformly to what is considered a usable size at the minimum cost of resources and

66    capital (Timmons et al., 2002). A well-informed feeding regimen can increase the likelihood

67    of optimum growth, reduce costs, and decrease environmental impacts from waste outputs

68    (Davidson et al., 2016). Despite  extensive monitoring and control opportunities, estimating

69    cohort properties such as growth rates, fish size distributions, and total biomass in

70    experimental or commercial fish populations poses challenges. Particularly in commercial

71    farms, true cohort values are often impossible to obtain due to the extensive sampling effort

72 involved and the negative effects of stress on the fish (Nilsson & Folkedal, 2019; Shieh &

73 Petrell, 1998). These are key inputs for many important decisions in the production process,

74 such as feed ration assignment, feed cost calculations, harvest planning, and estimation of

75 production yield (Føre et al., 2018; Lugert et al., 2016). Similarly, aquaculture experiments

76 continue to use mean body size as the primary currency by which studies measure the success

77 of experimental treatments in growth trials. The use of mean trait values, however,

78 potentially masks the meaningful effects of individual variation on cohort-level processes

79 (Fritschie & Olden, 2016). Furthermore, small biases in size distribution or biomass estimates

80 may produce significant deviations in scientific, management and economic outcomes

81 (Nilsson & Folkedal, 2019). Size-structured population models highlight the importance of

82 investigating growth variability and might be able to provide new insights into the

83 mechanisms that determine size variability of cohorts in aquaculture research.

84

85         Size-structured population models that incorporate individual-level variation are

86 useful for the exploration of population dynamics and ecosystem feedbacks (e.g. Filipe &

87 Kyriazakis, 2019; Griffiths et al., 2020; Vincenzi et al., 2014). The common denominator is

88 the understanding of body size as the fundamental functional trait  that influences organismal

89 vital rates such as metabolism, uptake, mortality, and reproduction rates. Individual vital rates

90 are then integrated and scaled up to the population, community or ecosystem level (Andersen

91 et al., 2016; Blanchard et al., 2017). Both the mean body size and the individual variation

92 around the mean, i.e. the frequency distribution of body size, are impacted by variation in

93 internal and external factors. Following Jensen's inequality, the aggregate sum of any

94 function that scales allometrically will be altered at the population level should either the

95 mean or the size distribution around the mean change (Fritschie & Olden, 2016). Therefore, it

96 is necessary to select a size-structured model approach which allows the projection of both

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

98  projection model.

99

100  Integral projection models (IPMs) are size-structured models that describe how

101  populations structured by continuous individual-level state variables change in discrete time

102  (Easterling et al., 2000). These models perform well with body size as the state variable.

103  Deterministic IPMs are data-driven and parameterised with simple regressions that relate an

104  individual's state to its vital rates, such as growth, survival and reproduction (Coulson, 2012;

105  Merow et al., 2014). The core of the IPM is the kernel which is the function that predicts how

106  the body size distribution of a population changes from one time step to the next. In addition

107  to the mean change in the state variable at the population level, the IPM allows the flexible

108  modelling of the changes in variance. The level of complexity of the biological processes

109  included in the model is determined by the extent and quality of the available data. One

110  exceptional feature of IPMs is that they provide insights into mechanistic population-level

111  processes from individual-level observations that cannot easily be inferred from statistical

112  models of vital rates alone, while remaining computationally simple. So far, IPMs have been

113  employed in ecological studies to estimate population growth rates under variable

114  environmental conditions (Coulson, 2012; Ellner & Rees, 2006; Heather et al., 2018). This

115  type of growth modelling has been shown to accurately capture growth trajectories in many

116  plant and animal species, including fishes (e.g. Heather et al., 2018; White et al., 2016). To

117  the authors' knowledge, the present study will be the first application of an IPM in

118  aquaculture.

119

120  To adapt the IPM framework for application in aquaculture it is necessary to identify

121  the relevant biological processes and select a state variable that allows inferences about said

122 processes. The present study uses body mass as the state variable, measured in grams of wet

123 weight, because body mass is a key determinant of fish performance in aquaculture. Since

124 grow-out and reproduction are isolated operations in commercial aquaculture, and because

125 the experimental animals were pre-reproductive juveniles, with negligible mortality rates,

126 only growth rates are considered. We use the IPM to assess the effects of ration on individual

127 growth performance in New Zealand King or Chinook salmon (*Oncorhynchus tshawytscha*)

128 reared in a freshwater recirculation aquaculture system (RAS). The advantage of using data

129 from RAS is that the majority of biotic and abiotic factors are kept stable and can hence be

130 excluded from the analysis. This case study is ideal because the experimental fish had not

131 undergone extensive selective breeding and their performance with respect to growth and

132 feed efficiency remains highly variable (Araujo et al., 2021; Semeniuk et al., 2019).

133

134 **2. Materials and methods**

135

136 The current project made retrospective use of data and did not require Animal Ethics

137 approval. The experimental setup has previously been described in detail by Esmaeili et al.

138 (2021) and Zhao et al. (2021). Below we focus only on the aspects of the experiment vital to

139 this study.

140

141 2.1 King salmon growth trial dataset

142

143 A single cohort of all-female king salmon juveniles were sourced from a local

144 hatchery (Clearwater Hatchery, Mt Cook Alpine Salmon, Twizel, New Zealand), where the

145 fish were individually implanted with a passive integrated transponder (PIT) tag (HID

146 Global, EM4305 684,230, 12 mm glass tags). The growth trial was conducted over a period

147    of 276 days in the Finfish Research Centre (FRC) at the Cawthron Aquaculture Park (CAP),

148    New Zealand. After a 21-to-24-day acclimation period to tank conditions at 15°C, 1625 fish

149    (average wet weight ± SD: 40.67 ± 8.13 g, wet weight range: 21.14g – 63.75 g) were

150    haphazardly distributed amongst nine 8000 L circular freshwater tanks. The initial stocking

151    was 176 to 187 fish per tank with a coefficient of variation for wet weight between 16% and

152    21%. Throughout the experiment, water temperature was maintained at $17 \pm 0.5$°C and

153    photoperiod was set to 24 h continuous light to prevent early maturation.

154

155    2.2 Feeding regimes and sampling

156

157        The experiment tested the effects of three feed rations, 60%, 80%, or 100% satiation

158    (n=3) on growth performance. One extruded feed with pellet sizes of 4 mm and 6 mm was

159    used throughout the experiment (Tasman Freshwater experimental diet, Ridley, Australia).

160    Fish were handfed one meal per day. The 100% satiation ration was determined by hand

161    feeding until apparent satiation, defined as the time when the feeding response of all

162    individuals within a tank had ceased. The respective feed amounts for the 60% and 80% feed

163    ration treatment groups were calculated using a feed model based on daily observations of

164    feed amount consumed by the 100% satiation treatment group and adjusted for predicted

165    average weight and tank biomass. For simplicity, the rations of 60%, 80% and 100% satiation

166    will be referred to as treatments 60S, 80S, and 100S, respectively. Fish were removed if they

167    ceased feeding or lost weight, or for biomass reduction at the later stages of the experiment.

168    Tank feed intake was measured daily: uneaten pellets were collected, counted, and subtracted

169    from the weight of feed delivered. In addition to repeated measurements of individual wet

170    weight and fork length under anaesthesia (65 ppm tricaine methane sulfonate (Syndel,

171    Canada)) on six occasions (days 0, 91, 124, 173, 221 and 276), individual daily feed intake

172    (DFI) was quantified using the x-ray "ballotini" bead method (McCarthy et al., 1993; Talbot

173    & Higgins, 1983; Walker et al., 2012) on days 124, 173, 221 and 276.

174

175    2.3 Integral projection model of the king salmon experiment

176

177         An IPM describes the probability density distribution of the body mass $w_i = w(t_i)$ of

178    a population at a sequence of discrete times $t_1, t_2, \ldots, t_n$ (Coulson, 2012). An IPM assumes

179    that the body mass $w_{i+1}$ of an individual at time $t_{i+1}$, conditional on its body mass $w_i$ at time

180    $t_i$, is given by the growth kernel $G(w_{i+1}|w_i, t_i)$. If the probability density distribution of

181    body masses at time $t_i$ is $n(w_i, t_i)$, it follows that (Rees et al., 2014) the probability density

182    distribution of body masses at time $t_{i+1}$ is

183

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

184

185    The growth kernel can relate the body mass at each time to the body mass at the previous

186    time through a linear model. If conditional on $w_i$, the body mass $w_{i+1}$ is normally distributed

187    with mean $\beta_{0i} + \beta_{1i}w_i$ and variance $\varsigma_i^2$,

188

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

189

190    and the body masses at time $i$ are also normal with mean $\mu_i$ and variance $\sigma_i^2$

191

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

192

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

194

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

195

196 and variance

197

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

198

199 The model parameters $\beta_{0i}$, $\beta_{0i}$, and $\varsigma_i^2$ 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

211  time (see Supplementary material for a more detailed description of the logistic model). The

212  logistic model can be expressed in terms of the weight $w_i = w(t_i)$ at time $t_i$

213

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

214

215  Expanding this expression in a Taylor Series in $w_i$ yields

216

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

217

218  This relation approximates the growth kernel of the IPM, and suggests the coefficients of the

219  linear regressions for the IPM should be approximately $\beta_{0i} = 0$ and $\beta_{1i} = e^{-k(t_{i+1}-t_i)}$.

220  All calculations were performed using the open-source software R (R Core Team, 2020).

221

## 3. Results

223

224      The linear regressions fitted to the time increment subsets of each ration agreed

225  closely with the predicted body size means from the logistic model as well as the data (Figs

226  1–2). The main difference between the model predictions of the two approaches was that the

227  linear regressions did not include predictions for low-performance individuals that had been

228  removed during a previous sampling interval while the logistic model did.

229

230    [Figure 1]

231

232         The goodness of fit of the linear regressions and the logistic model was assessed by

233    calculating the percentage error (PE) between the predicted mean body size and the observed

234    mean body size for each ration treatment group at each time point or time interval.

235    Interestingly, the highest deviation between observed mean body size and predicted mean

236    body size for the logistic model was found at the initial time point (i.e. $w_0$) for the 80S (18%

237    PE) and 100S (36% PE). Similarly, the linear regression predictions deviated most from the

238    observations during the first time increment (60S: 1.42%; 80S: 1.49%, 100S: 1.50%).

239    Predicted mean final body size, $w_{max}$, in the logistic model deviated less from the observed

240    values for all ration sizes, and the PE decreased with increasing ration size (60S: 5.37%; 80S:

241    3.04%; 100S: 2.97%). This trend for the last time interval was partially mirrored by the linear

242    regressions (60S: 0.31%; 80S: 0.24%; 100S: 0.46%). Mean percentage error (MPE) was

243    calculated as the mean of all PEs for each ration treatment over the entire experimental

244    period. For the logistic model, MPE was lowest for the 60S treatment at 3.97%, followed by

245    the 80S treatment at 5.7% and 9.12% for the 100S treatment. The higher MPEs of the 80S

246    and 100S treatments were significantly influenced by the deviation between observed and

247    predicted mean initial sizes ($w_0$, cf. Table 1 Supplementary Material). For the linear

248    regressions, the MPEs for all treatments were significantly lower than those of the logistic

249    model and the differences in MPE between the treatments was negligible at 0.57% for the

250    60S treatment, followed by the 80S treatment at 0.54% and the 100S treatment at 0.53%.

251

252    [Figure 2]

253

254        In addition to the growth trajectories, we visually compared the probability density

255    distributions of observed vs. predicted body mass (Fig. 3). Again, we found the predictions to

256    mirror the observations, capturing details such as a slight right-skew in the distributions of

257    the final time increments for the 60S and 80S treatments as well as the right-skew in the

258    penultimate time increment and the bimodality that is indicated in the last time increment of

259    the 100S treatment group (see Fig. 3, column five for the 60S and 80S treatment groups, and

260    columns four and five for the 100S treatment group).

261

262    [Figure 3]

263

264        Overall, ration size significantly influenced several aspects of growth, both at the

265    individual and at the cohort level. Mean final size as well as mean growth rate were

266    considerably augmented by increased ration size (see Fig. 1). Variance also significantly

267    increased with ration size through time (cf. Figs 1, 3). The initial coefficients of variation

268    (CVs) were found to be similar for all treatment groups, 19.9% in the 60S treatment group,

269    18.9% and 21.05% in the 80S and 100S treatments, respectively. While the variance

270    remained relatively constant in the 60S treatment group (final CV = 20.65%), the CVs of the

271    80S and 100S treatments were substantially elevated at 23% and 30.6%, respectively, by the

272    end of the experiment. This became especially evident when comparing the widths of the

273    growth kernels for each ration treatment (Supplementary Material, Fig. 2). While the 60S

274    treatment resulted in a relatively narrow, almost linear band of transition probabilities across

275    all sizes $w_t$, we observed an increased fanning effect at the higher rations which indicated a

276    higher variability of achieved sizes $w_{t+1}$ from the same value $w_t$. The trends in the individual

277    daily feed intake (DFI) data mirror the trends in growth in response to ration size and

278    individual body size: both mean and variance of individual DFI increased with increasing

279    ration and body size (Fig. 4).

280

281    [Figure 4]

282

283         Additionally, we examined the proportion of the experimental cohorts that grew to the

284    respective mean size or larger by the last time point to illustrate potential management

285    implications of the respective ration treatments. In the 60S treatment, the largest proportion,

286    63.4% or 196 of 309 individuals, grew to the cohort's mean size or larger (642 – 989g),

287    followed by the 80S cohort where 58.09% or 176 of 303 individuals reached the mean size or

288    larger (791 – 1343g). In the 100S treatment, less than half of the cohort, namely 48.44% or

289    124 of 256 individuals, grew to the cohort mean size or larger (873 – 1497g).

290

291    **4. Discussion**

292

293         Overall, our study demonstrates that feeding to satiation achieved the highest mean

294    and maximum growth rates but resulted in highly variable final body masses. Our results thus

295    question whether the common aquaculture practice of feeding to satiation produces the

296    desired effects of efficient, fast, and uniform growth in king salmon. They also highlight the

297    potential shortcomings of approaches that report growth in terms of mean and standard

298    deviation and demonstrate the importance of exploring the size structure of a fish cohort and

299    the processes that yield certain body mass distributions. One of the strengths of the IPM

300    framework that makes it very suitable to this kind of investigation is the mechanistic

301    projections of deterministic vital rate functions, such as growth rate, which allows insights

302    into cohort-level processes.

303

304      Improving fish growth performance while reducing the environmental footprint and

305    maintaining economic viability has been the main goal of empirical aquaculture research for

306    decades. Because aquaculture feed formulations rely on limiting resources and are the single

307    largest expense in fed aquaculture enterprises, with a share in production costs of over 50%

308    (Iversen et al., 2020), the sustainability of the sector depends on the continuous improvement

309    of feed formulations and feeding practices (e.g. Carter & Houlihan, 2001; Hasan & Soto,

310    2017).

311

312      Ration size is one of the most influential feeding regime factors and is readily

313    manipulated to enhance the likelihood of optimum growth as well as lower costs and

314    environmental impact from uneaten pellets or waste outputs (Davidson et al., 2016). Our

315    study on the growth performance of a cohort of all-female, juvenile king salmon fed three

316    rations of 60% (60S), 80% (80S) and 100% satiation (100S) for 276 days demonstrates that

317    there are large differences in mean and individual-level growth performance under different

318    feeding regimes. In accordance with earlier studies in salmonids, the data of the present study

319    showed that mean growth in the high ration group (100S) significantly exceeded mean

320    growth of the intermediate (80S) and the low ration groups (60S) (e.g. Kiessling et al., 2005;

321    Mazur et al., 1993; Shearer et al., 1997). The proportion of fish, however, that reached a body

322    size equal to the treatment group mean or larger decreased with increasing ration size, raising

323    questions about the efficiency of feeding to satiation. In contrast to previous findings, the

324    variance in growth performance as approximated by variance in body mass increased

325    significantly with ration size and over time. Davis and Olla (1987) as well as McCarthy et al.

326    (1992) had reported that reduced rations resulted in higher variability in growth rate than

327    medium or high ration sizes due to presumably higher competition under resource limitation.

328

329       Disproportionate growth and an increase in the variance in body mass or feed intake

330    have previously been attributed to the preferential acquisition of feed by dominant

331    individuals and interpreted as indicators of interference competition for resources, also called

332    a feeding hierarchy (Jobling, 1995). Within a strong feeding hierarchy, a small number of

333    dominant fish monopolise feed which may result in faster growth and larger body sizes.

334    Meanwhile, the feeding activity of subordinate fish is supressed, as they consume smaller

335    meals (Metcalfe, 1986; Ryer & Olla, 1996). The trends in individual daily feed intake and the

336    right-skewed or bimodal probability density distributions of body mass might indicate the

337    establishment of such feeding hierarchies as a source of the increased growth variability in

338    the treatment groups 80S and 100S towards the end of the experiment. During hand feeding,

339    the 60S and 80S fish exhibited a strong feeding response and completed their meals quickly,

340    whereas the feeding response was more variable in the 100S fish, with slower feeding. This

341    could have allowed more dominant fish to eat larger meals (Ryer & Olla, 1991; Thorpe et al.,

342    1990). Although the directionality of the relationship between individual body mass and

343    dominance status is contested, generally larger fish have been found to be more dominant in

344    husbandry conditions (Huntingford et al., 1990; Metcalfe et al., 1992).

345

346       Individual variation is increasingly recognised by ecologists and fisheries scientists as

347    important parameter for understanding and predicting the dynamics of wild populations and

348    their interactions with the surrounding ecosystem (e.g. Fritschie & Olden, 2016). Because

349    morphological and physiological functions scale allometrically with body mass, focussing

350    solely on the mean body mass will potentially bias predictions at the population level, when

351    there is high variance (Fritschie & Olden, 2016). Environmental variables, such as

352    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

378  (Higgs et al., 1995; Leblanc et al., 2019; Salin et al., 2019). Despite king salmon being a

379  commonly farmed species in New Zealand, not all the farmed stocks are selectively bred and

380  commercially important traits such as feed consumption, feed efficiency and growth remains

381  highly variable (Araujo et al., 2021; Esmaeili et al., 2021; Semeniuk et al., 2019; Walker et

382  al., 2012). The absence of systematic control of intraspecific genotypic variation and the

383  resulting phenotypic differences are likely to lead to divergent individual growth trajectories

384  in a controlled environment and under different resource availability treatments (Leblanc et

385  al., 2019; Semeniuk et al., 2019). Future applications of IPMs in aquaculture might consider

386  the inclusion of terms that allow the representation of phenotypic variability in factors that

387  contribute to growth variability and have been shown to affect dominance status, such as

388  standard metabolic rate (Cutts et al., 1998; Metcalfe et al., 1995).

389

390      Our study shows that deterministic IPMs are powerful tools to investigate processes

391  that shape a population's demography from the individual level. The employment of

392  phenomenological methods such as regression models makes this approach flexible and

393  accessible to practitioners. The deterministic core of the approach, however, means that

394  results can only be interpreted for the exact conditions of the underlying experiment. For the

395  prediction of aquaculture cohort responses to a changing environment, the incorporation of

396  fully mechanistic model formulations such as the dynamic energy budget into an IPM could

397  be instructive (e.g. Smallegange et al., 2017). Additionally, extending the IPM using Markov

398  chain theory (Tuljapurkar, 1990) might allow the model to represent stochastic processes,

399  such as variation in environmental factors or interactions between individual fish, which may

400  increase the approach's explanatory power and aid with capturing the observed variance. To

401  explore feeding hierarchies and their effects on growth (and survival) in more detail,

402  quantification of the strength of competitive interactions among individuals could be captured

403    within the IPM framework (Griffiths et al., 2020). Future work on the use of IPMs in

404    aquaculture research that focuses on both the incorporation of size-based mechanisms for

405    growth depensation as well as mortality would be promising extensions.

406

407

436

437

438    References
439    Andersen, K. H., Berge, T., Gonçalves, R. J., Hartvig, M., Heuschele, J., Hylander, S.,
440        Jacobsen, N. S., Lindemann, C., Martens, E. A., Neuheimer, A. B., Olsson, K., Palacz,
441        A., Prowe, A. E. F., Sainmont, J., Traving, S. J., Visser, A. W., Wadhwa, N., & Kiørboe,
442        T. (2016). Characteristic Sizes of Life in the Oceans, from Bacteria to Whales. *Annual
443        Review of Marine Science*, *8*(1), 217–241. https://doi.org/10.1146/annurev-marine-
444        122414-034144
445    Araujo, B. C., Symonds, J. E., Glencross, B. D., Carter, C. G., Walker, S. P., & Miller, M. R.
446        (2021). A review of the nutritional requirements of chinook salmon (*Oncorhynchus*

*tshawytscha*). *New Zealand Journal of Marine and Freshwater Research*, *0*(0), 1–30.
https://doi.org/10.1080/00288330.2021.1985530

Blanchard, J. L., Heneghan, R. F., Everett, J. D., Trebilco, R., & Richardson, A. J. (2017).
From Bacteria to Whales: Using Functional Size Spectra to Model Marine Ecosystems.
*Trends in Ecology and Evolution*, *32*(3), 174–186.
https://doi.org/10.1016/j.tree.2016.12.003

Carter, C. G., & Houlihan, D. F. (2001). Protein Synthesis. In P. A. Wright & P. M.
Anderson (Eds.), *Nitrogen excretion, Fish Physiology Vol. 20* (pp. 31–75). Academic
Press.

Coulson, T. (2012). Integral projections models, their construction and use in posing
hypotheses in ecology. *Oikos*, *121*(9), 1337–1350. https://doi.org/10.1111/j.1600-
0706.2012.00035.x

Cutts, C. J., Metcalfe, N. B., & Taylor, A. C. (1998). Aggression and growth depression in
juvenile Atlantic salmon: The consequences of individual variation in standard
metabolic rate. *Journal of Fish Biology*, *52*(5), 1026–1037.
https://doi.org/10.1006/jfbi.1998.0647

Davidson, J., May, T., Good, C., Waldrop, T., Kenney, B., Terjesen, B. F., & Summerfelt, S.
(2016). Production of market-size North American strain Atlantic salmon *Salmo salar* in
a land-based recirculation aquaculture system using freshwater. *Aquacultural
Engineering*, *74*, 1–16. http://10.0.3.248/j.aquaeng.2016.04.007

Davis, M. W., & Olla, B. L. (1987). Aggression and Variation in Growth of Chum Salmon
(*Oncorhynchus keta*) Juveniles in Seawater: Effects of Limited Ration. *Canadian
Journal of Fisheries and Aquatic Sciences*, *44*(1), 192–197. https://doi.org/10.1139/f87-
025

Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-specific sensitivity: Applying a
new structured population model. *Ecology*, *81*(3), 694–708.

Ellner, S. P., & Rees, M. (2006). Integral projection models for species with complex
demography. *American Naturalist*, *167*(3), 410–428. https://doi.org/10.1086/499438

Esmaeili, M., Carter, C. G., Wilson, R., Walker, S. P., Miller, M. R., Bridle, A., & Symonds,
J. E. (2021). Proteomic investigation of liver and white muscle in efficient and
inefficient Chinook salmon (*Oncorhynchus tshawytscha*): Fatty acid metabolism and
protein turnover drive feed efficiency. *Aquaculture*, *542*(October 2020).
https://doi.org/10.1016/j.aquaculture.2021.736855

FAO. (2016). *The State of World Fisheries and Aquaculture 2016 - Contributing to food
security and nutrition for all.*

FAO. (2018). *The State of World Fisheries and Aquaculture 2018 - Meeting the sustainable
development goals.*

FAO. (2020). *The State of the World Fisheries and Aquaculture 2020. Sustainability in
action.* https://doi.org/https://doi.org/10.4060/ca9229en

Filipe, J. A. N., & Kyriazakis, I. (2019). Bayesian, Likelihood-Free Modelling of Phenotypic
Plasticity and Variability in Individuals and Populations. *Frontiers in Genetics*, *10*, 727.
https://doi.org/10.3389/fgene.2019.00727

Føre, M., Alver, M., Alfredsen, J. A., Marafioti, G., Senneset, G., Birkevold, J., Willumsen,
F. V., Lange, G., Espmark, Å., & Terjesen, B. F. (2016). Modelling growth performance
and feeding behaviour of Atlantic salmon (*Salmo salar* L.) in commercial-size
aquaculture net pens: Model details and validation through full-scale experiments.
*Aquaculture*, *464*, 268–278. https://doi.org/10.1016/j.aquaculture.2016.06.045

Føre, M., Frank, K., Norton, T., Svendsen, E., Alfredsen, J. A., Dempster, T., Eguiraun, H.,
Watson, W., Stahl, A., Sunde, L. M., Schellewald, C., Skøien, K. R., Alver, M. O., &
Berckmans, D. (2018). Precision fish farming: A new framework to improve production

in aquaculture. *Biosystems Engineering*, *173*, 176–193.
https://doi.org/10.1016/j.biosystemseng.2017.10.014

Fritschie, K. J., & Olden, J. D. (2016). Disentangling the influences of mean body size and size structure on ecosystem functioning: An example of nutrient recycling by a non-native crayfish. *Ecology and Evolution*, *6*(1), 159–169. https://doi.org/10.1002/ece3.1852

Froehlich, H. E., Jacobsen, N. S., Essington, T. E., Clavelle, T., & Halpern, B. S. (2018). Avoiding the ecological limits of forage fish for fed aquaculture. *Nature Sustainability*, *1*(6), 298–303. https://doi.org/10.1038/s41893-018-0077-1

Griffiths, J. I., Childs, D. Z., Bassar, R. D., Coulson, T., Reznick, D. N., & Rees, M. (2020). Individual differences determine the strength of ecological interactions. *Proceedings of the National Academy of Sciences*, *117*(29), 17068–17073. https://doi.org/10.1073/pnas.2000635117

Hasan, M. R., & Soto, S. (2017). *Improving feed conversion ratio and its impact on reducing greenhouse gas emissions in aquaculture* (FAO Non-Serial Publication).

Heather, F. J., Childs, D. Z., Darnaude, A. M., & Blanchard, J. L. (2018). Using an integral projection model to assess the effect of temperature on the growth of gilthead seabream *Sparus aurata*. *PLoS ONE*, *13*(5). https://doi.org/10.1371/journal.pone.0196092

Higgs, D. A., Macdonald, J. S., Levings, C. D., & Dosanjh, B. S. (1995). Nutrition and feeding habits in relation to life history stage. In C. Groot, L. Margolis, & W. C. Clarke (Eds.), *Physiological ecology of Pacific salmon* (pp. 161–318). UBC Press.

Hopkins, K. D. (1992). Reporting Fish Growth: A Review of the Basics. *Journal of the World Aquaculture Society*, *23*(3), 173–179. https://doi.org/10.1111/j.1749-7345.1992.tb00766.x

Huntingford, F. A., Metcalfe, N. B., Graham, W. D., Adams, C. E., & Thorpe, J. E. (1990). Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology*, *36*(6), 877–881. https://doi.org/10.1111/j.1095-8649.1990.tb05635.x

Iversen, A., Asche, F., Hermansen, Ø., & Nystøyl, R. (2020). Production cost and competitiveness in major salmon farming countries 2003–2018. *Aquaculture*, *522*, 735089. https://doi.org/https://doi.org/10.1016/j.aquaculture.2020.735089

Jobling, M. (1995). Simple indices for the assessment of the influences of social environment on growth performance, exemplified by studies on Arctic charr. *Aquaculture International*, *3*(1), 60–65. https://doi.org/10.1007/BF00240922

Kiessling, A., Pickova, J., Eales, J. G., Dosanjh, B., & Higgs, D. (2005). Age, ration level, and exercise affect the fatty acid profile of chinook salmon (*Oncorhynchus tshawytscha*) muscle differently. *Aquaculture*, *243*(1), 345–356. http://10.0.3.248/j.aquaculture.2004.10.003

Leblanc, C. A., Horri, K., Skúlason, S., & Benhaim, D. (2019). Subtle temperature increase can interact with individual size and social context in shaping phenotypic traits of a coldwater fish. *PLoS ONE*, *14*(3), 1–21. https://doi.org/10.1371/journal.pone.0213061

Lugert, V., Thaller, G., Tetens, J., Schulz, C., & Krieter, J. (2016). A review on fish growth calculation: Multiple functions in fish production and their specific application. *Reviews in Aquaculture*, *8*(1), 30–42. https://doi.org/10.1111/raq.12071

Mazur, C. F., Tillapaugh, D., & Iwama, G. K. (1993). The effects of feeding level and rearing density on the prevalence of *Renibacterium salmoninarum* in Chinook salmon (*Oncorhynchus tshawytscha*) reared in salt water. *Aquaculture*, *117*(1–2), 141–147. https://doi.org/10.1016/0044-8486(93)90130-Q

McCarthy, I. D., Carter, C. G., & Houlihan, D. F. (1992). The effect of feeding hierarchy on individual variability in daily feeding of rainbow trout, *Oncorhynchus mykiss*

(Walbaum). *Journal of Fish Biology*, *41*(2), 257–263. https://doi.org/10.1111/j.1095-8649.1992.tb02655.x

McCarthy, I. D., Houlihan, D. F., Carter, C. G., & Moutou, K. (1993). Variation in individual food consumption rates of fish and its implications for the study of fish nutrition and physiology. *Proceedings of the Nutrition Society*, *52*(3), 427–436. https://doi.org/10.1079/pns19930083

Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E. K., Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R., & Mcmahon, S. M. (2014). Advancing population ecology with integral projection models: A practical guide. *Methods in Ecology and Evolution*, *5*(2), 99–110. https://doi.org/10.1111/2041-210X.12146

Metcalfe, N. B. (1986). Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *Journal of Fish Biology*, *28*, 525–531.

Metcalfe, N. B., Huntingford, F. A., & Thorpe, J. E. (1992). Social effects on appetite and development in Atlantic salmon. In J. E. Thorpe & F. A. Huntingford (Eds.), *The importance of feeding behavior for the efficient culture of salmonid fishes. World Aquaculture Workshops no.2* (pp. 29–40). World Aquaculture Society.

Metcalfe, N. B., Taylor, A. C., & Thorpe, J. E. (1995). Metabolic rate, social status and life history strategies in Atlantic salmon. *Animal Behaviour*, *49*(2), 431–436. https://doi.org/10.1006/anbe.1995.0056

Nilsson, J., & Folkedal, O. (2019). Sampling of Atlantic salmon *Salmo salar* from tanks and sea cages is size-biased. *Aquaculture*, *502*(December 2018), 272–279. https://doi.org/10.1016/j.aquaculture.2018.12.053

Pinheiro, J., & Bates, D. (2000). *Mixed-effects models in S and S-PLUS* (1st ed.). Springer. https://doi.org/https://doi.org/10.1007/b98882

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Rees, M., Childs, D. Z., & Ellner, S. P. (2014). Building integral projection models: A user's guide. *Journal of Animal Ecology*, *83*(3), 528–545. https://doi.org/10.1111/1365-2656.12178

Ryer, C. H., & Olla, B. L. (1991). Agonistic behavior in a schooling fish: form, function and ontogeny. *Environmental Biology of Fishes*, *31*(4), 355–363. https://doi.org/10.1007/BF00002360

Ryer, C. H., & Olla, B. L. (1996). Growth depensation and aggression in laboratory reared coho salmon: the effect of food distribution and ration size. *Journal of Fish Biology*, *48*, 686–694.

Salin, K., Villasevil, E. M., Anderson, G. J., Lamarre, S. G., Melanson, C. A., McCarthy, I., Selman, C., & Metcalfe, N. B. (2019). Differences in mitochondrial efficiency explain individual variation in growth performance. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1909), 20191466. https://doi.org/10.1098/rspb.2019.1466

Semeniuk, C. A. D., Capelle, P. M., Dender, M. G. E., Devlin, R., Dixon, B., Drown, J., Heath, J., Hepburn, R., Higgs, D. M., Janisse, K., Lehnert, S. J., Love, O. P., Mayrand, J., Mickle, M., Pitcher, T. E., Neff, B., Semple, S. L., Smith, J. L., Toews, S., … Heath, D. (2019). Domestic-wild hybridization to improve aquaculture performance in Chinook salmon. *Aquaculture*, *511*(December 2017). https://doi.org/10.1016/j.aquaculture.2019.734255

Shearer, K. D., Dickhoff, W. W., & Silverstein, J. T. (1997). Control of growth and adiposity of juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Aquaculture*, *157*(3–4), 311–323. https://doi.org/10.1016/S0044-8486(97)00170-1

Shepherd, C. J., & Jackson, A. J. (2013). Global fishmeal and fish-oil supply: Inputs, outputs and markets. *Journal of Fish Biology*, *83*(4), 1046–1066. https://doi.org/10.1111/jfb.12224

Shieh, A. C. R., & Petrell, R. J. (1998). Measurement of fish size in Atlantic salmon (*Salmo salar* L.) cages using stereographic video techniques. *Aquacultural Engineering*, *17*, 29–43.

Smallegange, I. M., Caswell, H., Toorians, M. E. M., & de Roos, A. M. (2017). Mechanistic description of population dynamics using dynamic energy budget theory incorporated into integral projection models. *Methods in Ecology and Evolution*, *8*(2), 146–154. https://doi.org/10.1111/2041-210X.12675

Talbot, C., & Higgins, P. J. (1983). A radiographic method for feeding studies on fish using metallic iron powder as a marker. *Journal of Fish Biology*, *23*(2), 211–220. https://doi.org/10.1111/j.1095-8649.1983.tb02896.x

Thorpe, J. E., Talbot, C., Miles, M. S., Rawlings, C., & Keay, D. S. (1990). Food consumption in 24 hours by Atlantic salmon (*Salmo salar* L.) in a sea cage. *Aquaculture*, *90*(1), 41–47. https://doi.org/10.1016/0044-8486(90)90281-Q

Timmons, M. B., Ebeling, J. M., Wheaton, F. W., Summerfelt, S. T., & Vinci, B. J. (2002). *Recirculation Aquaculture Systems* (2nd ed.). Cayuga Aqua Ventures.

Tuljapurkar, S. (1990). Population dynamics in variable environments. *Lecture Notes in Biomathematics*, *85*.

Vincenzi, S., Mangel, M., Crivelli, A. J., Munch, S., & Skaug, H. J. (2014). Determining Individual Variation in Growth and Its Implication for Life-History and Population Processes Using the Empirical Bayes Method. *PLOS Computational Biology*, *10*(9), 1–16. https://doi.org/10.1371/journal.pcbi.1003828

Walker, S. P., Ingram, M., Bailey, J., Dodds, K. G., Fisher, P. J., Amer, P. R., & Symonds, J. E. (2012). Chinook salmon (*Oncorhynchus tshawytscha*) feed conversion efficiency : evaluation and potential for selection. *Proceedings of the New Zealand Society of Animal Production*, *72*, 227–230.

White, J. W., Nickols, K. J., Malone, D., Carr, M. H., Starr, R. M., Cordoleani, F., Baskett, M. L., Hastings, A., & Botsford, L. W. (2016). Fitting state-space integral projection models to size-structured time series data to estimate unknown parameters. *Ecological Applications*, *26*(8), 2675–2692. https://doi.org/10.1002/eap.1398

Zhao, R., Symonds, J. E., Walker, S. P., Steiner, K., Carter, C. G., Bowman, J. P., & Nowak, B. F. (2021). Effects of feed ration and temperature on Chinook salmon (*Oncorhynchus tshawytscha*) microbiota in freshwater recirculating aquaculture systems. *Aquaculture*, *543*, 736965. https://doi.org/https://doi.org/10.1016/j.aquaculture.2021.736965

Zhou, C., Lin, K., Xu, D., Chen, L., Guo, Q., Sun, C., & Yang, X. (2018). Near infrared computer vision and neuro-fuzzy model-based feeding decision system for fish in aquaculture. *Computers and Electronics in Agriculture*, *146*(October 2017), 114–124. https://doi.org/10.1016/j.compag.2018.02.006

Zuur, A. F., Ieno, N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer.
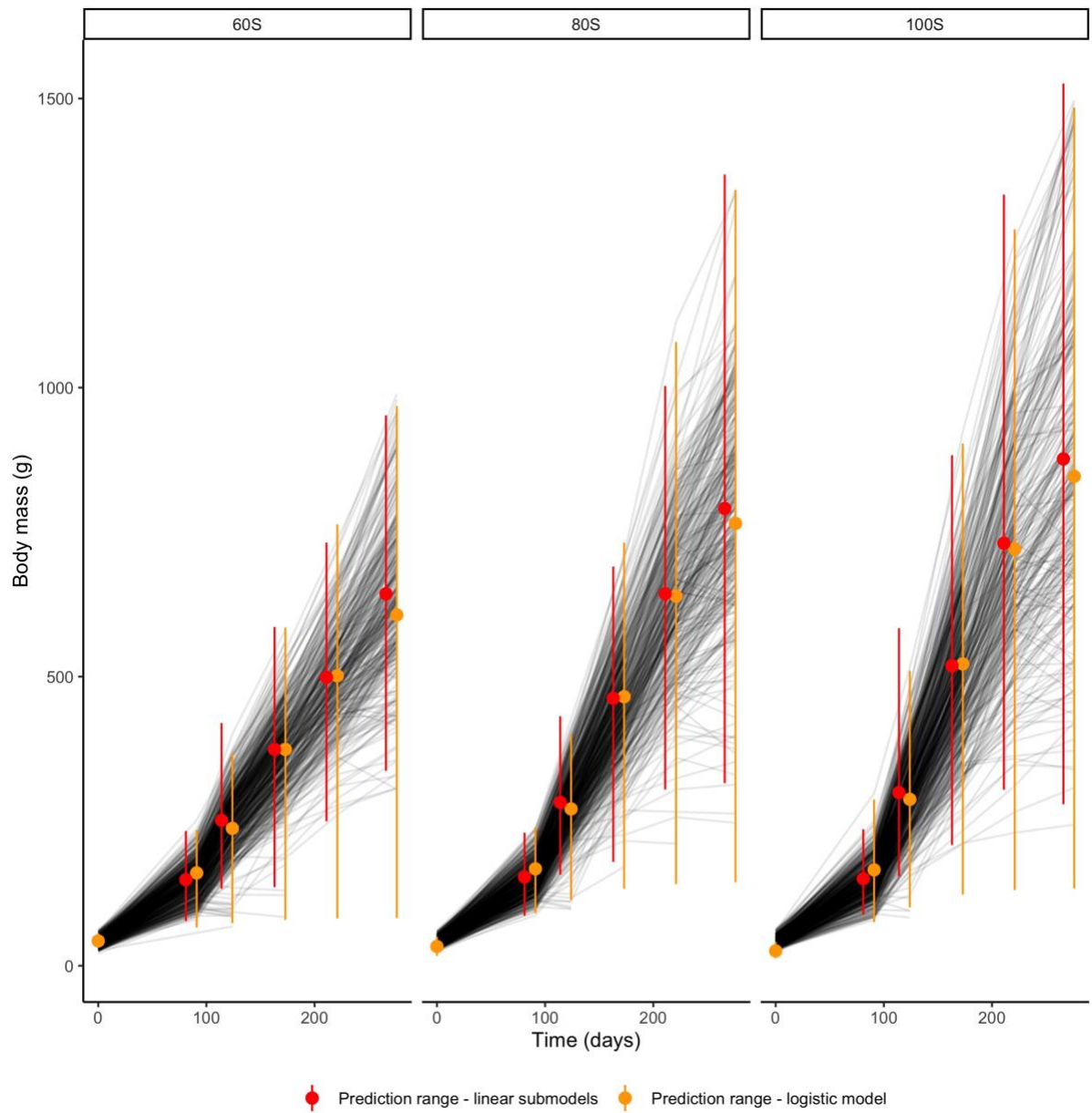
639

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

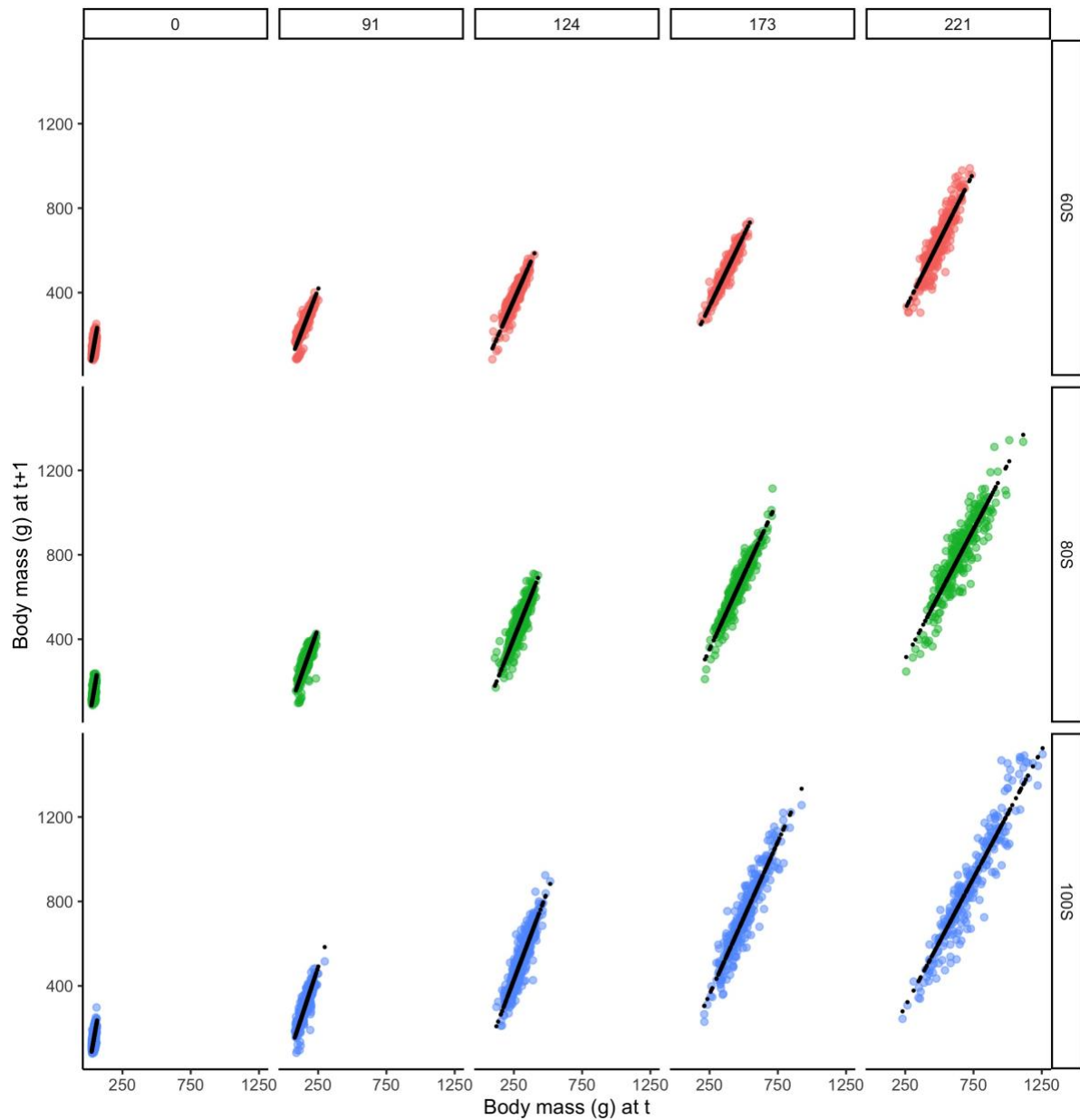642 x-axis) of the observed individual growth trajectories (grey lines).

643

644

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

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

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

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

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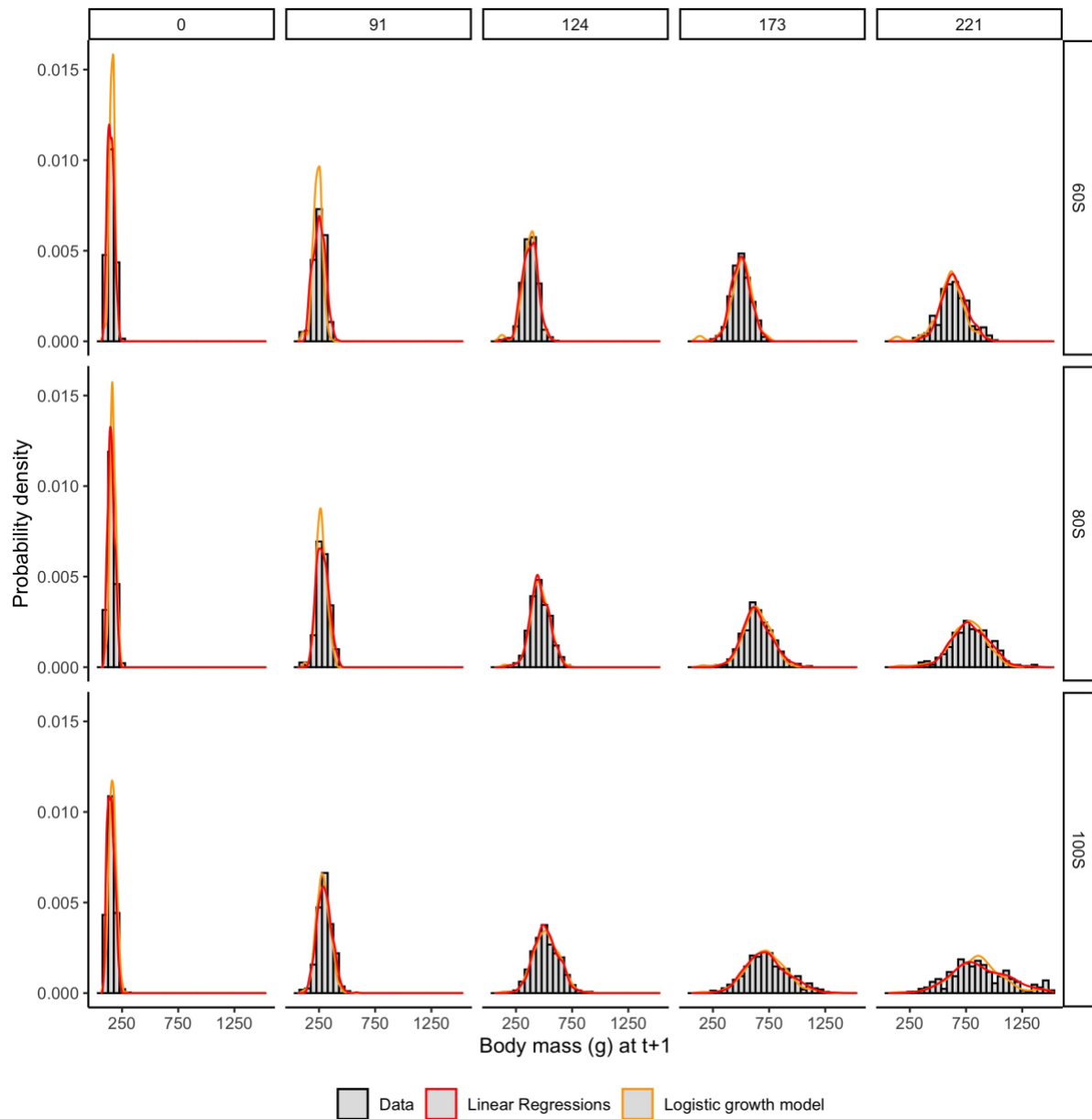
(black points).

651

Figure 3. The black histograms depict the probability density distributions of observed body mass $w_{t+1}$ while the overlaid red (linear regressions) and orange (logistic model) lines represent the probability densities of predicted body mass $w_{t+1}$ from the growth models. Each column represents one of five time increments (time t to time t+1), named after the number of days representing time t (i.e. day 0, day 91, day 124, etc.), and each row represents one of the three ration treatments 60S, 80S and 100S.
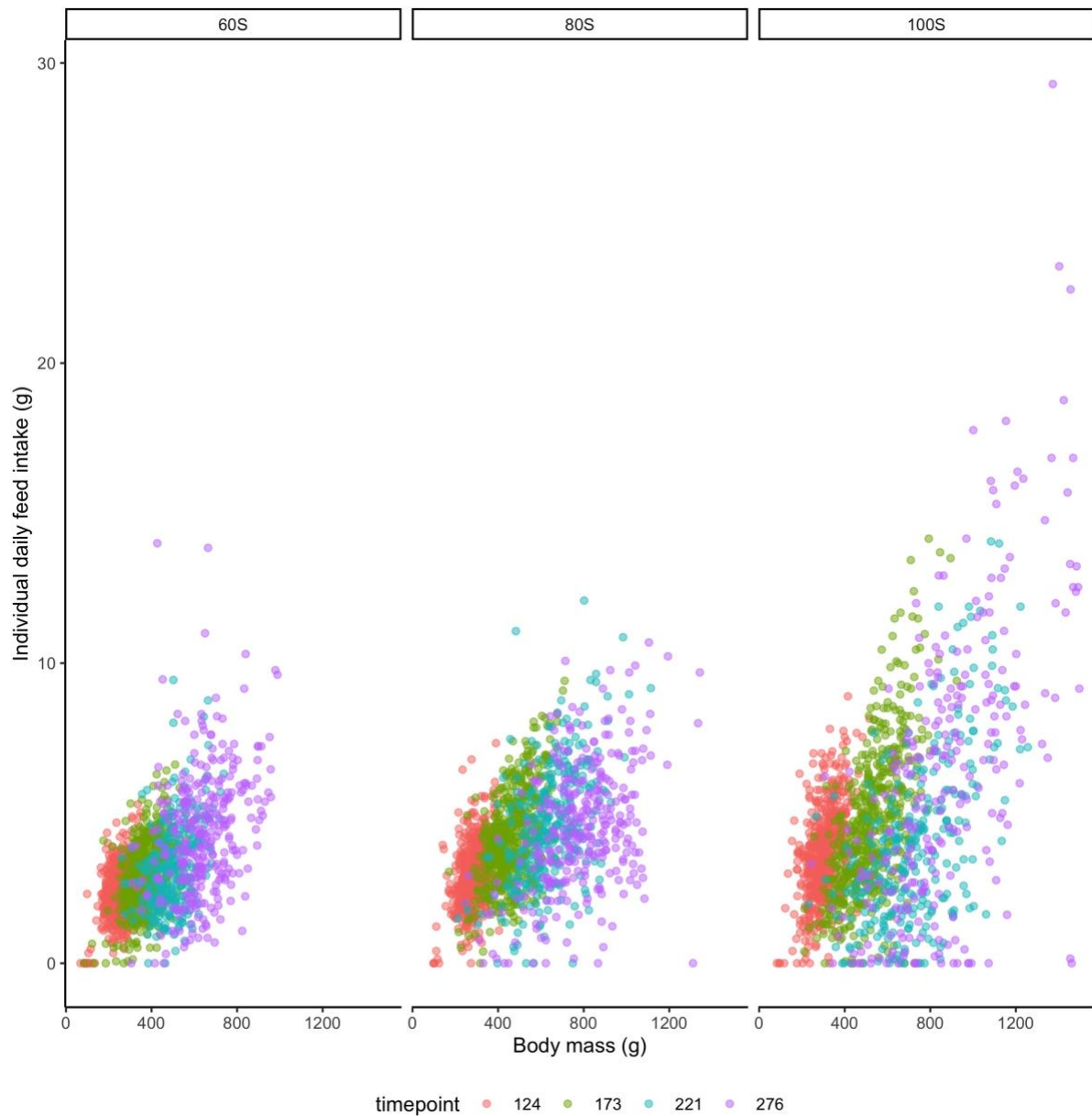
25

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

661

662

663

664

665

666

667