

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 • A sentence with caveat about the need for large sample sizes to produce “feasible” results is warranted.

21 **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.

47 1.1 Maternity function

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

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

51

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

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

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

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

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

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

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

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

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

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

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

1.2 Revisiting the maternity function

Wider use of maternity functions in studies of chondrichthyan reproductive biology is needed to improve calculation of reproductive capacity in the quantitative population assessments that are increasingly being used to support fisheries management and prioritize conservation actions (Cortés et al. 2012, Swenson et al. 2024). It may also help address the lack of empirical data on the periodicity of chondrichthyan reproductive cycles. Historically, reproductive periodicity has only been determined qualitatively, and has been assumed to be fixed (e.g. annual, biennial), despite observations of plasticity in this trait within discrete populations (Higgs et al. 2020, Nosal et al. 2021). Information on reproductive periodicity is contained within maternal data, however the existing approach of fixing P_{Max} in maternity functions prevents statistical inference from being made on these data. Changes to the way in which maternity functions are implemented may also

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

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

131 2 Materials and methods

132 2.1 Approach

133 To assess the feasibility of estimating maternity parameters a simulation study was carried out using the 3PLF
134 to generate data for populations with varying reproductive frequencies (Figure 1). Simulations were conducted
135 for a range of gear selectivities and sample sizes reflective of those typically available in reproductive studies
136 and fishery sampling programs. The performance of three methods in estimating ‘true’ maternity parameters
137 from simulated data was tested by examining accuracy, bias, and interval coverage. To illustrate the
138 effects of misspecifying maternity parameters, lifetime reproductive output was calculated for each simulated
139 population using parameters derived from each of the methods, and by substituting maturity parameters for
140 maternity parameters. Finally, empirical data from previously published studies were reanalysed to illustrate
141 possible strategies for estimating maternity parameters and making inferences on reproductive frequency. All
142 simulation modelling and data analysis was conducted using the R language [Version 4.2.0] (R Core Team
143 2022) and the Template Model Builder (TMB) R package [Version 1.9.1] (Kristensen et al. 2016).

144 2.2 Simulation

145 2.2.1 Data generation

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

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

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

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

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

158 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
159 probability density function at age $a = 0$ for a given length, l ,

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

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

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

163 Growth in subsequent age classes was modelled using a length transition matrix (Punt et al. 1997, Hall et al.
164 2000), $G = g_{j,k}$ that represents the probability that a fish in length class, j , will grow into length class, k ,
165 over a specified time interval

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

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

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

167 where l is mean length, f is the specified normal distribution, l_k^- and l_k^+ are the lower and upper limits of
168 length class j , and ϕ is a vector of parameters.

169 Selectivity in the model was assumed to follow a gamma function based on gillnet selectivity experiments
170 (Kirkwood and Walker 1986, Punt and Walker 1998), where the selectivity of an individual in length class, l
171 was given by

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

172 where θ_1 and θ_2 are estimated parameters (Kirkwood and Walker 1986). Two selectivity scenarios were
173 simulated corresponding to low and high selectivity of the maternal component of the population. For
174 consistency between species, gillnet mesh sizes were chosen that would result in peak relative selectivity
175 occurring at the lengths equal to 25% and 75% of the population in maternal condition (Table 1).

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

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

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

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

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

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

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

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

183 To examine the effect of varying sample size, six scenarios were conducted with catch ranging from 50 to 2500
 184 individuals, reflecting a gradient from data poor to rich. Length data were generated by randomly sampling,
 185 with replacement, from a vector of length classes, weighted by a vector of probabilities determined from the
 186 above catch equation.

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

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

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

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

190

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

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

192 2.2.2 Estimation approaches

193 Two approaches to estimating maternity parameters were compared: the 3PLF itself (3PLF-estimated) and
 194 the 3PLF function with a fixed asymptote (3PLF-fixed). Additionally, two approaches using a 2PLF were also
 195 examined, using maternity-at-length data (2PLF-maternity) and maturity-at-length data (2PLF-maturity).
 196 The 3PLF-estimated method was undertaken to validate the utility of this model, which has so far been used
 197 in only a single study (Colonello et al. 2016). The 3PLF-fixed is the method described by Walker (2005)
 198 and most commonly used in practice. The 2PLF-maternity method was used to examine what effect simply
 199 ignoring the upper asymptote had (i.e. P_{Max} fixed at 1). The 2PLF-maturity method is commonly used to
 200 approximate a maternity curve, and tacitly assumed to be similar. The resulting maturity curve can then be
 201 weighted by the proportion of gravid females to calculate annual reproductive output (although in practice
 202 annual fecundity is more often modified, for example halved for a species suspected to reproduce biennially
 203 (SEDAR 2023)).

204 Only the 3PLF-estimated method involves statistically estimating P_{Max} , which must be subjectively chosen
 205 in the case of the 3PLF-fixed and the 2PLF-maturity. P_{Max} is ideally chosen based on detailed study of the
 206 ovarian and uterine cycles (Walker 2005), or alternatively based on the proportion of mature females observed
 207 to be in maternal condition during sampling (Baremore and Hale 2012, Harry et al. 2013, Trinnie et al. 2016).
 208 For the purposes of the simulation, the timing and duration of the uterine and ovarian cycles were assumed to
 209 be unknown. The following procedure was used to ‘guess’ the fixed value of P_{Max} in each simulation. P_{Max}
 210 was chosen as the proportion of females in maternal condition above the length at which 99% of females
 211 were mature, $L > \Psi(L_{99\%})$. In some cases this procedure failed due to there being no maternal females in

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

2.2.3 Reproductive output

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

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

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

2.2.4 Performance

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

233 2.2.5 Empirical case study

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

248 3 Results

249 3.1 Simulation study

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

255 When using the 3PLF methods model performance typically declined as the periodicity of the reproductive
256 cycle increased. This is seen in the positive correlation between \hat{L}_{50}' and \hat{P}_{Max} , whereby true underlying
257 P_{Max} affected the magnitude and direction of bias in these parameters (Figure 2). With lower values of P_{Max}

258 it appeared to be more difficult for the model to separate the point of inflection in the logistic model and the
259 upper asymptote. As true underlying P_{Max} decreased there was also a greater potential for positive bias in
260 \hat{P}_{Max} . Additionally, longer reproductive cycles resulted in fewer maternal females, which was associated with
261 larger bias (Figure 2).

262 For the 3PLF methods, parameter estimates tended to be biased high at lower sample sizes (Figure S2,
263 Figure S3). In some scenarios, particularly with sample sizes ≤ 250 , fixing the asymptote was effective at
264 reducing bias, although for larger sample sizes neither method was clearly preferable (Figure S2, Figure S3).
265 The accuracy of parameter estimates varied considerably across different combinations of variables used and
266 among parameters (Figure S4, Figure S5). Again, in some scenarios with smaller sample sizes ≤ 250 , fixing
267 the asymptote improved accuracy with the 3PLF methods, although at larger sample sizes better accuracy
268 was achieved by estimating P_{Max} (Figure 3). Overall, P_{Max} was comparatively more challenging to estimate
269 accurately than L'_{50} (Figure S4, Figure S5).

270 While the 3PLF-fixed method was in some cases able to reduce bias at lower sample sizes, a trade off in
271 the use of this method was poorer interval coverage (Figure 4, Figure S6). For most simulations, interval
272 coverage for \hat{L}'_{50} was well below the expected level of 50%, irrespective of sample size. In contrast, for the
273 3PLF-estimated method interval coverage oscillated around 50% for both \hat{L}'_{50} and \hat{P}_{Max} .

274 Differences in life history and gear selectivity played an important role in the ability to obtain accurate
275 and unbiased maternity parameters. Certain combinations of variables in the simulated data resulted in
276 few females in maternal or immature condition, making parameter estimation difficult (Figure S8, Figure
277 S9). This was particularly the case for P_{Max} which required a relatively high maternal sample size to enable
278 accurate parameter estimation (Figure 5). These effects were not necessarily consistent between species
279 and seemed to reflect differences in the underlying population length structure. For example, in biennial
280 low selectivity scenarios for gummy sharks ~60% of individuals were immature compared to ~50% in the
281 corresponding scenarios for school sharks (Figure S9).

282 Overall, the 2PLF-maternity method performed the poorest. Ignoring P_{Max} introduced a fixed bias in this
283 parameter that increased in magnitude as reproductive periodicity increased (Figure S3). This manifested

in an overestimation of L'_{50} that was exacerbated by gear selectivity effects (Figure S2). In contrast, using a maturity function to approximate the maternity function (2PLF-maturity method) resulted in relatively good performance. L_{50} could usually be estimated with a higher accuracy than L'_{50} . For the gummy shark, where L_{50} and L'_{50} were relatively similar, using the 2PLF-maturity method led to a constant underestimate of L'_{50} of approximately 2%, exceeding the performance of the 3PLF-methods at most sample sizes.

The effect of the different methods in ultimately calculating R_0 varied considerably across the various scenarios. For school sharks, estimating P_{Max} , was the most effective way to minimize bias in most scenarios (Figure S10). Substituting maturity parameters (2PLF-maturity method) led to a median overestimation of R_0 by 3.4% across all scenarios, while the 2PLF-maternity method led to a median underestimate of 11.1%. (Figure S10). In contrast, for the gummy shark substituting maturity parameters led to a median overestimation of R_0 of just 1% across all scenarios which outperformed the 3PLF methods in several instances (Figure S10). Using the 2PLF method for gummy sharks led to a median overestimate of R_0 of 22% (Figure S10). For both species, better accuracy in calculating R_0 was achieved with the 3PLF methods, with the 3PLF-estimated method performing best in most scenarios tested (Figure 6, Figure S11). For gummy sharks the 3PLF-fixed method performed best at lower sample sizes and lower values of P_{Max} .

3.2 Empirical case study

Maternal data were re-analysed for 1087 sandbar sharks including 640 mature individuals of which 32% were in maternal condition. Using the 3PLF-estimated method, the maximum likelihood estimate for \hat{P}_{Max} was 0.48 (Table 2). Despite having a sample size of > 600 mature females, the proportion of maternal individuals at length was still uncertain and \hat{P}_{Max} was estimated to lie between 0.39 and 0.60 with 95% confidence (Figure 7). For 3PLF-fixed models a value of $P_{Max} = 0.5$ was strongly supported ($\Delta_{AIC} = 14.15$) over the alternative fixed value of $P_{Max} = 0.33$. The model with $P_{Max} = 0.5$ also outperformed the 3PLF-estimated method ($\Delta_{AIC} = 1.86$). Given the fixed model had one fewer estimated parameter, both models had essentially the same level of support given the data (Burnham and Anderson 2002).

308 4 Discussion

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

322 4.1 Implementing maternity functions

323 Using simulated data to compare the relative performance of the 3PLF-estimated and 3PLF-fixed methods
324 subject to a range of variables showed that it was feasible to estimate P_{Max} , but also identified situations
325 where it may be preferable to fix P_{Max} . While the estimation of maternity parameters in most simulations
326 was often possible, it was difficult to do so accurately. Outcomes of the simulation study showed that, for
327 non-annual reproductive cycles, ≥ 100 and ≥ 200 maternal females were typically needed to estimate P_{Max}
328 with $<10\%$ MARE for school and gummy sharks, respectively (Figure 5). This is a much larger error than is
329 achievable from conventional logistic maturity analysis (Roa et al. 1999). In the case of the gummy shark this
330 inaccuracy led to the 2PLF-maturity method performing comparably or better than the 3PLF methods in
331 ultimately quantifying R_0 . Relatively wide confidence intervals were also obtained for P_{Max} in the empirical
332 analysis for sandbar sharks, even with a total sample size of > 1000 females, of which 206 were in maternal
333 condition. 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.

Providing clear guidelines on when to fix or estimate P_{Max} is difficult as model performance was species-specific and influenced by life history traits and gear selectivity. Most instances where the 3PLF-fixed method outperformed the 3PLF-estimated method typically occurred at lower sample sizes. At sample sizes <100 it is therefore advisable to fix P_{Max} . It is also important to note that accurate estimation of the P_{Max} parameter required a sample size of 100 - 200 females in maternal condition in simulated data, and that larger sample sizes are needed with longer reproductive cycles.

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). For smaller samples sizes, placing a prior or penalty on P_{Max} may also help overcome issues of parameter inaccuracy, enabling existing information about reproductive periodicity to be incorporated from other populations or closely-related species (Smart and Grammer 2021). Information on length at maturity, which is likely to be relatively easier to estimate, may also be informative in the development of priors, with L_{50} effectively providing a lower bound for L'_{50} .

For the numerous data-poor chondrichthyan species, or where data on pregnant females are sparse or unattainable, the current practice of using maturity parameters as a proxy for maternity parameters will likely still be the only option. From this perspective, the outperformance of the 3PLF-methods by the 2PLF-methods for the gummy shark in several simulations is encouraging. However, the extent to which maturity parameters can provide a good approximation of maternity parameters may be species-specific, depending on how close L_{50} is to L'_{50} . While several studies have shown these parameters to be similar (Walker 2007, Soto-López et al. 2018), L'_{50} is more frequently shifted to the right of L_{50} (Braccini et al. 2006, Montealegre-Quijano et al. 2014, Colonello et al. 2016, Palacios-Hernández et al. 2020), and this length difference can equate to one or more years. For example, Harry et al. (2013) found both spot-tail shark, *C. sorrah*, and Australian blacktip shark, *C. tilstoni*, began reproducing the year after reaching sexual maturity. Similarly, Fujinami et al. (2017) found A'_{50} to be 1.4 years older than A_{50} in blue sharks.

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

360 within and among taxa. In general, this study confirms Walker’s (2005) assertion that the common practice
361 of weighting the maturity curve by the frequency of parturition overestimates recruitment. This study also
362 confirms that fitting a 2PLF to maternal data when $P_{Max} < 1$ (effectively ignoring P_{Max}) is likely to result
363 in biased parameters and can also overestimate recruitment. While not widely used, this approach has been
364 undertaken in several studies (Baremore and Hale 2012, Mejía-Falla et al. 2012, Baremore and Passerotti
365 2013, Rambahiniarison et al. 2018).

366 4.2 Empirical study

367 The empirical analysis carried out using data for the sandbar shark illustrates how novel insights can be
368 gained from maternal data by estimating P_{Max} . Detailed reproductive studies of the western North Atlantic
369 population by Baremore and Hale (2012) and Piercy et al. (2016) were ambiguous about the frequency of
370 reproduction. In both studies, the low proportion of pregnant females and bimodality in ovarian follicle size
371 led the authors to conclude that the reproductive cycle was most commonly triennial or possibly longer at
372 the population level. Reanalysis of these combined data sets using the 3PLF-estimated method, however,
373 resulted in a maximum likelihood estimate of $\hat{P}_{Max} = 0.48$, considerably larger than 0.37 - the proportion of
374 pregnant mature females observed by Baremore and Hale (2012). Similarly, based on AIC values, a fixed
375 value of $P_{Max} = 0.5$ had a much higher relative plausibility than a value of 0.33 (Table 2).

376 This unexpected result may be related to the gradual attainment of asymptotic maternal status. Maturity
377 in sandbar sharks appears to occur over an extended size range. L_5 and L_{95} are 146cm and 176cm – a
378 length interval that corresponds to around seven years given the sandbar shark’s slow growth rate (Hale and
379 Baremore 2013). With females maturing over a broad range of sizes and ages, it is possible that smaller
380 females reproduce less frequently. The outcomes of this study suggest that larger sharks may ultimately be
381 capable of reproducing biennially, although few females appear to attain this size (Hale and Baremore 2013).
382 As such, the modal reproductive frequency is still at least triennial. Further work would be required to confirm
383 this hypothesis, however, such an outcome would have important implications for management; not only are
384 larger females more fecund (Baremore and Hale 2012), they also reproduce more frequently. This implies
385 that size selective fishing or the removal of larger and older female sharks could have a disproportionately

greater impact on population productivity.

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, *Rhynchodon typus*, are two examples of intensively studied species where only

411 fragmentary observations of female reproductive biology exist (Joung et al. 1996, Sato et al. 2016). In
 412 both species lack of data on reproductive frequency is a major impediment to population modelling and
 413 the development of management strategies (Huvneers et al. 2018, Bowlby and Gibson 2020). With many
 414 of these populations the focus of ongoing monitoring, non-lethal methods for assessing maternal state may
 415 eventually provide a way of collecting sufficient data for estimation of P_{Max} (Sulikowski et al. 2016).
 416 A logical progression from estimating P_{Max} is the consideration of alternative functional forms for this
 417 parameter such as time- or space-varying P_{Max} or more complex length- or age-dependent forms (Winton
 418 et al. 2014). Despite the diverse range of reproductive modes found in chondrichthyan fishes, the current,
 419 limited knowledge of maternal investment has typically investigated variables such as litter size and pup
 420 condition (Hussey et al. 2010). Little is known about how reproductive frequency varies as a function of size
 421 or age, in response to environmental effects, or at changing population densities. Better understanding of
 422 these factors has the potential to improve understanding reproductive strategies and is, in many cases, of
 423 direct relevance to management.

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429 **6 Competing interests**

430 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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