

# 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.

## 1.1 Maternity function

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

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

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

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

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

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

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

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  $L_{\infty}$  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,  $\mu$ , was calculated from the growth curve. The standard deviation,  $\sigma$  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  $\phi$  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  $\theta_1$  and  $\theta_2$  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  $L'_{50}$  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  $P_{Max}$

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

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

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

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

281 Overall, the 2PLF-maternity method performed the poorest. Ignoring  $P_{Max}$  introduced a fixed bias in this  
282 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).

## 307 4 Discussion

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

### 321 4.1 Implementing maternity functions

322 Using simulated data to compare the relative performance of the 3PLF-estimated and 3PLF-fixed methods  
323 subject to a range of variables showed that it was feasible to estimate  $P_{Max}$ , but was difficult to do so  
324 accurately. For non-annual reproductive cycles,  $> 100$  school sharks and  $> 200$  gummy sharks in maternal  
325 condition were typically needed to estimate  $P_{Max}$  with  $<10\%$  MARE (Figure 5). This indicates that the both  
326 sample size requirements and levels of uncertainty are likely to be larger than conventional logistic maturity  
327 analysis (Roa et al. 1999). In the case of the gummy shark this inaccuracy led to the 2PLF-maturity method  
328 performing comparably or better than the 3PLF methods in minimizing bias in  $R_0$  (Figure S11). Relatively  
329 wide confidence intervals were also obtained for  $P_{Max}$  in the empirical analysis for sandbar sharks, even with  
330 a total sample size of  $> 1000$  females, 206 of which were in maternal condition. A similar sample size was  
331 used by Colonello *et al.* (2016) to estimate plausible values of  $P_{Max}$  and maternity parameters for south  
332 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 ( $\leq 100$  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 elasmobranchs:  
463 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.