

1 Quantifying maternal reproductive output of chondrichthyan fishes

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7 **Abstract**

8 For the live-bearing and egg-laying class of chondrichthyan fishes a three parameter logistic ‘maternity’
9 function with a variable upper asymptote, P_{Max} , can be used to calculate the average probability of a
10 female giving birth or laying eggs in a season. Although fundamental to calculating the reproductive
11 capacity of a population, relatively few studies report maternity functions. Instead, maturity functions
12 have typically been used as a proxy, despite evidence of a delay between attainment of functional maturity
13 and pregnancy in some species. This study examined the relative performance of alternative approaches
14 for quantifying maternal reproductive output. Applying logistic models to a combination of simulated
15 and empirical data showed that it was feasible to estimate P_{Max} from data and that precision, bias, and
16 confidence interval coverage often improved compared to when a fixed value was used. At sample sizes <
17 250 individuals a fixed-value for P_{Max} was more effective at reducing bias in simulated data for gummy
18 sharks, *Mustelus antarcticus*. Maturity parameters could be estimated with greater precision however
19 substituting them in place of maternity parameters overestimated lifetime reproductive output. The extent
20 to which maturity functions can provide a good approximation for maternity functions may be species
21 specific and requires further research. Greater use of maternity functions has the potential to improve
22 calculation of reproductive output in quantitative populations models. We proposed that estimation of
23 P_{Max} is generally preferable to using a fixed value. In addition to improvements in parameter estimation,
24 this method involves fewer assumptions and enables statistical inferences to be made on frequency of
25 reproduction.

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26 1 Introduction

27 Many ecological and evolutionary applications need quantitative data on the reproductive capacity of a
28 population and in fisheries science this information forms the basis of widely-used management reference
29 points such as spawning stock biomass (Quinn and Deriso 1999). Calculating reproductive capacity requires
30 data on the sexually mature proportion of the population contributing to reproduction at a given size or age.

31 For most populations of teleost fishes a simple two-parameter logistic regression function (2PLF) is sufficient
32 to model this process using dichotomous sexual maturity stage data (immature / mature) from a sample of
33 individuals (Jennings et al. 2001, King 2007). While the mathematical formulae and methods of statistically
34 estimating parameters for a 2PLF vary, the estimated values are similar and can be obtained with the built
35 in generalised linear model (GLM) programs in most modern statistical software.

36 In chondrichthyan fishes (sharks, rays, skates, and chimaeras), the process of maturation can be modelled in
37 a similar manner to teleost fishes with a simple 2PLF; however, for the intents and purposes of calculating
38 reproductive capacity, chondrichthyans differ in several ways to most teleosts. Firstly, in many chondrichthyans
39 the duration of the reproductive cycle is longer than a year, meaning the proportion of females that will
40 give birth in the population in a given season is less than one (Frisk et al. 2005, Dulvy et al. 2008, Rigby
41 and Simpfendorfer 2015). Secondly, there may be a lag between when females reach sexual maturity and
42 when they begin reproducing (Harry et al. 2013, Fujinami et al. 2017). This is confounded by the adopted
43 definition of maturity, which can lead to variable estimates of size and age at maturity (Braccini et al. 2006,
44 Walker 2007, Montealegre-Quijano et al. 2014). Finally, because female fecundity is low (usually $\ll 100$
45 embryos), total pup or egg production and recruitment are likely to be closely related to the number of
46 reproductively active females, exhibiting little interannual variability (Taylor et al. 2013). This contrasts the
47 often highly variable relationship between stock size and recruitment in teleost fish, and warrants a precise
48 definition and calculation of reproductive output. For these reasons, unlike in teleosts, a maturity function
49 may not be the most appropriate tool to quantify reproductive capacity.

50 1.1 Maternity function

51 Walker (2005) recognised the need for a maternity function, as distinct from a maturity function, to accurately
52 quantify reproductive capacity in chondrichthyans. For this purpose he used a non-linear, three-parameter
53 logistic function (3PLF) of the form:

$$Y_i \sim B(x_i; n_i, P_i)$$

54

$$E[Y_i] = n_i P_i = \frac{\alpha}{1 + e^{-(b_0 + b_1 x)}}$$

55 where the proportion of individuals in a given length or age category, x_i , that are in maternal condition, Y_i ,
56 is a binomially distributed random variable, with an expected value equal to the probability of an individual
57 from that category being in maternal condition, P_i , multiplied by the total number of individuals in the
58 category, n_i . If x is a continuous rather than categorical variable (i.e. $n = 1$), Y_i reduces to a Bernoulli
59 random variable (Zuur et al. 2007). α is the upper asymptote of the curve, controlling the maximum value
60 of Y as x approaches infinity. The lesser-used 3PLF reduces to the ubiquitous 2PLF when $\alpha = 1$, as is
61 appropriate for most teleost and chondrichthyan populations if modeling maturity (Quinn and Deriso 1999,
62 Roa et al. 1999). When $\alpha = 1$, the function also belongs to the class of generalised linear models; logistic
63 transformation of the dependent variable allows Y to be modeled as a linear function of x_i , where b_0 and b_1
64 are the intercept and slope, respectively (Zuur et al. 2007). Alternatively, the model can be expressed in
65 more biologically relevant terms as:

$$E[Y_i] = P_{Max} \left(1 + e^{-ln(19) \left(\frac{x_i - x_{50}}{x_{95} - x_{50}} \right)} \right)^{-1}$$

66 where x_{50} and x_{95} are the sizes or ages at which 50% and 95% of the maximum proportion of individuals
67 (P_{Max}) are in maternal condition. Instead of being fit to data on female maturity condition the model is fit
68 to dichotomous data on female maternal condition (non maternal / maternal).

69 Walker (2005) defines individual females as being in maternal condition if they would have given birth or
70 laid eggs by the end of a given year such that they contribute to annual recruitment (age 0+ cohort) at
71 the beginning of the next year. Pregnancy is a necessary, but not sufficient, condition for maternity, and

72 the two conditions are not always synonymous. For example, reproduction in the Australian population of
73 school shark, *Galeorhinus galeus*, occurs triennially, such that approximately one third of mature females
74 give birth annually and $P_{Max} \approx 1/3$ (Walker 2005). Gestation lasts 20 months, and includes a protracted
75 period of ovulation. Newly pregnant females are not considered to be in maternal condition until the year of
76 pre-recruitment. Walker's (2005) definition is specific to species that reproduce during a single, well-defined
77 period of the year, but the concept can be generalised to accommodate asynchronously reproducing species
78 or those that reproduce more than once a year.

79 Numerous authors have adopted Walker's (2005) maternity function, including for species with biennial or
80 longer reproductive cycles (Huveneers et al. 2007, Rochowski et al. 2015, Trinnie et al. 2016) as well as those
81 with annual or shorter reproductive cycles (Trinnie et al. 2009, Mejía-Falla et al. 2012, Harry et al. 2013,
82 Taylor et al. 2016). Techniques have been described for determining maternal output in asynchronously
83 reproducing species (Braccini et al. 2006, Colonello et al. 2016), and maternity functions are also increasingly
84 being used directly in shark and ray population assessments (SEDAR 2012, 2023, SEDAR 2017).

85 Despite an increase in use, only a small fraction of reproductive studies in recent years have reported
86 maternity functions. Classification of maternal condition is more data-intensive than maturity condition,
87 ideally requiring monthly sampling over a year or longer in order to establish the timing and duration of the
88 female ovarian and uterine cycles. Such data can be difficult and costly to collect for sharks and rays, which
89 are often data-poor and sampled opportunistically. The teleost-oriented foundations of fisheries science have
90 also contributed to the general lack of awareness of maternity functions; Walker (2005) is the sole description
91 on this type of analysis for chondrichthyans and there are no primary literature sources that describe specific
92 methods for chondrichthyan fishes.

93 For practitioners that are aware of maternity functions, lack of information on implementation may also have
94 discouraged use. Walker's (2005) approach to estimating parameters in the maternity function is difficult to
95 reproduce, apparently due to the constraints of the proprietary statistical program first used to implement the
96 analysis. Specifically, the method as described involves adjusting the raw data prior to parameter estimation
97 and then weighting it during analysis (Walker 2005). Additionally, the use of a fixed value for P_{Max} , as in the

98 original analysis, has the potential to bias parameter estimates and reduce their standard errors (Motulsky
99 and Christopoulos 2004). Alternative approaches to estimating maternal parameters have also arisen in the
100 literature, indicative of a lack of guidance on implementation. For example, some authors have obtained
101 maternity parameters by fitting a 2PLF to maternity data (Baremore and Hale 2012, Baremore and Passerotti
102 2013).

103 A consequence of the low uptake in use of maternity functions is that most practitioners undertaking
104 population assessments invariably take an *ad hoc* approach to quantifying maternal reproductive output.
105 This typically involves approximating maternal output using a maturity function. Under such an approach
106 all mature females are tacitly assumed to reproduce in each breeding season (Cortes 1998). Non-annual
107 reproduction is accounted for by weighting fecundity or the maturity function by the assumed (but often
108 unknown) duration of the reproductive cycle (2005). In some cases, calculations of reproductive output may
109 use the age-at-first-reproduction, defined as the mean age at maturity plus the gestation period (Mollet and
110 Cailliet 2002). This accounts for the protracted gestation period of many chondrichthyans, but still assumes
111 that all individuals begin reproducing immediately after maturity. Measures of annual reproductive output
112 that follow this approach are hence built upon a series of assumptions that are rarely tested in practice.

113 1.2 Revisiting the maternity function

114 Wider use of maternity functions in studies of chondrichthyan reproductive biology is needed to improve
115 calculation of reproductive capacity in the quantitative population assessments that are increasingly being
116 used to support fisheries management and prioritize conservation actions (Cortés et al. 2012). It may also
117 help address the lack of empirical data on the periodicity of chondrichthyan reproductive cycles. Historically,
118 reproductive periodicity has only been determined qualitatively, and has been assumed to be fixed (e.g. annual,
119 biennial), despite observations of plasticity in this trait within discrete populations (Higgs et al. 2020).
120 Information on reproductive periodicity is contained within maternal data, however the existing approach of
121 fixing P_{Max} in maternity functions prevents statistical inference from being made on these data. Changes to
122 the way in which maternity functions are implemented may also contribute to quantifying uncertainty in
123 reproductive frequency and help understand the temporal stability of reproductive cycles. To date only a

124 single study on spiny dogfish, *Squalus acanthias*, has statistically estimated P_{Max} from data (Colonello et al.
125 2016), and the feasibility of doing so for a wider range of species has not been investigated.

126 This study revisits the use of maternity functions with the objectives of providing guidance on implementation
127 and appropriate use. To address this objective a combination of simulated and empirical data were used to 1)
128 evaluate the performance of two alternative methods for estimating maternity parameters, subject to varying
129 reproductive frequency, sample size, and gear selectivity, 2) illustrate the effect of not using using maternity
130 functions on calculations of lifetime reproductive output, and 3) outline strategies for making inferences on
131 reproductive frequency from maternity data.

132 2 Methods

133 2.1 Approach

134 To assess the feasibility of estimating maternity parameters a simulation study was carried out using the 3PLF
135 to generate data for populations with varying reproductive frequencies (Figure 1). Simulations were conducted
136 for a range of gear selectivities and sample sizes reflective of those typically available in reproductive studies
137 and fishery sampling programs. The performance of three methods in estimating ‘true’ maternity parameters
138 from simulated data was tested by examining precision, bias, and interval coverage. To illustrate the
139 effects of misspecifying maternity parameters, lifetime reproductive output was calculated for each simulated
140 population using parameters derived from each of the methods, and by substituting maturity parameters for
141 maternity parameters. Finally, empirical data from previously published studies were reanalysed to illustrate
142 possible strategies for estimating maternity parameters and making inferences on reproductive frequency. All
143 simulation modelling and data analysis was conducted using the R language (R Core Team 2018) and the
144 Template Model Builder (TMB) R package (Kristensen et al. 2016).

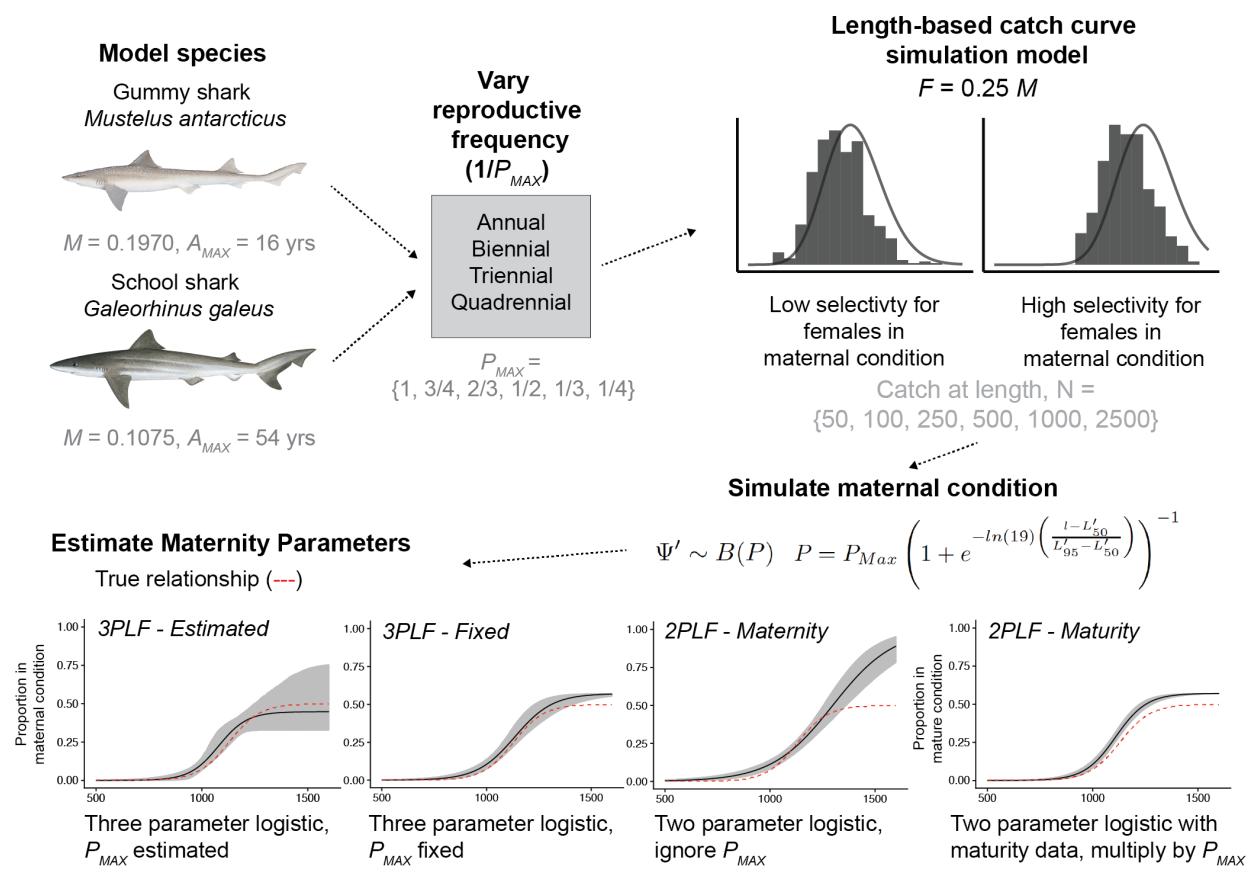


Figure 1: Approach used to generate simulated data and test the performance of four methods for calculating maternity parameters.

145 **2.2 Simulation**

146 **2.2.1 Data generation**

147 Data were generated for the gummy shark, *Mustelus antarcticus*, and school shark, *Galeorhinus galeus*,
148 using parameters from studies conducted on southern Australian populations (Table 1) (Grant et al. 1979,
149 Kirkwood and Walker 1986, Moulton et al. 1992, Walker 1992, Punt and Walker 1998, Walker 2005, 2007).
150 Both species are well-studied and were chosen to be representative of r- and K-selected chondrichthyan life
151 history styles, respectively (Stevens 1999).

152 Catch at length data were simulated using a female-only, length-based catch curve model (Hesp 2023). The
153 approach involved calculating expected survival and catches per recruit subject to specified life history
154 parameters, gear selectivity, and total mortality. Growth was modelled using a von Bertalanffy growth
155 function with length l , of a fish of age, a , calculated as

$$l(a) = L_\infty(1 - e^{-K(a-a_0)})$$

156 where L_∞ is asymptotic length, K is the growth coefficient and a_0 is the hypothetical age at zero length.
157 Recruitment into the population was assumed to occur at age 0 with length conforming to a normal distribution.
158 The proportion of fish of length, l , at age, $a = 0$, was calculated as

$$\Theta_k = \int_{l^-}^{l^+} f_{a=0}(l) dl$$

159 where l^- and l^+ are the lower and upper limits of each 1cm length class, k . $f_{a=0}(l)$ is the value of the normal
160 probability density function at age $a = 0$ for a given length, l ,

$$f_{a=0}(l) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left[\frac{(l-\mu)^2}{2\sigma^2}\right]$$

161 where mean length, μ , was calculated from the growth curve. The standard deviation, σ was not available for
162 either species so was assumed to be directly proportional to length, with a constant of proportionality of 5%

163 (Table 1), i.e. $\sigma = 0.05\mu$.

164 Growth in subsequent age classes was modelled using a length transition matrix (Punt et al. 1997, Hall et al.

165 2000), $G = g_{j,k}$ that represents the probability that a fish in length class, j , will grow into length class, k ,

166 over a specified time interval

$$G = \begin{bmatrix} g_{1,1} & 0 & 0 & 0 \\ g_{2,1} & g_{2,2} & 0 & 0 \\ \dots & \dots & \ddots & 0 \\ g_{n,1} & g_{n,2} & \cdots & g_{n,n} \end{bmatrix}$$

167 where the elements of the matrix followed the general form of Punt *et al* (1997) and are given by

$$g_{k,j} = \begin{cases} \int_{l_k^-}^{l_k^+} f[\phi(l, j)]dl & \text{if } k = 1 \\ \int_{l_k^-}^{l_k^+} f[\phi(l, j)]dl & \text{if } k = 1 < k < n \\ \int_{l_k^-}^{\infty} f[\phi(l, j)]dl & \text{if } k = n \end{cases}$$

168 where l is mean length, f is the specified normal distribution, l_k^- and l_k^+ are the lower and upper limits of

169 length class j , and ϕ is a vector of parameters.

170 Selectivity in the model was assumed to follow a gamma function based on gillnet selectivity experiments

171 (Kirkwood and Walker 1986, Punt and Walker 1998), where the selectivity of an individual in length class, l

172 was given by

$$S(l) = \left[\frac{l}{\theta_1 \theta_2} \right]^{\theta_1} \exp(\theta_1 - \frac{l}{\theta_2})$$

173 where θ_1 and θ_2 are estimated parameters (Kirkwood and Walker 1986). Two selectivity scenarios were

174 simulated corresponding to low and high selectivity of the maternal component of the population. For

175 consistency between species, gillnet mesh sizes were chosen that would result in peak relative selectivity

176 occurring at the lengths equal to 25% and 75% of the population in maternal condition (Table 1).

177 Fishing mortality, F , in length class l , was calculated as

$$F(l) = S(l) \cdot F$$

178 where F was assumed to be constant and nominally set to 25% of natural mortality, M (i.e. $0.25M$). The
179 effects of varying levels of F were not investigated further in this study. Total mortality, Z , in length class, l ,
180 was further given by

$$Z(l) = F(l) \cdot M$$

181 The number of fish, N , per recruit in length class, l , that survived to age, a , was calculated as

$$N_{l,a} = \begin{cases} 1 & \text{if } a = 0 \\ N_{l,a-1} \exp(-Z_l) & \text{if } a = 1 < a < A_{Max} \\ N_{l,a-1} \exp(-Z_l)/(1 - \exp(-Z_l)) & \text{if } a = A_{Max} \end{cases}$$

182 where A_{Max} is the maximum age (Table 1). The estimated numbers of fish caught in length class, l , at age,
183 a , was calculated using the Baranov catch equation as

$$\hat{C}_l = \sum_a (F_l/Z_l)(1 - \exp(-Z_l))N_{l,a}$$

184 To examine the effect of varying sample size, six scenarios were conducted with catch ranging from 50 to
185 2500 individuals, reflecting a gradient from data poor to rich.

186 Next, maturity-at-length data, $\psi(l)$, were randomly generated by simulating from a Bernoulli distribution,
187 $\Psi(l) \sim B(P)$, where P was given by the 2PLF:

$$P = \left(1 + e^{-\ln(19)\left(\frac{l-L_{50}}{L_{95}-L_{50}}\right)}\right)^{-1}$$

188 This process was then repeated to generate maternity-at-length data, $\Psi'(l)$, using the 3PLF:

$$\Psi' \sim B(P)$$

189

$$P = P_{Max} \left(1 + e^{-\ln(19) \left(\frac{l - L'_{50}}{L'_{95} - L'_{50}} \right)} \right)^{-1}$$

190 Finally, 300 iterations were run for each of the 144 unique variables combinations.

191 **2.2.2 Estimation approaches**

192 Two approaches to estimating maternity parameters were compared: the 3PLF itself (3PLF-estimated) and

193 the 3PLF function with a fixed asymptote (3PLF-fixed). Additionally, two approaches using a 2PLF were also

194 examined, using maternity-at-length data (2PLF-maternity) and maturity-at-length data (2PLF-maturity).

195 The 3PLF-estimated method was undertaken to validate the utility of this model, which has so far been used

196 in only a single study (Colonello et al. 2016). The 3PLF-fixed is the method described by Walker (2005)

197 and most commonly used in practice. The 2PLF-maternity method was used to examine what effect simply

198 ignoring the upper asymptote had (i.e. P_{Max} fixed at 1). The 2PLF-maturity method is commonly used to

199 approximate a maternity curve, and tacitly assumed to be similar. The resulting maturity curve can then be

200 weighted by the proportion of gravid females to calculate annual reproductive output (although in practice

201 annual fecundity is more often modified, for example halved for a species suspected to reproduce biennially

202 (SEDAR 2023)).

203 Only the 3PLF-estimated method involves statistically estimating P_{Max} , which must be subjectively chosen

204 in the case of the 3PLF-fixed and the 2PLF-maturity. P_{Max} is ideally chosen based on detailed study of the

205 ovarian and uterine cycles (Walker 2005), or alternatively based on the proportion of mature females observed

206 to be in maternal condition during sampling (Baremore and Hale 2012, Harry et al. 2013, Trinnie et al. 2016).

207 For the purposes of the simulation, the timing and duration of the uterine and ovarian cycles were assumed to

208 be unknown. The following procedure was used to ‘guess’ the fixed value of P_{Max} in each simulation. P_{Max}

209 was chosen as the proportion of females in maternal condition above a the length at which 99% of females

210 were mature, $L > \Psi(L_{99\%})$. In some cases this procedure failed due to there being no maternal females in

211 the simulated data set meeting this criteria. If this occurred, L_{95} was used, followed by L_{50} , and finally the
212 proportion of all mature females in the sample that were in maternal condition. Statistical estimation of all
213 non-fixed parameters in each of the methods was undertaken using maximum likelihood. Nonparametric
214 bootstrapping was used to calculate approximate 50% confidence intervals for the best-fit parameters from
215 250 resampled data sets.

216 **2.2.3 Reproductive output**

217 For each iteration, the per-generation rate of multiplication, R_0 , or lifetime female pup production, was
218 calculated as:

$$R_0 = \int_0^{\infty} R\beta(a)e^{\int_0^a Mds}da$$

219 where R and M are the embryonic sex ratio and natural mortality rate (Table 1) and $\beta(a)$ is the age-specific
220 reproductive rate which incorporates $\Psi'(L)$ (Xiao and Walker 2000).

221 **2.2.4 Performance**

222 Model performance was evaluated in each iteration where 1) the fitted model successfully converged as indicated
223 by a positive definite Hessian matrix, and 2) the estimated parameters L'_{50} and L'_{95} remained within specified
224 bounds ($0 - 10^4$). An iteration was also not attempted if there were no maternal females in the randomly
225 generated sample. Model performance was evaluated by quantifying precision, bias, and interval coverage for
226 L'_{50} , P_{Max} and R_0 . Bias was quantified using the mean relative error, $MRE = \text{mean}[(x_{\text{Estimated}} - x_{\text{True}})/x_{\text{True}}]$
227 and precision using the mean absolute relative error, $MARE = \text{mean}|[(x_{\text{Estimated}} - x_{\text{True}})/x_{\text{True}}]|$. Interval
228 coverage measures the ability of the model to capture uncertainty and was calculated by taking the proportion
229 of the estimated parameters for each simulation that fell within the 50% confidence intervals (Rudd and
230 Thorson 2018). For a well-performing model, approximately 50% of parameters would be expected to fall
231 within the nominal 50% confidence intervals.

232 **2.2.5 Empirical case study**

233 An empirical case study was also undertaken to show how maternity functions can be used in practice.
234 Data from two studies of the reproductive biology of the sandbar shark, *Carcharhinus plumbeus*, in the
235 Gulf of Mexico and western North Atlantic Ocean were combined and reanalysed using both 3PLF methods.
236 The sandbar shark is a relatively long-lived ($A_{Max} = 33$ years) and slow growing species ($K = 0.12\text{yr}^{-1}$)
237 with a protracted reproductive cycle lasting longer than a year (Springer 1960). The Gulf of Mexico and
238 western North Atlantic Ocean population has been considered overfished since the late 1970s (Sminkey and
239 Musick 1995) and during the 2000s detailed studies of sandbar shark reproductive biology and growth were
240 undertaken for stock assessment purposes (Baremore and Hale 2012, Piercy et al. 2016). In their study,
241 Baremore and Hale (2012) estimated maternity parameters using the 2PLF-maternity method, weighting
242 the final curve by 0.37 based on the proportion of pregnant females observed, most closely aligning with a
243 triennial reproductive cycle. Piercy et al (2016) did not estimate maternity parameters but also suggested
244 that the average reproductive cycle was likely to be longer than two years based on examination of ovarian
245 follicles. To examine relative support for either a biennial or triennial reproductive cycle, 3PLF-fixed models
246 were fit with P_{Max} estimated and fixed at 0.5 and 0.33, respectively.

247 **3 Results**

248 **3.1 Simulation study**

249 Parameter estimation was generally straightforward; with sample sizes > 50 a success rate of $\geq 95\%$ was
250 achieved in all scenarios (Figure S1, Table S1). Overall, convergence and parameter boundary failures
251 were most common with the 2PLF-maternity method which essentially involved fitting data to an under-
252 parameterized model where P_{Max} was always fixed at 1. In addition to convergence failures, 12 simulations
253 also generated insufficient maternal data (zero or one maternal females in the simulated data), and were
254 discarded.

255 Generally when using the 3PLF methods model performance declined as the periodicity of the reproductive
256 cycle increased. The nature of this problem can be seen in the positive correlation between the \hat{L}_{50} and $\hat{P_{Max}}$

parameters whereby P_{Max} affects the magnitude and direction of bias in these parameters (Figure 2). With lower values of P_{Max} it was apparently more difficult for the model to separate the point of inflection in the logistic model and the upper asymptote. As true underlying P_{Max} decreased there was a greater potential for positive bias in \hat{P}_{Max} (Figure 2).

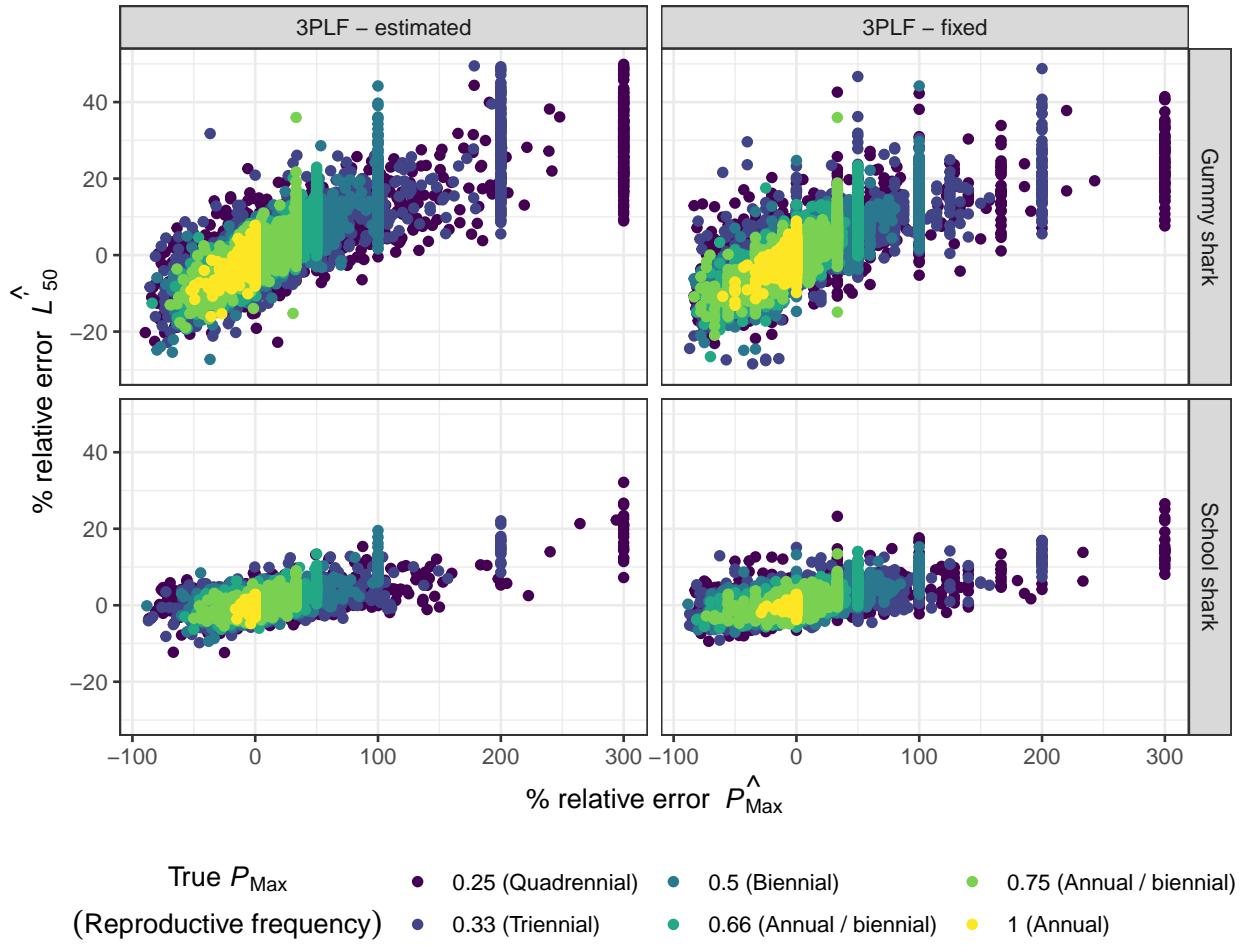


Figure 2: Bias (per cent relative error) in parameter estimates for \hat{L}_{50} and \hat{P}_{Max} for 3PLF methods. Each point represents parameter estimates from one iteration of simulated data. Bias tended to increase as the true underlying P_{Max} decreased.

For the 3PLF methods, parameter estimates tended to be biased high at lower sample sizes (Figure S2, Figure S3). In some scenarios, particularly with sample sizes ≤ 250 , fixing the asymptote was effective at reducing bias, although for larger sample sizes neither method was clearly preferable (Figure S2, Figure S3). The accuracy of parameter estimates varied considerably across different combinations of variables used in the simulation and among parameters (Figure S4, Figure S5). Again, in some scenarios with smaller sample

266 sizes ≤ 250 , fixing the asymptote improved precision with the 3PLF methods, although at larger sample
 267 sizes better precision was achieved by estimating P_{Max} (Figure 3). Overall, P_{Max} was comparatively more
 268 challenging to estimate accurately than L'_{50} (Figure S4, Figure S5).

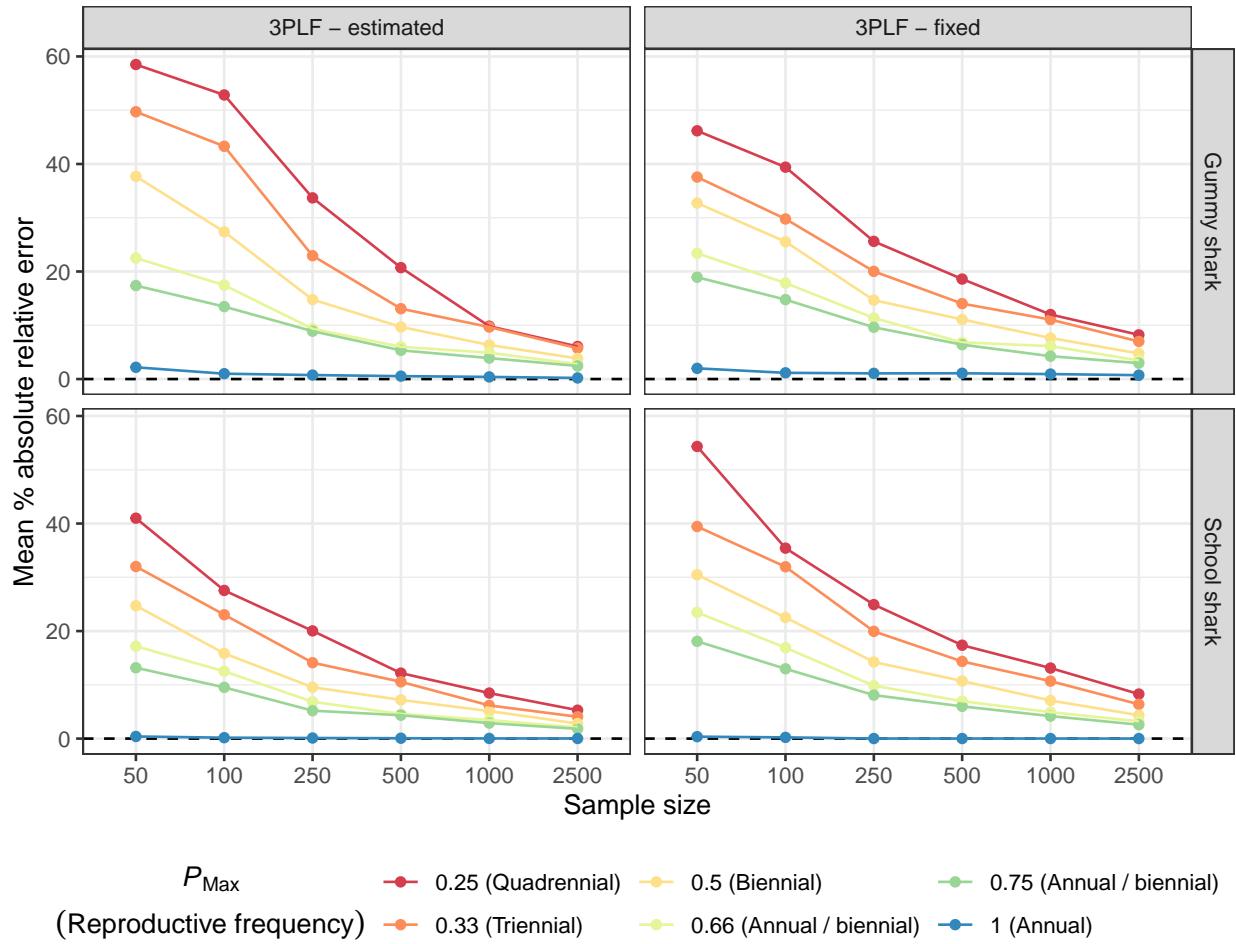


Figure 3: Precision (per cent absolute error) in parameter estimates of \hat{P}_{Max} for 3PLF methods. Large sample sizes were needed to accurately estimate \hat{P}_{Max} and precision decreased as the duration of the reproductive cycle increased

269 While the 3PLF-fixed method was in some cases able to reduce bias at lower sample sizes, a trade off in
 270 the use of this method was poorer interval coverage (Figure 4, Figure S6). For most simulations, interval
 271 coverage for L'_{50} was well below the expected level of 50%, irrespective of sample size. In contrast, for the
 272 3PLF-estimated method interval coverage oscillated around 50% for both L'_{50} and P_{Max} .

273 Differences in life history and gear selectivity played an important role in the ability to obtain precise and
 274 unbiased maternity parameters. Certain combinations of variables in the simulated data resulted in captures

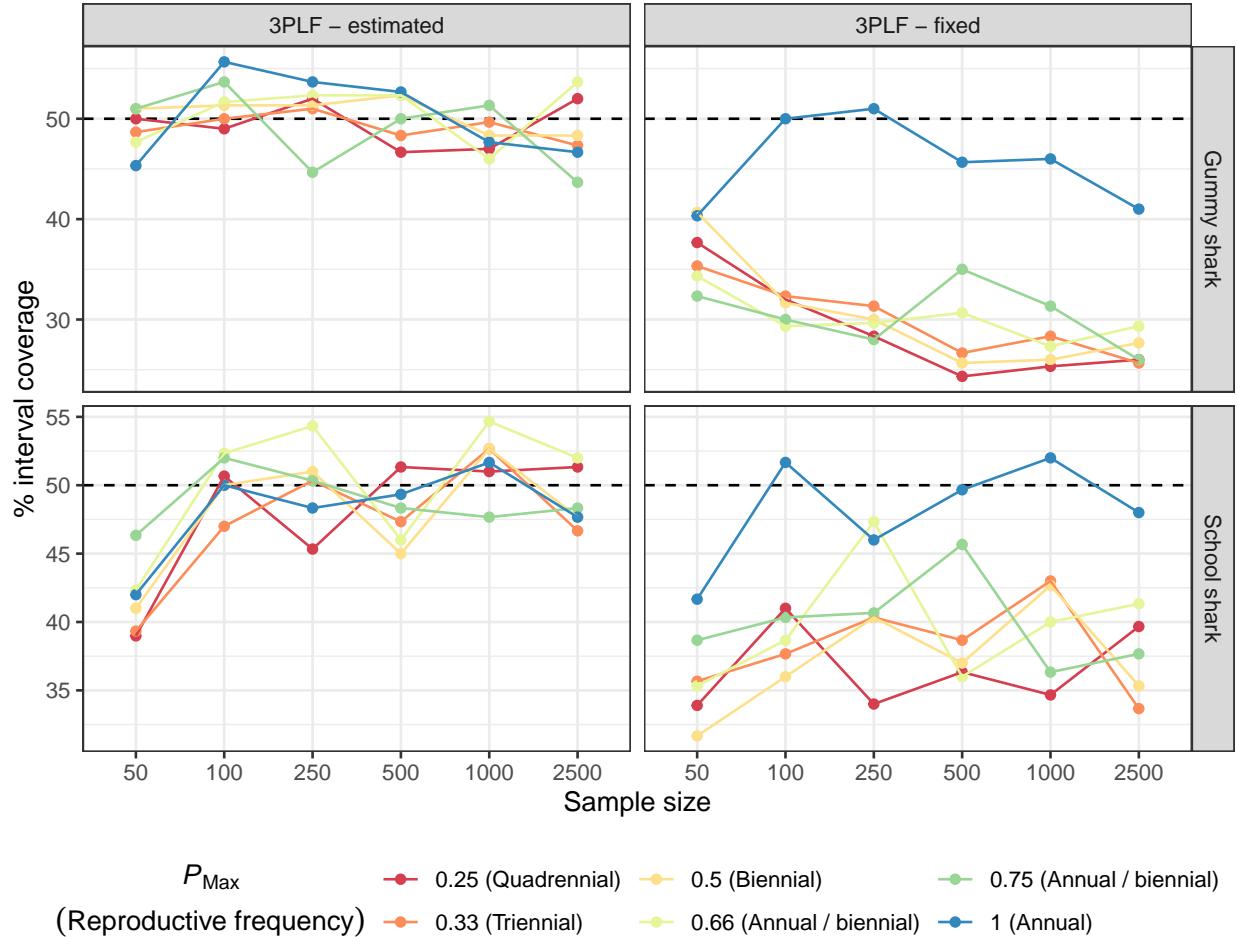


Figure 4: Interval coverage for \hat{L}_{50} for 3PLF methods (high selectivity scenarios). Figure shows the percentage of simulations where the true parameter value fell within the 50% bootstrap confidence interval.

275 of few females in maternal or immature condition making parameter estimation difficult (Figure S8, Figure
276 S9). These effects were not necessarily consistent between species and seemed to reflect differences in the
277 underlying population length structure. For example, in low selectivity scenarios for gummy sharks ~60% of
278 individuals were immature compared to ~50% in the corresponding scenarios for school sharks (Figure S9).

279 As P_{Max} decreased the proportion of maternal females in the analysis also decreased.

280 Overall, the 2PLF-maternity method performed the worst. Ignoring P_{Max} introduced a fixed bias in this
281 parameter that increased in magnitude as reproductive periodicity increased (Figure S3). This manifested
282 in an overestimation of L'_{50} that was exacerbated by gear selectivity effects (Figure S2). In contrast, using
283 a maturity function to approximate the maternity function (2PLF-maturity method) resulted in relatively
284 good performance. L_{50} could usually be estimated with a higher precision than L'_{50} . For the gummy shark,
285 where L_{50} and L'_{50} were relatively similar, using the 2PLF-maturity method led to a constant underestimate
286 of L'_{50} of approximately 2% and exceeding the performance of the 3PLF-methods at most sample sizes.

287 The effect of the different methods in ultimately calculating R_0 varied considerably and was also influenced
288 by life history and selectivity characteristics. For school sharks, estimating P_{Max} , was the most effective way
289 to minimize bias in most scenarios for the school shark (Figure 5, Figure S11). In contrast, using a fixed
290 P_{Max} or substituting maturity parameters often led to better performance for the gummy shark (Figure 5,
291 Figure S11).

292 Greater precision in calculating R_0 was achieved with the 3PLF methods, with the 3PLF-estimated method
293 performing best in most scenarios tested (Figure 6, Figure S11). For gummy sharks the 3PLF-fixed method
294 performed best at lower sample sizes and lower values of P_{Max} , consistent with decreasing performance of
295 3PLF methods as P_{Max} decreased (Figure 2, Figure 3).

296 3.2 Empirical case study

297 Maternal data were re-analysed for 1087 sandbar sharks including 640 mature individuals of which 32%
298 were in maternal condition. Using the 3PLF-estimated method the maximum likelihood estimate for \hat{P}_{Max}
299 was 0.48 (Table 2). Despite having a sample size of > 600 mature females, the proportion of maternal

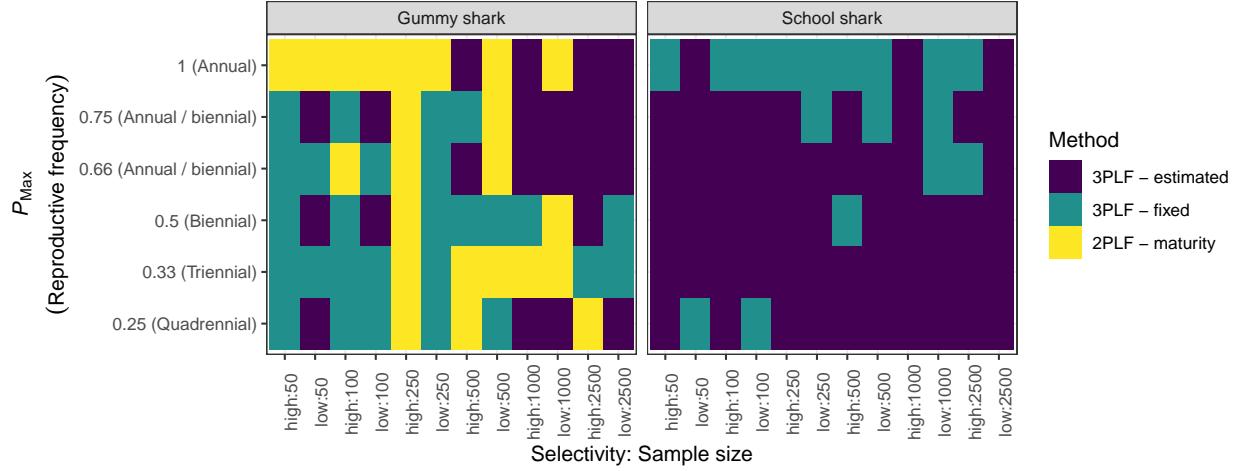


Figure 5: Performance of alternative maternity functions in minimising bias in calculations of R_0 . The preferred method was that which minimised bias, $|\text{relative error}|$ across 300 simulated datasets. Note 2PLF-maternity (Annual) scenarios were excluded for this comparison.

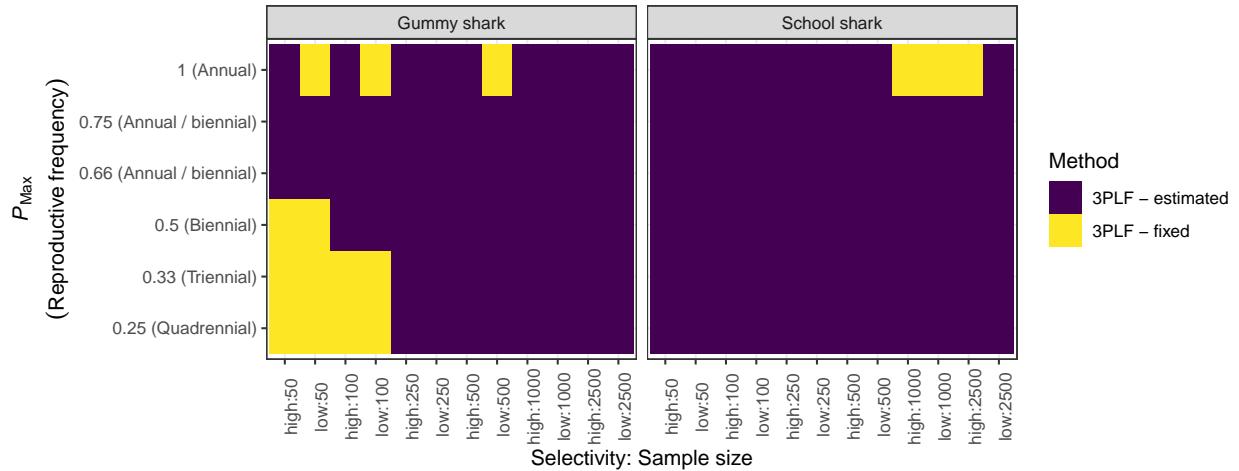


Figure 6: Performance of alternative maternity functions in accurately calculating R_0 . The best performing method was that which minimised mean absolute error across 250 simulated datasets. Note 2PLF-maternity (Annual) scenarios were excluded for this comparison.

300 individuals at length was still uncertain and \hat{P}_{Max} was estimated to lie between 0.39 and 0.60 with 95%
 301 confidence. Comparison of 3PLF-fixed models with values of $P_{Max} = 0.33$ and $P_{Max} = 0.5$ showed much
 302 greater support for a biennial cycle ($\Delta AIC = 14.15$). The model with $P_{Max} = 0.5$ also outperformed the
 303 3PLF-estimated method ($\Delta AIC = 1.86$). Given the fixed model had one fewer estimated parameters, both
 304 models had essentially the same level of support given the data (Burnham and Anderson 2002).

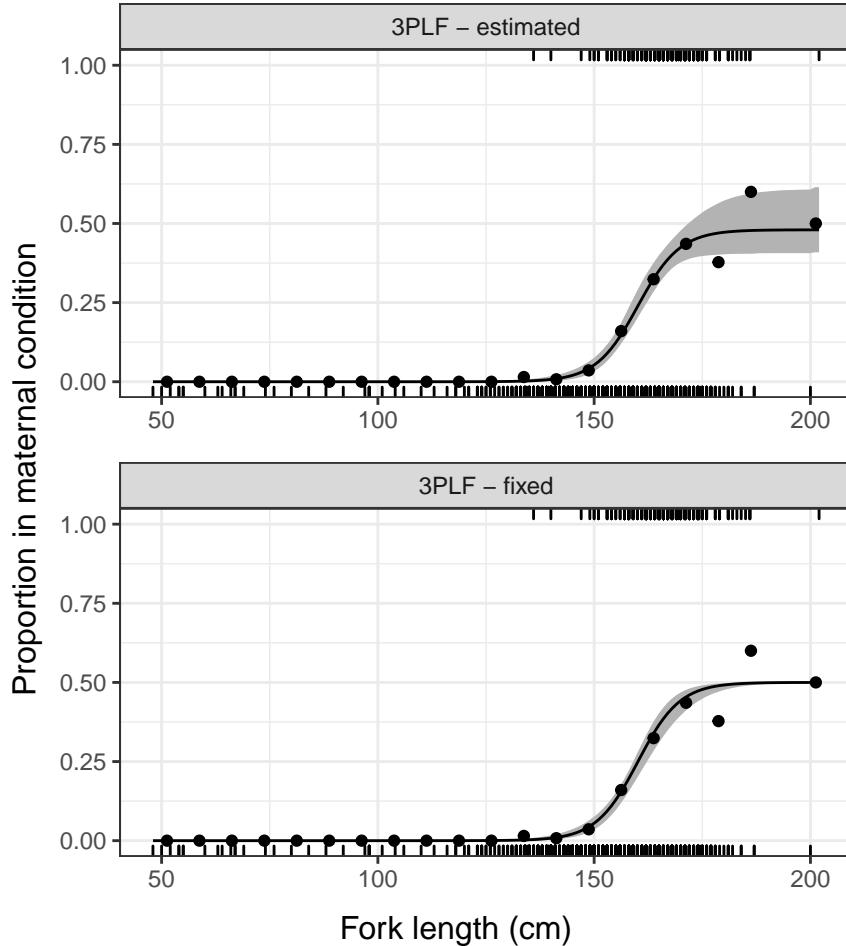


Figure 7: Comparison of 3PLF-estimated and 3PLF-fixed methods used to estimate maternal parameters for sandbar shark, *C. plumbeus*, in the Gulf of Mexico and Western North Atlantic. Solid line is the expected proportion in maternal condition at length, $\Psi'(L)$. The grey shaded region denotes 95% confidence intervals based on bootstrap resampling. P_{Max} was fixed at 0.5 in the lower panel

305 4 Discussion

306 Relatively few reproductive biology studies have used maternity functions to model maternal reproductive
 307 output in chondrichthyan fishes. Where they have been employed the approach has typically been to use

308 a three parameter logistic function with a fixed, user-defined value for the upper asymptote, P_{Max} . Here
309 we show that it is feasible to estimate P_{Max} from maternal data, in turn enabling statistical inferences on
310 reproductive periodicity. Applying 3PLF models with estimated and fixed values of P_{Max} to simulated data
311 showed that precision, bias, and confidence interval coverage often improved when P_{Max} was estimated.
312 Using a fixed value for P_{Max} in some cases resulted in lower bias at low sample sizes. This study also
313 demonstrated that recruitment can be overestimated when maturity data were used to approximate maternal
314 data and if P_{Max} was ignored when estimating maternity parameters. Based on these findings we outline
315 considerations for practitioners using these methods and illustrate how they can provide novel insights into
316 reproductive biology. We conclude by discussing the advantages of adopting this approach to quantifying
317 maternal reproductive output and future directions.

318 4.1 Implementing maternity functions

319 Using simulated data to compare the relative performance of the 3PLF-estimated and 3PLF-fixed methods
320 subject to a range of variables showed that it was feasible to estimate P_{Max} from data, but also identified
321 some situations where it may be preferable to fix P_{Max} . In most scenarios sample sizes of at least 100 were
322 needed for the 3PLF-estimated method to approach or exceed the performance of the 3PLF-fixed method. At
323 sample sizes below this is therefore advisable to fix P_{Max} . Due to the decline in performance associated with
324 longer reproductive cycles, larger sample sizes are desirable before attempting to estimate P_{Max} in species
325 with a triennial or longer reproductive cycle.

326 While the estimation of maternity parameters in most simulations was possible, it was difficult to do so
327 accurately. Outcomes of the simulation study suggested that samples sizes of ≥ 500 would be needed to
328 estimate P_{Max} with $<10\%$ MARE for a triennially reproducing species. This is a much larger error than
329 is achievable from conventional logistic maturity analysis (Roa et al. 1999). In the case of the gummy
330 shark this imprecision led to the 2PLF-maturity method performing comparably or better than the 3PLF
331 methods in ultimately quantifying R_0 . Relatively wide confidence intervals were also obtained for P_{Max} in
332 the empirical analysis for sandbar sharks, even with a sample size of > 1000 . A similar sample size was used
333 by Colonello *et al* (2016) to successfully estimate P_{Max} and maternity parameters for south Atlantic spiny

334 dogfish. These results suggest that data requirements of the 3PLF analyses may be prohibitively large for
335 many chondrichthyans and therefore best suited to use on commercially captured species where large sample
336 sizes can be obtained (Oddone et al. 2010, Tribuzio and Kruse 2012).

337 In light of the data requirements suggested by this study, the current practice of using maturity parameters as
338 a proxy for maternity parameters will likely still be the only option for numerous data-poor chondrichthyans.
339 From this perspective, the outperformance of the 3PLF-methods by the 2PLF-methods for the gummy shark
340 in several simulations is encouraging. However, the extent to which maturity parameters can provide a good
341 approximation of maternity parameters may be species-specific, depending on how close L_{50} is to L'_{50} . While
342 several studies have shown these parameters to be similar (Walker 2007, Soto-López et al. 2018), L'_{50} is more
343 frequently shifted to the right of L_{50} (Braccini et al. 2006, Montealegre-Quijano et al. 2014, Colonello et
344 al. 2016, Palacios-Hernández et al. 2020), and this length difference can equate to one or more years. For
345 example, Harry *et al* (2013) found both spot-tail shark, *C. sorrah*, and Australian blacktip shark, *C. tilstoni*,
346 began reproducing the year after reaching sexual maturity. Similarly, Fujiyama found A'_{50} to be 1.4 years
347 older than A_{50} in blue sharks.

348 More research is needed to understand the relationship between size at maturity and maternity and variability
349 within and among taxa. In general, this study confirms Walker's (2005) assertion that the common practice
350 of weighting the maturity curve by the frequency of parturition overestimates recruitment. This study also
351 confirms that fitting a 2PLF to maternal data when $P_{Max} < 1$ (effectively ignoring P_{Max}) is likely to result
352 in biased parameters and can also overestimate recruitment. While not widely used, this approach has been
353 undertaken in several studies (Baremore and Hale 2012, Mejía-Falla et al. 2012, Baremore and Passerotti
354 2013, Rambahiniarison et al. 2018).

355 The success of any analysis using the 3PLF-estimated method, and its ability to outperform the 3PLF-fixed
356 method, ultimately depends on the analyst choosing a suitable value for P_{Max} . In this study, the value
357 for P_{Max} used in the fixed analyses was chosen based on the proportion of maternal females observed in
358 the simulated data. The potential to introduce a greater level of bias in the analysis through the incorrect
359 selection of P_{Max} should also be considered if using this approach.

360 **4.2 Empirical study**

361 The empirical analysis carried out using data for the sandbar shark illustrates the potential for the 3PLF-
362 estimated method to provide novel insights from maternal data. Detailed reproductive studies of the western
363 North Atlantic population by Baremore and Hale (2012) and Piercy *et al* (2016) were ambiguous about the
364 frequency of reproduction. In both studies, the low proportion of pregnant females and bimodality in ovarian
365 follicle size led the authors to conclude that the reproductive cycle was most commonly triennial or longer at
366 the population level. Reanalysis of these combined data sets using the 3PLF-estimated method, however,
367 resulted in a maximum likelihood estimate of $P_{Max} = 0.48$, more consistent with biennial cycle. Using AIC
368 values to compare the relative plausibility of 3PLF-fixed models corresponding to biennial and triennial cycles
369 also supported a biennial cycle.

370 This counter intuitive result may stem from the gradual attainment of asymptotic maternal status as a
371 function of length. Maturity in sandbar sharks appears to occur over an extended period; L_5 and L_{95} are
372 146cm and 176cm, a length interval that corresponds to around seven years given the sandbar shark's slow
373 growth rate (Hale and Baremore 2013). With females maturing over a broad range of sizes and ages, it is
374 possible that smaller females may be reproducing less frequently, with the largest females potentially capable
375 of reproducing biennially. Further work would be required to confirm this hypothesis, however, such an
376 outcome would have implications for management of this stock; not only are larger females more fecund
377 (Baremore and Hale 2012), they also reproduce more frequently. This implies removal of larger and older
378 female sharks could have a disproportionately greater impact on population productivity.

379 **4.3 Advantages and future directions**

380 Despite the simplicity of the 3PLF-estimated method, it nonetheless represents a conceptual shift for
381 chondrichthyan reproductive and population biology. Until now reproductive periodicity has largely been
382 determined qualitatively from observations of female reproductive biology or inferred based on circumstantial
383 evidence. Using the 3PLF-estimated method to estimate P_{Max} within a maternity function transforms it
384 from a nuisance parameter to one of direct inferential interest that can be seen as a valuable output of the
385 modelling process itself. In addition to the potential benefits of using this method to improve estimation of

386 maternal parameters, there are also a range of other advantages that arise from estimating P_{Max} .

387 One benefit of this approach is that it reduces the need for subjective modelling assumptions relating
388 to P_{Max} . Such assumptions can have important implications for population modelling. For example, to
389 account for uncertainty in temporal and spatial frequency of reproduction in sparsely-spotted stingarees,
390 *Urolophus paucimaculatus*, Trinnie *et al* (2014) estimated maternity parameters for ten plausible scenarios. In
391 stock assessment of western North Atlantic sandbar sharks a breeding frequency of 2.5 years was assumed to
392 account for uncertainty in the duration of the reproductive cycle (SEDAR 2017).

393 More commonly, practitioners have chosen fixed values of the form $P_{Max} = 1/n$, where n is the apparent
394 duration of the reproductive cycle in years. This process also has the potential to introduce bias if a small
395 proportion of females reproduce more or less frequently than the larger population. Long-term study of
396 offspring from genetically profiled lemon sharks, *Negaprion brevirostris*, confirmed that most individuals
397 reproduced biennially, but also revealed some cases of triennial reproduction (Feldheim *et al.* 2014). Statistical
398 estimation of P_{Max} from data avoids these decisions and enables uncertainty in this parameter to be included
399 in subsequent population models.

400 Estimation of P_{Max} using the 3PLF-estimated method may also be a means to resolving the longstanding
401 question of reproductive frequency in some rare and threatened chondrichthyans. White sharks, *Carcharodon*
402 *carcharias*, and whale shark, *Rhinichodon typus*, are two examples of intensively studied species where only
403 fragmentary observations of female reproductive biology exist (Joung *et al.* 1996, Sato *et al.* 2016). In
404 both species lack of data on reproductive frequency is a major impediment to population modelling and
405 the development of management strategies (Huveneers *et al.* 2018, Bowlby and Gibson 2020). With many
406 of these populations the focus of ongoing monitoring, non-lethal methods for assessing maternal state may
407 eventually provide a way of collecting sufficient data for estimation of P_{Max} (Sulikowski *et al.* 2016).

408 A logical progression from estimating P_{Max} is the consideration of alternative functional forms for this
409 parameter such as time- or space-varying P_{Max} or more complex length- or age-dependent forms. Despite
410 the diverse range of reproductive modes found in chondrichthyan fishes, the current, limited knowledge of
411 maternal investment has typically investigated variables such as litter size and pup condition (Hussey *et*

412 al. 2010). Little is known about how reproductive frequency varies as a function of size or age, in response
413 to environmental effects, or at changing population densities. Better understanding of these factors has
414 the potential to improve understanding reproductive strategies and is, many cases, of direct relevance to
415 management.

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