The influence of sample distribution on growth model output for a highly-exploited marine fish, the Gulf Corvina (*Cynoscion othonopterus*)

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Estimating the growth of fishes is critical to understanding their life history and conducting fisheries assessments. It is imperative to sufficiently sample each size and age class of fishes to construct models that accurately reflect biological growth patterns, but this may be a challenging endeavor for highly-exploited species in which older fish are rare. Here, we use the Gulf Corvina (*Cynoscion othonopterus*), a vulnerable marine fish that has been persistently overfished for two decades, as a model species to compare the performance of several growth models. We fit the von Bertalanffy, Gompertz, logistic, Schnute, and Schnute-Richards growth models to length-at-age data by nonlinear least squares regression and used simple indicators to reveal biased data and ensure our results were biologically feasible. We then explored the consequences of selecting a biased growth model with a per-recruit model that estimated female spawning-stock-biomass-per-recruit and yield-per-recruit. Based on statistics alone, we found that the Schnute-Richards model described our data best. However, it was evident that our data were biased by a bimodal distribution of samples and underrepresentation of large, old individuals, so we found the Schnute-Richards model output to be biologically implausible. By simulating an equal distribution of samples across all age classes, we found that sample distribution distinctly influenced model output for all growth models tested. Consequently, we determined that the growth pattern of the Gulf Corvina was best described by the von Bertalanffy growth model, which was the most robust to biased data, comparable across studies, and statistically comparable to the Schnute-Richards model. Growth model selection had important consequences for assessment, as the per-recruit model employing the Schnute-Richards model fit to raw data predicted the stock to be in a much healthier state than

per-recruit models employing other growth models. Our results serve as a reminder of the importance of complete sampling of all size and age classes when possible, and transparent identification of biased data when complete sampling is not possible.

1   **The influence of sample distribution on growth model output for a highly-exploited marine**

2   **fish, the Gulf Corvina (*Cynoscion othonopterus*)**

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17   **Abstract**

18   Estimating the growth of fishes is critical to understanding their life history and conducting

19   fisheries assessments. It is imperative to sufficiently sample each size and age class of fishes to

20   construct models that accurately reflect biological growth patterns, but this may be a challenging

21   endeavor for highly-exploited species in which older fish are rare. Here, we use the Gulf Corvina

22   (*Cynoscion othonopterus*), a vulnerable marine fish that has been persistently overfished for two

23   decades, as a model species to compare the performance of several growth models. We fit the

24   von Bertalanffy, Gompertz, logistic, Schnute, and Schnute-Richards growth models to length-at-

25   age data by nonlinear least squares regression and used simple indicators to reveal biased data

26   and ensure our results were biologically feasible. We then explored the consequences of

27   selecting a biased growth model with a per-recruit model that estimated female spawning-stock-

28   biomass-per-recruit and yield-per-recruit. Based on statistics alone, we found that the Schnute-

29   Richards model described our data best. However, it was evident that our data were biased by a

30   bimodal distribution of samples and underrepresentation of large, old individuals, so we found

31   the Schnute-Richards model output to be biologically implausible. By simulating an equal

32   distribution of samples across all age classes, we found that sample distribution distinctly

33   influenced model output for all growth models tested. Consequently, we determined that the

34   growth pattern of the Gulf Corvina was best described by the von Bertalanffy growth model,

35   which was the most robust to biased data, comparable across studies, and statistically

36   comparable to the Schnute-Richards model. Growth model selection had important consequences

37   for assessment, as the per-recruit model employing the Schnute-Richards model fit to raw data

38   predicted the stock to be in a much healthier state than per-recruit models employing other

39   growth models. Our results serve as a reminder of the importance of complete sampling of all

40   size and age classes when possible, and transparent identification of biased data when complete

41   sampling is not possible.

42   **Introduction**

43   Age and size data inform estimates of life history parameters that are crucial to fisheries

44   stock assessments. In early assessments such as Beverton and Holt's yield-per-recruit model

45   (1957), size at age was critical for estimating reproductive output and thus the sustainability of

46   fisheries. In today's age-structured stock assessments, size at age is used to convert from biomass

47   to number of fish, determine selectivity, and calculate expected length compositions (Francis,

48   2016). Similarly, size (i.e., length or weight) at age is used in size-structured stock assessment

49   models to inform transitions between size bins and determine length composition (Punt et al.,

50   2016). Accurately representing the relationship between size and age is particularly important for

51   vulnerable fish and in data-poor fisheries, in which life-history parameters and population

52   structure often drive stock assessments and management decisions (Dulvy et al., 2004; Froese,

53   2004; Honey et al., 2010; Hordyk et al., 2016). Specifically, these types of assessments rely

54   heavily on age-length data to confer insights on vulnerability and overfishing (Erisman et al.,

55   2014).

56   When modelling the relationship between age and size for the purposes of assessment, and

57   for any purpose, each age and size class must be sufficiently represented to generate growth

58   parameters that reflect biological growth (Cailliet et al., 1986; Cailliet and Tanaka, 1990; Francis

59   and Francis, 1992; Cailliet and Goldman, 2004). It is important to make the distinction between

60   this type of sampling and sampling to reflect population structure, which should not be the goal

61   of age and growth studies as this reflects bias due to the relative scarcity of large and old

62 individuals. Sufficiently representing each size and age class may be especially difficult in

63 highly-exploited species, as exploitation alters the population structure of fishes by preferentially

64 selecting for large and old fish individuals (Mason, 1998; Berkeley et al., 2004). The

65 ramifications for failing to acknowledge selection are clear, as length-selective fishing mortality

66 distorts growth curves (Walker et al., 1998). Further, the lack of representation of large and old

67 individuals could result in underestimation of lifespan and longevity, which makes fishery

68 management measures less effective (Campana, 2001; Cailliet and Andrews, 2008; Goldman et

69 al., 2012). Large and old fish drive estimates of the maximum average length parameter L_∞, and

70 without them, L_∞ is underestimated and the growth rate (typically denoted by K) is

71 overestimated. The underestimation of L_∞ and the overestimation of K lead to the assumptions of

72 a shorter generation time and less mortality, and thus more resiliency to high levels of fishing

73 pressure (Campana, 2001; Goldman et al., 2012; Harry, 2017). The L_∞ term is particularly

74 important when growth models are incorporated into stock assessment (Wells et al., 2013). This

75 problem may also occur in growth modelling for vulnerable fish or in data-poor fisheries, where

76 lack of representation of each age and size class due to sampling constraints or the scarcity of

77 individuals may similarly affect parameter estimates. Fishery dependent data are often the only

78 data available for growth modelling, which may be acceptable only as long as the inherent biases

79 and limitations are acknowledged.

80 Several models have been developed to quantify the relationship between age and size,

81 with body length being the most common metric of size. Typically, asymptotic growth models

82 are used to quantify this relationship. These models describe fast growth rate in the earliest years

83 of life and slower growth in later years. Despite some criticism (Roff, 1980; Czarnołe'ski and

84 Kozlowski, 1998), the most widely used is the von Bertalanffy growth model (Chen et al., 1992;

85   Kimura, 2008). Rooted in bioenergetics, this model is intended to give a biologically relevant

86   representation of how catabolic and anabolic processes work within a fish to change growth over

87   the lifespan of fishes (von Bertalanffy, 1938; Pauly, 2010). Over the years, there have been many

88   re-parameterizations of von Bertalanffy with incorporation of growth-influencing factors and

89   applications to a variety of situations (Gallucci II and Quinn, 1979; Ratkowsky, 1986; Helser and

90   Lai, 2004; Kimura, 2008; Brunel and Dickey-Collas, 2010; van Poorten and Walters, 2016), but

91   the original parametrization is still the most commonly used (Lorenzen, 2016). Other asymptotic

92   growth models are commonly used in fisheries, such as the Gompertz growth model (Gompertz,

93   1825) and the logistic growth model (Ricker, 1975).

94   In recent years, fish growth models have moved from a foundation in bioenergetics to

95   being more statistically driven (van Poorten and Walters, 2016). These models are inherently

96   more flexible, allowing them to capture subtleties in growth patterns that may not be captured by

97   the more inflexible growth models. The Schnute model (Schnute, 1981), for example, has four

98   curve families that the model may assume based on which types of data the model is fit to and

99   what other functions are incorporated into the framework. Another flexible growth model, the

100   Schnute-Richards model (Schnute and Richards, 1990), can describe biphasic growth among

101   several other forms. By design, the Schnute-Richards model may be equivalent to the other

102   growth models discussed above when the proper values are specified for its dimensionless

103   parameters. Fish growth is inherently plastic and fish do not all grow the same way (Weatherley,

104   1990; Lorenzen, 2016), so a flexible growth model may be advantageous in certain situations.

105   However, these flexible models may also be more sensitive to sampling biases in data,

106   potentially producing growth patterns that reflect the size-frequency distribution of fish collected

107   rather than the biological growth pattern of the species.

108   The Gulf Corvina *(Cynoscion othonopterus)* is an ideal species to examine the

109   performance of multiple growth models in a vulnerable marine fish. Endemic to the northern

110   Gulf of California, Mexico (Robertson and Allen, 2008), it is currently listed as vulnerable under

111   the International Union for the Conservation of Nature (IUCN) Redlist (Chao et al., 2016). Gulf

112   Corvina have experienced persistent overfishing on their spawning aggregations for the past two

113   decades, which have resulted in growing concern for the fishery's stability and longevity

114   (Erisman et al., 2012; Ruelas-Peña et al., 2013; Erisman et al., 2014; Ortiz et al., 2016). The life

115   history of this species has been well documented and provides an ideal foundation for future

116   analysis of individual and population growth (Román-Rodriguez, 2000; Gherard et al., 2013.

117   With a documented maximum size of 1013 mm total length (TL) and a documented maximum

118   age of 9 years, Gulf Corvina is a fast growing, short lived species which reaches sexual maturity

119   at 2 years of age (Gherard et al., 2013). However, the combination of highly efficient, size-

120   selective gear and persistent overfishing have severely truncated the age structure of the

121   population (Erisman et al., 2014; Ortiz et al., 2016). The mean age of capture of Gulf Corvina is

122   5 years (*ca.* 700 mm TL), and few individuals older than age 7 or younger than age 4 have been

123   observed in the fishery (Gherard et al., 2013; Erisman et al., 2014; Ortiz et al., 2016).

124   Past studies of Gulf Corvina growth, which have relied solely on fishery-dependent data

125   with incomplete sampling of all size and age classes, have produced different results due to

126   differences in model selection approach. Based on the congruence of the model with the growth

127   pattern of many species of the genus *Cynoscion* and other sciaenid fishes (Rutherford et al.,

128   1982; Lowerre-Barbieri et al., 1995; Rodriguez and Hammann, 1997), Gherard et al. (2013) took

129   a conservative, single model approach and fit the von Bertalanffy growth model to Gulf Corvina

130   age-length data. Conversely, Aragón-Noriega (2014) chose a statistically-driven approach and fit

131   several models to multiple datasets, concluding that Gulf Corvina grew in a biphasic pattern with

132   slow growth in the beginning of life, rapid growth after age two, and slow growth after age four.

133   Notably, Aragón-Noriega's (2014) estimates for the L_∞ parameter varied greatly, from 735.0 to

134   1126.6 mm, depending on which dataset was used. Given this variability, absence of biphasic

135   growth patterns in similar sciaenids, and the distance from the maximum observed length of Gulf

136   Corvina (1013 mm; Gherard et al., 2013), Aragón-Noriega's (2014) estimates may be

137   biologically unrealistic. Mendivil-Mendoza et al. (2017) took a similar approach and found a

138   similarly wide range of L_∞ values (666.7 – 1306.0 mm). However, despite fitting models to

139   similar data and selecting the same model as Aragón-Noriega (2014), Mendivil-Mendoza et al.

140   (2017) did not describe the biphasic growth pattern recorded by Aragón-Noriega (2014). The

141   existence of discrepancies between the previous Gulf Corvina growth studies and the importance

142   of the age-length relationship to the stock assessment of the fishery merit further investigation on

143   the growth pattern of the species.

144   Here, we model the growth of Gulf Corvina and draw conclusions about data needs and

145   fisheries assessments. Our specific objectives were to: (1) assess how representation of size and

146   age classes affected growth parameter estimates and (2) compare the performance of multiple

147   growth models for describing age-at-length data for Gulf Corvina. Through generating a more

148   complete dataset than previous studies and testing for biases in our data with simple indicators,

149   we addressed these objectives. Moreover, using the results of simulations with a per-recruit

150   model, we discussed the implications of misrepresenting growth in highly-exploited, vulnerable

151   marine fishes.

152   **Materials and Methods**

153   *Data collection*

154   Seven hundred and forty-nine Gulf Corvina were sampled from 2009 through 2013 at the

155   three locations in the upper Gulf of California: El Golfo de Santa Clara (Sonora), San Felipe

156   (Baja California), and El Zanjón (Baja California). Information on total length (TL) was

157   recorded to the nearest mm for each fish collected, and the sagittal otoliths were removed, dried

158   whole and stored until further use. Five hundred and thirty of these samples were collected from

159   the commercial Gulf Corvina fishery and from bycatch from the shrimp fishery. These data were

160   used by Gherard et al. (2013). In order to increase representation of size and age classes that

161   were scarce in the dataset used by Gherard (2013), we collected 219 additional samples in 2012-

162   2013 from the bycatch of other fisheries (e.g., shrimp), fishery-independent sampling of small

163   individuals (<30 cm TL), and the commercial Gulf Corvina fishery. All fish were deceased at the

164   time of collection from fishers. The research protocol was approved under UCSD IACUC ID no.

165   S13240 and data were collected under CONANP permit no. CNANP-00-007.

166   Otolith preparation and ageing protocols were followed according to the methods

167   developed by Gherard et al. (2013) for Gulf Corvina. Whole sagittal otoliths were first mounted

168   on wood blocks with a cyanoacrylate adhesive and a 0.5 mm dorsal-ventral cross-section was cut

169   through the otolith focus using a double-bladed Buehler Isomet 1000 precision saw (Allen et al.,

170   1995). Sub-sections were then mounted on a glass slide using thermoplastic glue and submerged

171   in a glass petri dish with water and a black background. Transmitted light under a Zeiss Stemi

172   2000-C microscope with a Zeiss Axiocam 105 color camera at 6.25x total magnification was

173   used to count the alternating opaque and translucent growth zones that define an annulus (Figure

174   1). For the purposes of this study, an annulus was defined as one full opaque and translucent

175   zone of growth (Cailliet et al., 1996), which was validated for Gulf Corvina by previous studies

176   (Rowell et al., 2005; Román-Rodriguez, 2000; Gherard et al., 2013) Each otolith was aged by

177 two independent readers from digital images of cross-sections, as direct observation through the

178 scope did not distort band pattern and did not affect age estimates. Samples were excluded from

179 analysis when discrepancies between readers occurred.

180 *Model fitting and assessment of fit*

181 *Growth modelling*

182 A suite of growth models was fit to age data determined from otoliths as described, and

183 length data obtained in the field. Model parameters were estimated using non-linear least squares

184 regression with the Levenberg-Marquardt algorithm, and confidence limits were placed around

185 parameter estimates in R studio (using the R packages FSA, minpack.lm, and nlstools).

186 The specialized von Bertalanffy growth model (von Bertalanffy, 1938) is given by:

187 Eq. 1:
$$L(t) = L_\infty[1 - e^{-K(t - t_0)}]$$

188 where *L(t)* is size (in mm TL) at age *t*, L_∞ is the maximum average length (in mm TL), *K* is the

189 growth rate coefficient (in year^{-1}), and t_0 is the theoretical age at which length is zero (in years).

190 The Gompertz growth model (Gompertz, 1825) is given by:

191 Eq. 2:
$$L(t) = L_\infty e^{\left(-\left(\frac{1}{K}\right)e^{-K(t - t_0)}\right)}$$

192 where the parameters are the same as described for Eq. 1.

193 The logistic model (Ricker, 1975) is given by:

194 Eq. 3:
$$L(t) = L_\infty[1 + e^{-K(t - t_0)}]^{-1}$$

195   where the parameters are the same as described for Eqs. 1 and 2.

196   The Schnute model where a and b are not equal to zero (Schnute, 1981) is given by:

197   Eq. 4:
$$L(t) = \left[L_1^b + (L_2^b - L_1^b)\frac{1 - e^{-a(t-T_1)}}{1 - e^{-a(T_2-T_1)}}\right]^{1/b}$$

198   where T_1 is the first specified age, T_2 is the second specified age, L_1 is size at age T_1, L_2 is size at

199   age T_2, a is the constant relative rate of relative growth (in year^{-1}), and b is the incremental

200   relative rate of relative growth (dimensionless),

201   Finally, the Schnute-Richards model (Schnute and Richards, 1990) is given by:

202   Eq. 5:
$$L(t) = L_\infty \left(1 + \alpha e^{-at^c}\right)^{1/b}$$

203   where α, b, and c are dimensionless parameters, and a has the unit of year^{-b}.

204   *Statistical measures of fit*

205   Model fit was assessed with the bias-corrected Akaike Information Criterion (AICc)

206   (Shono, 2000; Burnham and Anderson, 2004), and Bayesian Information Criterion (Schwarz,

207   1978) in R Studio (using the R package AICcmodavg).

208   The formula for AICc is given by:

209   Eq. 6:
$$AIC_c = AIC + \frac{2k(k+1)}{n-k-1}$$

210   where:

211   Eq. 7:
$$AIC = -2\log(L) + 2k$$

212   and n is the number of observations, k is the number of model parameters, and L is the likelihood.

213   The formula for BIC is given by:

214   Eq. 8: $BIC = 2\ln(L) + k\log(n)$

215   where parameter definitions are the same as described for Eq. 7.

216   The smallest AICc and BIC values indicate the best model. The difference between the

217   two criteria is that AICc is designed to select the model that describes reality the best while

218   treating no models as true, which is consistent with an information theory approach, whereas

219   BIC is designed to select the true model. Practically, BIC penalizes for the number of parameters

220   more heavily than AICc. AICc was used instead of AIC as it is bias-corrected at small n values

221   or high $k{:}n$ ratios; AICc converges to AIC at large n values (Burnham and Anderson, 2004).

222   AICc and BIC values were calculated to show the absolute difference between model fits. Next,

223   AICc weights were calculated for model averaging of parameter estimates; the AIC weighting

224   formula is given by:

225   Eq. 9: $w_i = \dfrac{e(-0.5\Delta_i)}{\sum_{k=1}^{5} e(-0.5\Delta_k)}$

226   where parameter definitions are the same as described for Eqs. 7 and 8.

227   *Simple indicators of biased data*

228   *Simulation of an ideal sampling outcome*

229   To test for the influence of sampled population structure on growth model output, different

230   amounts of simulated data were added to raw data so that each age observed (1-8) had 200 total

231   observations. Data were simulated from a normal distribution with the same mean and standard

232   deviation as the raw data at each age class. This simulation was not intended to generate the true

233   population structure of Gulf Corvina in the Gulf of California, but rather to generate an equal

234   number of samples in each age and size class. This simulation did not explicitly account for

235   selectivity or limits in sampling effort, but filled in gaps left by these factors and others that

236   prevented more equal representation of each size and age class in the raw data. Models were fit

237   to the new dataset and goodness of fit was assessed in the same manner as was described above.

238   *Froese and Binohlan's empirical relationship*

239   Froese and Binohlan's (2000) empirical relationship between the longest fish in the data

240   set (L_{max}) and L_∞ was used to specifically test for the influence of the lack of large and old fish in

241   the raw dataset, which is likely due to heavy exploitation. If large and old fish are insufficiently

242   represented in the dataset, it stands to reason that the L_∞ predicted by this relationship will be

243   greater than the modelled L_∞. This relationship is given by:

244   Eq. 10: $logL_\infty = 0.044 + 0.9841 * \log(L_{max})$

245

246   *Literature review*

247   A brief literature review of sciaenid growth modelling was conducted to assess how the

248   results of this study compared with other studies on fishes closely related to the Gulf Corvina

249   (e.g., other species in the genus *Cynoscion*). In conjunction with Froese and Binohlan's empirical

250   relationship and the simple simulation of an ideal sampling scenario, this brief literature review

251   was intended to check if the samples used in this study produced a biologically plausible growth

252   pattern when growth was modelled.

253   *Simulations with a per-recruit model*

254   To be able to discuss the implications of misrepresenting growth in Gulf Corvina, we ran

255   simulations with a per-recruit model detailed in Appendix S1. In brief, this per-recruit model

256   estimates the female spawning-stock-biomass-per-recruit (SSBR; a proxy of reproductive

257   capacity) and yield-per-recruit (YPR; exploitable biomass) of Gulf Corvina in relation to the

258   annual exploitation rates of the old adults ($\geq$ 5 year-old individuals) of the species (E_{OA}). In this

259   per-recruit model, Gulf Corvina is assumed to grow according to one of five alternative growth

260   models: (1) the von Bertalanffy model developed in Gherard et al. (2013), referred to as the

261   "Gherard model"; (2) the von Bertalanffy model fit to raw data in the present study; (3) the von

262   Bertalanffy model fit to raw data bolstered by simulation values in this study; (4) the Schnute-

263   Richards model fit to raw data in the present study; and (5) the Schnute-Richards model fit to

264   raw data bolstered by simulation values in this study. The current E_{OA} was estimated to be 0.825

265   year^{-1} (Appendix S1). We first ran simulations with the per-recruit model to determine the

266   maximum value of the YPR of Gulf Corvina (YPR$_{max}$) and the natural SSBR of Gulf Corvina

267   (NSSBR), i.e., its SSBR in the absence of fishing (Appendix S1). Then, we estimated the current

268   fraction of NSSBR (current FNSSBR, i.e., the ratio of current SSBR to NSSBR) and the current

269   YPR over YPR$_{max}$ of Gulf Corvina, when each of the five abovementioned growth models is

270   used to represent the growth in length of Gulf Corvina.

271   **Results**

272   *Length and age structure*

273   A bimodal distribution was observed in the length and age structure of the fish used in

274   this study (Figures 2 and 3). The first mode of the distribution represents Gulf Corvina caught as

275   bycatch, whereas the second represents Gulf Corvina caught in the targeted fishery. Lengths

276   ranged from 141-1013 mm TL, and ages ranged from 1-8 years.

277   *Model fitting and assessment of fit for models fit to raw data*

278   *Growth patterns and parameter estimates for models fit to raw data*

279   The Gompertz, logistic, and von Bertalanffy models yielded asymptotic growth patterns,

280   while the Schnute-Richards model described biphasic growth and the Schnute model described

281   near-linear growth after 1.5 years of life (Figure 4). Modelled length at age was most similar

282   among models at intermediate ages, where samples were most abundant (Figure 4). Conversely,

283   modelled length at age was most variable at young and old ages, where samples were most

284   scarce (Figure 4). Estimates of L_∞ ranged from 730.91 mm (Schnute-Richards model) to 916.05

285   mm (von Bertalanffy model). All parameter estimates are summarized in Table 1, while

286   confidence intervals around parameter estimates are reported in Appendix S2.

287   *Measures of statistical fit for models fit to raw data*

288   AICc and BIC values indicated that the Schnute-Richards model described the raw data

289   best, followed by the logistic, Gompertz, von Bertalanffy, and Schnute models (Table 2). The

290   AIC weighting formula gave full support to the Schnute-Richards model, so no model averaging

291   of parameters was necessary.

292   *Simple indicators of biased data*

293   *Growth patterns and parameter estimates for models fit to raw data bolstered by*

294   *simulated values*

295   The Schnute-Richards, Gompertz, logistic and von Bertalanffy growth models yielded

296   asymptotic growth patterns, while the Schnute model described near-linear growth after 1.5 years

297   of age (Figure 5). Modelled length at age was similar at intermediate ages among all growth

298   models except for the Schnute one, but differed slightly at young and old ages (Figure 5).

299 Estimates of L_∞ ranged from 834.34 mm (logistic model) to 951.30 mm (von Bertalanffy model)

300 (Table 3). All parameter estimates for each growth model are summarized in Table 3.

301 *Measures of statistical fit for models fit to raw data bolstered by simulated values*

302 The von Bertalanffy growth model described the raw data bolstered by simulated values

303 best according to AICc and BIC values (Table 4). However, it was only marginally better than

304 the Schnute-Richards and Gompertz models based on AICc. Thus, the von Bertalanffy growth

305 model received 53% of AICc weighting to the Schnute-Richards' 33%, and Gompertz' 15%. The

306 logistic model fit the data better than the Schnute model, but neither models received any support

307 from AICc weighting. Model averaging L_∞ based on AICc weights resulted in an estimated L_∞ of

308 945 mm, an estimate 6 mm shorter than the that predicted by the von Bertalanffy model. In

309 contrast to AICc values, BIC values indicated that the Gompertz model fit the data better than

310 the Schnute-Richards model. Both Gompertz and Schnute-Richards models fit the data better

311 than the logistic and Schnute models according to BIC values, as was indicated by AICc values.

312 *Froese and Binohlan's empirical relationship*

313 Froese and Binohlan's empirical relationship between L_{max} and L_∞ predicted a L_∞ of 1006

314 mm from a maximum observed length of 1013 mm. This estimate is larger than all estimates of

315 L_∞ derived from growth models fit to raw data (Table 1) and raw data bolstered by simulated

316 values (Table 3).

317 *Literature review*

318 Results from our review of 24 sciaenid growth studies and citations are summarized in Table

319 5. Age and body length relationships in sciaenids were represented by the von Bertalanffy

320 growth model in 20 of 24 (83%) of the studies we reviewed, as reported in Atlantic Croaker

321   (*Micropogonias undulatus*), Black Drum (*Pogonias chromis*), Red Drum (*Scianops ocellatus*),

322   Southern Kingfish (*Menticirrhus americanus*), Spotted Seatrout (*Cynoscion nebulosus*),

323   Weakfish (*Cynoscion regalis*), and Whitemouth Croaker (*Micropogonias furnieri*). Notably,

324   growth of the Totoaba (*Totoaba macdonaldi*), a sciaenid closely related to Gulf Corvina and also

325   found in the Gulf of California, was modelled by the von Bertalanffy growth model. Growth of

326   the Gulf Corvina was modelled using the von Bertalanffy growth model in two previous studies.

327   Other growth models have been used to describe age and body length relationships in

328   sciaenids in 5 of 24 (21%) the studies we reviewed. The Gompertz model was used to model

329   growth in female Spotted Seatrout. A linear model was used to model growth in male Spotted

330   Seatrout, although it was noted that the linear growth pattern may have been due to lack of

331   sampling of large and old individuals. Multi-model approaches similar to this study were

332   employed three times (13%). One study on the Gulf Corvina selected the von Bertalanffy growth

333   model for two datasets, and the Schnute-Richards model for two other datasets. As such, this

334   study was counted in as one of the 20 studies that used the von Bertalanffy growth model to

335   model sciaenid growth, and as one of the five studies that employed other growth models. The

336   most recent age and growth study on Gulf Corvina selected the Schnute-Richards model, but did

337   not describe a biphasic growth pattern. The other study that employed multiple models fit them

338   to Spotted Seatrout age-length data and found the most statistical support for the three-parameter

339   logistic model.

340   *Model selection*

341   Synthesis of the above considerations and assessments led to the selection of the von

342   Bertalanffy growth model as the best model to represent Gulf Corvina growth. Of models fit in

343   this study, the von Bertalanffy growth model had the 4th best statistical fit to raw data (AICc =

344 8813.66, Δ AICc = 53.84, AICc weight = 0; BIC = 8832.08, Δ BIC = 44.66; Table 2) and the

345 best statistical fit to raw data bolstered by simulated values (AICc = 18678.72, Δ AICc = 0. AICc

346 weight = 0.53; BIC = 18700.20, Δ BIC = 0; Table 4). Of models fit in this study, the von

347 Bertalanffy growth model produced an L_∞ closest to the L_∞ predicted by Froese and Binohlan's

348 empirical relationship of 1006 mm (raw data: 916.05 mm; raw data bolstered by simulated

349 values: 951.30 mm; Tables 1 and 3). Further, the von Bertalanffy growth model was used to

350 represent sciaenid growth in 83% of studies reviewed.

351 *Simulations with a per-recruit model*

352   The current value of the exploitation rate of old adults of Gulf Corvina E_{OA} that we

353 estimated is *ca.* twice larger than the value of E_{OA} at which the YPR of Gulf Corvina reaches a

354 maximum, regardless of the growth model employed for simulations with the per-recruit model

355 (Appendix S1). However, the current FNSSBR of Gulf Corvina predicted when using the

356 Schnute-Richards growth model fit to raw data only (0.60) is noticeably greater than the current

357 FNSSBR of Gulf Corvina predicted when using all the other growth models (0.42-0.53) (Figure

358 6A). The value of fraction of natural SSBR that causes population collapse typically is in the

359 range of 0.1-0.6 and lower for short-lived fish species such as Gulf Corvina (Myers et al., 1999;

360 Grüss et al., 2014). Thus, the per-recruit model employing Schnute-Richards growth model

361 predicts the Gulf Corvina stock to be in a much healthier state than the per-recruit models

362 employing other growth models. The current YPR over YPR_{max} of Gulf Corvina predicted when

363 using the Schnute-Richards growth model fit to raw data only (0.80) is also greater than the

364 current YPR over YPR_{max} of Gulf Corvina predicted when using all the other growth models

365 (0.70-0.74) (Figure 6B).

366 **Discussion**

367   This study illustrates the pitfalls of using statistical considerations alone when selecting a

368   growth model for a vulnerable and highly-exploited species, due to the high likelihood of a

369   biased distribution of samples. The combination of highly efficient, size-selective gear and high

370   fishing effort have altered the age structure of the Gulf Corvina population (Ortiz et al., 2016),

371   making sufficient representation of each size and age class difficult (Erisman et al., 2014). The

372   influence of the lack of large and old fish in the dataset used for this study is clear, as Froese and

373   Binohlan's (2000) empirical relationship predicted an L_∞ that was 89.95 – 275.09 mm greater

374   than the L_∞ predicted by growth modeled fit to raw data. This predicted L_∞ from Froese and

375   Binohlan's (2000) empirical relationship of 1006 mm was identical to the L_∞ estimated by

376   Gherard et al. (2013) with the von Bertalanffy growth model. Growth patterns (Figures 4 and 5)

377   and parameter estimates (Tables 1 and 3) were far less variable for models fit to data where

378   sample size was equal at age, compared to models fit to raw data alone.

379   Unfortunately, heavy exploitation of Gulf Corvina makes the use of biased data in age

380   and growth studies an unavoidable reality. Length data collected from the continuous monitoring

381   of the fishery (Erisman et al., 2015; Ortiz et al., 2016) indicate that Gulf Corvina may be able to

382   grow longer than their maximum reported length of 1013 mm and live longer than their

383   maximum reported age of 9 years, but heavy exploitation (exploitation rate of 0.825 year^{-1} for

384   Gulf Corvina five years-old and older; Erisman et al. 2014) prevents them from doing so. Thus,

385   despite our best efforts, we were unable to sufficiently represent large and old fish in our dataset.

386   Further, while we made a concerted effort to sample small individuals, our data set would have

387   been improved if we were able to collect more. This led to our decision to employ our simulation

388   exercise to understand how the biases in our data affected our results. Similarly biased data have

389   been the only data available for age and growth studies with Gulf Corvina, and previous studies

390   have taken markedly different approaches to dealing with its limitations. Gherard et al. (2013)

391   chose to use the inflexible and widely comparable von Bertalanffy growth model while

392   acknowledging the data's limitations and caveating results accordingly. Alternatively, Aragón-

393   Noriega (2014) and Mendivil-Mendoza (2017) employed a multi-model approach that leaned

394   exclusively on statistics. Their statistical procedures led to the selection of the flexible Schnute-

395   Richards model to describe Gulf Corvina growth. Despite reporting different growth patterns

396   depending on which dataset was used, Aragón-Noriega (2014) did not acknowledge the

397   limitations of fishery-dependent data and concluded that Gulf Corvina grew in a biphasic pattern.

398   The same suite of models employed by Aragón-Noriega (2014) and Mendivil-Mendoza

399   et al. (2017) were fit to our data, and statistical measures of fit similarly supported the Schnute-

400   Richards model as the best model for Gulf Corvina. Further, a biphasic growth pattern was

401   described by the model, as it did in Aragón-Noriega's (2014) study. However, our review of 24

402   sciaenid growth studies indicated that only two (8%) studies used the Schnute-Richards model to

403   describe sciaenid growth (Aragon-Noriega, 2014; Mendivil-Mendoza et al., 2017), of which only

404   one described biphasic growth (Aragón-Noriega, 2014). The biological implausibility of this

405   growth pattern was further supported by the distance between Froese and Binohlan's predicted

406   L_∞ and the L_∞ estimated by the Schnute-Richards model (1006 vs. 730.91 mm, i.e., a 275.09 mm

407   difference). Finally, simulating an ideal sampling scenario where each age class was equally

408   represented revealed that this biphasic growth pattern was due to bimodal distribution of samples

409   and a lack of large, old fish. Both the parameter estimates and growth pattern changed

410   substantially when simulated data was added to raw data so that sample size was equal for each

411   age (Figure 5 and Table 3). The Schnute-Richards model is flexible by design, and is, therefore,

412   not suited for use with datasets that do not sufficiently represent each size and age class. Thus,

413 by integrating the results of our statistical measures of fit, literature review, and simple indicators

414 of biased data, we selected the von Bertalanffy growth model as the best model to represent Gulf

415 Corvina growth.

416   The results of our study reinforce the well-established, but often forgotten, principle that

417 each size and age class must be sufficiently represented for growth modelling to produce

418 biologically reasonable results (Cailliet et al., 1986; Cailliet and Tanaka, 1990; Francis and

419 Francis, 1992; Cailliet and Goldman, 2004). Ensuring sufficient representation may be difficult

420 for highly-exploited fishes, as exploitation alters the population structure of fishes by

421 preferentially selecting for large and old fish individuals (Berkeley et al., 2004; Mason, 1998).

422 Similar challenges are faced when studying growth for vulnerable fishes or in data-poor

423 fisheries, where there may not be resources available for extensive fishery-independent sampling

424 or fish are scarce in general. Despite difficulty, ensuring sufficient representation of each size

425 and age class should be a priority. The distinction between sampling to sufficiently represent

426 each size and age class and sampling to represent population structure is an important one to

427 make, as sampling to represent population structure should not be a goal of age and growth

428 studies due to the bias created by the natural scarcity of large and old fish. As such, the simple

429 simulation of an ideal sampling scenario with an equal number of samples at each age was not

430 intended to represent the population structure of Gulf Corvina or to reflect the relative

431 probability of obtaining samples of particular size and age classes in the real world.

432   Life-history parameters such as those estimated in growth models are influential in

433 assessments for vulnerable and data-poor species (Fournier et al., 1990; Dulvy et al., 2004;

434 Froese, 2004; Honey et al., 2010; Hordyk et al., 2016). These types of assessments rely on age-

435 length data to determine vulnerability and overfishing, and problems emerge when all size and

436 age classes are not sufficiently represented. The average maximum length (L_∞) is underestimated

437 and the growth rate (K) is overestimated when large and old fish are absent. Accordingly, a short

438 generation time and lower levels of mortality are estimated, conferring more resilience to

439 exploitation that the population possesses (Campana, 2001; Goldman et al., 2012; Harry, 2017).

440 This idea was demonstrated with simulations with a per-recruit model, where the per recruit

441 model using the Schnute-Richards growth model fit to raw data (which had the lowest L_∞ in the

442 present study) predicted Gulf Corvina reproductive capacity to be in a much healthier state than

443 the per recruit models using other growth models (Fig. 6A). This false resiliency makes fishery

444 management measures less effective (Campana, 2001; Cailliet and Andrews, 2008; Goldman et

445 al., 2012), and may be present in Gulf Corvina assessments, as length and age truncation in the

446 catch has increased progressively since biological monitoring of the fishery began in 1997

447 (Erisman et al., 2014). Given this length and age truncation, published growth models reported

448 for this species may not be representing biology but rather the influence of exploitation.

449   Our results have implications for estimating growth within a stock assessment. Piner

450 (2016) documented an increase in precision in parameter estimates, ability to account for

451 selectivity, and ability to incorporate multiple data sources when growth was estimated within a

452 stock assessment. However, the influence of sample distribution on model output should be

453 carefully examined if this approach is to be taken. So-called haphazard sampling strategies that

454 ensure that all age and size classes are represented (e.g. Wells et al., 2013) make growth

455 estimation within a stock assessment model more difficult, though are necessary if the density of

456 samples at a particular age is driving model fit or preventing accurate estimation of L_∞. Precision

457 may be improved, but care must be taken to ensure that precision is being improved around

458 biological reality.

459   We found that Gulf Corvina exhibit a high degree of variation in length-at-age, a pattern

460   that is common among coastal fishes in the Gulf of California and other regions of the eastern

461   Pacific characterized by significant annual variations in precipitation, ocean temperatures, and

462   productivity in response to climate forcing that are known to influence growth rates in marine

463   fishes (e.g., El Niño Southern Oscillation, ENSO; (Wells et al., 2006; Williams et al., 2007;

464   Black, 2009). Specifically, growth rate is higher in Gulf Corvina during El Niño years, mainly in

465   association with increased sea surface temperatures in the region (Reed, 2017). ENSO has been

466   shown to affect fish growth in other areas, such as the waters of New Caledonia (Lehodey and

467   Grandperrin, 1996), New Zealand (Gillanders et al., 2012), and north-western Australia (Ong et

468   al., 2016, 2015). As the present study was conducted over multiple years, it is reasonable to

469   assume that variations in ENSO over the study period (i.e., a succession of El Niño/La Niña

470   events) could have affected the fish harvested for this study, explaining the observed variation in

471   length-at-age. These effects may affect estimates of growth derived with growth models, but in

472   order to identify these effects with confidence, complete sampling must be conducted with this

473   purpose in mind. Another explanation for length-at-age variation could be measurement error

474   (Neilson, 1992; Campana, 2001). Most of the fish in this study were harvested during their

475   spawning season, which is around the time when they form new annuli. Therefore, it would be

476   reasonable to conservatively assume that the precision of this study is more or less one year of

477   age. However, we have high confidence in our reading of these otoliths, as annuli are clearly

478   seen with minimal preparation (Figure 1) and we excluded any samples for which there was a

479   disagreement between readers.

480   Assessing the biological feasibility of growth model output, here accomplished with the

481   use of simple indicators of biased data and literature review, is crucial for age and growth

482   studies. Statistical measures of fit alone may not lead to the selection of a model that represents

483   biological reality (Wang et al., 1995; Cailliet et al., 2006; Araya and Cubillos, 2006). By

484   integrating measures of statistical fit with results from the simple indicators and literature review,

485   we concluded that the von Bertalanffy growth model best described the growth of Gulf Corvina

486   and was most appropriate for the quality of available data. Though the Schnute-Richards model

487   had the best statistical fit, it was not biologically reasonable, comparable between studies, or

488   robust to biased data. Simple indicators such as those described in this paper should be used to

489   reveal biases in data, and the use of flexible growth models such as the Schnute-Richards model

490   to represent the growth of Gulf Corvina and similarly exploited fishes should be halted if biases

491   are not accounted for.

492   **Conclusions**

493   Sample distribution influences growth model output, especially for flexible, statistically-driven

494   models. Data used in growth modelling studies should be thoroughly examined for bias, as

495   statistical measures of fit are insufficient for selecting a model that reflects biological reality.

496   Reflecting biological reality in growth models is critical for vulnerable fish and in data-poor

497   fisheries, where age-length data are integral to assessing vulnerability and overfishing. In this

498   case, the von Bertalanffy growth model represented biological reality best among the models

499   tested. We warn against the production and use of growth models without recognizing biases in

500   data given the serious implications for stock assessments and the management of vulnerable fish

501   populations and data-poor fisheries.

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Figure 1

Transverse section of a sagittal otolith from a five-year old Gulf Corvina

Annuli are numbered and marked by white rectangles. Transmitted light under a Zeiss Stemi 2000-C microscope with a Zeiss Axiocam 105 color camera at 6.25x total magnification was used to count the alternating opaque and translucent growth zones that define an annulus.

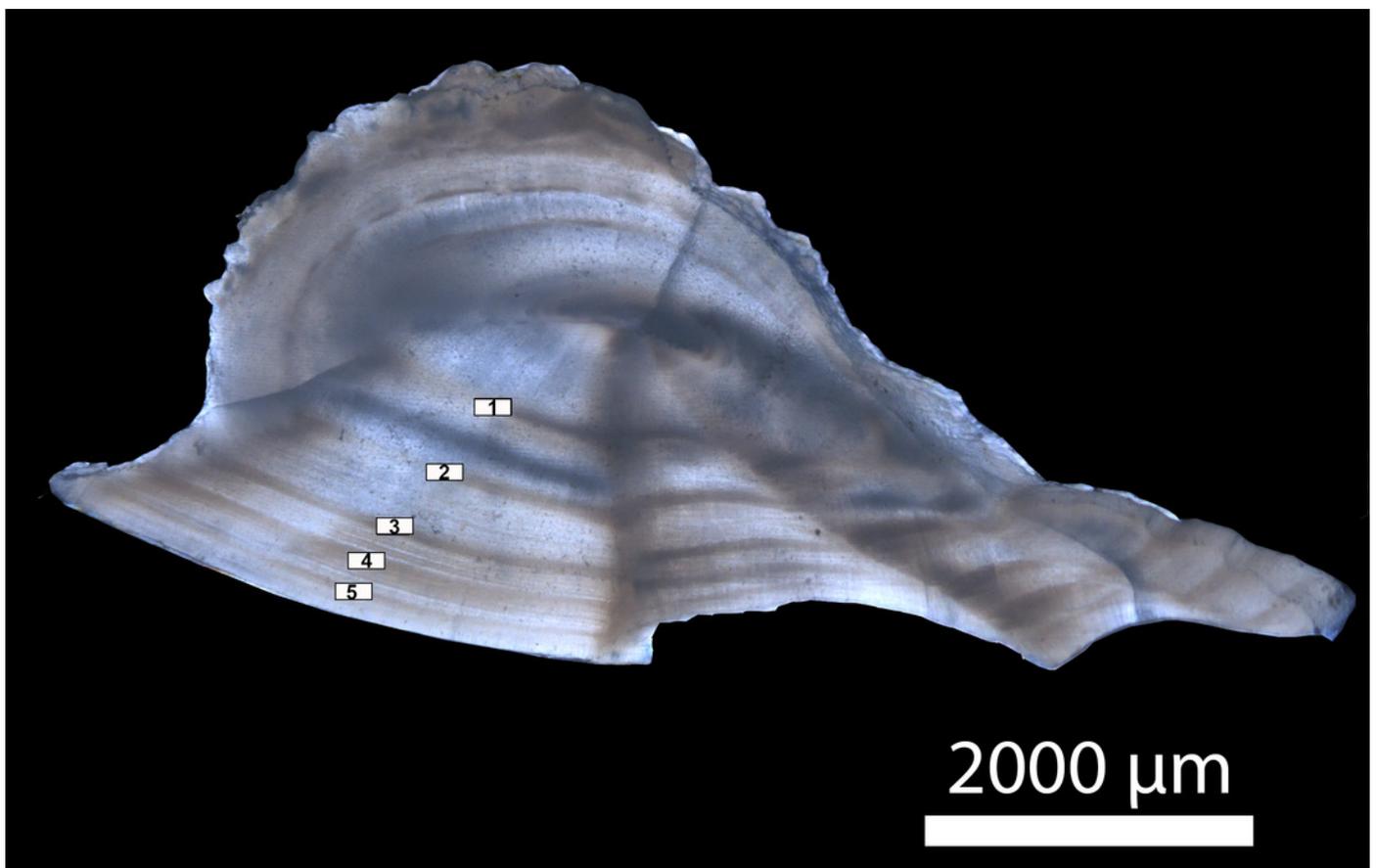



Figure 2

Length frequency of Gulf Corvina from raw data represented in 10 mm bins

A bimodal distribution is observed, with the first consisting of Gulf Corvina caught as bycatch, and the second largely consisting of fish from the directed fishery. Few fish larger than 750 mm are present in this dataset.

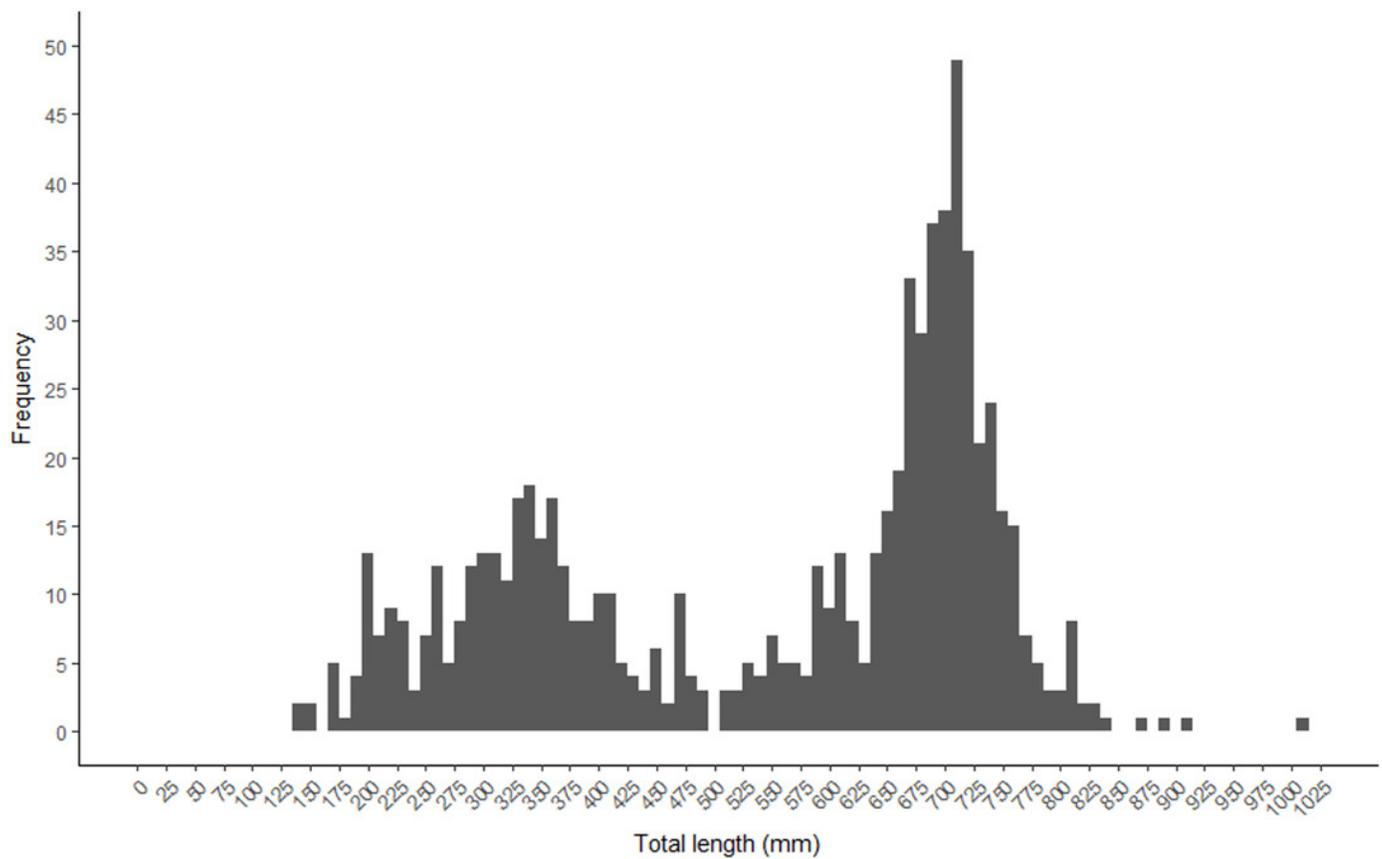



Figure 3

Age frequency of Gulf Corvina from raw data

A bimodal distribution is observed, with the first consisting of Gulf Corvina caught as bycatch, and the second largely consisting of fish from the directed fishery. Few fish older than age 6 are present in this dataset.

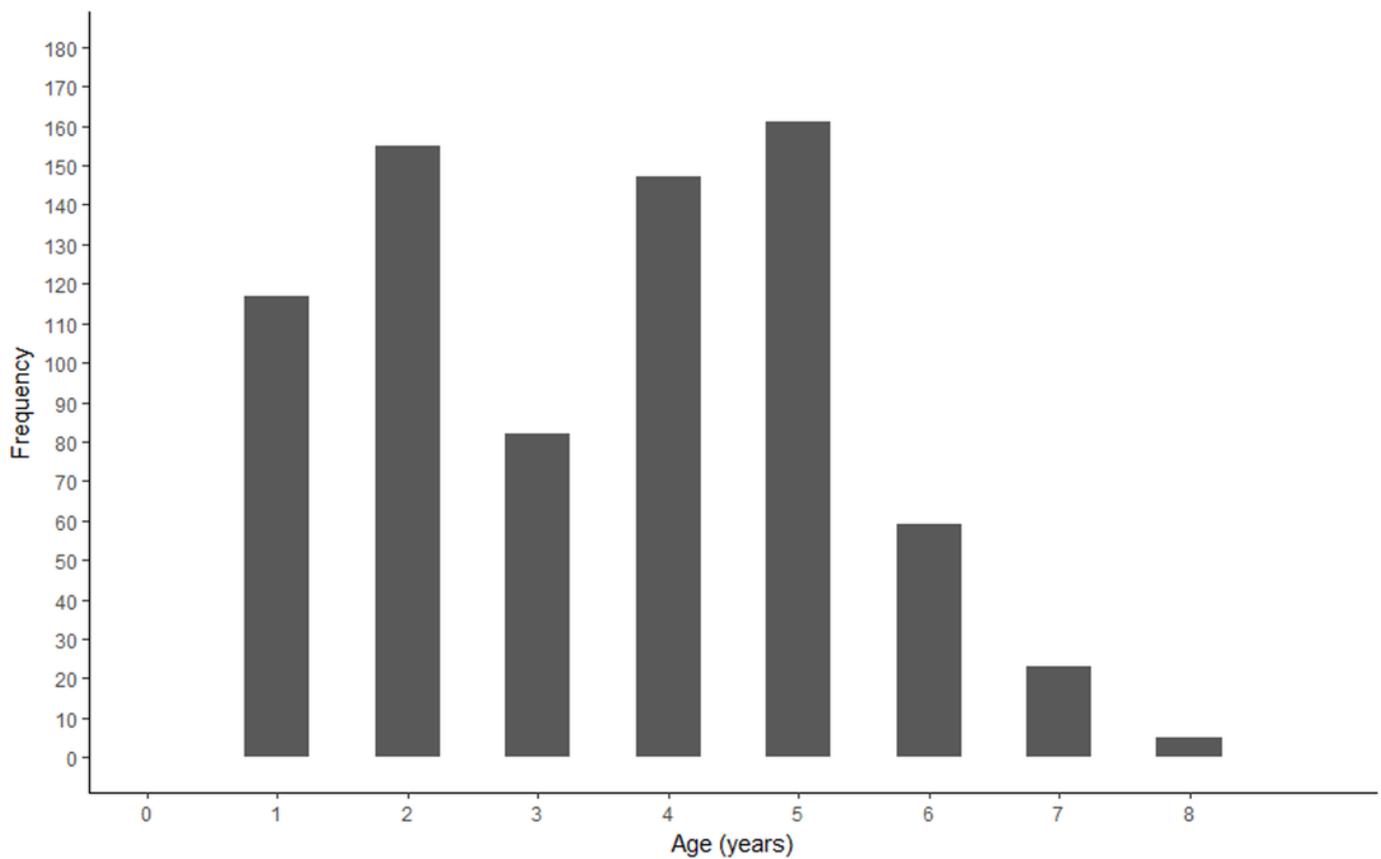



Figure 4

Growth models fit to raw age-length data for Gulf Corvina

The Gompertz, Logistic, and von Bertalanffy models yield asymptotic growth patterns. However, the Schnute-Richards model describes bi-phasic growth, and the Schnute model describes near-linear growth after the first 1.5 years of life. Differences in modelled size at age are most pronounced at the beginning and end of life, where samples are most scarce.

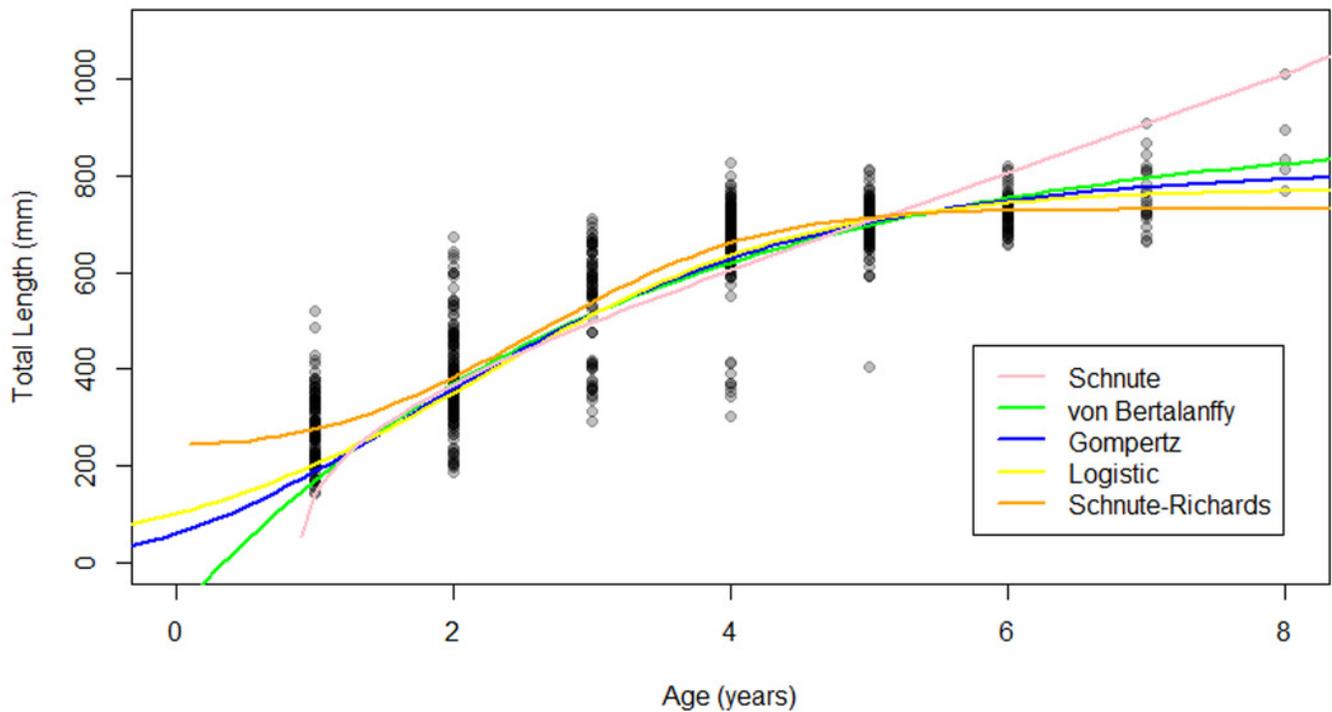



Figure 5

Growth models fit to raw Gulf Corvina age-length data bolstered by simulated values

All models except for the Schnute describe asymptotic growth, and only show slight differences in modelled size at age. Differences in modelled size at age are most pronounced at the beginning and end of life.

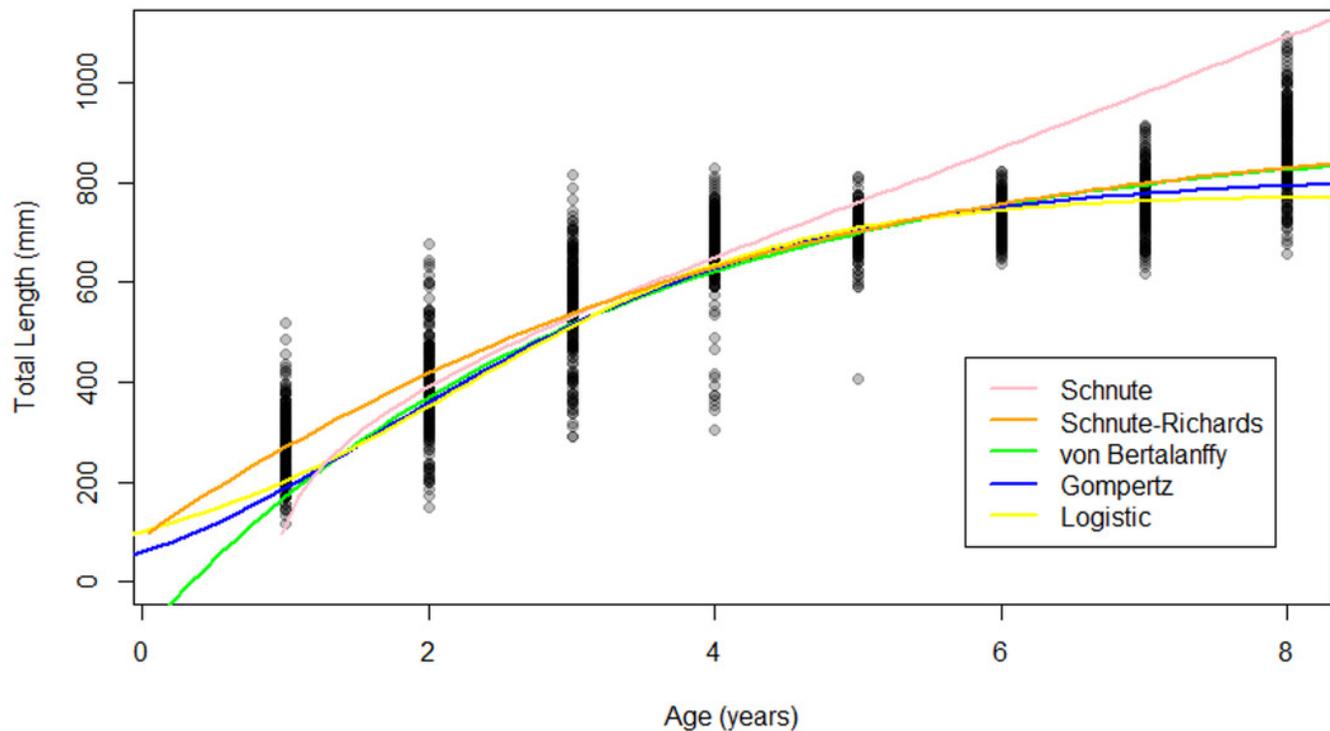
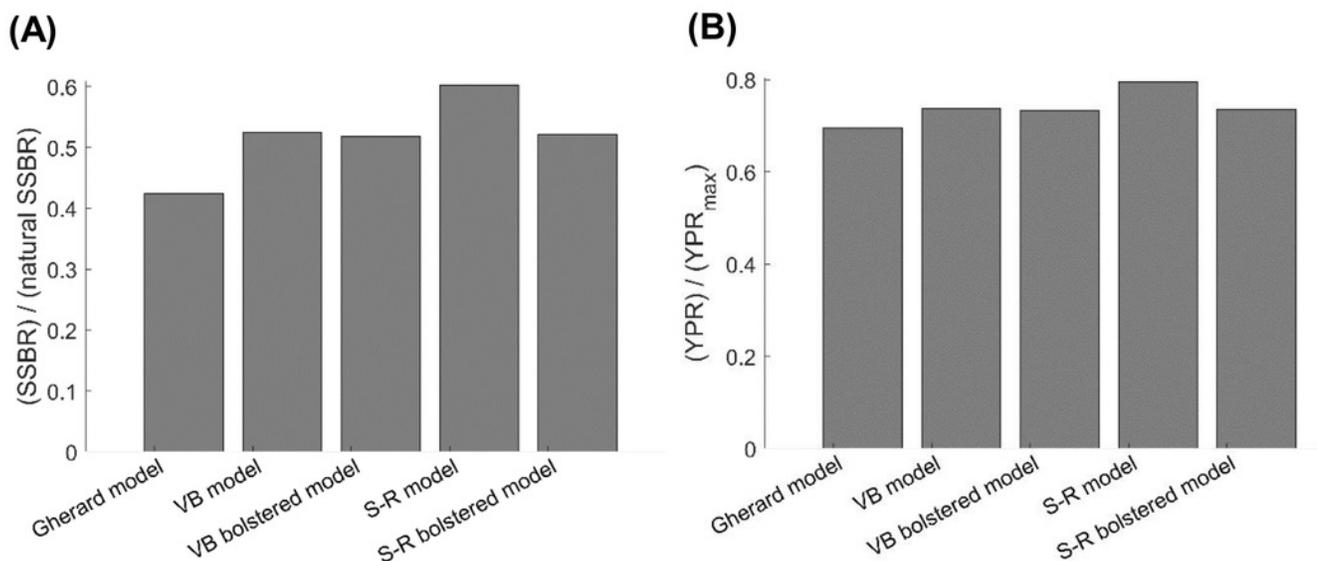



Figure 6

Consequences of using different growth models on (A) the current female SSBR over natural SSBR and (B) current YPR over YPR_{max} of Gulf Corvina (*Cynoscion othonopterus)*

SSBR = spawning-stock-biomass-per-recruit. YPR = yield-per-recruit. Gherard model = von Bertalanffy model developed in Gherard et al. (2013). VB model = von Bertalanffy model fit to raw data in the present study. VB bolstered model = von Bertalanffy model fit to raw data bolstered by simulation values in this study. S-R model = Schnute-Richards model fit to raw data in the present study. S-R bolstered model = Schnute-Richards model fit to raw data bolstered by simulation values in this study.

Parameter estimates for growth models fit to raw age-length data for Gulf Corvina

Estimates of L_∞ are variable, but not as variable as those reported in previous multi-model studies of Gulf Corvina growth (Aragón-Noriega, 2014; Mendivil-Mendoza, 2017). Confidence intervals around parameter estimates may be found in the supplemental information.

Model name	Model equation when fit to raw data
von Bertalanffy	$L(t) = 916.05[1 - e^{-0.28(t - (-0.17))}]$
Gompertz	$L(t) = 820.64e^{(-(\frac{1}{0.51})e^{-0.51(t - 1.29)})}$
Logistic	$L(t) = 778.88[1 + e^{-0.76(t - 1.92)}]^{-1}$
Schnute	$L(t) = \left[141^{-0.33} + (1013^{-0.33} - 141^{-0.33})\dfrac{1 - e^{-3.36(t - 1)}}{1 - e^{-3.36(8 - 1)}}\right]^{1/-0.33}$
Schnute-Richards	$L(t) = 730.91\left(1 + (-0.003)e^{-(0.12)t^{2.18}}\right)^{1/0.003}$

Statistical measures of fit for growth models fit to raw age-length data for Gulf Corvina

The Schnute-Richards model fits the data best according to AICc and BIC values, but is only marginally better than the logistic, Gompertz, and von Bertalanffy models. Note: K indicates the number of parameters in each model.

*3 parameters were estimated by nonlinear least squares, but 4 additional parameters were manually inputted (maximum and minimum ages and lengths) for the Schnute model.

Model	K	AICc	Δ AICc	AICc weight	BIC	Δ BIC
Schnute-Richards	6	8759.82	0.00	1	8787.42	0.00
Logistic	4	8773.62	13.80	0	8792.04	4.62
Gompertz	4	8789.69	29.87	0	8808.11	20.69
von Bertalanffy	4	8813.66	53.84	0	8832.08	44.66
Schnute	3*	9148.78	388.96	0	9162.61	375.19

Parameter estimates for growth models fit to raw Gulf Corvina age-length data bolstered by simulated values

Compared to parameter estimates for models fit to raw data alone, estimates of L_∞ are less variable and generally increase. These estimates are closer to the L_∞ of 1006 predicted by Froese and Binohlan's (2000) empirical relationship between L_∞ and the longest fish in a dataset

Model	Model fit to data bolstered by simulated values
von Bertalanffy	$L(t) = 951.30[1 - e^{-0.25(t-(-0.33))}]$
Gompertz	$L(t) = 870.48e^{(-(\frac{1}{0.62})e^{-0.62(t-1.34)})}$
Logistic	$L(t) = 834.34[1 + e^{-0.62(t-2.10)}]^{-1}$
Schnute	$L(t) = \left[141^{-0.78} + (1013^{-0.78} - 141^{-0.78})\dfrac{1 - e^{-6.06(t-1)}}{1 - e^{-6.06(8-1)}}\right]^{1/-0.78}$
Schnute-Richards	$L(t) = 938.80\left(1 + (-0.0046)e^{-(0.67)t^{0.72}}\right)^{1/0.0019}$

Statistical measures of fit for growth models fit to raw Gulf Corvina age-length data bolstered by simulated values

The von Bertalanffy growth model describes the data best according to AICc and BIC values. However, AICc weighting indicates that the Schnute- Richards and Gompertz models have nearly equivalent fits. Note: K indicates the number of parameters in each model.

*3 parameters were estimated by nonlinear least squares, but 4 additional parameters were manually inputted (maximum and minimum ages and lengths) for the Schnute model.

Model	K	AICc	Δ AICc	AICc weight	BIC	Δ BIC
von Bertalanffy	4	18678.72	0.00	0.53	18700.20	0.00
Schnute-Richards	6	18679.65	0.94	0.33	18711.87	11.67
Gompertz	4	18681.29	2.57	0.15	18702.77	2.57
Logistic	4	18702.60	23.89	0	18724.09	23.89
Schnute	3*	19891.72	1213.01	0	19907.84	1207.64

Models used to describe growth in sciaenid fishes similar to and including the Gulf Corvina

A review of 24 sciaenid growth studies indicates that sciaenid growth is most commonly modelled by the von Bertalanffy growth model (20 studies; 83 % of studies reviewed).

Growth model selected	Genus and species	References
Gompertz	*Cynoscion nebulosus*	Murphy and Taylor, 1994 (females only)
Linear	*Cynoscion nebulosus*	Murphy and Taylor, 1994 (males only); Nieland et al., 2001
Logistic	*Cynoscion nebulosus*	Dippold et al., 2016
Schnute-Richards	*Cynoscion othonopterus*	Aragón-Noriega, 2014 (selected for two datasets); Mendivil-Mendoza, 2017
von Bertalanffy	*Cynoscion nebulosus*	Rutherford et al., 1982; Maceina et al., 1987; Wieting, 1989; Cottrell, 1990
	Cynoscion othonopterus	Gherard et al. 2013; Aragón-Noriega, 2014 (selected for two datasets)
	Cynoscion regalis	Lowerre-Barbieri et al., 1995; Hatch and Jiao, 2016; White, 2017
	Menticirrhus americanus	Clardy et al., 2014
	Micropogonias funieri	Manickchand-Heileman and Kenny, 1990; Santos et al., 2017
	Micropogonias undulates	Barger, 1985; Barbieri, 1993; Franco, 2014
	Pogonias chromis	Murphy and Taylor, 1989
	Sciaenops ocellatus	Beckman et al., 1988; Murphy and Taylor, 1990; Ross et al., 1995
	Totoaba macdonaldi	Rodriguez and Hammann, 1997