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Bayesian state-space estimation of von Bertalanffy growth parameters for gray triggerfish, Balistes capriscus, incorporating multiple readers and ageing structures

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Manuscripts

1   **Bayesian state-space estimation of von Bertalanffy growth parameters for gray triggerfish,**

2   ***Balistes capriscus*, incorporating multiple readers and ageing structures**

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Abstract

24

25   Uncertainty in growth parameter estimates is derived from both natural variability in

26   growth and ageing error. However, these sources of error are rarely considered discretely as

27   growth is generally estimated from a single age reader's age estimates. Here, we developed a

28   sex-specific Bayesian state space formulation of the von Bertalanffy growth model (VBGM) to

29   estimate gray triggerfish (*Balistes capriscus*) growth parameters from multiple (n = 3) reader age

30   estimates derived from otolith opaque zone counts, a new dorsal spine protocol, and the

31   historical (old) dorsal spine protocol. For all three ageing protocols, estimates of length-at-age

32   were significantly different between sexes, resulting in significantly higher estimates of L_∞ for

33   males compared to females. Estimates of the Brody growth coefficient (k) from both the otolith

34   and new spine ageing protocols were significantly lower than the old spine protocol estimate.

35   Study results provide a framework for comparing VBGMs, suggest it is most appropriate to fit

36   sex-specific growth models for this species, and suggest stock assessments using ages estimated

37   with the old spine ageing protocol would produce biased results.

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Introduction

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40   Accurate estimation of growth parameters is fundamental to accurate fisheries stock

41   assessment models. Size-structured stock assessment models rely on estimates of growth to

42   determine the progression of fish across timesteps, while age-structured models frequently use

43   growth to calculate total biomass or biomass-at-age and often outperform their size-structured

44   counterparts (Fisch et al., 2019). Proxy estimates of fecundity, mortality, and vulnerability are

45   also frequently derived from growth estimates, which are also critical to determining how size

46   limits or changes in selectivity may affect yield (Stawitz et al., 2019; von Bertalanffy, 1934;

47   Walters and Martell, 2004; Zhou et al., 2012). Thus, accurate estimation of growth parameters,

48   and the attendant uncertainty in those estimates, is fundamental to accurate stock assessment

49   outputs and effective fisheries management.

50   Growth estimation has advanced from fitting growth functions with least squares or

51   likelihood methods (Quinn II and Deriso, 1999), to incorporating multiple readers as random

52   effects (Cope and Punt, 2007) and considering marginal increment data or multiple readers

53   within a Bayesian framework (Caltabellotta et al., 2021; Chamberlin et al., 2023b). Early

54   implementation of growth models estimated growth parameters without uncertainty parameters

55   (von Bertalanffy, 1934). Under that framework, growth estimates represent mean growth and

56   process error (natural variability) and observation error (ageing error) were not estimated. As

57   statistical and computational capabilities have improved uncertainty in parameter estimates is

58   typically estimated. However, it is not uncommon for modern age and growth papers to report

59   growth estimates without an estimate of uncertainty or to incorrectly report these data. When

60   uncertainty is estimated, non-linear least squares or likelihood formulations typically assume that

61   variance in growth is due solely to process error (Cope and Punt, 2007; Quinn II and Deriso,

62 1999), and fail to consider how observation error may contribute to the overall variance

63 structure. By incorporating multiple age estimates the relative contribution of observation error

64 to the total variance can be quantified (Chamberlin et al., 2023b; Cope and Punt, 2007) and the

65 total variance can subsequently be incorporated into stock assessments.

66 Gray triggerfish (*Balistes capriscus*) in the Gulf of Mexico (GOM) is a stock for which

67 there has historically been substantial ageing error (Chamberlin et al., 2024; Potts et al., 2023).

68 This may have contributed to the failure of the stock to recover at expected rates following

69 decades of overfishing and the implementation of a rebuilding plan in the early 1990s (SEDAR,

70 2006; SEDAR, 2015). Gray triggerfish were historically aged by counting translucent zones in

71 dorsal spine sections using the methods of Kolmos et al. (2013), hereafter referred to as the old

72 spine protocol. However, this method results in biased underestimates of age (Chamberlin et al.,

73 2024; Potts et al., 2023). Underestimation of age results in biased estimates of growth, mortality,

74 recruitment, and the overestimation of the fishing mortality that produces the maximum

75 sustainable yield (Beamish and McFarlane, 1983; Bradford, 1991; Campana, 2001; Lin Lai and

76 Gunderson, 1987; Reeves, 2003; Tyler et al., 1989). Therefore, considering ageing error (i.e.,

77 bias and imprecision) as a source of uncertainty is essential to effectively characterizing

78 parameters derived from age data, particularly in the case of gray triggerfish.

79 Potts et al. (2023) recently reported the annual periodicity of growth zone formation in

80 gray triggerfish dorsal spines and otoliths and proposed a modified protocol for estimating age

81 from dorsal spine thin sections, referred to as the new spine protocol. Chamberlin et al. (2024)

82 later validated age estimates derived from whole otoliths and the Potts et al. (2023) new spine

83 protocol as being accurate via application of the bomb radiocarbon chronometer to eye lens core

84 (birth year) $\Delta^{14}C$ values. However, it is also important to consider how differences in between-

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85   reader precision affect parameter estimates derived from either ageing structure as between-

86   reader precision differs between the two protocols. Additionally, it is important to consider how

87   growth parameters estimated from these validated methods compare to estimates derived from

88   the biased methods of the Kolmos et al. (2013), which historically was used to estimate age as

89   well as growth parameters for use in GOM gray triggerfish stock assessments (e.g., Allman et al.

90   2016, 2018). However, the direct comparison of growth parameter estimates is complicated by

91   the effects of samples sizes and presence or absence of small or large fish (Gwinn et al., 2010;

92   Wilson et al., 2015). Bayesian methods allow parameters from different models to be estimated

93   simultaneously and can consider the joint distribution across correlated growth parameters,

94   allowing for a direct comparison of parameter estimates between different models, which is

95   critical in estimating and comparing growth under alternate ageing protocols.

96   The objectives of this study were to develop a modeling framework to 1) estimate GOM

97   gray triggerfish growth parameters from age estimates produced by multiple readers; 2) test for

98   differences in growth parameters computed from age estimates derived from whole otoliths

99   versus those produced from the new spine-based method reported by Potts et al. (2023) and the

100   old method of Kolmos et al. (2013); and, 3) test whether gray triggerfish exhibit sexually

101   dimorphic growth. Study results are discussed in the context of their implications for estimating

102   gray triggerfish growth and population dynamics, as well as broader applicability of the methods

103   presented here to fish growth estimation.

Methods

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Sample Collection

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106   Fishery-independent and fishery-dependent gray triggerfish samples were collected in the

107   GOM with hook and line, longline, trawl, and spear. Animal collection was permitted by the

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108   National Marine Fisheries Service and animals were handled in accordance with the Guide for

109   the Care and Use of Laboratory Animals under protocols approved by the University of Florida

110   Institutional Animal Care and Use Committee (Protocol #202211613). Fishery-dependent and

111   independent samples collected with hook and line were targeted in the northern Gulf of Mexico

112   (nGOM) off Dauphin Island, Alabama to Destin, Florida, and the eastern Gulf of Mexico

113   (eGOM) on the west Florida continental shelf (WFS). Fishery-dependent samples collected with

114   longline were targeted by commercial fishers on natural and artificial reefs also on the WFS.

115   Trawl caught samples were collected throughout the GOM during the Southeast Area Monitoring

116   and Assessment Program trawl survey. Finally, gray triggerfish that were speared were collected

117   in the western Gulf of Mexico (wGOM) off the coast of Texas.

118   Fishery-dependent samples had been filleted and the carcasses were transported to the

119   University of Florida on ice. Each carcass was measured to the nearest millimeter filleted fork

120   length (FL). Sex was determined by macroscopic examination of the gonads, if the gonads had

121   been removed sex was indicated as unknown. Fishery-independent samples were transported to

122   the University of Florida whole on ice to be processed. Each fish was measured to the nearest

123   mm fork length (FL) and weighed to the nearest gram (g). A subset of fishery-independent

124   samples were subsequently filleted and the filleted FL was measured. A linear-regression was

125   then fitted to the whole FL and filleted FL, which was used to convert filleted FL to whole FL

126   for fishery-dependent samples. Right and left vestibular systems were extracted whole, with

127   otoliths contained within the saccule, and stored dry in 0.5-ml microcentrifuge tubes. The first

128   dorsal spine, including the condyle, was removed by cutting anterior and posterior to the spine.

129   **Age Estimation and Size-at-Age**

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130   Sagittae were removed from vestibular tissue with tweezers in the laboratory following

131   rehydration of the tissue, then stored dry in microcentrifuge vials. Each otolith sample was read

132   whole by an experienced reader (R1; DWC) and a subset of otoliths were read by two additional

133   experienced fish agers (R2; JCP and R3; WDR) using the methods of Chamberlin et al. (2024).

134   Dorsal spines were prepared for ageing by boiling in water and subsequently scraping to remove

135   any adhering tissue (Allman et al., 2016). A 0.5-mm thick transverse section was cut near the

136   spine's base with a diamond-bladed, low-speed saw. The section was then affixed to a slide and

137   covered with a toluene-based mounting medium. Translucent zones were initially enumerated by

138   R1 using the old spine protocol (Kolmos et al., 2013). Second and third reads were not

139   conducted using this protocol as R2 and R3 had developed a new spine protocol and reverting to

140   the old spine protocol would likely have produced biased results. Following training by R2 and

141   R3, translucent zones were also enumerated by R1 using the new spine protocol (Potts et al.,

142   2023). A subset of these samples were also read by R2 and R3. All reads were performed

143   double-blind, without knowledge of other reader's opaque or translucent zone counts or

144   morphometric data.

145   The index of average percent error (iAPE) was calculated to assess the precision of

146   growth zone counts between readers for each ageing structure (Beamish and Fournier, 1981).

147   Bias plots were also constructed to compare growth zone counts between readers for each ageing

148   structure (Campana et al., 1995), as well as between ageing structures or spine protocols for each

149   reader. Fractional age was estimated for age-0 fish by dividing the measured fork length by and

150   estimated juvenile growth rate of 0.95 mm/day and then dividing by 365 days (Ingram, 2001;

151   Moore, 2001). The effects of sex on estimated size-at-age derived from R1 data were tested with

152   three-factor ANOVA models ($\alpha = 0.05$) in R (R Core Team, 2023). Fork length was the

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153 dependent factor, with age, ageing structure, and sex as independent factors. The ageing

154 structure*age*sex interaction was sliced by ageing structure and age to test for sex-specific

155 differences in size-at-age. All analyses were performed in R (R Core Team, 2023).

von Bertalanffy Growth Estimation

von Bertalanffy growth model formulation

158   We used the size-at-birth formulation of the von Bertalanffy growth model (VBGM; von

159 Bertalanffy, 1934) as a template to build a growth model for gray triggerfish (Equation 1).

160       $$L_{i,t} = L_\infty - (L_\infty - L_0)e^{-kt_i} \qquad \text{(Eq. 1)}$$

161 where $L_{i,t}$ is the length at some predicted time t (age) of individual i, L_∞ is the asymptotic length

162 or average maximum size, L_0 is the size at birth, and k is the Brody growth coefficient. We

163 adapted this growth model to 1) compare between ages derived from otoliths and both spine

164 protocols; 2) compare growth parameters between sexes; 3) incorporate unknown sex

165 individuals; and 4) account for between-reader variability. To compare among otolith-derived

166 and old and new spine-derived ages, we fit separate instances of Equation 1 while sharing a

167 common L_0 among models (Equation 2) and specifying $L_{i,t}$ to be described by a log-normal

168 process (Equation 3).

169       $$\hat{L}_{ip,t} = L_{\infty,p} - (L_{\infty,p} - L_0)e^{-k_p t_{ip}} \qquad \text{(Eq. 2)}$$

170       $$L_{ip,t} \sim \text{logNormal}\left(\log\left(\hat{L}_{ip,t}\right), \sigma_p\right) \qquad \text{(Eq. 3)}$$

171 where p denotes different protocols, ip describes individual i aged with hard part/protocol p, $\hat{L}_{i,t}$

172 describes the predicted length, $L_{i,t}$ now describes the observed length, and σ_p describes the log-

173 normal scale. We then further separated Equations 2–3 to account for sex (Equation 4–5).

174       $$\hat{L}_{ip,t} = L_{\infty,p,s} - (L_{\infty,p,s} - L_0)e^{-k_{p,s} t_{ip}} \qquad \text{(Eq. 4)}$$

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175 $$L_{ip,t} \sim \text{logNormal}\left(\log\left(\hat{L}_{ip,t}\right), \sigma_{p,s}\right) \quad \text{(Eq. 5)}$$

176 where s denotes the sex-specific parameter. As we did not know the sex of every individual, we

177 modified the sex-specific parameters such that Equation 2 receives additive effects of sex to L_∞,

178 k, and σ_p to generate Equation 4 (Equations 6–8) in the spirit of Siders et al. (2023).

179 $$\log(L_{\infty,p,s}) = \log(L_{\infty,p}) + \beta_{L_\infty,s} \quad \text{(Eq. 6)}$$

180 $$\log(k_{p,s}) = \log(k_p) + \beta_{k,s} \quad \text{(Eq. 7)}$$

181 $$\log(\sigma_{p,s}) = \log(\sigma_p) + \beta_{\sigma,s} \quad \text{(Eq. 8)}$$

182 where $\beta_{X,s}$ is the sex-specific additive effect to a given von Bertalanffy growth model parameter.

183 Lastly, we accounted for between-reader variability in the assigned age, which is a major

184 source of error in variables in the age-growth modeling process. We adopted the state-space

185 approach of Chamberlin et al. (2023b) that uses the multiple reads as observations of the true age

186 for each individual coming from a Student's T distribution (Equation 9),

187 $$t_{ip,r} \sim \text{Student's T}\left(v_{ip}, \hat{t}_{ip}, \sigma_{obs,p}\right) \quad \text{(Eq. 9)}$$

188 where $t_{ip,r}$ is the observed age coming from reader r per individual i and protocol p, v_{ip} is the

189 degrees of freedom equal to the number of reads, $\hat{t}_{ip}$ is the latent true age, and $\sigma_{obs,p}$ is the inter-

190 reader variability. Including $\sigma_{obs,p}$ separates the ageing observation error from σ_p and $\sigma_{p,s}$ such

191 that these now reflect process error or growth variability, which now we denote as $\sigma_{VB,p}$ and

192 $\sigma_{VB,p,s}$. A Student's T distribution was used due to the incorporation of fractional ages for fish

193 with 0 observed growth zones (Age-0) and has the added benefit of accounting for the number of

194 individual reads per sample.

195 Within the Bayesian von Bertalanffy growth model, we predicted length-at-age for each

196 sex and protocol over a range of hypothetical ages from zero to $t_{\max}$ by 0.1 year increments. For

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197   integration with the more common t_0 formulation of the von Bertalanffy growth model in

198   teleosts, we derived t_0 (Equation 10),

199      $$t_0 = \frac{1}{k}\log\left(\frac{L_\infty - L_0}{L_\infty}\right)$$ (Eq. 10)

200   *von Bertalanffy growth model implementation*

201   We used STAN (Stan Development Team, 2022) and *cmdstanr* (Gabry and Češnovar,

202   2022) to implement the Bayesian von Bertalanffy growth model for gray triggerfish. We first fit

203   Equation 1 using maximum-likelihood estimation to generate weakly informative priors

204   following Caltabellotta et al. (2019), Chamberlin et al. (2023b), and Rolim et al. (2020) for L_∞, k

205   , and σ_{VB} using the predicted mean for the prior location and a 50% coefficient of variation to

206   generate the corresponding scale. For L_∞, k, σ_{VB}, and σ_{obs}, we specified normal priors on the

207   log-transformed parameters. A weakly-informative prior was put on σ_{obs} with a mean of 1 and a

208   standard deviation of 0.5. The only parameter that received a strongly informative prior was L_0

209   with a mean of 2.2 mm and standard deviation of 0.04 mm, which was derived data reported by

210   Simmons and Szedlmayer (2013). For the sex-specific additive effects, we specified normal

211   priors with mean 0 and a standard deviation of 1 as these effects were on the log-transformed

212   scale (Equation 6–8). We used the No U-Turn sampler in STAN with eight chains that had 5,000

213   warmup iterations and 125 sampling iterations each. We combined the chain-specific posterior

214   samples to generate a single posterior of each parameter after assessing chain coverage using the

215   Gelman and Rubin (1992) statistic below 1.1 for all parameters. We assessed significant

216   differences between parameters using the maximum a posteriori (MAP) value at $\alpha = 0.10$ using

217   the bayestestR package (Makowski et al., 2019).

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219   **Results**

Sample Collection

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221   In total, 1,270 gray triggerfish were samples across the GOM, consisting of 925 fishery-

222   dependent samples and 345 fishery-independent samples. Of these, 706 samples were collected

223   in the nGOM, 391 in the seGOM, and 122 in the wGOM. Among fishery-dependent samples, 51

224   did not have a sample location noted. There were 18 fish sampled with deck-reels, 667 with hook

225   and line, 412 with longline, 122 with spear, and 51 with trawl. There was a significant

226   relationship between whole FL and filleted FL (n = 42; R^2 = 0.99; $FL_{Whole} = 0.99 * FL_{Filleted}$

227   +0.30), which was used to convert filleted FL to whole FL for fishery-dependent samples.

Age Estimation and Size-at-Age

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229   Age was estimated by R1 for 1,182 samples by counting whole otolith opaque zones,

230   1,219 samples using the new spine protocol (Potts et al., 2023), and 1,243 samples using the old

231   spine protocol (Kolmos et al., 2013). Differences in sample sizes are due to missing structures or

232   differences in interpretability. Between-reader growth zone counts derived from whole otoliths

233   and the new spine protocol showed strong agreement among readers (see Chamberlin et al. 2024,

234   Figure 3 for reader bias plots). Overall, iAPE among all three readers was 10.1% for whole

235   otolith-derived age estimates and 9.4% for new spine protocol age estimates. Therefore, age

236   estimates were slightly more consistent between readers using the new spine protocol compared

237   to reading whole otoliths (Chamberlin et al. 2024). There are no precision metrics for the old

238   spine protocol as only R1 read the dorsal spine samples using that protocol.

239   Otolith-derived age estimates ranged from 0 to 14 y for female gray triggerfish and 0 to

240   12 y for males. New spine protocol age estimates ranged from 1 to 16 y for female gray

241   triggerfish and 0 to 14 y for males, while old spine protocol age estimates ranged from 1 to 12 y

242   for female gray triggerfish and 0 to 9 y for males. Otolith and new spine protocol age estimates

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243 corresponded well across ages with no apparent relationship between sex and protocol-specific

244 age estimates (Figure S1). Conversely, age estimates derived from the old spine protocol

245 consistently underestimated age relative to ages derived from the validated whole otolith and the

246 new spine protocols, for ages ≥ 5 (Figure S1). Males were significantly larger at age than females

247 when age was estimated from either whole otoliths, the new spine protocol, or the old spine

248 protocol (Figure 1; Table S1).

249 **von Bertalanffy Growth Estimation**

250 The Bayesian state-space von Bertalanffy growth model with size-at-age data from all

251 three ageing protocols converged with a mean Gelman and Rubin (1992) statistic of 1.01 across

252 all parameters and no parameters over 1.1. Differences between the von Bertalanffy parameter

253 estimates based on otolith-, new spine protocol-derived ages, or old spine protocol-derived ages

254 were insignificant, with the exception of k and t_0 (Figures 2 and 3; Table S2). At the median k

255 for the combined sex model, the differences between otolith- $\left(k = 0.42 \text{ y}^{-1}\right)$ and new spine

256 protocol-derived $\left(k = 0.39 \text{ y}^{-1}\right)$ parameter estimates were only 0.03 y^{-1} (Table 1). However,

257 the combined sex old spine protocol estimate $\left(k = 0.55 \text{ y}^{-1}\right)$ was greater than estimated k in

258 either the combined sex otolith or new spine protocol models. This difference was not significant

259 due to variability in posterior estimates, which likely resulted from sexually dimorphic growth

260 (Table S2). The greater between-reader variability for otolith-derived ages compared to new

261 spine protocol-derived ages was not statistically significantly (Table S2, $p_{\text{MAP}} = 0.67$ of $\Delta\sigma_{obs}$).

262 Inclusion of multiple readers resulted in increased uncertainty in the combined sex otolith and

263 new spine protocol models ($\sigma_{total} = \sigma_{VB} + \sigma_{obs} = 0.68$ for both the otolith and new spine

264 protocols, respectively) compared to the single reader old spine model ($\sigma_{total} = \sigma_{VB} = 0.14$).

265   Differences between protocols were more pronounced in the sex-specific models where

266   female- and male-specific old spine protocol-derived estimates for k and t_0 significantly differed

267   from the otolith and new spine protocols (Figure 3; Table S2). For k, these estimates were,

268   across otolith and new spine protocol-derived estimates, 0.18 y^{-1} higher for females and 0.12

269   y^{-1} higher for males, on average, compared to the old spine protocol-derived estimates (Table

270   1). The significant differences in k were driven by the relative underestimation of age using the

271   old spine protocol compared to the otolith or new spine protocols (Figure S1). While there were

272   significant differences in estimates of t_0, this was due to the strong prior L_0 resulting in narrow

273   posterior distributions of t_0 (Table 1).

274   In terms of sex-specific growth, males were expected to grow significantly larger than

275   females ($L_{\infty,M} = 501$ mm, $L_{\infty,F} = 446$ mm, new spine protocol-derived; $p_{\text{MAP}} < 0.01$) but both

276   sexes are roughly the same size until age 2 to age 3 (Figures 1, 2, and 4; Table 1). Females had

277   significantly higher variability in growth (Figure 4; $p_{\text{MAP}} < 0.01$ of $\Delta\sigma_{VB}$). Females generally

278   had higher estimates of k but not significantly so due to uncertainty in the posterior parameter

279   estimates of k regardless of otolith- or spine-derived ages (Figure 4; Table 1; $p_{\text{MAP}} = 0.18 -$

280   1.00). Otolith-derived estimates of k were more different between sexes than the new spine

281   protocol-derived ages (Figure 4), due to great between-reader variability and a tendency for

282   female otolith-derived ages to be slightly lower at younger ages than the corresponding female

283   new spine protocol-derived ages (Figure S1).

284   **Discussion**

285   Our results demonstrate that gray triggerfish age estimates derived from whole otoliths

286   and the Potts et al. (2023) dorsal spine protocol produce similar growth parameter estimates,

287   while age estimates using the Kolmos et al. (2013) dorsal spine protocol result in a significantly

288   higher estimate of the Brody growth coefficient, k. The Brody growth coefficient is a common

289   proxy for stock productivity, with a higher k indicating a more productive stock, thus

290   overestimating k could result in overestimating stock productivity leading to overfishing (Pauly,

291   1980; Walters and Martell, 2004). Additionally, our results clearly demonstrate gray triggerfish

292   exhibit sexually dimorphic growth with males growing to a larger maximum size than females on

293   average. This suggests future assessments should consider incorporating sex specific estimates of

294   growth and landings data to better capture the true population dynamics.

295   Growth misspecification can bias stock assessment estimates resulting in overly

296   optimistic estimates of management reference points (Stawitz et al., 2019), which increases the

297   likelihood of overfishing. Increasingly stock assessments are able to incorporate uncertainty

298   parameters and propagate that uncertainty into assessment outputs (Methot et al., 2020).

299   Incorporating multiple readers into growth estimation and estimating observation error allows for

300   sources of process error, such as annual or spatial growth variability, to be investigated explicitly

301   (Cope and Punt, 2007). While process error would generally be reduced, the estimation of

302   observation error results in an overall increase in total uncertainty because the parameter

303   estimates now incorporate error in variables. The increase in overall uncertainty would have

304   attendant effects by increasing uncertainty in any derived parameter, such as M or fecundity,

305   whereas under a single reader model this uncertainty could not be captured and accounted for.

306   Given these advantages future growth estimation should explicitly acknowledge and incorporate

307   ageing error by estimating growth parameters based on multiple reads.

308   Direct comparison of growth parameter estimates is difficult as parameter estimates are

309   affected by samples size and the presence or absence of small and/or large fish (Gwinn et al.,

310   2010; Wilson et al., 2015). Alternatively, differences in size-at-age can be tested directly

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311   (Chamberlin et al., 2023a; Shepard et al., 2010). However, the direct comparison of growth

312   parameter estimates is often necessary to determine how changes in ageing protocols may affect

313   derived parameter estimates or assessment outcomes. This is particularly salient in the context of

314   ageing error and sexually dimorphic growth. Ageing protocols are frequently amended when

315   ageing error is detected, thus the difference in growth estimates under an altered paradigm must

316   be assessed. Additionally, many fish exhibit sexually dimorphic growth necessitating the

317   investigation of the effect of sex on growth parameter estimates beyond size-at-age. Bayesian

318   methods can directly facilitate this comparison as the parameter estimates from different growth

319   models can be simultaneously estimated. In our application, fitting sexually dimorphic growth

320   models for each protocol allowed us to compare differences between sexes within an ageing

321   protocol and between protocols. This ensures that significantly different comparisons take into

322   account the joint distribution across all growth parameters. As L_∞ and k are highly correlated in

323   the von Bertalanffy growth model, the error in the joint distribution is more representative of the

324   true error.

325   Bias in age estimates propagates as bias in growth parameter estimates, principally the

326   overestimation of the Brody growth coefficient (k), which can result in the overestimation of

327   stock productivity. This is not exceptionally surprising as ageing error does not change the range

328   of lengths included in a model. Therefore, ageing error primarily affects k and not the parameters

329   more strongly influenced by the lengths included in the model like L_∞ and σ_{VB}. The sex-specific

330   VBGF estimates of k reported here, based on otolith-derived and new spine protocol age

331   estimates, were significantly lower than k estimated here with the old spine protocol.

332   Additionally, they are generally lower than estimates, based on the old dorsal spine protocol,

333   reported in several previous studies of gray triggerfish in the nGOM and southeastern Atlantic (k

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334   = 0.52 – 0.95 y^{-1}; Allman et al., 2018; Kelly-Stormer et al., 2017). These combined results

335   support the conclusion that estimates of k will be elevated, and growth overestimated, if age is

336   estimated using the Kolmos et al. (2013) protocol.

337   Several authors have reported estimates of k, derived from whole otolith opaque zone

338   counts, for Atlantic gray triggerfish that are lower than those reported here ($k = 0.27 – 0.30$ y^{-1};

339   Shervette et al., 2021; Shervette and Rivera Hernández, 2022). However, VBGFs in those studies

340   were fit to data sets that have a distinct lack of young, small fish in the $50 – 250$ mm range due to

341   gear selectivity (Shervette et al., 2021; Shervette and Rivera Hernández, 2022). This manifests in

342   the negative t_0 estimates ranging from -0.30 to -0.19 y which results in L_0 estimates of 22.6 to

343   36.2 mm, 10 to 16 times larger than the observed L_0 (Shervette et al., 2021; Shervette and Rivera

344   Hernández, 2022; Simmons and Szedlmayer, 2013). Size-selective sampling can result in a

345   dampening of the estimate of k, thus growth appears to occur at a slower rate than would be

346   estimated if the samples were representative of the population (Gwinn et al., 2010). The

347   incorporation of additional information, such as an informative prior on L_0, in a Bayesian

348   framework can reduce biases in VBGF estimates due to size-selective sampling.

349   Ageing error and growth parameter misspecification can result in misestimation of stock

350   status benchmarks, increasing the likelihood of overfishing (Reeves, 2003; Stawitz et al., 2019).

351   Accurate estimation of growth parameters is thus vital to effective fisheries management. Here,

352   we have demonstrated the utility of a novel modeling approach for estimating and statistically

353   comparing growth parameters across sex and multiple ageing protocols while incorporating

354   multiple readers. This approach explicitly acknowledges and quantifies uncertainty due to reader

355   imprecision and is broadly applicable within growth estimation. Beyond this we have

356   demonstrated gray triggerfish otoliths and the newly proposed and validated dorsal spine

357   protocol (Potts et al., 2023; Chamberlin et al., 2024) produce similar growth estimates while the

358   old dorsal spine protocol (Kolmos et al., 2013) overestimates k, erroneously indicating a more

359   productive stock.

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364

365 **Author Contributions**

366 **Derek Chamberlin:** Conceptualization, Formal analysis, Investigation, Methodology,

367 Visualization, Writing – original draft. **Zach Siders:** Conceptualization, Formal analysis,

368 Methodology, Visualization, Writing - original draft. **Jennifer Potts:** Conceptualization,

369 Investigation, Methodology, Writing - Review & Editing. **Walter Rogers:** Conceptualization,

370 Investigation, Methodology, Writing - Review & Editing. **Miaya Taylor:** Resources, Project

371 Administration, Writing - Review & Editing. **William Patterson:** Conceptualization, Formal

372 analysis, Funding acquisition, Investigation, Methodology, Supervision, Writing - Review &

373 Editing.

374

375 **Declaration of Competing Interest**

376   The authors declare that they have no known competing financial interests or personal

377 relationships that could have appeared to influence the work reported in this paper.

378

379 **Data Availability**

380   Data are currently provided within the manuscript and/or supplemental files, but will be

381 uploaded to an appropriate public repository and a DOI will be provided at the time of

382 acceptance.

383

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390

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520

521 Table 1. Posterior median estimates and 90% credible intervals (CI) for gray triggerfish von
522 Bertalanffy growth model (VBGM) parameters. L_∞ (mm) is the asymptotic length, k (y^{-1}) is the
523 Brody growth coefficient, σ_{VB} and σ_{obs} are the likelihood standard deviations, and t_0 is the age
524 (y) at length zero. Only one reader was used for the old spine protocol so there is no inter-reader
525 variability (σ_{obs}) estimate.

Protocol	Sex	θ	Median (90% CI)	90% credible interval
Otolith	Combined	L_∞	467	458 – 478
		k	0.42	0.38 - 0.45
		t_0	-0.012	-0.013 - -0.011
		σ_{VB}	0.130	0.125 - 0.137
		σ_{obs}	0.55	0.52 - 0.58
Spine - new	Combined	L_∞	473	463 – 484
		k	0.39	0.36 - 0.42
		t_0	-0.012	-0.013 - -0.012
		σ_{VB}	0.125	0.119 - 0.131
		σ_{obs}	0.56	0.53 - 0.59
Spine - old	Combined	L_∞	454	446 – 463
		k	0.55	0.51 - 0.59
		t_0	-0.009	-0.010 - -0.009
		σ_{VB}	0.143	0.137 - 0.150
		σ_{obs}	—	—
Otolith	Female	L_∞	430	416 – 445
	Male	L_∞	508	495 - 521
	Female	k	0.46	0.40 - 0.53
	Male	k	0.38	0.35 - 0.41
	Female	t_0	-0.012	-0.013 - -0.010
	Male	t_0	-0.012	-0.013 - -0.011
	Female	σ_{VB}	0.157	0.147 - 0.169
	Male	σ_{VB}	0.108	0.101 - 0.115
	Female	σ_{obs}	0.57	0.53 - 0.62
	Male	σ_{obs}	0.53	0.49 - 0.57
Spine - new	Female	L_∞	446	430 – 464
	Male	L_∞	501	489 – 513
	Female	k	0.39	0.35 - 0.45
	Male	k	0.39	0.36 - 0.43
	Female	t_0	-0.013	-0.014 - -0.012
	Male	t_0	-0.012	-0.012 - -0.011
	Female	σ_{VB}	0.147	0.138 - 0.157
	Male	σ_{VB}	0.107	0.100 - 0.114
	Female	σ_{obs}	0.54	0.50 - 0.58
	Male	σ_{obs}	0.57	0.53 - 0.62
Spine - old	Female	L_∞	424	413 – 437
	Male	L_∞	486	476 – 498
	Female	k	0.60	0.53 - 0.68
	Male	k	0.51	0.47 - 0.55
	Female	t_0	-0.009	-0.010 - -0.008
	Male	t_0	-0.009	-0.010 - -0.009
	Female	σ_{VB}	0.161	0.150 - 0.172
	Male	σ_{VB}	0.128	0.120 - 0.136
	Female	σ_{obs}	—	—
	Male	σ_{obs}	—	—

23

527
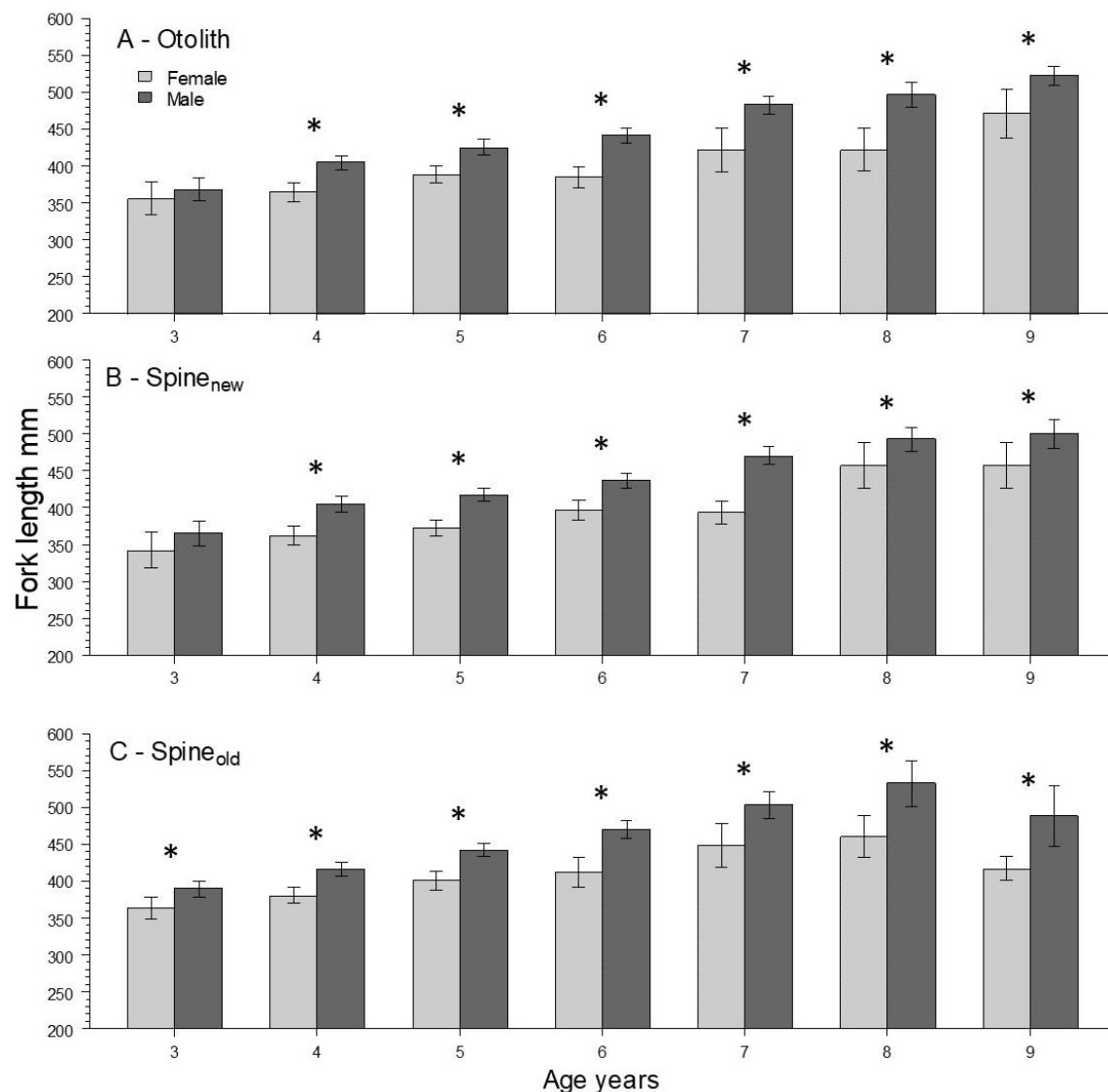
Figure 1. A) Mean sex-specific size-at-age (±95% CI) for gray triggerfish for otolith-derived age estimates for ages 3-9 years. Age-specific sample sizes were 86, 161, 185, 170, 76, 52, and 41 for ages 3-9 years, respectively. B) Mean sex-specific size-at-age (±95% CI) for gray triggerfish for new spine protocol-derived age estimates for ages 3-9 years. Age-specific sample sizes were 76, 144, 180, 195, 92, 57, and 43 for ages 3-9 years, respectively. C) Mean sex-specific size-at-age (±95% CI) for gray triggerfish for old spine protocol-derived age estimates for ages 3-9 years. Age-specific sample sizes were 115, 226, 247, 136, 62, 18, and 6 for ages 3-9 years, respectively. Asterisks denote a significant ($\alpha < 0.05$) effect of sex within year class.
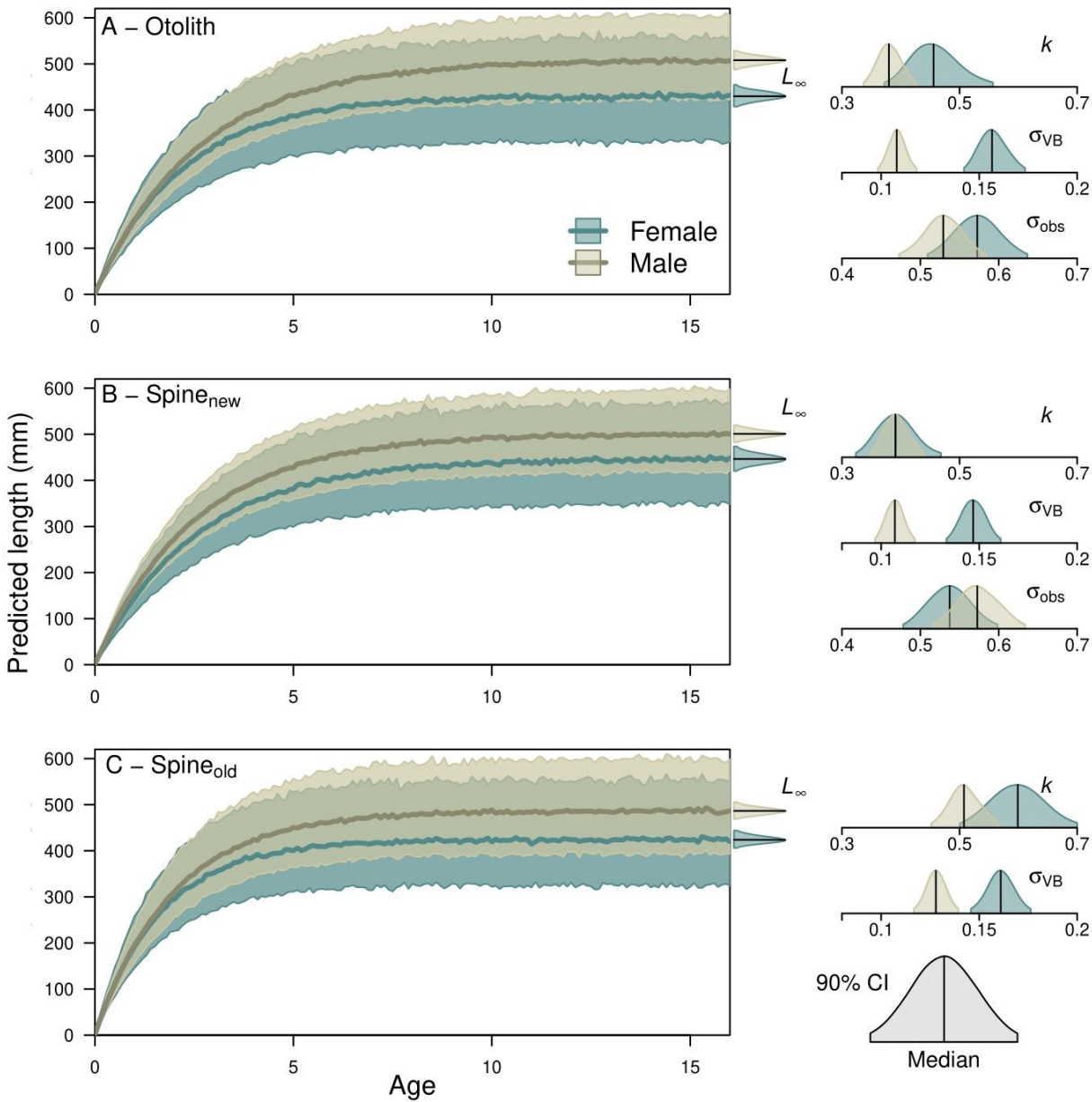
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Figure 2. Sex-specific von Bertalanffy growth models fitted to A) otolith-derived age estimates,
B) dorsal spine-derived age estimates using the new Potts et al. (2023) protocol, and C) dorsal
spine-derived age estimates using the old Kolmos et al. (2013) protocol. Data from multiple
readers were utilized in otolith and new spine growth models. The median (solid line) and 90%
credible intervals (CIs) (shaded areas) are shown for sex-specific growth model predictions in
each panel. Posterior distributions, median estimate (solid, vertical line), and 90% CIs are shown
for asymptotic length (L_∞), the Brody growth coefficient (k), and the likelihood standard
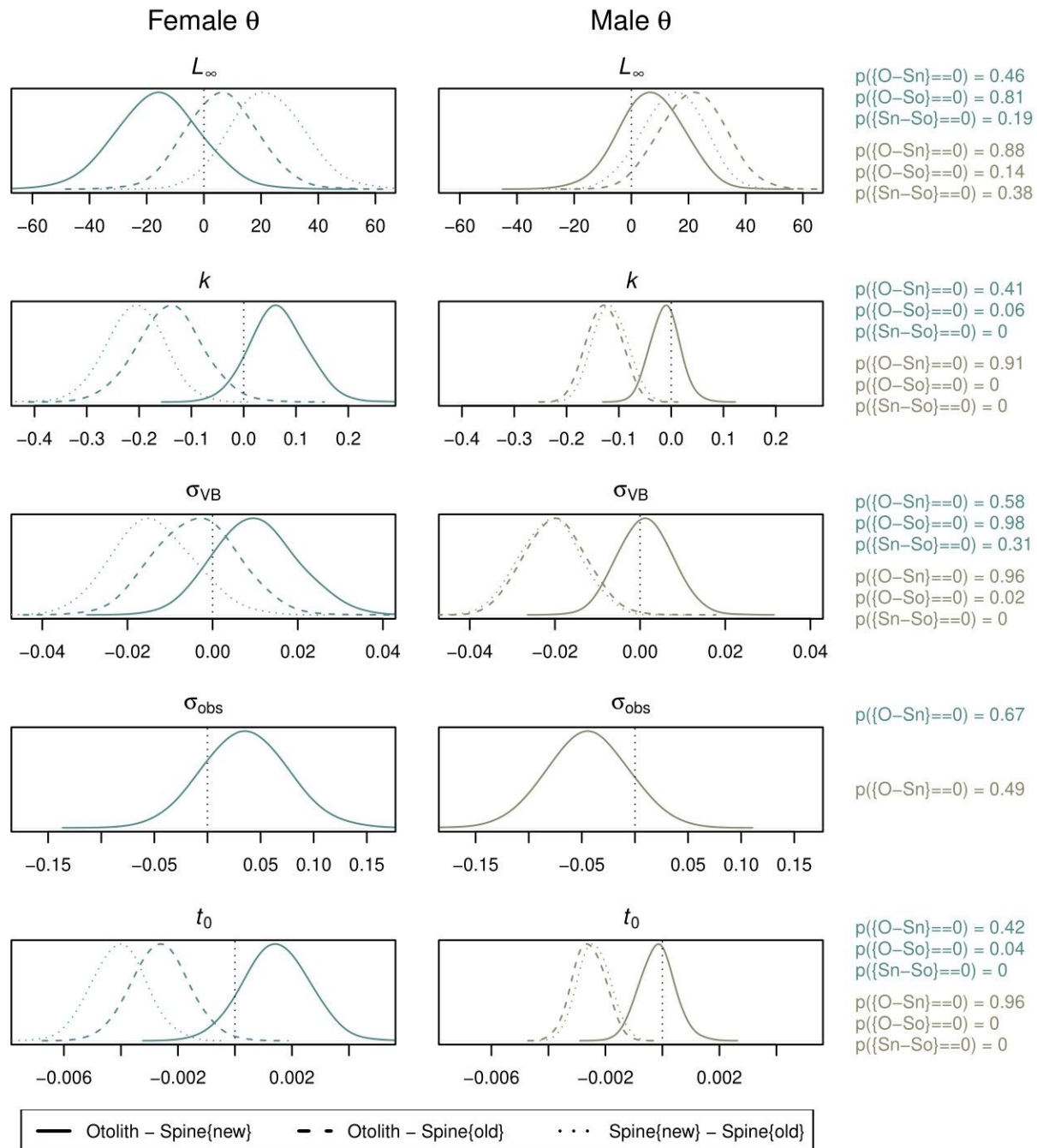deviations (σ_{vb} and σ_{obs}).

Figure 3. Posterior distribution of the difference, by sex, in asymptotic length (L_∞; top), the Brody growth coefficient (k; 2nd from top), the likelihood standard deviations (σ_{vb}; middle), the likelihood standard deviation due to observation error (σ_{obs}; 2nd from bottom), and size at length zero (t_0; bottom) estimates between age estimation methods for otolith- and new spine protocol- (solid line), otolith- and the old spine protocol- (dashed line), and new spine protocol- and old spine protocol- (dotted line) derived age estimates. The maximum *a posteriori* (MAP) value is reported for ageing method comparison to the right of each panel with significant differences assessed at $\alpha = 0.10$.
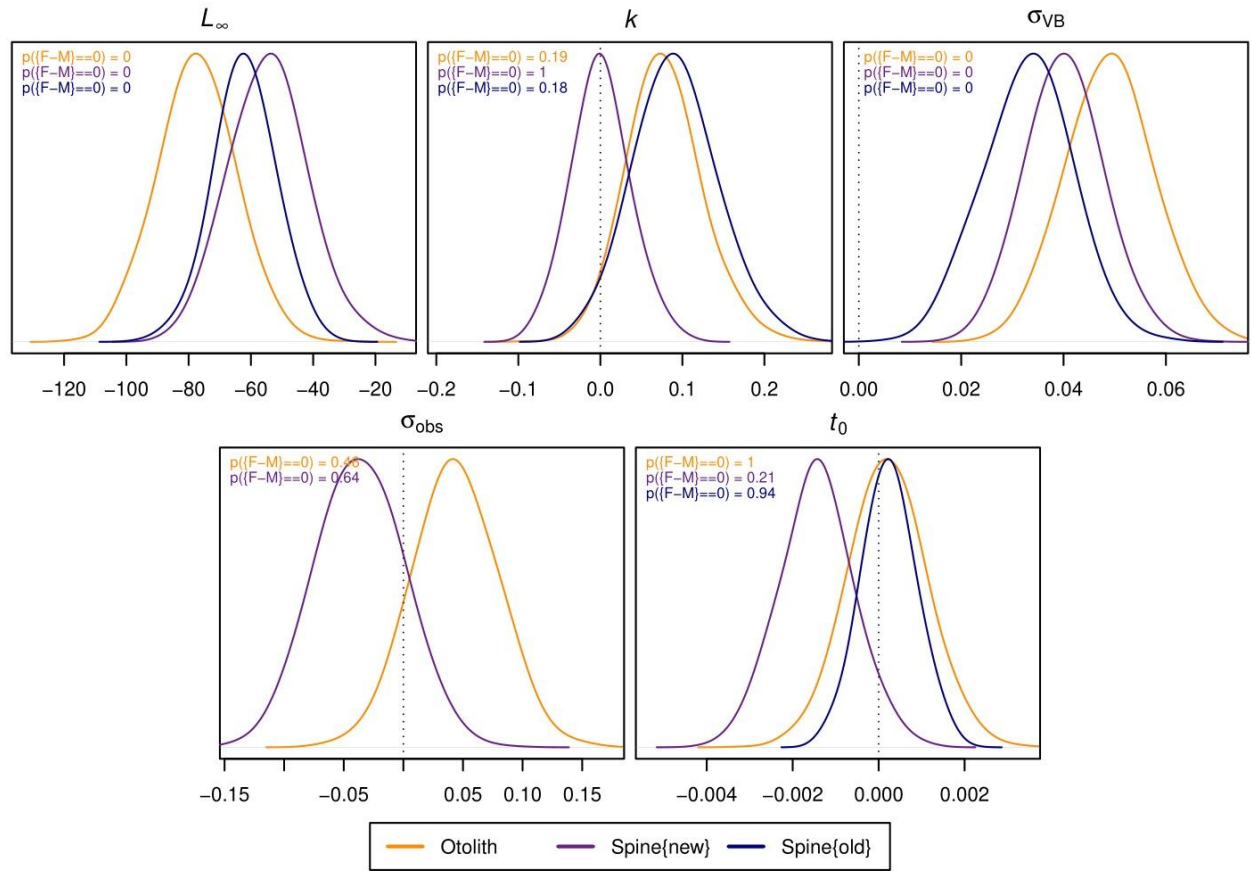
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Figure 4. Posterior distribution of the difference in asymptotic length (L_∞; top left), the Brody
growth coefficient (k; top middle), the likelihood standard deviations (σ_{vb}; top right), the
likelihood standard deviation due to observation error (σ_{obs}; bottom left), and size at length zero
(t_0; bottom right) estimates between males and females for otolith- (orange line), new spine
protocol- (purple line), and old spine protocol- (blue line) derived age estimates. The maximum *a*
posteriori (MAP) value, by ageing method, is reported for comparison between sex in the top left
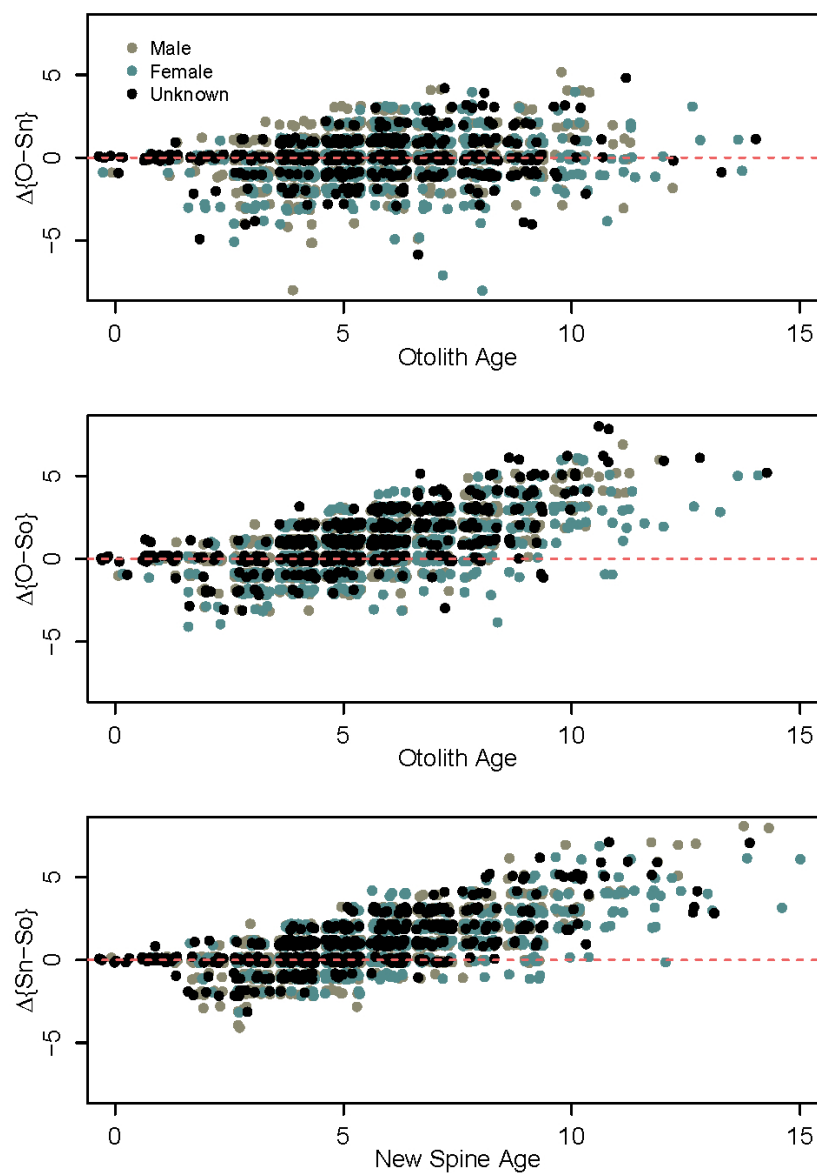of each panel with significant differences assessed at $\alpha = 0.10$.

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Figure S1. Difference in age estimates derived from A) whole otoliths and the new spine protocol (Potts et al., 2023), B) whole otoliths and the old spine protocol (Kolmos et al., 2013), and C) the new spine protocol and the old spine protocol by sex and age. Age on the x-axis is jittered for ease of viewing.

315x444mm (79 x 79 DPI)