

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. However, sample sizes of 100 - 200 maternal females were typically required for accurate
15 estimation of P_{Max} . While maturity parameters could be estimated with greater accuracy, substituting them
16 for maternity parameters overestimated lifetime reproductive output. Greater use of maternity functions has
17 the potential to improve calculation of reproductive output in quantitative populations models. In addition
18 to improvements in parameter estimation, this method involves fewer assumptions and enables statistical
19 inferences to be made on frequency of reproduction.

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.

46 1.1 Maternity function

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

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

50

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

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

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

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

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

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

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

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

89 For practitioners that are aware of maternity functions, lack of information on implementation may also have
90 discouraged use. Walker’s (2005) approach to estimating parameters in the maternity function is difficult to
91 reproduce, apparently due to the constraints of the proprietary statistical program first used to implement the
92 analysis. Specifically, the method as described involves adjusting the raw data prior to parameter estimation
93 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

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

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

130 2 Materials and methods

131 2.1 Approach

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

143 2.2 Simulation

144 2.2.1 Data generation

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

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

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

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

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

157 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
158 probability density function at age $a = 0$ for a given length, l ,

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

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

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

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

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).

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:

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

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 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

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.

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 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 zero maternal females, and were discarded.

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

it appeared to be 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 also a greater potential for positive bias in \hat{P}_{Max} . Additionally, longer reproductive cycles resulted in fewer females in maternal condition, which was associated with larger bias (Figure 2).

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 and among parameters (Figure S4, Figure S5). Again, in some scenarios with smaller sample sizes ≤ 250 , fixing the asymptote improved accuracy with the 3PLF methods, although at larger sample sizes better accuracy was achieved by estimating P_{Max} (Figure 3). Overall, P_{Max} was comparatively more challenging to estimate accurately than L'_{50} (Figure S4, Figure S5).

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

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

Overall, the 2PLF-maternity method performed the poorest. Ignoring P_{Max} introduced a fixed bias in this 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 many instances (Figure S11). 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 S12). 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).

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 reduced bias. Overall, however, relatively large sample sizes were needed to accurately estimate P_{Max} , particularly with longer reproductive cycles. This study also demonstrated that, in some cases, recruitment was 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 and future directions.

4.1 Implementing maternity functions

Using simulated data to compare the relative performance of the 3PLF-estimated and 3PLF-fixed methods subject to a range of variables showed that it was feasible to estimate P_{Max} , but was difficult to do so accurately. For non-annual reproductive cycles, > 100 school sharks and > 200 gummy sharks in maternal condition were typically needed to estimate P_{Max} with $<10\%$ MARE (Figure 5). This indicates that the both sample size requirements and levels of uncertainty are likely to be larger than 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 minimizing bias in R_0 (Figure S11). Relatively wide confidence intervals were also obtained for P_{Max} in the empirical analysis for sandbar sharks, even with a total sample size of > 1000 females, 206 of which were in maternal 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.

333 The simulation study also identified some situations where it may be preferable to fix P_{Max} , particularly
334 at lower sample sizes (≤ 100 individuals total). Providing clear guidelines on this is difficult as model
335 performance was species-specific and influenced by life history and gear selectivity. The success of any
336 analysis using a fixed value also ultimately depends on the analyst choosing a suitable value. The potential
337 to introduce a greater level of bias through the incorrect selection of P_{Max} should also be considered if using
338 this approach (Natanson et al. 2019).

339 Together, these results suggest that data requirements of the 3PLF analyses may be prohibitively large
340 for many chondrichthyans and therefore best suited to use on commercially captured species where large
341 sample sizes can be obtained (Oddone et al. 2010, Tribuzio and Kruse 2012). For smaller samples sizes,
342 placing a prior or penalty on P_{Max} may also help overcome issues of parameter inaccuracy, enabling existing
343 information about reproductive periodicity to be incorporated from other populations or closely-related
344 species (Smart and Grammer 2021). Information on length at maturity, which is likely to be relatively easier
345 to estimate, may also be informative in the development of priors, with L_{50} effectively providing a lower
346 bound for L'_{50} .

347 For data-poor chondrichthyan species, or where data on pregnant females are sparse or unattainable, the
348 current practice of using maturity parameters as a proxy for maternity parameters will likely still be the
349 only option. From this perspective, the outperformance of the 3PLF-methods by the 2PLF-methods for the
350 gummy shark in several simulations is encouraging. However, the extent to which maturity parameters can
351 provide a good approximation of maternity parameters may be species-specific, depending on how close L_{50}
352 is to L'_{50} . While several studies have shown these parameters to be similar (Walker 2007, Soto-López et al.
353 2018), L'_{50} is more frequently shifted to the right of L_{50} (Braccini et al. 2006, Montealegre-Quijano et al.
354 2014, Colonello et al. 2016, Palacios-Hernández et al. 2020), and this length difference can equate to one or
355 more years. For example, Harry et al. (2013) found both spot-tail shark, *C. sorrah*, and Australian blacktip
356 shark, *C. tilstoni*, began reproducing the year after reaching sexual maturity. Similarly, Fujinami et al. (2017)
357 found A'_{50} to be 1.4 years older than A_{50} in blue sharks.

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

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

365 4.2 Empirical study

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

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

385 population productivity.

386 4.3 Advantages and future directions

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

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

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

407 Estimation of P_{Max} using the 3PLF-estimated method may also be a means to resolving the longstanding
408 question of reproductive frequency in some rare and threatened chondrichthyans. White sharks, *Carcharodon*
409 *carcharias*, and whale shark, *Rhincodon typus*, are two examples of intensively studied species where only

410 fragmentary observations of female reproductive biology exist (Joung et al. 1996, Sato et al. 2016). In
411 both species lack of data on reproductive frequency is a major impediment to population modelling and
412 the development of management strategies (Huvneers et al. 2018, Bowlby and Gibson 2020). With many
413 of these populations the focus of ongoing monitoring, non-lethal methods for assessing maternal state may
414 eventually provide a way of collecting sufficient data for estimation of P_{Max} (Sulikowski et al. 2016).

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

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428 6 Competing interests

429 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.

References

- Baremore, I.E., and Hale, L.F. 2012. Reproduction of the Sandbar Shark in the Western North Atlantic Ocean and Gulf of Mexico. *Marine and Coastal Fisheries* **4**(1): 560–572. doi: 10.1080/19425120.2012.700904.
- Baremore, I.E., and Passerotti, M.S. 2013. Reproduction of the Blacktip Shark in the Gulf of Mexico. *Marine and Coastal Fisheries* **5**(1): 127–138. doi: 10.1080/19425120.2012.758204.
- Bowlby, H.D., and Gibson, A.J.F. 2020. Implications of life history uncertainty when evaluating status in the Northwest Atlantic population of white shark (*Carcharodon carcharias*). *Ecology and Evolution* **10**(11): 4990–5000. doi: 10.1002/ece3.6252.
- Braccini, J.M., Gillanders, B.M., and Walker, T.I. 2006. Determining reproductive parameters for population assessments of chondrichthyan species with asynchronous ovulation and parturition: Piked spurdog (*Squalus megalops*) as a case study. *Mar. Freshwater Res.* **57**: 105–119. doi: 10.1071/Mf05076.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd edn. Springer, New York, NY.
- Colonello, J.H., Cortés, F., Belleggia, M., and Massa, A.M. 2016. Reproductive and population parameters of spiny dogfish *Squalus acanthias* in the south-western Atlantic Ocean. *J. Fish Biol.* **88**(5): 1758–1775. doi: 10.1111/jfb.12940.
- Cortes, E. 1998. Demographic analysis as an aid in shark stock assessment and management. *Fish. Res.* **39**: 199–208. doi: 10.1016/S0165-7836(98)00183-0.
- Cortés, E., Brooks, E.N., and Gedamke, T. 2012. Population dynamics, demography, and stock assessment.

453 *In* Biology of Sharks and Their Relatives, Second Edition. *Edited by* J.C. Carrier, J.A. Musick, and M.R.
454 Heithaus. CRC Press, New York. pp. 453–86.

455 Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortes, E., Domingo, A., Fordham, S., Fowler, S.,
456 Francis, M.P., Gibson, C., Martínez, J., Musick, J.A., Soldo, A., Stevens, J.D., and Valenti, S. 2008. You can
457 swim but you can't hide: The global status and conservation of oceanic pelagic sharks and rays. *Aquatic*
458 *Conservation: Marine and Freshwater Ecosystems*.

459 Feldheim, K.A., Gruber, S.H., DiBattista, J.D., Babcock, E.A., Kessel, S.T., Hendry, A.P., Pikitch, E.K., Ash-
460 ley, M.V., and Chapman, D.D. 2014. Two decades of genetic profiling yields first evidence of natal philopatry
461 and long-term fidelity to parturition sites in sharks. *Mol. Ecol.* **23**(1): 110–117. doi: 10.1111/mec.12583.

462 Frisk, M.G., Miller, T.J., and Dulvy, N.K. 2005. Life histories and vulnerability to exploitation of elasma-
463 branches: Inferences from elasticity, perturbation and phylogenetic analyses. *Journal of Northwest Atlantic*
464 *Fishery Science* **35**: 27–45. doi: 10.2960/J.v35.m514.

465 Fujinami, Y., Semba, Y., Okamoto, H., Ohshimo, S., and Tanaka, S. 2017. Reproductive biology of the
466 blue shark (*Prionace glauca*) in the western North Pacific Ocean. *Mar. Freshwater Res.* **68**(11): 2018–2027.
467 Available from <https://doi.org/10.1071/MF16101>.

468 Grant, C., Sandland, R., and Olsen, A. 1979. Estimation of growth, mortality and yield per recruit of the
469 Australian school shark, *Galeorhinus australis* (Macleay), from tag recoveries. *Mar. Freshwater Res.* **30**(5):
470 625–637. doi: 10.1071/MF9790625.

471 Hale, L.F., and Baremore, I.E. 2013. Age and Growth of the Sandbar Shark (*Carcharhinus plumbeus*) from
472 the Northern Gulf of Mexico and the Western North Atlantic Ocean. *Gulf of Mexico Science* **1**(2): 28–39.

473 Hall, N., Cao, L., Chubb, C., Caputi, N., Cheng, H., Melville-Smith, R., and Shanks, S. 2000. Modelling
474 to explore management strategies to optimise the value of the Rock Lobster Fishery of Western Australia.
475 Fisheries Research Development Corporation Final Report Project (97/104).

476 Harry, A.V., Tobin, A.J., and Simpfendorfer, C.A. 2013. Age, growth and reproductive biology of the
477 spot-tail shark, *Carcharhinus sorrah*, and the Australian blacktip shark, *Carcharhinus tilstoni*, from the

Great Barrier Reef World Heritage Area, north-eastern Australia. Mar. Freshwater Res. **64**: 277–293. doi:
10.1071/MF12142.

Hesp, A. 2023. L3Assess: Catch curve and per recruit analyses. R package version 0.1.0.

Higgs, J.M., Hoffmayer, E.R., Sulikowski, J.A., Driggers, W.B., Stiller, D.A., and Hendon, J.M. 2020. Reproductive biology of the finetooth shark (*Carcharhinus isodon*) in the northern Gulf of Mexico, with evidence of both annual and biennial reproduction. Mar. Freshwater Res. Available from <https://doi.org/10.1071/MF20120>.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. Springer, New York, NY.

Hussey, N.E., Wintner, S.P., Dudley, S.F.J., Cliff, G., Cocks, D.T., and MacNeil, M.A. 2010. Maternal investment and size-specific reproductive output in carcharhinid sharks. J. Anim. Ecol. **79**: 184–193. doi: 10.1111/j.1365-2656.2009.01623.x.

Huveneers, C., Apps, K., Becerril-García, E.E., Bruce, B., Butcher, P.A., Carlisle, A.B., Chapple, T.K., Christiansen, H.M., Cliff, G., Curtis, T.H., Daly-Engel, T.S., Dewar, H., Dicken, M.L., Domeier, M.L., Duffy, C.A.J., Ford, R., Francis, M.P., French, G.C.A., Galván-Magaña, F., García-Rodríguez, E., Gennari, E., Graham, B., Hayden, B., Hoyos-Padilla, E.M., Hussey, N.E., Jewell, O.J.D., Jorgensen, S.J., Kock, A.A., Lowe, C.G., Lyons, K., Meyer, L., Oelofse, G., Oñate-González, E.C., Oosthuizen, H., O’Sullivan, J.B., Ramm, K., Skomal, G., Sloan, S., Smale, M.J., Sosa-Nishizaki, O., Sperone, E., Tamburin, E., Towner, A.V., Weisel, M.A., Weng, K.C., and Werry, J.M. 2018. Future research directions on the “Elusive” white shark. Frontiers in Marine Science **5**: 455. doi: 10.3389/fmars.2018.00455.

Huveneers, C., Walker, T.I., Otway, N.M., and Harcourt, R.G. 2007. Reproductive synchrony of three sympatric species of wobbegong shark (genus *orectolobus*) in New South Wales, Australia: Reproductive parameter estimates necessary for population modelling. Mar. Freshwater Res. **58**: 765–777. doi: 10.1071/MF06187.

Jennings, S., Kaiser, M., and Reynolds, J.D. 2001. Marine fisheries ecology. John Wiley & Sons, Oxford.

Joung, S.-J., Chen, C.-T., Clark, E., Uchida, S., and Huang, W.Y.P. 1996. The whale shark, *Rhincodon typus*,

503 is a livebearer: 300 embryos found in one “megamamma” supreme. Environ. Biol. Fish. **46**(3): 219–223. doi:
504 10.1007/BF00004997.

505 King, M. 2007. Fisheries biology, assessment and management. Blackwell Publishing, Oxford.

506 Kirkwood, G.P., and Walker, T.I. 1986. Gill net mesh selectivities for gummy shark, *Mustelus antarcticus*
507 Gunther, taken in southeastern Australian waters. Aust. J. Mar. Fresh. Res. **37**: 689–697.

508 Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., and Bell, B.M. 2016. TMB: Automatic Differentiation
509 and Laplace Approximation. J. Stat. Softw. **70**(5): 1–21. doi: 10.18637/jss.v070.i05.

510 Mejía-Falla, P.A., Navia, A.F., and Cortés, E. 2012. Reproductive variables of *Urotrygon rogersi* (Batoidea:
511 Urotrygonidae): A species with a triannual reproductive cycle in the eastern tropical Pacific Ocean. J. Fish
512 Biol. **80**(5): 1246–1266. doi: 10.1111/j.1095-8649.2012.03237.x.

513 Mollet, H.F., and Cailliet, G.M. 2002. Comparative population demography of elasmobranchs using life
514 history tables, Leslie matrices and stage-based matrix models. Mar. Freshwater Res. **53**: 503–516.

515 Montealegre-Quijano, S., Cardoso, A.T.C., Silva, R.Z., Kinas, P.G., and Vooren, C.M. 2014. Sexual
516 development, size at maturity, size at maternity and fecundity of the blue shark *Prionace glauca* (Linnaeus,
517 1758) in the Southwest Atlantic. Fish. Res. **160**: 18–32. doi: <https://doi.org/10.1016/j.fishres.2014.03.003>.

518 Motulsky, H., and Christopoulos, A. 2004. Fitting models to biological data using linear and nonlinear
519 regression: A practical guide to curve fitting. Oxford University Press, San Diego.

520 Moulton, P.L., Walker, T.I., and Saddler, S.R. 1992. Age and growth-studies of gummy shark, *Mustelus*
521 *antarcticus* Gunther, and school shark, *Galeorhinus galeus*(Linnaeus), from Southern Australian waters. Aust.
522 J. Mar. Fresh. Res. **43**: 1241–1267. doi: 10.1071/MF9921241.

523 Natanson, L.J., Deacy, B.M., Joyce, W., and Sulikowski, J. 2019. Presence of a resting population of female
524 porbeagles (*Lamna nasus*), indicating a biennial reproductive cycle, in the western North Atlantic Ocean.
525 Fish. B-noaa. **117**.

526 Nosal, A.P., Cartamil, D.P., Ammann, A.J., Bellquist, L.F., Ben-Aderet, N.J., Blincow, K.M., Burns, E.S.,
527 Chapman, E.D., Freedman, R.M., Klimley, A.P., Logan, R.K., Lowe, C.G., Semmens, B.X., White, C.F.,

528 and Hastings, P.A. 2021. Triennial migration and philopatry in the critically endangered soupfin shark
529 *Galeorhinus galeus*. J. Appl. Ecol. **58**(8): 1570–1582. doi: 10.1111/1365-2664.13848.

530 Oddone, M.C., Paesch, L., and Norbis, W. 2010. Size structure, abundance and preliminary information on
531 the reproductive parameters of the shortspine spurdog (*Squalus mitsukurii*) in the argentinean-uruguayan
532 common fishing zone from the mid-1990s. J. Northw. Atl. Fish. Sci. **43**: 13–26. doi: 10.2960/j.v.43.m662.

533 Palacios-Hernández, D., Castillo-Géniz, J.L., Méndez-Loeza, I., and Pérez-Jiménez, J.C. 2020. Temporal and
534 latitudinal comparisons of reproductive parameters in a heavily exploited shark, the bonnethead, *Sphyrna*
535 *tiburo* (L. 1758), in the southern Gulf of Mexico. J. Fish Biol. **97**(1): 100–112. doi: 10.1111/jfb.14330.

536 Piercy, A.N., Murie, D.J., and Gelsleichter, J.J. 2016. Histological and morphological aspects of reproduction
537 in the sandbar shark *Carcharhinus plumbeus* in the U.S. South-eastern Atlantic Ocean and Gulf of Mexico. J.
538 Fish Biol. **88**(5): 1708–1730. doi: 10.1111/jfb.12945.

539 Punt, A.E., Kennedy, R.B., and Frusher, S.D. 1997. Estimating the size-transition matrix for Tasmanian
540 rock lobster, *Jasus edwardsii*. Mar. Freshwater Res. **48**(8): 981–992. Available from [https://doi.org/10.1071/](https://doi.org/10.1071/MF97017)
541 MF97017.

542 Punt, A.E., and Walker, T.I. 1998. Stock assessment and risk analysis for the school shark (*Galeorhinus*
543 *galeus*) off southern Australia. Mar. Freshwater Res. **49**: 719–731. doi: 10.1071/MF96101.

544 Quinn, I.I., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York, NY.

545 R Core Team. 2022. R: A Language and Environment for Statistical Computing. Vienna, Austria. Available
546 from <https://www.R-project.org/>.

547 Rambahiniarison, J.M., Lamoste, M.J., Rohner, C.A., Murray, R., Snow, S., Labaja, J., Araujo, G., and
548 Ponzo, A. 2018. Life history, growth, and reproductive biology of four mobulid species in the Bohol Sea,
549 Philippines. Frontiers in Marine Science **5**: 269. doi: 10.3389/fmars.2018.00269.

550 Rigby, C., and Simpfendorfer, C.A. 2015. Patterns in life history traits of deep-water chondrichthyans. Deep
551 Sea Research Part II: Topical Studies in Oceanography **115**: 30–40. doi: [https://doi.org/10.1016/j.dsr2.2013.](https://doi.org/10.1016/j.dsr2.2013.09.004)
552 09.004.

553 Roa, R., Ernst, B., and Tapia, F. 1999. Estimation of size at sexual maturity: An evaluation of analytical
554 and resampling procedures. *Fish. B-noaa.* **97**: 570–580.

555 Rochowski, B.E.A., Graham, K.J., Day, R.W., and Walker, T.I. 2015. Reproductive biology of the greeneye
556 spurdog *Squalus chloroculus* (Squaliformes, Squalidae). *J. Fish Biol.* **86**(2): 734–754. doi: 10.1111/jfb.12593.

557 Rudd, M.B., and Thorson, J.T. 2018. Accounting for variable recruitment and fishing mortality in length-based
558 stock assessments for data-limited fisheries. *Can. J. Fish. Aquat. Sci.* **75**(7): 1019–1035.

559 Sato, K., Nakamura, M., Tomita, T., Toda, M., Miyamoto, K., and Nozu, R. 2016. How great white sharks
560 nourish their embryos to a large size: Evidence of lipid histotrophy in lamnoid shark reproduction. *Biology*
561 *Open* **5**(9): 1211–1215. doi: 10.1242/bio.017939.

562 SEDAR. 2012. SEDAR 29 stock assessment report: HMS Gulf of Mexico blacktip shark. North Charleston,
563 SC.

564 SEDAR. 2017. SEDAR 54 stock assessment report: HMS sandbar shark. North Charleston, SC.

565 SEDAR. 2023. HMS Hammerhead Sharks: Scalloped Hammerhead Shark. Section III: Assessment Report.
566 North Charleston, SC.

567 Smart, J.J., and Grammer, G.L. 2021. Modernising fish and shark growth curves with bayesian length-at-age
568 models. *Plos One* **16**(2): 1–21. doi: 10.1371/journal.pone.0246734.

569 Sminkey, T.R., and Musick, J.A. 1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before
570 and after population depletion. *Copeia*: 871–883.

571 Soto-López, K., Ochoa-Báez, R.I., Tovar-Ávila, J., and Galván-Magaña, F. 2018. Reproductive biology of the
572 brown smooth-hound shark, *Mustelus henlei* (Chondrichthyes: Triakidae), off northwestern Mexico based on
573 macroscopic and histological analyses. *Cienc. Mar.* **44**(2): 125–139.

574 Springer, S. 1960. Natural history of the sandbar shark, *Eulamia milberti*. US Fish Wildl. Serv. Fish. Bull.
575 **61**: 1–38.

576 Stevens, J.D. 1999. Variable resilience to fishing pressure in two sharks: The significance of different ecological

577 and life history parameters. Am. Fish. S. S. **23**: 11–15.

578 Sulikowski, J.A., Wheeler, C.R., Gallagher, A.J., Prohaska, B.K., Langan, J.A., and Hammerschlag, N. 2016.
579 Seasonal and life-stage variation in the reproductive ecology of a marine apex predator, the tiger shark
580 *Galeocerdo cuvier*, at a protected female-dominated site. Aquat. Biol. **24**(3): 175–184.

581 Swenson, J.D., Brooks, E.N., Kacev, D., Boyd, C., Kinney, M.J., Marcy-Quay, B., Sévêque, A., Feldheim,
582 K.A., and Komoroske, L.M. 2024. Accounting for unobserved population dynamics and aging error in close-kin
583 mark-recapture assessments. Ecology and Evolution **14**(2). doi: 10.1002/ece3.10854.

584 Taylor, I.G., Gertseva, V., Methot, R.D., and Maunder, M.N. 2013. A stock–recruitment relationship based
585 on pre-recruit survival, illustrated with application to spiny dogfish shark. Fish. Res. **142**: 15–21. doi:
586 <https://doi.org/10.1016/j.fishres.2012.04.018>.

587 Taylor, S.M., Harry, A.V., and Bennett, M.B. 2016. Living on the edge: Latitudinal variations in the
588 reproductive biology of two coastal species of sharks. J. Fish Biol. **89**(5): 2399–2418. doi: 10.1111/jfb.13126.

589 Tribuzio, C.A., and Kruse, G.H. 2012. Life history characteristics of a lightly exploited stock of *Squalus*
590 *suckleyi*. J. Fish Biol. **80**(5): 1159–1180. doi: 10.1111/j.1095-8649.2012.03241.x.

591 Trinnie, F.I., Walker, T.I., Jones, P.L., and Laurenson, L.J. 2009. Reproductive biology of the eastern
592 shovelnose stingaree *Trygonoptera imitata* from south-eastern Australia. Mar. Freshwater Res. **60**: 845–860.

593 Trinnie, F.I., Walker, T.I., Jones, P.L., and Laurenson, L.J. 2014. Regional differences in the reproductive
594 parameters of the sparsely-spotted stingaree, *Urolophus paucimaculatus*, from south-eastern Australia. Mar.
595 Freshwater Res. **65**(11): 943. doi: 10.1071/mf13275.

596 Trinnie, F.I., Walker, T.I., Jones, P.L., and Laurenson, L.J. 2016. Reproductive cycle of *Urolophus cruciatus*
597 in south-eastern Australia: Does the species exhibit obligate or facultative diapause? Mar. Biol. **163**(11):
598 226. doi: 10.1007/s00227-016-2976-x.

599 Walker, T. 1992. Fishery simulation model for sharks applied to the Gummy Shark, *Mustelus antarcticus*
600 Gunther, from Southern Australian waters. Mar. Freshwater Res. **43**(1): 195–212. Available from
601 <https://doi.org/10.1071/MF9920195>.

602 Walker, T.I. 2005. Reproduction in fisheries science. *In* Reproductive biology and phylogeny of Chon-
603 drichthyans: Sharks, batoids, and chimaeras. *Edited by* W.C. Hamlett. Science Publishers Inc., Enfield. pp.
604 81–127.

605 Walker, T.I. 2007. Spatial and temporal variation in the reproductive biology of gummy shark *Mustelus*
606 *antarcticus* (Chondrichthyes : Triakidae) harvested off southern Australia. Mar. Freshwater Res. **58**: 67–97.
607 doi: 10.1071/MF06074.

608 Winton, M.V., Wuenschel, M.J., and McBride, R.S. 2014. Investigating spatial variation and temperature
609 effects on maturity of female winter flounder (*Pseudopleuronectes americanus*) using generalized additive
610 models. Can. J. Fish. Aquat. Sci. **71**(9): 1279–1290. doi: 10.1139/cjfas-2013-0617.

611 Xiao, Y.S., and Walker, T.I. 2000. Demographic analysis of gummy shark (*Mustelus antarcticus*) and school
612 shark (*Galeorhinus galeus*) off southern Australia by applying a generalized Lotka equation and its dual
613 equation. Can. J. Fish. Aquat. Sci. **57**: 214–222. doi: 10.1139/f99-224.

614 Zuur, A., Ieno, E.N., and Smith, G.M. 2007. Analyzing ecological data. New York, NY.