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 predict the average probability of a female

10 giving birth or laying eggs in a season. Although fundamental to calculating the reproductive capacity of a

11 population, few studies report maternity functions, with maturity functions often used as a proxy. Applying

12 logistic models to simulated and empirical data showed that it was feasible to estimate P_{Max} from maternal

13 data and that accuracy, bias, and confidence interval coverage often improved compared to when a fixed

14 value was used. Maturity parameters could be estimated with greater accuracy; however, substituting them

15 for maternity parameters overestimated lifetime reproductive output. Greater use of maternity functions

16 has the potential to improve calculation of reproductive output in quantitative populations models. In

17 addition to improvements in parameter estimation, this method involves fewer assumptions and enables

18 statistical inferences to be made on frequency of reproduction. This study suggests that for sample sizes $>$

19 100, estimation of P_{Max} is generally preferable to using a fixed value.

20 **Key words** Logistic regression; reproductive biology; maturity ogive; fisheries management

1   Introduction

Many ecological and evolutionary applications need quantitative data on the reproductive capacity of a population and in fisheries science this information forms the basis of widely-used management reference points such as spawning stock biomass (Hilborn and Walters 1992, Quinn and Deriso 1999). Calculating reproductive capacity requires data on the sexually mature proportion of the population contributing to reproduction at a given size or age. For most populations of teleost fishes a simple two-parameter logistic regression function (2PLF) is sufficient to model this process using dichotomous sexual maturity stage data (immature / mature) from a sample of individuals (Jennings et al. 2001, King 2007). While the mathematical formulae and methods of statistically estimating parameters for a 2PLF vary, the estimated values are similar and can be obtained with the built in generalised linear model (GLM) programs in most modern statistical software.

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

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1.1 Maternity function

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

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

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

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

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

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

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

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

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

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

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

94 original analysis, has the potential to bias parameter estimates and reduce their standard errors (Motulsky

95 and Christopoulos 2004). Alternative approaches to estimating maternal parameters have also arisen in the

96 literature, indicative of a lack of guidance on implementation. For example, some authors have obtained

97 maternity parameters by fitting a 2PLF to maternity data (Baremore and Hale 2012, Baremore and Passerotti

98 2013).

99 A consequence of the low uptake in use of maternity functions is that most practitioners undertaking

100 population assessments invariably take an *ad hoc* approach to quantifying maternal reproductive output.

101 This typically involves approximating maternal output using a maturity function. Under such an approach

102 all mature females are tacitly assumed to reproduce in each breeding season (Cortes 1998). Non-annual

103 reproduction is accounted for by weighting fecundity or the maturity function by the assumed (but often

104 unknown) duration of the reproductive cycle (Walker 2005). In some cases, calculations of reproductive

105 output may use the age-at-first-reproduction, defined as the mean age at maturity plus the gestation period

106 (Mollet and Cailliet 2002). This accounts for the protracted gestation period of many chondrichthyans,

107 but still assumes that all individuals begin reproducing immediately after maturity. Measures of annual

108 reproductive output that follow this approach are hence built upon a series of assumptions that are rarely

109 tested in practice.

1.2 Revisiting the maternity function

111 Wider use of maternity functions in studies of chondrichthyan reproductive biology is needed to improve

112 calculation of reproductive capacity in the quantitative population assessments that are increasingly being

113 used to support fisheries management and prioritize conservation actions (Cortés et al. 2012, Swenson et al.

114 2024). It may also help address the lack of empirical data on the periodicity of chondrichthyan reproductive

115 cycles. Historically, reproductive periodicity has only been determined qualitatively, and has been assumed

116 to be fixed (e.g. annual, biennial), despite observations of plasticity in this trait within discrete populations

117 (Higgs et al. 2020, Nosal et al. 2021). Information on reproductive periodicity is contained within maternal

118 data, however the existing approach of fixing P_{Max} in maternity functions prevents statistical inference from

119 being made on these data. Changes to the way in which maternity functions are implemented may also

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contribute to quantifying uncertainty in reproductive frequency and help understand the temporal stability of reproductive cycles. To date only a single study on spiny dogfish, *Squalus acanthias*, has statistically estimated P_{Max} from data (Colonello et al. 2016), and the feasibility of doing so for a wider range of species has not been investigated.

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

2 Materials and methods

2.1 Approach

To assess the feasibility of estimating maternity parameters a simulation study was carried out using the 3PLF to generate data for populations with varying reproductive frequencies (Figure 1). Simulations were conducted for a range of gear selectivities and sample sizes reflective of those typically available in reproductive studies and fishery sampling programs. The performance of three methods in estimating 'true' maternity parameters from simulated data was tested by examining accuracy, bias, and interval coverage. To illustrate the effects of misspecifying maternity parameters, lifetime reproductive output was calculated for each simulated population using parameters derived from each of the methods, and by substituting maturity parameters for maternity parameters. Finally, empirical data from previously published studies were reanalysed to illustrate possible strategies for estimating maternity parameters and making inferences on reproductive frequency. All simulation modelling and data analysis was conducted using the R language [Version 4.2.0] (R Core Team 2022) and the Template Model Builder (TMB) R package [Version 1.9.1] (Kristensen et al. 2016).

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2.2 Simulation

2.2.1 Data generation

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

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

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

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

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

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 probability density function at age $a = 0$ for a given length, l,

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

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

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

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

163 2000), $G = g_{j,k}$ that represents the probability that a fish in length class, j, will grow into length class, k,

164 over a specified time interval

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

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

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

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

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

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

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

170 was given by

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

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

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

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

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

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

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

176 where F was assumed to be constant and nominally set to 25% of natural mortality, M (i.e. $0.25M$). The

177 effects of varying levels of F were not investigated further in this study. Total mortality, Z, in length class, l,

178 was further given by

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

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

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

180 where A_{Max} is the maximum age (Table 1). The estimated numbers of fish caught in length class, l, at age,

181 a, was calculated using the Baranov catch equation as

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

182 To examine the effect of varying sample size, six scenarios were conducted with catch ranging from 50 to 2500

183 individuals, reflecting a gradient from data poor to rich. Length data were generated by randomly sampling,

184 with replacement, from a vector of length classes, weighted by a vector of probabilities determined from the

185 above catch equation.

186 Next, dichotomous maturity-at-length data, $\psi(l)$, were randomly generated by simulating from a Bernoulli

187 distribution, $\Psi(l) \sim B(P)$, where P was given by the 2PLF:

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

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

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

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

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

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 asmyptote 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 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.

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).

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 accuracy, 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 accuracy 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 withing the nominal 50% confidence intervals.

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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 ($K = 0.12$ 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.

3   Results

3.1   Simulation study

249   Parameter estimation was generally straightforward; with sample sizes > 50 a convergence success rate of

250   $\geq 95\%$ was achieved in all scenarios (Figure S1, Table S1). Overall, convergence and parameter boundary

251   failures were most common with the 2PLF-maternity method which essentially involved fitting data to

252   an under-parameterized model where P_{Max} was always fixed at 1. In addition to convergence failures, 12

253   simulations also generated insufficient maternal data (zero or one maternal females in the simulated data),

254   and were 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

257 $P_{\hat{Max}}$ parameters whereby P_{Max} affects the magnitude and direction of bias in these parameters (Figure 2).

258 With lower values of P_{Max} it was apparently more difficult for the model to separate the point of inflection

259 in the logistic model and the upper asymptote. As true underlying P_{Max} decreased there was also a greater

260 potential for positive bias in $P_{\hat{Max}}$ (Figure 2).

261 For the 3PLF methods, parameter estimates tended to be biased high at lower sample sizes (Figure S2,

262 Figure S3). In some scenarios, particularly with sample sizes ≤ 250, fixing the asymptote was effective at

263 reducing bias, although for larger sample sizes neither method was clearly preferable (Figure S2, Figure S3).

264 The accuracy of parameter estimates varied considerably across different combinations of variables used in

265 the simulation and among parameters (Figure S4, Figure S5). Again, in some scenarios with smaller sample

266 sizes ≤ 250, fixing the asymptote improved accuracy with the 3PLF methods, although at larger sample

267 sizes better accuracy 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).

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 $L'_{\hat{50}}$ 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 $L'_{\hat{50}}$ and $P_{\hat{Max}}$.

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 fewer

275 females in maternal or immature condition making parameter estimation difficult (Figure S8, Figure S9).

276 These effects were not necessarily consistent between species and seemed to reflect differences in the underlying

277 population length structure. For example, in low selectivity scenarios for gummy sharks ~60% of individuals

278 were immature compared to ~50% in the corresponding scenarios for school sharks (Figure S9). As P_{Max}

279 decreased the proportion of maternal females in the analysis also decreased.

280 Overall, the 2PLF-maternity method performed the poorest. 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

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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 accuracy 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%, 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 across the various scenarios.

288   For school sharks, estimating P_{Max}, was the most effective way to minimize bias in most scenarios (Figure 5,

289   Figure S10). Substituting maturity parameters (2PLF-maturity method) led to a median overestimation

290   of R_0 by 3.4% across all scenarios, while the 2PLF-maternity method led to a median underestimate of

291   11.1%. (Table S1, Figure S10). In contrast, for the gummy shark substituting maturity parameters led to a

292   median overestimation of R_0 of just 1% across all scenarios which outperformed the 3PLF methods in several

293   instances (Figure 5, Figure S10). Using the 2PLF method for gummy sharks led to a median overestimate of

294   R_0 of 22% (Figure S10). For both species, better accuracy in calculating R_0 was achieved with the 3PLF

295   methods, with the 3PLF-estimated method performing best in most scenarios tested (Figure 6, Figure S11).

296   For gummy sharks the 3PLF-fixed method performed best at lower sample sizes and lower values of P_{Max}.

297   ## 3.2   Empirical case study

298   Maternal data were re-analysed for 1087 sandbar sharks including 640 mature individuals of which 32% were

299   in maternal condition. Using the 3PLF-estimated method, the maximum likelihood estimate for $\hat{P_{Max}}$ was

300   0.48 (Table 2). Despite having a sample size of > 600 mature females, the proportion of maternal individuals

301   at length was still uncertain and $\hat{P_{Max}}$ was estimated to lie between 0.39 and 0.60 with 95% confidence (Figure

302   7). For 3PLF-fixed models a value of $P_{Max} = 0.5$ was strongly supported ($\Delta_{AIC} = 14.15$) over the alternative

303   fixed value of $P_{Max} = 0.33$. The model with $P_{Max} = 0.5$ also outperformed the 3PLF-estimated method

304   ($\Delta_{AIC} = 1.86$). Given the fixed model had one fewer estimated parameter, both models had essentially the

305   same level of support given the data (Burnham and Anderson 2002).

4 Discussion

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

4.1 Implementing maternity functions

While the estimation of maternity parameters in most simulations was possible, it was difficult to do so accurately. Outcomes of the simulation study suggested that samples sizes of ≥ 500 would be needed to estimate P_{Max} with <10% MARE for a triennially reproducing species. This is a much larger error than is achievable from conventional logistic maturity analysis (Roa et al. 1999). In the case of the gummy shark this inaccuracy led to the 2PLF-maturity method performing comparably or better than the 3PLF methods in ultimately quantifying R_0. Relatively wide confidence intervals were also obtained for P_{Max} in the empirical analysis for sandbar sharks, even with a sample size of > 1000. A similar sample size was used by Colonello *et al.* (2016) to estimate plausible values of P_{Max} and maternity parameters for south Atlantic spiny dogfish. These results suggest that data requirements of the 3PLF analyses may be prohibitively large for many chondrichthyans and therefore best suited to use on commercially captured species where large sample sizes can be obtained (Oddone et al. 2010, Tribuzio and Kruse 2012).

In light of the data requirements suggested by this study, placing a penalty function on P_{Max} or using a the

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332 use of a prior distribution

333 For some species, and data on pregnant females are particularly sparse, the current practice of using maturity

334 parameters as a proxy for maternity parameters will likely still be the only option for numerous data-poor

335 chondrichthyans. From this perspective, the outperformance of the 3PLF-methods by the 2PLF-methods for

336 the gummy shark in several simulations is encouraging. However, the extent to which maturity parameters

337 can provide a good approximation of maternity parameters may be species-specific, depending on how close

338 L_{50} is to L'_{50}. While several studies have shown these parameters to be similar (Walker 2007, Soto-López et

339 al. 2018), L'_{50} is more frequently shifted to the right of L_{50} (Braccini et al. 2006, Montealegre-Quijano et

340 al. 2014, Colonello et al. 2016, Palacios-Hernández et al. 2020), and this length difference can equate to

341 one or more years. For example, Harry et al. (2013) found both spot-tail shark, *C. sorrah*, and Australian

342 blacktip shark, *C. tilstoni*, began reproducing the year after reaching sexual maturity. Similarly, Fujinami et

343 al. (2017) found A'_{50} to be 1.4 years older than A_{50} in blue sharks.

344 More research is needed to understand the relationship between size at maturity and maternity and variability

345 within and among taxa. In general, this study confirms Walker's (2005) assertion that the common practice

346 of weighting the maturity curve by the frequency of parturition overestimates recruitment. This study also

347 confirms that fitting a 2PLF to maternal data when $P_{Max} < 1$ (effectively ignoring P_{Max}) is likely to result

348 in biased parameters and can also overestimate recruitment. While not widely used, this approach has been

349 undertaken in several studies (Baremore and Hale 2012, Mejía-Falla et al. 2012, Baremore and Passerotti

350 2013, Rambahiniarison et al. 2018).

351 Another approach to overcoming the

352 Using simulated data to compare the relative performance of the 3PLF-estimated and 3PLF-fixed methods

353 subject to a range of variables showed that it was feasible to estimate P_{Max} from data, but also identified

354 situations where it may be preferable to fix P_{Max}. In most scenarios sample sizes of at least 100 were needed

355 for the 3PLF-estimated method to approach or exceed the performance of the 3PLF-fixed method. At sample

356 sizes below this it is therefore advisable to fix P_{Max}. Larger sample sizes are necessary before attempting to

357 estimate P_{Max} in species with a triennial or longer reproductive cycle, due to the decline in the performance

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358   of the 3PLF-estimated method as P_{Max} decreases.

359   The success of any analysis using the 3PLF-fixed or 2PLF-maturity methods, as implemented here, ultimately

360   depends on the analyst choosing a suitable value for P_{Max}. In this study, the value for P_{Max} used in the

361   fixed analyses was chosen based on the proportion of maternal females observed in the simulated data. The

362   potential to introduce a greater level of bias in the analysis through the incorrect selection of P_{Max} should

363   also be considered if using this approach.

4.2   Empirical study

365   The empirical analysis carried out using data for the sandbar shark illustrates how novel insights can be

366   gained from maternal data by estimating P_{Max}. Detailed reproductive studies of the western North Atlantic

367   population by Baremore and Hale (2012) and Piercy et al. (2016) were ambiguous about the frequency of

368   reproduction. In both studies, the low proportion of pregnant females and bimodality in ovarian follicle size

369   led the authors to conclude that the reproductive cycle was most commonly triennial or possibly longer at

370   the population level. Reanalysis of these combined data sets using the 3PLF-estimated method, however,

371   resulted in a maximum likelihood estimate of $\hat{P_{Max}} = 0.48$, considerably larger than 0.37 - the proportion of

372   pregnant mature females observed by Baremore and Hale (2012). Similarly, based on AIC values, a fixed

373   value of $P_{Max} = 0.5$ had a much higher relative plausibility than a value of 0.33 (Table 2).

374   This unexpected result may be related to the gradual attainment of asymptotic maternal status. Maturity

375   in sandbar sharks appears to occur over an extended size range. L_5 and L_{95} are 146cm and 176cm – a

376   length interval that corresponds to around seven years given the sandbar shark's slow growth rate (Hale and

377   Baremore 2013). With females maturing over a broad range of sizes and ages, it is possible that smaller

378   females reproduce less frequently. The outcomes of this study suggest that larger sharks may ultimately be

379   capable of reproducing biennially, although few females appear to attain this size (Hale and Baremore 2013).

380   Further work would be required to confirm this hypothesis, however, such an outcome would have important

381   implications for management; not only are larger females more fecund (Baremore and Hale 2012), they also

382   reproduce more frequently. This implies that size selective fishing or the removal of larger and older female

383   sharks could have a disproportionately greater impact on population productivity.

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4.3 Advantages and future directions

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

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

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

Estimation of P_{Max} using the 3PLF-estimated method may also be a means to resolving the longstanding question of reproductive frequency in some rare and threatened chondrichthyans. White sharks, *Carcharodon carcharias*, and whale shark, *Rhinchodon typus*, are two examples of intensively studied species where only fragmentary observations of female reproductive biology exist (Joung et al. 1996, Sato et al. 2016). In both species lack of data on reproductive frequency is a major impediment to population modelling and

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the development of management strategies (Huveneers et al. 2018, Bowlby and Gibson 2020). With many of these populations the focus of ongoing monitoring, non-lethal methods for assessing maternal state may eventually provide a way of collecting sufficient data for estimation of P_{Max} (Sulikowski et al. 2016).

A logical progression from estimating P_{Max} is the consideration of alternative functional forms for this parameter such as time- or space-varying P_{Max} or more complex length- or age-dependent forms (Winton et al. 2014). Despite the diverse range of reproductive modes found in chondrichthyan fishes, the current, limited knowledge of maternal investment has typically investigated variables such as litter size and pup condition (Hussey et al. 2010). Little is known about how reproductive frequency varies as a function of size or age, in response to environmental effects, or at changing population densities. Better understanding of these factors has the potential to improve understanding reproductive strategies and is, in many cases, of direct relevance to management.

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6 Competing interests

The authors declare there are no competing interests.

7 Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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