Title: Variation in growth among individuals and over time: a case study and simulation experiment involving tagged Antarctic toothfish

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Dear Fisheries Research Editorial Board,

RE: Variation in growth among individuals and over time: a case study and simulation experiment involving tagged Antarctic toothfish

Please find attached our paper for consideration in the special issue on Growth Modeling in Fisheries Research. In our paper we develop growth models in which we decompose variation in growth among individuals into persistent or transient components. We apply the model to a wild marine population of Antarctic toothfish and validate using a simulation study. We find that transient variation accounts for up to half of the total variability in Antarctic toothfish and the simulation study suggests that these models are approximately unbiased given the available sample sizes. While variation in growth rates is also an active area of research, our study is the first to our knowledge to apply these methods to a wild marine population.

We make the code publically available on GitHub as an R package *TagGrowth* in an attempt to encourage future research comparing the magnitude of persistent and transient variation in growth among marine populations in different taxa and environments.

All data used within this paper are owned by CCAMLR and the New Zealand Ministry for Primary Industries (MPI). The rights to use these data in our paper, and make the data publically available, were granted by MPI.

Thank you for your consideration. We look forward to hearing from you.

Yours faithfully,
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Highlights

- We decompose variation in growth among individuals into persistent (faster throughout their lifetime) or transient (faster in one year) components.

- We apply the model to a wild marine population of Antarctic toothfish and validate using a simulation study.

- Transient variation accounts for up to half of the total variability in Antarctic toothfish.

- The simulation study suggests that these models are approximately unbiased given the available sample sizes.

- The code is made publically available as an R package *TagGrowth*.

1   **Variation in growth among individuals and over time: a case study and**

2   **simulation experiment involving tagged Antarctic toothfish**

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20 **Abstract**

21 Organisms in the marine environment are likely to exhibit variation in growth rates among

22 individuals, and this variation may be persistent (particular individuals growing faster/slower

23 throughout their entire lifetime) or transient (particular individuals growing faster in one year

24 than another year). Understanding variation in growth is necessary when interpreting data

25 regarding size (length or weight) in population models, or when estimating growth given data for

26 tagged individuals. In this study, we explicitly model persistent and transient variation in growth

27 rates among individuals in a wild marine population of Antarctic toothfish (*Dissostichus*

28 *mawsoni*) in the Ross Sea, in addition to sex-specific differences in average growth rates. The

29 model is implemented using maximum marginal likelihood estimation and validated using a

30 simulation study. The code is distributed as a publicly available package *TagGrowth* in the R

31 statistical environment. Using simulated data, we show that we can accurately estimate

32 parameters representing the magnitude of persistent and transient variation in growth rates, and

33 that parameters estimated in these models are reasonably precise given the case study sample

34 sizes (315 individuals tagged and recaptured over 10 years). The case study application suggests

35 that transient variation among individuals accounts for up to half of the total variability in

36 Antarctic tootfish. We conclude by recommending further research to additionally estimate

37 temporal and spatial variation in growth rates. Estimating the relative magnitude of multiple

38 sources of growth variation will improve our ability to assess the sensitivity of existing

39 population models to growth variation, as well as to understand the range of variation exhibited

40 by wild marine populations.

41

42 **Keywords:** Antarctic toothfish; time-varying growth; random effect; von Bertalanffy growth

1 Introduction

Variation in growth rates has been discussed for over 100 years for fish populations. Growth in fishes arises from complex behavioral trade-offs for each individual in a population. Growth (measured as an increase in standard length) arises from the allocation of energy between increased size (length) and increased condition (i.e., weight at length). Individuals can also increase their rate of energy acquisition via increased foraging activity, but increased foraging may also cause changes in the risk of predation. Environmental conditions modify the potential for growth, as well as the trade-offs faced by individual fish. For example, increases in water temperature are associated with increased activity levels but also increased energetic demands for maintaining existing body tissue, such that the net effect of changing temperature on growth may vary among individuals (Shelton et al., 2013). Similarly, changes in survival rates (via fishery harvest) may favor earlier maturation, thus affecting the relative allocation of energy between growth and reproduction.

Many recent studies of captive or wild populations have demonstrated persistent differences in behavioral or phenotypic traits among individuals (termed differences in "personality", Wolf and Weissing, 2012). Persistent differences in activity level or tolerance of predation risk (i.e., a tendency to forage in high vs. low-quality habitat) will likely lead to persistent differences in growth rates among individuals. For example, persistent differences in growth rate, combined with size-selective harvest, will result in older individuals being composed primarily of slow-growing individuals (termed "Rosa Lee's Phenomenon"), and has been demonstrated to occur in small-lake mesocosm experiments (Biro and Post, 2008). Failure to account for persistent differences in growth rate can lead to biased estimation of average growth rates in wild

65 populations, and population dynamics models are increasingly developed to account for these

66 effects (Taylor and Methot, 2013).

67   In addition, individuals are likely to experience transient variation in growth rates. Transient

68 variation could be caused by many different processes including movement between

69 warmer/colder ambient temperatures (and hence transient variation in metabolic rates), periodic

70 access to improved feeding (Armstrong and Schindler, 2011), and year-specific decisions

71 regarding the allocation of resources between growth and reproduction (Jørgensen and Fiksen,

72 2006). Finally, sex-specific differences in behavior can result in differences in average growth

73 rates between males and females (Biro and Sampson, 2015). Sex-specific differences in growth

74 rate are commonly included in population models for marine species (Methot and Wetzel, 2013).

75 We therefore hypothesize that most marine populations will have multiple sources of variability

76 in individual growth rates, including:

77 1. Persistent variation among individuals (i.e., some individuals grow faster or to a larger size

78   than others)

79 2. Transient variation over time for a given individual (i.e., individuals will have spurts and

80   drops in growth rates).

81 3. Variation in average growth rates between males and females

82 Estimation of growth rates among individuals and over time therefore requires partitioning

83 variation among multiple potential types, and mixed-effects models are generally advocated for

84 this task (Thorson and Minto, In press). Mixed-effects models partition variation among

85 multiple sources by estimating true size at age as a latent variable, which is integrated across

86 during estimation of growth parameters. True growth rates can therefore vary among

87 individuals, and the magnitude of this variation can be explained by multiple putative sources.

4

88   Hierarchical models are increasingly advocated as a strategy to partition variability into multiple

89   sources, and hence to interpret which source of variance is worth further study (Gelman, 2005;

90   Larsen et al., 2001).

91   Growth rates in natural populations are generally estimated using capture-mark-recapture

92   (CMR) models. In CMR studies for marine fishes, thousands of individuals are typically

93   captured and marked with a persistent and unique tag, and then measured and released. If a

94   tagged individual is recaptured, it is often killed and its age at recapture identified via analysis of

95   hard parts (e.g., otoliths). Given the known time between capture and recapture, its size and age

96   at both times can be calculated. This study design allows a model for growth increments to be

97   fitted to size and age data for two times for each individual in a data set. Many studies have

98   examined the impact of persistent or transient growth variation on estimation of growth patterns

99   using CMR data for wild marine populations (Francis, 1988; Sainsbury, 1980). However, few

100 studies have explicitly modeled multiple sources of variability in growth rates. One exception is

101 Shelton et al. (2013), which modeled persistent, temporal, and transient variation in growth rates

102 in the analysis of data from a growth experiment for steelhead trout.

103   In this study, we present a model for partitioning variation in growth into persistent,

104 transient, and sex-specific factors, and parameters are then estimated using maximum marginal

105 likelihood methods. The code is distributed as a publicly available package *TagGrowth* in the R

106 statistical environment, and is illustrated using CMR data for Antarctic toothfish (*Dissostichus*

107 *mawsoni*). Using these data, we show that we can accurately estimate parameters for a model

108 that includes multiple sources of individual variation in growth, and that estimates are reasonably

109 precise given a feasible number of individual recaptures (250 or more). Our case study

110   application suggests that transient variation over time accounts for up to half of the total

111   variability in Antarctic toothfish in the Ross Sea.

112

113   **2 Methods**

114   We start with the specialized von Bertalanffy growth function:

115     $dL/dt = a - kL$ (1)

116   where *dL/dt* is change in length *L* as a function of time *t*, *a* scales with energy acquisition, and *k*

117   represents metabolic upkeep costs. Persistent variation among individuals can be estimated by

118   treating each individual's demographic parameters as a random effect that arises from a

119   population-level distribution (Thorson and Minto, In press). Here, we treat average metabolic

120   upkeep costs k_i as varying among individuals (where subscript *i* signifies the upkeep rate for the

121   *i*-th individual), due to differences in ambient temperature, intrinsic variation in activity levels,

122   and other factors:

123     $k_i = \mu_k \exp(\varepsilon_i^k)$ (2)

124   where $\varepsilon_i^k \sim N(0, \sigma_k^2)$, μ_k is the median k_i among individuals in the population, and σ_k^2 is the

125   variance of individual upkeep cost deviations (ε_i^k).

126   Individuals that are more highly active may obtain more food (increased *a*) and

127   simultaneously have greater upkeep costs (increased *k*). Following Shelton et al. (2013), we

128   include this association via the following equation:

129     $a_i = \gamma k_i^{\Psi}$ (3)

130   where Ψ determines whether upkeep costs (k_i) and energy acquisition rate (a_i) are highly

131   correlated ($\Psi=1$) or independent among individuals ($\Psi=0$), and γ controls the average energy

132   acquisition rate among individuals.

133   We also assume that environmental conditions experienced by each individual will vary over

134   time, such that each individual will have "transient" variation over time in their upkeep costs (k_i),

135   in turn affecting their access to food (a_i). In particular, we assume that upkeep costs for a given

136   individual i for a short time interval t can be approximated by a constant value ($k_{i,t}$), which will

137   vary around the average value for this individual (k_i). In the proceeding, we use a time interval

138   of one week (7 days), while confirming that results are similar for other small time intervals.

139   Integration then yields:

140    $L(t + \Delta_t) = L(t)\exp\left(-\frac{k}{n_\Delta}\Delta_t\right) + \left(\frac{k}{n_\Delta}\right)^{\Psi-1}\left(1 - \exp\left(-\frac{k}{n_\Delta}\right)\right)\frac{\gamma}{n_\Delta}\sum_{j=0}^{\Delta_t-1}\exp\left(-\frac{k}{n_\Delta}j\right) + z_{\Delta_t}$

141   (4)

142   where

$$z_{\Delta_t} \sim N\left(0, \sigma_z^2\left[\left(\frac{k}{n_\Delta}\right)^{\Psi-1}\left(1 - \exp\left(-\frac{k}{n_\Delta}\right)\right)\right]^2 \sum_{j=0}^{\Delta_t-1}\exp\left(-2\frac{k}{n_\Delta}j\right)\right)$$

143   where Δ_t is the number of time-periods (weeks) elapsed between two times (e.g., tagging and

144   subsequent recapture) and n_Δ is the number of time-periods per year (52.15), such that k is the

145   Brody growth coefficient (with units years^{-1}), and σ_z is the magnitude of transient growth

146   variation (see Appendix A for derivation of z_{Δ_t}, derived from Shelton et al., 2013).   In this

147   study, we use a time interval of one week (7 days). We confirm that results are similar for other

148   small time intervals (i.e., days or months), but found that an annual time interval resulted in

149   parameter estimates yielding biased high growth schedules. We assume that all age-0

150   individuals have a length $L_{0,s}$ that differs between males $(s=0)$ and females $(s=1)$, and estimate

151   length-at-birth for each sex. Eq. 4 can then be used to calculate the predicted length at of first

152   capture $L(t_1)$ and upon recapture $L(t_1+t_2)$, where t_2 is the time between first tagging and recapture

153   (time at liberty), and t_1+t_2 is the age at recapture as determined from conventional ageing

154   methods.

155   The observed length for each individual upon first tagging $L_{obs}(t_1)$ and upon recapture

156    $L_{obs}(t_1+t_2)$ is assumed to follow a normal distribution with a fixed coefficient of variation (c.v.,

157   representing observation error caused by at-sea length measurements) given the estimated length

158   at that age $L(t)$:

159    $$L_{obs}(t) \sim N(L(t), \sigma_{obs}^2) \tag{5}$$

160   where $\sigma_{obs} = c_{obs}L(t)$, and and c_{obs} is the c.v. of observed growth.

161

2.1 Estimation

163   We estimate the value of fixed effects in this model (L_0, μ_k, σ_k, γ, σ_z, c_{obs}) using maximum

164   marginal likelihood while integrating across the probability of all random variables representing

165   persistent and transient variation among individuals (Thorson and Minto, In press). Preliminary

166   exploration using data for the case study (explained below) suggested that Ψ was not estimable

167   for our data set, so we proceed by fixing $\Psi=0$. Parameter estimation is conducted using

168   Template Model Builder (TMB; Kristensen, 2014; Kristensen et al., In press; available from:

169   https://github.com/kaskr/adcomp) software called from the R statistical environment (R Core

170   Development Team, 2013) and all code necessary for replicating the case study and simulation

171   experiment are publicly available (https://github.com/quantifish/TagGrowth; Appendix B). The

172   marginal likelihood is then maximized using conventional nonlinear minimization tools in R,

173   while using the gradient of the marginal likelihood with respect to fixed effects as calculated by

174   TMB. Standard errors are then estimated via the information matrix and delta-method.

175   After fixed effects have been estimated, the median asymptotic length ($\mu_{L\infty}$) for individuals

176   in the population can be calculated as:

177    $\mu_{L\infty} = \gamma \mu_k^{\psi-1}$ (6)

178   which is obtained by setting Eqn. 1 equal to zero, substituting in Eqn. 3, and rearranging.

179   Readers are referred to Shelton et al. (2013) for an expanded model that also incorporates

180   variability in average energy acquisition rates (γ) for all individuals in a given time period. All

181   of the variables used in this paper are outlined in Table 1.

182

183   **2.2 Case study application**

184   Antarctic toothfish are large Nototheniids native to the Southern Ocean. They can grow to be

185   more than 2m in length, weighing over 100kg, and can live for up to 50 years of age. The

186   exploratory toothfish fishery in the Ross Sea region began in 1997 and is managed by The

187   Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Since

188   then the fishery has increased to about 3000 tonnes per year. Fishing is restricted to the summer

189   months (December usually until to March), once the ice shelf recedes allowing vessels access to

190   the region. The Antarctic toothfish tagging programme was initiated in the in the 2001 fishing

191   season by New Zealand vessels involved in the fishery. In 2004, toothfish tagging was made

192   compulsory for all vessels participating in the fishery. Currently toothfish are required to be

193   double tagged at a rate of 1 fish per tonne landed. The tagging programme records information

194   on the date, depth, location, sex, and size of each tagged/recaptured fish. A small subset of the

195   recaptured fish are aged by reading their otolith.

196   We identified those fish that had been tagged, recaptured and aged upon recapture. This

197   yielded 315 individuals of which 166 were female and 149 male. All individuals were originally

198   tagged between 2001 and 2008, and were subsequently recaptured between 2002 and 2013.

199   These data allowed us to identify the observed length (cm) at first capture $L_{obs}(t_1)$ and recapture

200    $L_{obs}(t_1+t_2)$. The time at liberty (t_2) and the measured age of the fish at recapture (t_1+t_2) was used

201   to calculate the age of the fish at tagging (t_1). We fit several different versions of the model to

202   these data, these included: no random-effects, random-effects for the persistent differences in

203   upkeep costs ($k_{i,s}$ only) for each sex, transient variation in growth ($z_{\Delta_t,i}$ only), and random-effects

204   representing both persistent and transient variation in growth ($k_{i,s}$ and $z_{\Delta_t,i}$).

205   Length at birth ($L_{0,s}$), average upkeep costs ($\mu_{k,s}$), the magnitude of persistent variation in

206   growth ($\sigma_{k,s}$) and average energy acquisition rates (γ_s) were all assumed to be sex-specific in the

207   application of this model. The magnitude of transient variation in growth (σ_z) and the magnitude

208   of error when measuring length (c_{obs}) were assumed to be constant for males and females. The

209   simulation study illustrated that the model had little ability to identify the value of Ψ. We

210   therefore fixed the value of $\Psi=0$. Preliminary exploration indicated that seasonal effects could

211   not be explored because all tagging and recaptures are observed during a few months

212   (December-March and a few in May) and hence seasonal and annual effects are confounded.

213

214   2.1 Simulation

215   A simulation study was done to ensure that the model could generate estimates of growth

216   rates that are unbiased and reasonably precise. Four different scenarios were simulated

217   including: no random-effects, random-effects for persistent individual variation in upkeep costs

218   ($k_{i,s}$ only) for each sex, transient variation in growth ($z_{\Delta_t,i}$ only), and both persistent and transient

219   variation in growth (both $k_{i,s}$ and $z_{\Delta_t,i}$). A power analysis was done for each of the four scenarios

220   where data were simulated for 50, 100, 250 and 500 recaptured individuals. This yielded 16

221   different simulation experiments. We did 200 replicates for each of the 16 combinations of

222   scenario and sample size (n).

223   Average age at length zero ($t_{0,s}$), average upkeep costs (k_s), and asymptotic maximum length

224   ($L_{\infty,s}$) were taken from Dunn et al. (2006) and used to derive the values of the length at birth ($L_{0,s}$)

225   and average energy acquisition rate (γ_s) parameters used in the simulation study. These can be

226   calculated as:

227    $$L_0 = L_\infty \left(1 - exp \left(\frac{kt_0}{n_\Delta} \right) \right)$$ (7)

228   and

229    $$\gamma = \frac{k}{n_\Delta} L_\infty / \left(\frac{k}{n_\Delta} \right)^\Psi$$ (8)

230   The length at birth ($L_{0,s}$), average upkeep cost ($\mu_{k,s}$), magnitude of persistent variation in

231   growth ($\sigma_{k,s}$) and average energy acquisition rate (γ_s) parameters were all assumed to be sex-

232   specific in the simulation study, the magnitude of transient variation in growth (σ_z) and the

233   magnitude of error when measuring length (c_{obs}) were not (Table 2,

234   Table 3). The c.v. of observed growth (c_{obs}) was set at the value in Dunn et al. 2006 in the

235   scenario with no random-effects. In the remaining scenarios, the c.v. of observed growth (c_{obs}),

236   magnitude of persistent variation among individuals ($\sigma_{k,s}$) and magnitude of transient variation

237   ($\sigma_{z,}$) were set at values that resulted in reasonable variation in individual length trajectories (

238   Table 3).

239   For each individual in each of the scenario/power simulations, sex was sampled with

240   replacement from the observed sex of individuals in the toothfish data set. The age at release,

241   age at recapture and time at liberty were sampled independently from the observed individuals in

242   the toothfish data set also, then one of the three variables was chosen at random and calculated

243   using the other two variables and rounded to the nearest integer. For instance:

244   1. if age at first capture (t_1) was chosen at random it was calculated as the age at recapture

245   (t_1+t_2) minus the time at liberty (t_2), i.e., $t_1 = (t_1+t_2) - t_2$;

246   2. if age at recapture (t_1+t_2) was chosen it was calculated as the age at first capture (t_1) plus

247   the time at liberty (t_2), i.e., $(t_1+t_2) = t_1 + t_2$;

248   3. if time at liberty (t_2) was chosen it was calculated as the age at recapture (t_1+t_2) minus the

249   age at first capture (t_1), i.e., $t_2 = (t_1+t_2) - t_1$.

250   Sampling in this way ensured that the distribution of each of the variables approximated those

251   observed the real-world data set, without the need for sampling from complex joint distributions

252   (e.g., copulas). The model was fit to the data for each of the 200 replicates in each of the 16

253   simulation experiments. Instead of reporting average energy acquisition rate (γ_s) we present the

254   derived value median asymptotic length ($\mu_{L_\infty,s}$) which is calculated using Eqn. 6.

255

256   **3 Results**

257   **3.1 Case study application**

258   When applied to data for Antarctic toothfish in Ross Sea, the model without random-

259   effects looks much like a standard von Bertalanffy growth curve for both females and males (

260   *Figure 1*). The residual fit of this model is poor, given that many individuals have a

261   positive/negative residual at both tagging and resighting, and therefore residuals are correlated

262   for a given individual (*Figure 2*). The model without persistent or transient growth variation was

263   the least parsimonious model of the four according to the Akaike information criterion (AIC;

264   Akaike 1998; Table 4). Compared to Dunn et al. (2006) this model estimated a larger size at

265   birth ($L_{0,s}$) and larger median asymptotic maximum length ($\mu_{L_{\infty,s}}$). Using Eqn. 7, the length at

266   birth ($L_{0,s}$) from Dunn et al. (2006) is -0.34cm and 3.98cm for females and males, respectively.

267   Here the length at birth ($L_{0,s}$) was estimated to be 46.51cm and 51.54cm (*Table 4*). Using Eqn. 6,

268   the median asymptotic maximum length ($\mu_{L_{\infty,s}}$) was 216cm and 177cm for females and males,

269   respectively (compared with 180.20cm and 169.07cm in Dunn et al. 2006). Our estimate of the

270   magnitude of residual variation (c_{obs}) was very similar at 0.111 (compared to 0.102 in Dunn et al.

271   2006).

272   The most parsimonious model (which has AIC 160 lower than the model without random

273   effects; *Table 4*), included transient individual variation in growth rates ($z_{\Delta_t,i}$, *Figure 3*). In this

274   model, the standard deviation in log-space of transient variation (σ_z) was 0.632, representing a

275   70% coefficient of variation in transient growth rates for each individual in each week. This

276   model produced a tighter fit than the model described above (*Figure 4*). The distribution of

277   residuals for each individual at tagging and recapture are approximately uncorrelated, with the

278   exception of a few males that are either smaller than expected at tagging and larger than expected

279   at resighting (or vice versa, Figure 4). Values for most estimated parameters were similar to

280   those estimated in the model without the inclusion of any random-effects, however, the estimated

281   c.v. of residual errors is lower (AIC-selected model: c_{obs}=0.05 vs. model without random effects:

282    $c_{obs} = 0.102$) as over half of the variability is apportioned into the time-varying individual

283   variation (σ_z, Table 4).

284   The model that included both persistent and transient variation in individual growth rates

285   ($k_{s,i}$ and also $z_{\Delta_t,i}$) resulted in no decrease in marginal likelihood, and hence was deemed to not

286   be parsimonious by AIC. This occurred because the maximum likelihood estimate of the

287   magnitude of persistent variation ($\sigma_{k,s}$) approached zero for both sexes.

288

3.2 Simulation

289 **3.2 Simulation**

290   In the simulation study, estimates of average upkeep costs ($\mu_{k,s}$) and average asymptotic

291 maximum length ($\mu_{L_{\infty,s}}$) are unbiased in each of the four estimation models, and the precision

292 (i.e., the distribution of estimates around the true value) gets tighter as the sample size (n) is

293 increased from 50 to 500 individuals (Figure 5 and Figure 6). The size at birth ($L_{0,s}$) is also

294 unbiased for all sample sizes, but has very high imprecision (i.e., an SD of 15.1 and 15.7, for

295 females and males respectively, when estimated with both transient and persistent variation in

296 growth rates) given low sample sizes (i.e., $n=50$ individuals). The precision improves markedly

297 with increasing sample size (Figure 7), and has an SD of 2.6 and 2.7, for females and males

298 respectively, for large sample sizes when estimating both persistent and transient variation

299 ($n=500$ individuals).

300   The magnitude of persistent variation among individuals ($\sigma_{k,s}$) parameter was approximately

301 unbiased for all sample sizes, and relatively precise at sample sizes above $n=100$, with a small

302 proportion of parameter estimates hitting the lower bound when sample sizes were small (Figure

303 8). Finally, the magnitude of transient variation (σ_z) was estimated to approach 0 for the majority

304 of simulation replicates when sample sizes were low ($n=50$), and particularly when estimating

305 both persistent and transient variation (estimating variation in $k_{s,i}$ and $z_{\Delta_t,i}$). However, by large

306 sample sizes ($n=500$), the magnitude of residual variation was estimated well for either model

307 (Figure 9).

308   Not all fits to simulated data had a positive definite Hessian, signifying that some

309 combinations of simulation replicate and estimation model had parameters that were either (1)

310 not converged or (2) not uniquely identifiable. When the estimation model included no random-

311 effects, or random-effects for upkeep costs ($k_{i,s}$) only, almost all model fits were positive definite.

312 Fewer simulation replicates were positive definite when the model incorporated transient

313 individual random effects ($z_{\Delta_t,i}$), particularly at lower sample sizes (see Figure 5, Figure *6*,

314 Figure *7*, Figure *8*, and Figure *9*). However, we conclude that most models were positive

315 definite for sample sizes above 250 individuals, and that non-positive definite models can be

316 used as indication that the model is likely to be overfitted relative to the available data.

317

318 **4 Discussion**

319   In this study, we have used a case study application for Antarctic toothfish and a simulation

320 experiment to demonstrate that it is feasible to simultaneously estimate persistent and transient

321 variation in growth among individuals, as well as differences in growth rate between males and

322 females and residual (measurement error) variation. Early studies incorporated variability in

323 growth via individual variation in growth parameters (Sainsbury, 1980) or both time-dependent

324 and time-independent variation in growth increments (Francis, 1988). Recent studies have

325 developed mixed-effect models for estimating variation in growth rates over time and/or among

326 individuals in wild or experimental settings involving fish (Shelton et al., 2013; Stawitz et al., In

327 review; Thorson and Minte-Vera, In press; Vincenzi et al., 2014). Variation in growth rates is

328 also an active area of research and method development in other ecological taxa (Brooks et al.,

329 2013). However, our study is the first to our knowledge to apply these methods to a wild marine

330 population. Our case study application suggests that transient variation among individuals

331 accounts for up to half of the total variability in Antarctic toothfish.

332   By estimating persistent and transient variation among individuals and between sexes, we

333 have largely eliminated the correlations in residual size between tagging and recapture, as was

334 seen in the toothfish data set for the model without random effects. However, we have neglected

335 two obvious types of variation in growth rates: persistent variation over space, and synchronous

336 variation that is similar among individuals (i.e., annual variation). Populations may experience

337 synchronous variation in growth rates for several reasons. For example, annual variation in

338 water temperature may drive changes in metabolic costs as well as food availability in upwelling

339 systems such as the California Current (Black et al., 2010), and this may cause all individuals to

340 have elevated or depressed growth rates in a given year. Recent meta-analytic work supports the

341 hypothesis that time-variation in average growth rates is the rule rather than the exception for

342 marine populations (Thorson and Minte-Vera, In press). Similarly, many studies have illustrated

343 persistent spatial differences in growth rates (Gertseva et al., 2010), e.g., where populations often

344 have a smaller maximum size in warmer waters. Previous research has demonstrated the

345 prevalence of spatial variation in growth (Gertseva et al., 2010) and condition (Thorson, In

346 press). The modelling framework we present here could easily be modified to include spatial

347 variation in growth rates, either among spatial strata or using geostatistical techniques (Shelton et

348 al., 2014; Thorson et al., In press), but in this study we have chosen instead to focus on testing

349 the individual, temporal, and sex-specific variation that we presented here. We hypothesize that

350 including spatial variation would decrease the magnitude of among-individual variation in

351 growth rates, because spatial variation would explain some portion of individual-level variation.

352 We note that our model (and results for Antarctic toothfish in the Ross Sea) does not account

353 for the effects of fish handling and tagging on growth rates. Growth rates for untagged

354 individuals may be higher because tagging is likely to cause physiological stress that depresses

355 activity and metabolic levels (Dubula et al., 2005; Santos and Groeneveld, 2015; Xiao, 1994).

356 Future studies could estimate the impact of tagging on growth rates by jointly analyzing CMR

357   and other fishery data types (termed "integrated growth models"; Eveson et al. 2004). In

358   particular, the length-frequency of fishery and survey catches and the direct ageing of hard parts

359   from catches provide a separate source of information regarding size at age. These latter two

360   sources of information do not generally provide information to discriminate between persistent

361   and transient variation in growth rates (because each involves measuring size only once for each

362   individual). However, both sources can provide complementary information regarding average

363   growth rates for untagged individuals. We therefore believe that estimating persistent and

364   transient variation in growth rates within integrated growth models is an important topic for

365   future research.

366   Information regarding the magnitude of persistent and transient variation in growth is

367   important for at least three reasons. First, stock assessment models and fisheries management

368   strategies are routinely evaluated using simulation experiments (termed "management strategy

369   evaluation"; Sainsbury et al., 2000). However, simulation experiments depend upon having

370   information regarding plausible states-of-nature, which are used to simulate available data (Punt,

371   2008). Models estimating time-variation in growth can be used to simulate more plausible data

372   for use in testing assessment methods. Second, estimation the magnitude of persistent variation

373   in growth will lead to improved methods for approximating growth in population models. In

374   particular, persistent individual variation in growth has recently been approximated by tracking

375   individual platoons of fishes having the same age but different average growth rates (Taylor and

376   Methot, 2013). Tracking abundance by platoon then allows stock assessment models to account

377   for the impact of size-selective fishing on average growth rates. In particular, improved

378   accounting for growth is likely to be important for models that are highly dependent upon growth

379   information, e.g., length-based spawning potential ratio assessments (Hordyk et al., 2015).

380   Third, previous research has indicated that growth estimates are biased when variation estimated

381   via models that do not account for variation in growth (Sainsbury, 1980), and that these biases

382   can in turn result in biased estimates of stock status and productivity (Punt et al., In review). We

383   therefore hypothesize that improved treatment of transient and persistent individual variation in

384   growth will improve estimates of growth rates obtained from CMR data sets, and that this

385   improvement may result in improved estimates of fishery productivity.

386

387   **5 Conclusions**

388   In this study, we have estimated the magnitude of persistent and transient variation in growth

389   rates among individuals in a wild marine population of Antarctic toothfish in the Ross Sea during

390   2001-2013, in addition to differences in average growth rates between males and females.

391   Model selection suggests that transient variation is more significant than persistent variation

392   among individuals during these years. Estimating transient variation decreased the coefficient of

393   variation of residual (measurement error) variation by nearly half. Our simulation study

394   corroborates that all models provide parameters estimates that are approximately unbiased and

395   reasonably precise given sample sizes similar to those available here. Finally, we provide an R

396   package *TagGrowth*, containing code to applying our estimation model to other data sets. We

397   encourage future research comparing the magnitude of persistent and transient variation in

398   growth among marine populations in different taxa and environments.

399

400   **Acknowledgements**

18

409   **Bibliography**

410   Akaike, H., 1998. Information Theory and an Extension of the Maximum Likelihood Principle,

411   in: Parzen, E., Tanabe, K., Kitagawa, G. (Eds.), Selected Papers of Hirotugu Akaike.

412   Springer New York, New York, NY, pp. 199–213.

413   Armstrong, J.B., Schindler, D.E., 2011. Excess digestive capacity in predators reflects a life of

414   feast and famine. Nature 476, 84–87. doi:10.1038/nature10240

415   Biro, P.A., Post, J.R., 2008. Rapid depletion of genotypes with fast growth and bold personality

416   traits from harvested fish populations. Proc. Natl. Acad. Sci. 105, 2919–2922.

417   doi:10.1073/pnas.0708159105

418   Biro, P.A., Sampson, P., 2015. Fishing directly selects on growth rate via behaviour:

419   implications of growth-selection that is independent of size. Proc. R. Soc. B Biol. Sci.

420   282, 20142283–20142283. doi:10.1098/rspb.2014.2283

421   Black, B.A., Schroeder, I.D., Sydeman, W.J., Bograd, S.J., Lawson, P.W., 2010. Wintertime

422   ocean conditions synchronize rockfish growth and seabird reproduction in the central

423   California Current ecosystem. Can. J. Fish. Aquat. Sci. 67, 1149–1158.

424   Brooks, M.E., McCoy, M.W., Bolker, B.M., 2013. A Method for Detecting Positive Growth

425   Autocorrelation without Marking Individuals. PLoS ONE 8, e76389.

426   doi:10.1371/journal.pone.0076389

427   Dubula, O., Groeneveld, J.C., Santos, J., van Zyl, D.L., Brouwer, S.L., van den Heever, N.,

428   McCue, S.A., 2005. Effects of tag-related injuries and timing of tagging on growth of

429   rock lobster, Jasus lalandii. Fish. Res. 74, 1–10. doi:10.1016/j.fishres.2005.04.004

430   Dunn, A., Horn, P.L., Hanchet, S.M., 2006. Revised estimates of the biological parameters for

431   Antarctic toothfish (Dissostichus mawsoni) in the Ross Sea. WG-FSA-SAM 06/8, 1–14.

432   Eveson, J.P., Laslett, G.M., Polacheck, T., 2004. An integrated model for growth incorporating

433   tag-recapture, length-frequency, and direct aging data. Can. J. Fish. Aquat. Sci. 61, 292–

434   306. doi:10.1139/f03-163

435   Francis, R., 1988. Maximum likelihood estimation of growth and growth variability from tagging

436   data. N. Z. J. Mar. Freshw. Res. 22, 43–51.

437   Gelman, A., 2005. Analysis of variance—why it is more important than ever. Ann. Stat. 33, 1–

438   53.

439   Gertseva, V.V., Cope, J.M., Matson, S.E., 2010. Growth variability in the splitnose rockfish

440   Sebastes diploproa of the northeast Pacific Ocean: pattern revisited. Mar. Ecol. Prog. Ser.

441   413, 125–136.

442   Hordyk, A.R., Loneragan, N.R., Prince, J.D., 2015. An evaluation of an iterative harvest strategy

443   for data-poor fisheries using the length-based spawning potential ratio assessment

444   methodology. Fish. Res. doi:10.1016/j.fishres.2014.12.018

445   Jørgensen, C., Fiksen, Ø., 2006. State-dependent energy allocation in cod (*Gadus morhua*).

446   Can. J. Fish. Aquat. Sci. 63, 186–199. doi:10.1139/f05-209

447   Kristensen, K., 2014. General random effect model builder tool inspired by ADMB.

448   Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H.J., In press. Template Model Builder TMB. J.

449   Stat. Softw.

450   Larsen, D.P., Kincaid, T.M., Jacobs, S.E., Urquhart, N.S., 2001. Designs for Evaluating Local

451   and Regional Scale Trends. BioScience 51, 1069–1078. doi:10.1641/0006-

452   3568(2001)051[1069:DFELAR]2.0.CO;2

453   Methot, R.D., Wetzel, C.R., 2013. Stock synthesis: A biological and statistical framework for

454   fish stock assessment and fishery management. Fish. Res. 142, 86–99.

455   Punt, A.E., 2008. Refocusing stock assessment in support of policy evaluation, in: Tsukamoto,

456   K., Kawamura, T., Takeuchi, T., Beard, T.D., Kaiser, M.J. (Eds.), Fisheries for Global

457   Welfare and Environment. TerraPub, Tokyo, pp. 139–152.

458   Punt, A.E., Haddon, M., McGarvey, R., In review. Estimating Growth within size-structured

459   fishery stock assessments: What is the state of the art and what does the future look like?

460   R Core Development Team, 2013. R: A Language and Environment for Statistical Computing. R

461   Foundation for Statistical Computing, Vienna, Austria.

462   Sainsbury, K.J., 1980. Effect of individual variability on the von Bertalanffy growth equation.

463   Can. J. Fish. Aquat. Sci. 37, 241–247.

464   Sainsbury, K.J., Punt, A.E., Smith, A.D.., 2000. Design of operational management strategies for

465   achieving fishery ecosystem objectives. ICES J. Mar. Sci. J. Cons. 57, 731–741.

466   Santos, J., Groeneveld, J.C., 2015. Accounting for tag-induced growth retardation in spiny

467   lobsters using censoring and modelling approaches. Fish. Res. 161, 166–173.

468   doi:10.1016/j.fishres.2014.07.008

469   Shelton, A.O., Satterthwaite, W.H., Beakes, M.P., Munch, S.B., Sogard, S.M., Mangel, M.,

470   2013. Separating intrinsic and environmental contributions to growth and their population

471   consequences. Am. Nat. 181, 799–814.

472   Shelton, A.O., Thorson, J.T., Ward, E.J., Feist, B.E., 2014. Spatial semiparametric models

473   improve estimates of species abundance and distribution. Can. J. Fish. Aquat. Sci. 71,

474   1655–1666. doi:10.1139/cjfas-2013-0508

475   Stawitz, C.C., Essington, T.E., Branch, T.A., Haltuch, M.A., Hollowed, A.B., Spencer, P.D., In

476   review. A state-space approach for measuring growth variation and application to North

477   Pacific groundfish.

478   Taylor, I.G., Methot, R.D., 2013. Hiding or dead? A computationally efficient model of selective

479   fisheries mortality. Fish. Res. 142, 75–85. doi:10.1016/j.fishres.2012.08.021

480   Thorson, J.T., In press. Spatio-temporal variation in fish condition is not consistently explained

481   by density, temperature, or season for Northeast Pacific groundfishes.

482   Thorson, J.T., Minte-Vera, C., In press. Relative magnitude of cohort, age, and year effects on

483   size at age of exploited marine fishes. Fish. Res.

484   Thorson, J.T., Minto, C., In press. Mixed effects: a unifying framework for modelling in aquatic

485   ecology. ICES J. Mar. Sci.

486   Thorson, J.T., Skaug, H., Kristensen, K., Shelton, A.O., Ward, E.J., Harms, J., Benante, J., In

487   press. The importance of spatial models for estimating the strength of density

488   dependence. Ecology. doi:http://dx.doi.org/10.1890/14-0739.1

489   Vincenzi, S., Mangel, M., Crivelli, A.J., Munch, S., Skaug, H.J., 2014. Determining Individual

490   Variation in Growth and Its Implication for Life-History and Population Processes Using

491   the Empirical Bayes Method. PLoS Comput Biol 10, e1003828.

492   doi:10.1371/journal.pcbi.1003828

493   Wolf, M., Weissing, F.J., 2012. Animal personalities: consequences for ecology and evolution.

494   Trends Ecol. Evol. 27, 452–461. doi:10.1016/j.tree.2012.05.001

495   Xiao, Y., 1994. Growth Models with Corrections for the Retardative Effects of Tagging. Can. J.

496   Fish. Aquat. Sci. 51, 263–267. doi:10.1139/f94-027

497

498   Table 1: List and definition of symbols used in the text and equations with their units.

499

500   Table 2: Sex-specific parameter values used in all four scenarios in the simulation experiment.

501

502   Table 3: Sex-specific parameter values that vary among each of the four scenarios in the

503   simulation experiment.

504

505   Table 4: Estimated parameter values in each of the four case study models by sex (s). ΔAIC is

506   the difference in Akaike Information Criterion between the current model and the most

507   parsimonious model. Values marked with an asterisks (*) are hitting the lower bound.

508

509   Figure 1: Observed and expected length (cm) at age (years) for individual female and male

510   Antarctic toothfish using the model with no random-effects.

511

512   Figure 2: Standardized residual in length at tagging vs. the standardized residual in length at

513   recapture (cm) for individual female and male Antarctic toothfish using the model with no

514   random-effects. The standardized residual is calculated as $L_{obs}(t) - L(t)/SD(L_{obs}(t) - L(t))$

515   where SD is the standard deviation.

516

517   Figure 3: Observed and expected length (cm) at age (years) for individual female and male

518   Antarctic toothfish using the model with transient variation in growth ($z_{\Delta_t,i}$ only).

519

520   Figure 4: Standardized residual in length at tagging vs. the standardized residual in length at

521   recapture (cm) for individual female and male Antarctic toothfish using the model with transient

522   variation in growth. The standardized residual is calculated as

523    $L_{obs}(t) - L(t)/SD(L_{obs}(t) - L(t))$ where SD is the standard deviation.

524

525   Figure 5: Estimated value of the median upkeep cost ($\mu_{k,s}$, years^{-1}) in each of the simulation study

526   experiments. The vertical red lines show the true simulated values of the parameter, the number

527   of fits that are positive definite Hessian (pdH) are given in the top right of each panel.

528

529   Figure 6: Estimated value of the median asymptotic length ($\mu_{L_{\infty,s}}$, cm) in each of the simulation

530   study experiments (derived using Eqn. 6). The vertical red lines show the true simulated values

531   of the parameter, the number of fits that are positive definite Hessian (pdH) are given in the top

532   right of each panel.

533

534   Figure 7: Estimated value of the length at birth ($L_{0,s}$, cm) in each of the simulation study

535   experiments. The vertical red lines show the true simulated values of the parameter, the number

536   of fits that are positive definite Hessian (pdH) are given in the top right of each panel.

537

538   Figure 8: Estimated value of the magnitude of persistent variation among individuals ($\sigma_{k,s}$) in

539   each of the simulation study experiments. The vertical red lines show the true simulated values

540   of the parameter, the number of fits that are positive definite Hessian (pdH) are given in the top

541   right of each panel.

542

543   Figure 9: Estimated value of the magnitude of transient variation among individuals (σ_z) in each

544   of the simulation study experiments. The vertical red lines show the true simulated values of the

545   parameter, the number of fits that are positive definite Hessian (pdH) are given in the top right of

546   each panel.

547

Table 1

Table 1: List and definition of symbols used in the text and equations with their units.

Parameter name	Symbol	Units
The number of time periods per year	n_Δ	-
The hypothetical length at which time $t = 0$	$L_{0,s}$	cm
Anabolic rate	a_i	-
Energy expenditure rate ("Brody growth coefficient")	$\mu_{k,s}$, $k_{i,s}$	years^{-1}
Anabolism coefficient	γ_s	years^{-1}
Allometric scaling of anabolism and energy expenditure	Ψ	-
Time variation	$z_{\Delta_t, i}$	cm
Asymptotic maximum length	$\mu_{L_\infty, s}$, $L_{\infty, i, s}$	cm
The hypothetical time at which $L(t) = 0$	$t_{0,s}$	years
Observation coefficient of variation (c.v.)	c_{obs}	-
Energy expenditure rate standard deviation	$\sigma_{k,s}$	years^{-1}
Time variation standard deviation	σ_z	cm
Data	**Symbol**	**Units**
Time interval	Δ_t	weeks
Length at time t	$L(t)$	cm
Indices	**Symbol**	**Units**
Individual	i	-
Time	t	weeks
Sex	s	-

Table 2

Table 1: Sex-specific parameter values used in all four scenarios in the simulation experiment.

| Parameter	Units	Female	Male
$L_{0,s}$	cm	-0.3409	3.9777
$\mu_{k,s}$	years^{-1}	0.090	0.093
γ_s	years^{-1}	16.218	15.724

Table 3

Table 1: Sex-specific parameter values that vary among each of the four scenarios in the

simulation experiment.

Scenario	Parameter	Female	Male
No variation	c_{obs}	0.102	0.102
	$\sigma_{k,s}$	-	-
	σ_z	-	-
Variation in $k_{i,s}$	c_{obs}	0.05	0.05
	$\sigma_{k,s}$	0.1	0.2
	σ_z	-	-
Variation in $z_{\Delta_t,i}$	c_{obs}	0.05	0.05
	$\sigma_{k,s}$	-	-
	σ_z	0.3	0.3
Variation in $k_{i,s}$ and $z_{\Delta_t,i}$	c_{obs}	0.05	0.05
	$\sigma_{k,s}$	0.1	0.2
	σ_z	0.3	0.3

Table 4

Table 1: Estimated parameter values in each of the four case study models by sex (s). ΔAIC is the difference in Akaike Information Criterion between the current model and the most parsimonious model. Values marked with an asterisks (*) are hitting the lower bound.

Model	ΔAIC	Parameter	Units	Female	Male
No variation	160	$L_{0,s}$	cm	46.51	51.45
		k_s	years^{-1}	0.040	0.054
		γ_s	years^{-1}	8.669	9.534
		c_{obs}	-	0.111	
Variation in $k_{i,s}$	92	$L_{0,s}$	cm	45.70	52.11
		$\mu_{k,s}$	years^{-1}	0.041	0.046
		γ_s	years^{-1}	8.864	8.801
		c_{obs}	-	0.083	
		$\sigma_{k,s}$	years^{-1}	0.240	0.217
Variation in $z_{\Delta t,i}$	0	$L_{0,s}$	cm	34.66	45.82
		k_s	years^{-1}	0.062	0.054
		γ_s	years^{-1}	11.371	9.896
		c_{obs}	-	0.048	
		σ_z	cm	0.632	
Variation in $k_{i,s}$ and $z_{\Delta t,i}$	4	$L_{0,s}$	cm	34.66	45.82
		$\mu_{k,s}$	years^{-1}	0.062	0.054
		γ_s	years^{-1}	11.371	9.896
		c_{obs}	-	0.048	
		$\sigma_{k,s}$	years^{-1}	0.001*	0.001
		σ_z	cm	0.632	
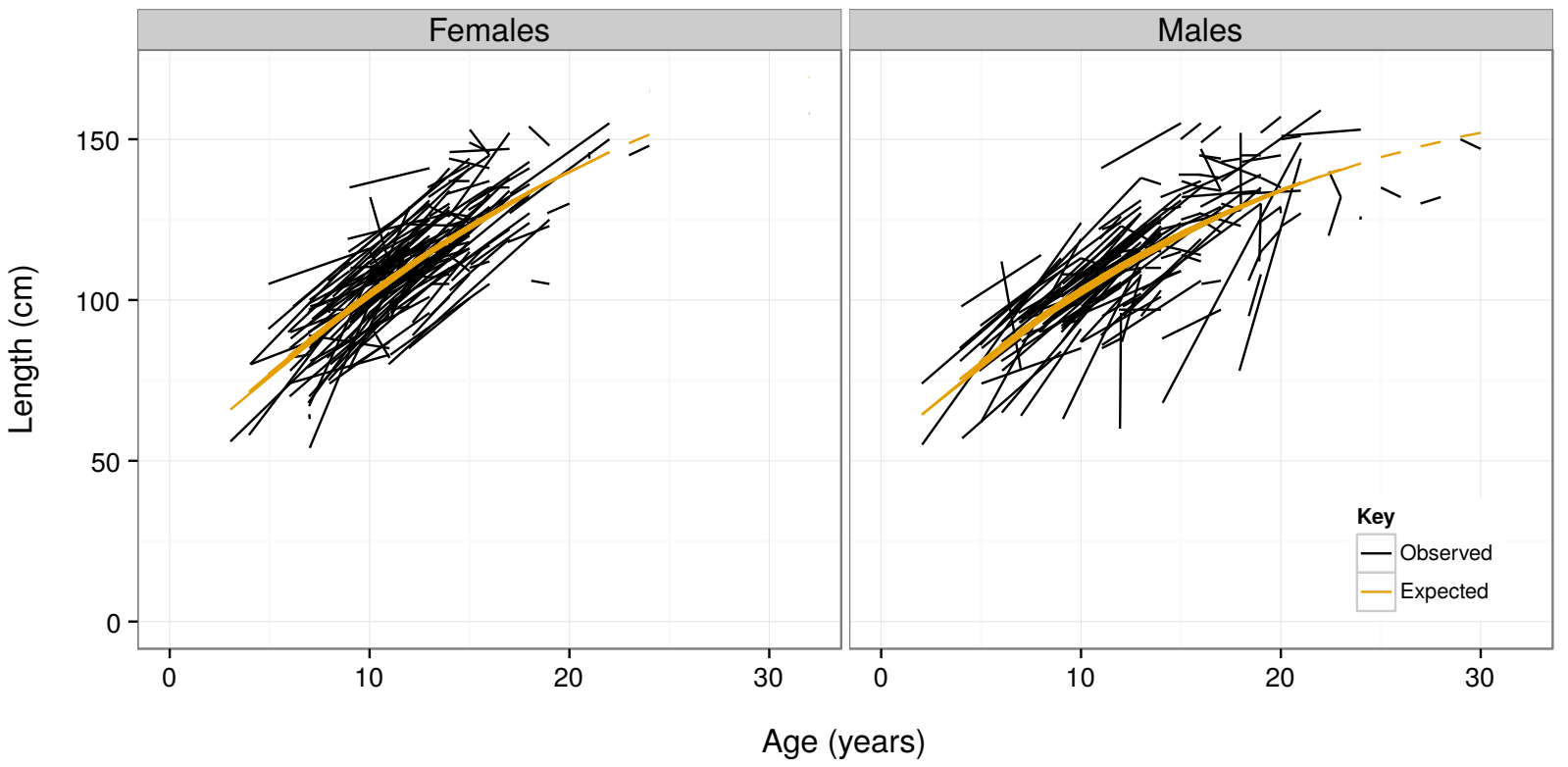
Figure 1

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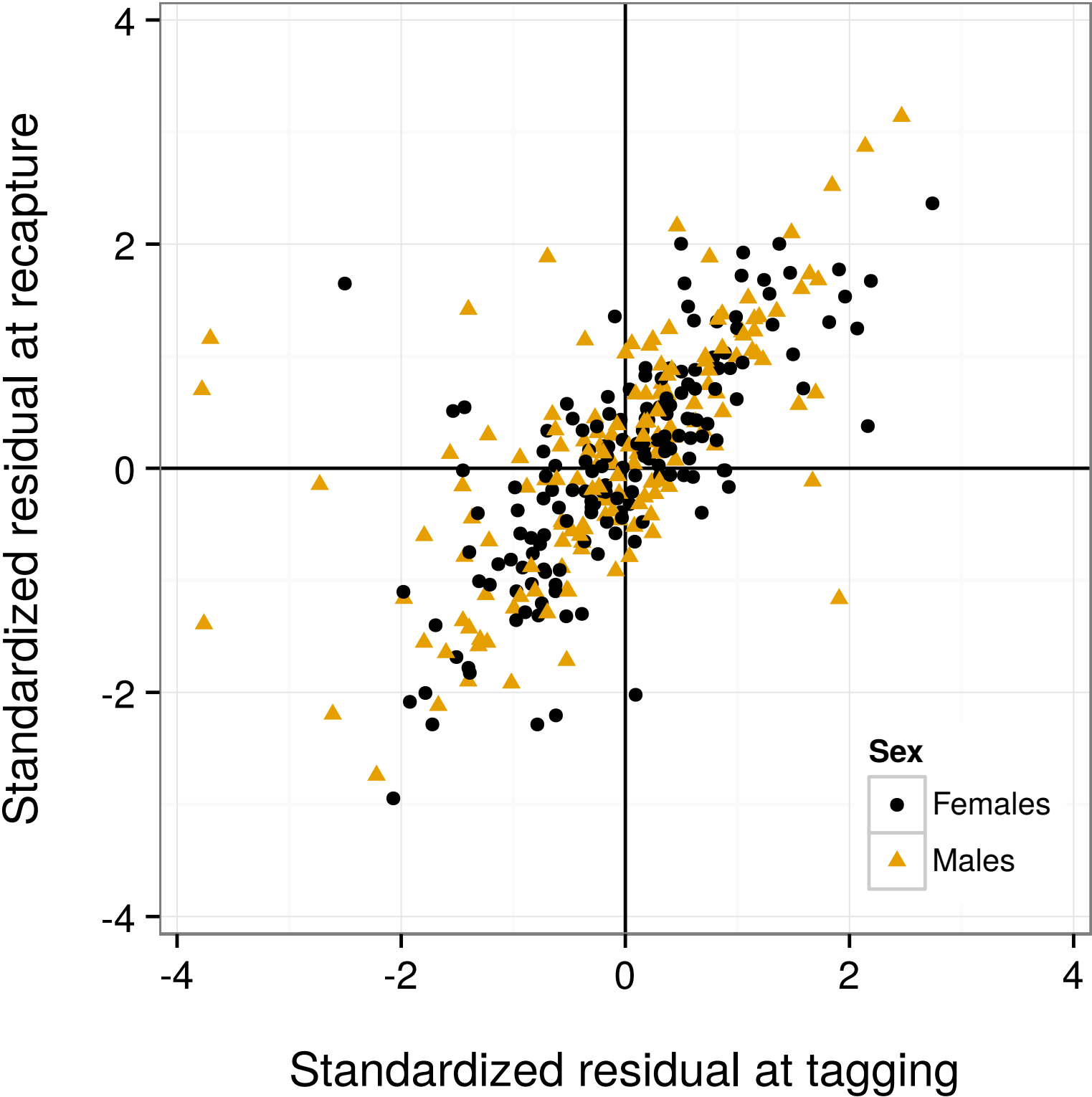
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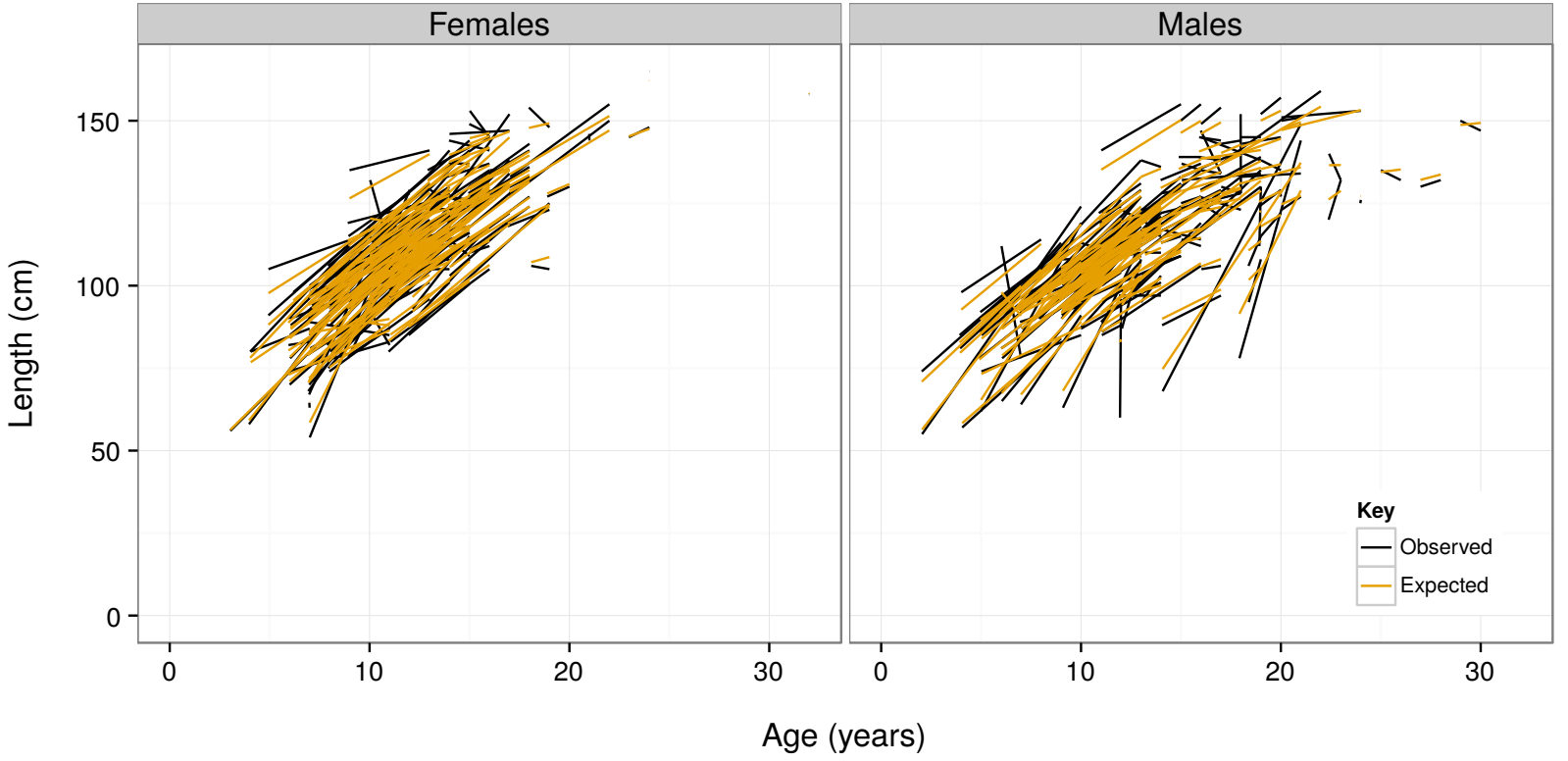
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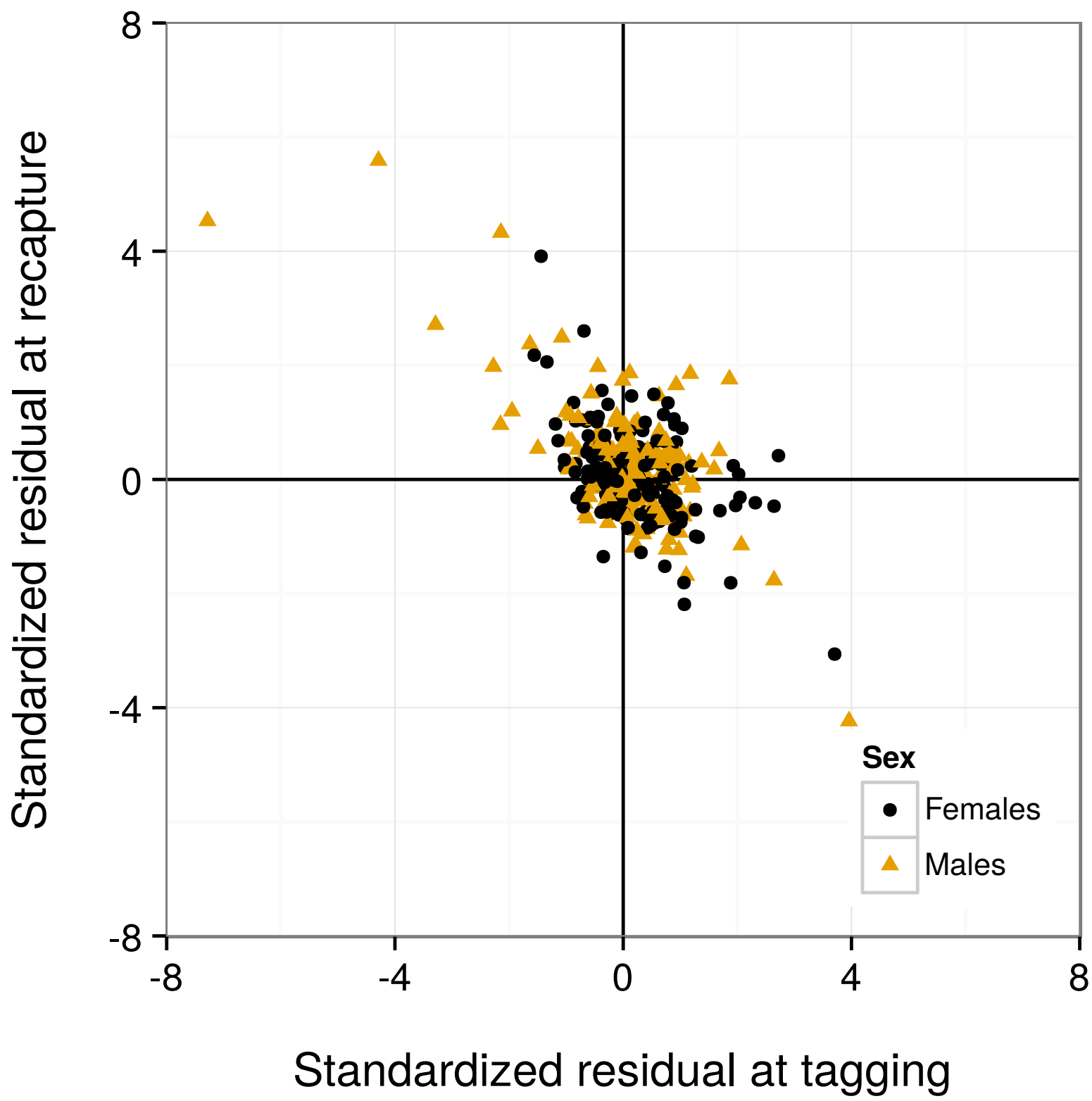
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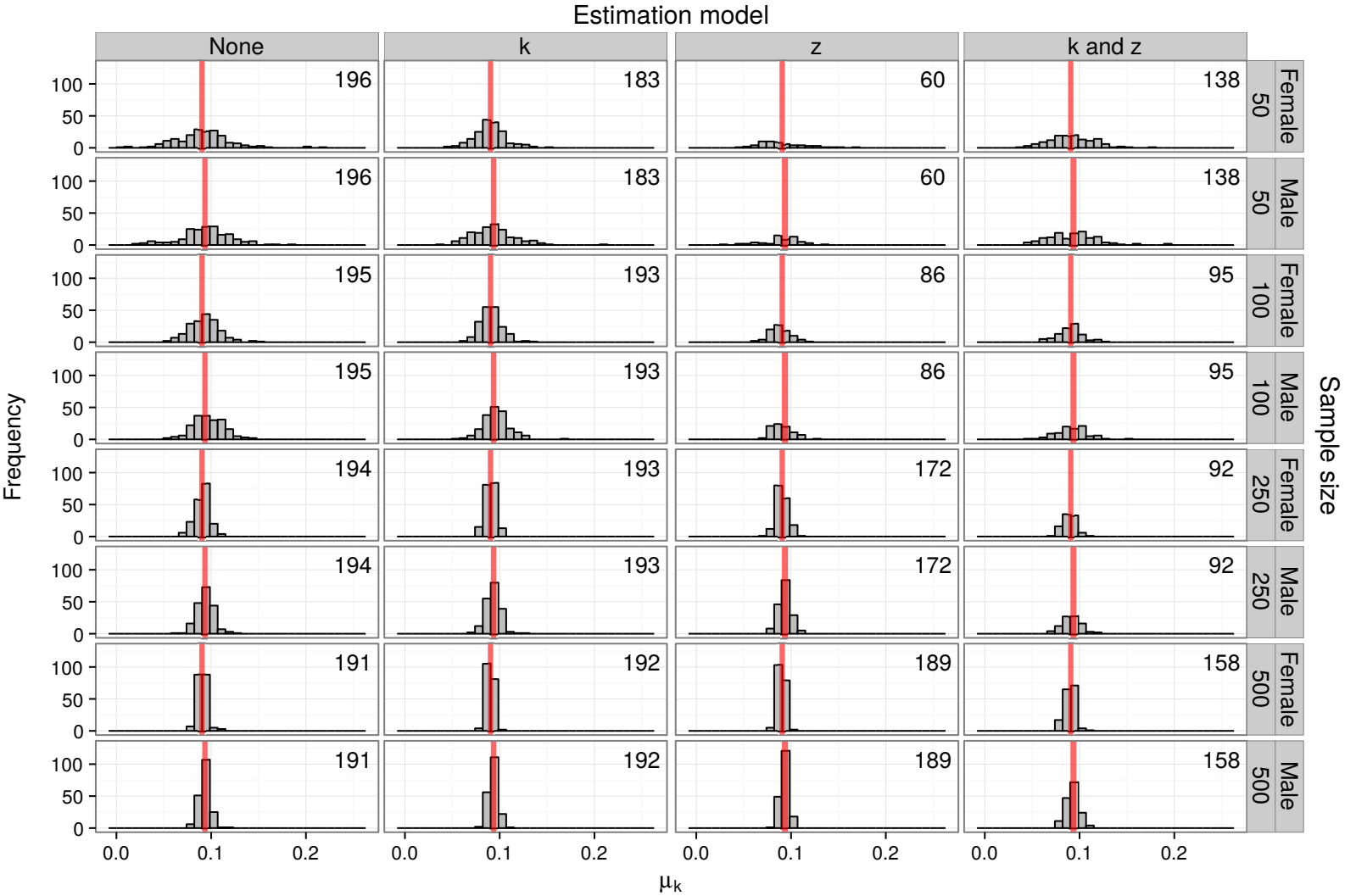
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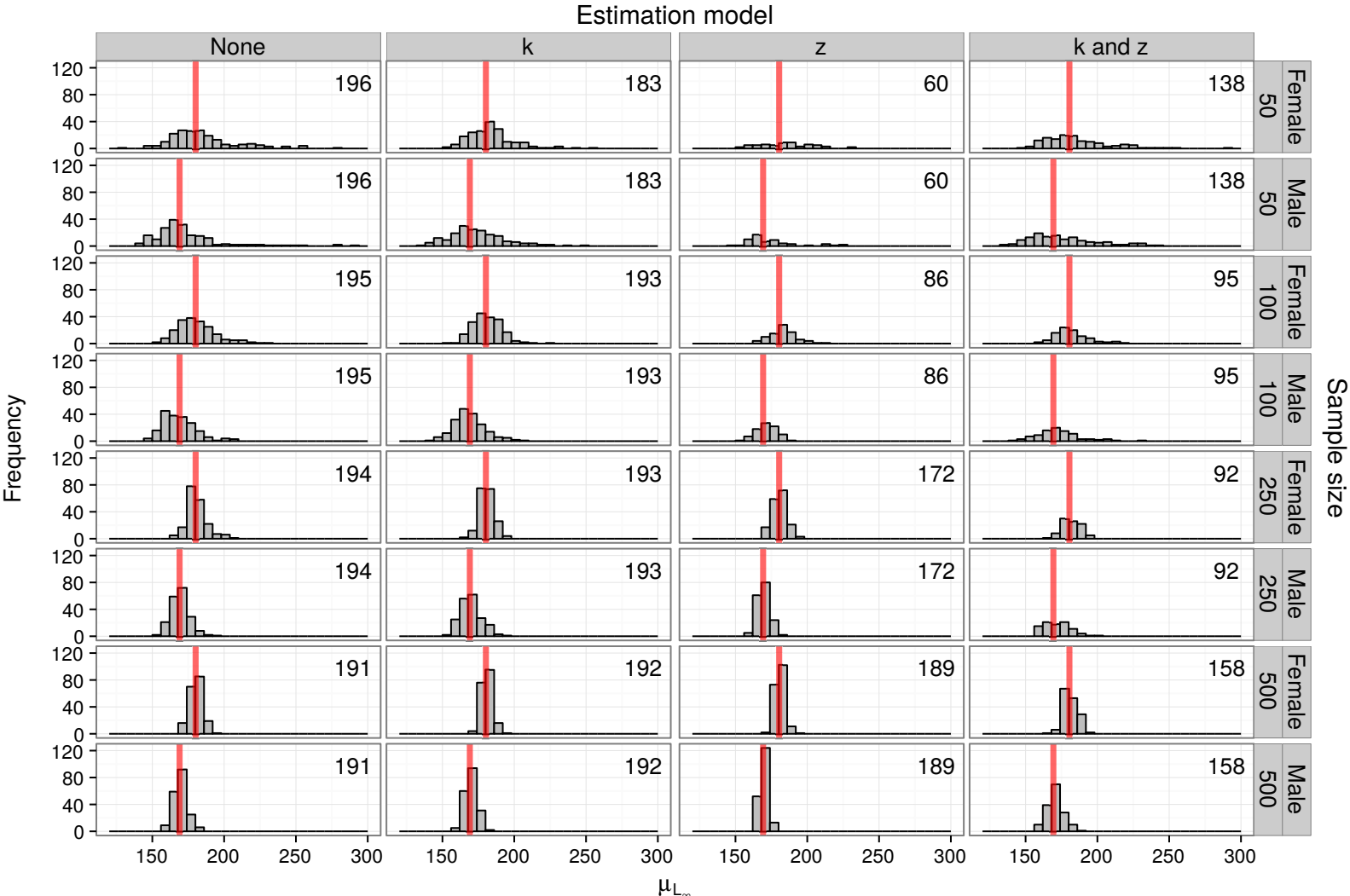
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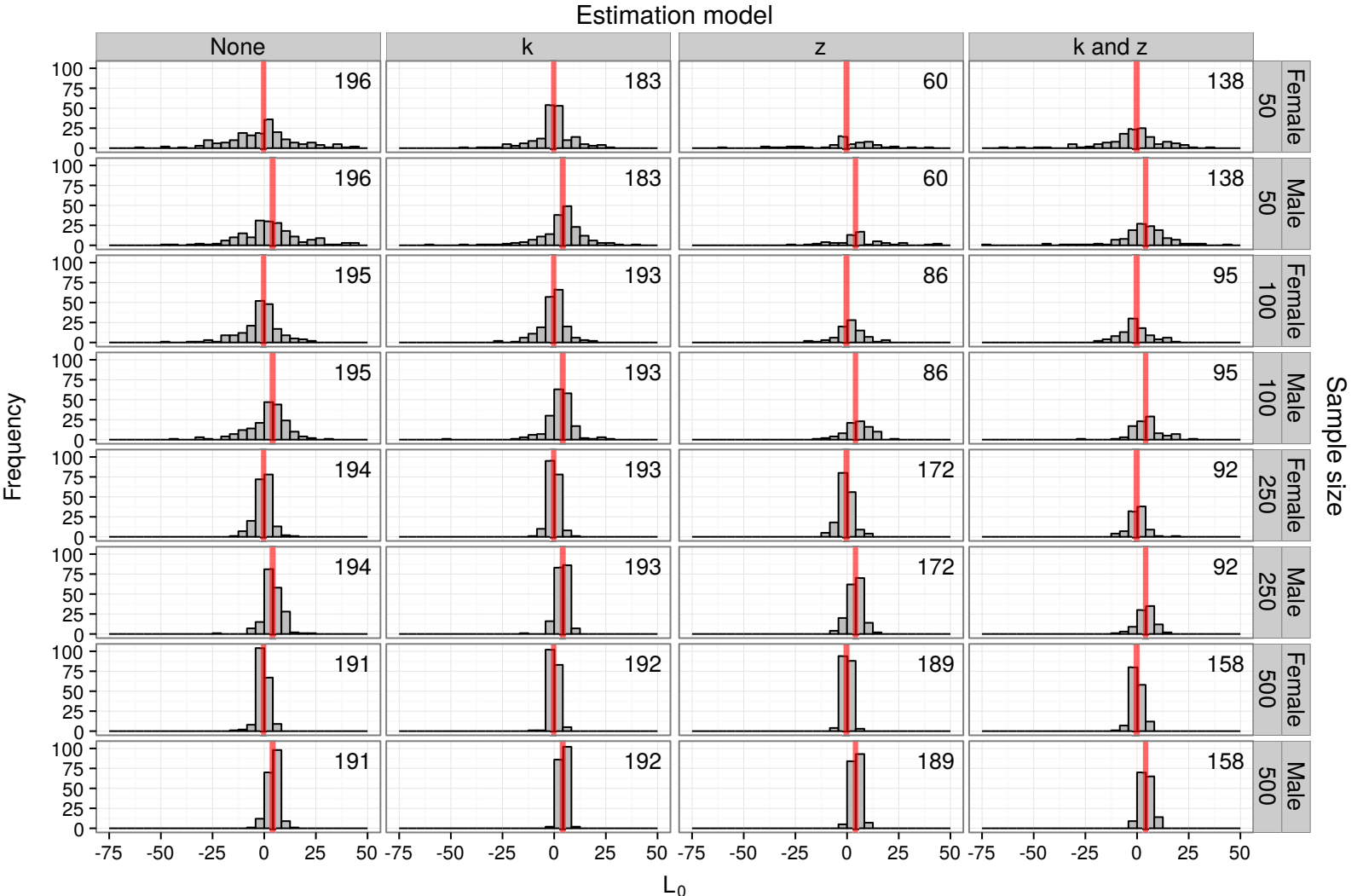
Figure 8

Figure 9

Appendices