Quantifying maternal reproductive output of chondrichthyan fishes

Alastair V Harry[1], Ivy Baremore[2], and Andrew Piercy[3]

[1]Fisheries & Agriculture Resource Management, Department of Primary Industries and Regional Development, 39 Northside Drive, Hillarys, 6025, WA, Australia *

[2]MarAlliance, Roatán, Islas de la Bahía, Honduras

[3]College of Southern Maryland, La Plata MD 20646, United States

Abstract

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

---

*alastair.harry@gmail.com

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 (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, skates, 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 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.

2

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:

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

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

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

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

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

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

3

72 the two conditions are not always synonymous. For example, reproduction in the Australian population of

73 school shark, *Galeorhinus galeus*, occurs triennially, such that approximately one third of mature females

74 give birth annually and $P_{Max} \approx 1/3$ (Walker 2005). Gestation lasts 20 months, and includes a protracted

75 period of ovulation. Newly pregnant females are not considered to be in maternal condition until the year of

76 pre-recruitment. Walker's (2005) definition is specific to species that reproduce during a single, well-defined

77 period of the year, but the concept can be generalised to accommodate asynchronously reproducing species

78 or those that reproduce more than once a year.

79 Numerous authors have adopted Walker's (2005) maternity function, including for species with biennial or

80 longer reproductive cycles (Huveneers et al. 2007, Rochowski et al. 2015, Trinnie et al. 2016) as well as those

81 with annual or shorter reproductive cycles (Trinnie et al. 2009, Mejía-Falla et al. 2012, Harry et al. 2013,

82 Taylor et al. 2016). Techniques have been described for determining maternal output in asynchronously

83 reproducing species (Braccini et al. 2006, Colonello et al. 2016), and maternity functions are also increasingly

84 being used directly in shark and ray population assessments (SEDAR 2012, 2017, 2023).

85 Despite an increase in use, only a small fraction of reproductive studies in recent years have reported

86 maternity functions. Classification of maternal condition is more data-intensive than maturity condition,

87 ideally requiring monthly sampling over a year or longer in order to establish the timing and duration of the

88 female ovarian and uterine cycles. Such data can be difficult and costly to collect for sharks and rays, which

89 are often data-poor and sampled opportunistically. The teleost-oriented foundations of fisheries science have

90 also contributed to the general lack of awareness of maternity functions; Walker (2005) is the sole description

91 on this type of analysis for chondrichthyans and there are no primary literature sources that describe specific

92 methods for chondrichthyan fishes.

93 For practitioners that are aware of maternity functions, lack of information on implementation may also have

94 discouraged use. Walker's (2005) approach to estimating parameters in the maternity function is difficult to

95 reproduce, apparently due to the constraints of the proprietary statistical program first used to implement the

96 analysis. Specifically, the method as described involves adjusting the raw data prior to parameter estimation

97 and then weighting it during analysis (Walker 2005). Additionally, the use of a fixed value for P_{Max}, as in the

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

4

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

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

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

102 2013).

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

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

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

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

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

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

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

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

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

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

113 tested in practice.

1.2   Revisiting the maternity function

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

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

117 used to support fisheries management and prioritize conservation actions (Cortés et al. 2012). It may also

118 help address the lack of empirical data on the periodicity of chondrichthyan reproductive cycles. Historically,

119 reproductive periodicity has only been determined qualitatively, and has been assumed to be fixed (e.g. annual,

120 biennial), despite observations of plasticity in this trait within discrete populations (Higgs et al. 2020).

121 Information on reproductive periodicity is contained within maternal data, however the existing approach of

122 fixing P_{Max} in maternity functions prevents statistical inference from being made on these data. Changes to

123 the way in which maternity functions are implemented may also contribute to quantifying uncertainty in

124 reproductive frequency and help understand the temporal stability of reproductive cycles. To date only a

5

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

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

2   Methods

2.1   Approach

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

6

2.2 Simulation

2.2.1 Data generation

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

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

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

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

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

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

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

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

7

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

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

166   2000), $G = g_{j,k}$ that represents the probability that a fish in length class, j, will grow into length class, k,

167   over a specified time interval

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

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

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

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

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

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

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

173   was given by

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

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

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

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

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

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

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

8

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

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

181   was further given by

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

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

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

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

184   a, was calculated using the Baranov catch equation as

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

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

186   2500 individuals, reflecting a gradient from data poor to rich.

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

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

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

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

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

190

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

9

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

192   **2.2.2   Estimation approaches**

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

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

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

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

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

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

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

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

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

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

203   (SEDAR 2023)).

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

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

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

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

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

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

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

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

212   the simulated data set meeting this criteria. If this occurred, L_{95} was used, followed by L_{50}, and finally the

213   proportion of all mature females in the sample that were in maternal condition. Statistical estimation of all

214   non-fixed parameters in each of the methods was undertaken using maximum likelihood. Nonparametric

215   bootstrapping was used to calculate approximate 50% confidence intervals for the best-fit parameters from

216   250 resampled data sets.

10

2.2.3 Reproductive output

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

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

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 precision, bias, and interval coverage for L'_{50}, P_{Max} and R_0. Bias was quantified using the mean relative error, $\mathrm{MRE} = \mathrm{mean}[(x_{\mathrm{Estimated}} - x_{\mathrm{True}})/x_{\mathrm{True}}]$ and precision using the mean absolute relative error, $\mathrm{MARE} = \mathrm{mean}|[(x_{\mathrm{Estimated}} - x_{\mathrm{True}})/x_{\mathrm{True}}]|$. 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 withing the nominal 50% confidence intervals.

2.2.5 Empirical case study

An empirical case study was also undertaken to show how maternity functions can be used in practice. Data from two studies of the reproductive biology of the sandbar shark, *Carcharhinus plumbeus*, in the Gulf of Mexico and western North Atlantic Ocean were combined and reanalysed using both 3PLF methods. The sandbar shark is a relatively long-lived ($A_{Max} = 33$ years) and slow growing species ($K = 0.12\mathrm{yr}^{-1}$) with a protracted reproductive cycle lasting longer than a year (Springer 1960). The Gulf of Mexico and western North Atlantic Ocean population has been considered overfished since the late 1970s (Sminkey and

11

240 Musick 1995) and during the 2000s detailed studies of sandbar shark reproductive biology and growth were

241 undertaken for stock assessment purposes (Baremore and Hale 2012, Piercy et al. 2016). In their study,

242 Baremore and Hale (2012) estimated maternity parameters using the 2PLF-maternity method, weighting

243 the final curve by 0.37 based on the proportion of pregnant females observed, most closely aligning with a

244 triennial reproductive cycle. Piercy *et al* (2016) did not estimate maternity parameters but also suggested

245 that the average reproductive cycle was likely to be longer than two years based on examination of ovarian

246 follicles. To examine relative support for either a biennial or triennial reproductive cycle, 3PLF-fixed models

247 were fit with P_{Max} estimated and fixed at 0.5 and 0.33, respectively.

248 3 Results

249 3.1 Simulation study

250 Parameter estimation was generally straightforward; with sample sizes > 50 a success rate of $\geq 95\%$ was

251 achieved in all scenarios (Figure S1, Table S1). Overall, convergence and parameter boundary failures

252 were most common with the 2PLF-maternity method which essentially involved fitting data to an under-

253 parameterized model where P_{Max} was always fixed at 1. In addition to convergence failures, 12 simulations

254 also generated insufficient maternal data (zero or one maternal females in the simulated data), and were

255 discarded.

256 Generally when using the 3PLF methods model performance declined as the periodicity of the reproductive

257 cycle increased. The nature of this problem can be seen in the positive correlation between the $\hat{L_{50}}$ and

258 $\hat{P_{Max}}$ parameters whereby P_{Max} affects the magnitude and direction of bias in these parameters (Figure 2).

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

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

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

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

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

12

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

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

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

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

268 sizes better precision was achieved by estimating P_{Max} (Figure 3). Overall, P_{Max} was comparatively more

269 challenging to estimate accurately than L'_{50} (Figure S4, Figure S5).

270 While the 3PLF-fixed method was in some cases able to reduce bias at lower sample sizes, a trade off in

271 the use of this method was poorer interval coverage (Figure 4, Figure S6). For most simulations, interval

272 coverage for $\hat{L'_{50}}$ was well below the expected level of 50%, irrespective of sample size. In contrast, for the

273 3PLF-estimated method interval coverage oscillated around 50% for both $\hat{L'_{50}}$ and $\hat{P_{Max}}$.

274 Differences in life history and gear selectivity played an important role in the ability to obtain precise and

275 unbiased maternity parameters. Certain combinations of variables in the simulated data resulted in fewer

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

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

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

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

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

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

283 in an overestimation of L'_{50} that was exacerbated by gear selectivity effects (Figure S2). In contrast, using

284 a maturity function to approximate the maternity function (2PLF-maturity method) resulted in relatively

285 good performance. L_{50} could usually be estimated with a higher precision than L'_{50}. For the gummy shark,

286 where L_{50} and L'_{50} were relatively similar, using the 2PLF-maturity method led to a constant underestimate

287 of L'_{50} of approximately 2%, exceeding the performance of the 3PLF-methods at most sample sizes.

288 The effect of the different methods in ultimately calculating R_0 varied considerably across the various scenarios.

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

13

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

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

292 11.1%. (Table S1, Figure S10). In contrast, for the gummy shark substituting maturity parameters led to a

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

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

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

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

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

298 ## 3.2   Empirical case study

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

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

301 0.48 (Table 2). Despite having a sample size of > 600 mature females, the proportion of maternal individuals

302 at length was still uncertain and $\hat{P_{Max}}$ was estimated to lie between 0.39 and 0.60 with 95% confidence. For

303 3PLF-fixed models a value of $P_{Max} = 0.5$ was strongly supported ($\Delta_{AIC} = 14.15$) over the alternative fixed

304 value of $P_{Max} = 0.33$. The model with $P_{Max} = 0.5$ also outperformed the 3PLF-estimated method ($\Delta_{AIC} =$

305 1.86). Given the fixed model had one fewer estimated parameters, both models had essentially the same level

306 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 precision, bias, and confidence interval coverage often improved when P_{Max} was estimated. Using

14

314   a fixed value for P_{Max} in some cases resulted in lower bias at low sample sizes. This study also demonstrated

315   that recruitment can be overestimated when maturity data were used to approximate maternal data and

316   inaccurate if P_{Max} was ignored when estimating maternity parameters. Based on these findings we outline

317   considerations for practitioners using these methods and illustrate how they can provide novel insights into

318   reproductive biology. We conclude by discussing the advantages of adopting this approach to quantifying

319   maternal reproductive output and future directions.

4.1   Implementing maternity functions

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

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

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

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

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

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

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

328   While the estimation of maternity parameters in most simulations was possible, it was difficult to do so

329   accurately. Outcomes of the simulation study suggested that samples sizes of ≥ 500 would be needed to

330   estimate P_{Max} with <10% MARE for a triennially reproducing species. This is a much larger error than

331   is achievable from conventional logistic maturity analysis (Roa et al. 1999). In the case of the gummy

332   shark this imprecision led to the 2PLF-maturity method performing comparably or better than the 3PLF

333   methods in ultimately quantifying R_0. Relatively wide confidence intervals were also obtained for P_{Max} in

334   the empirical analysis for sandbar sharks, even with a sample size of > 1000. A similar sample size was used

335   by Colonello *et al* (2016) to successfully estimate P_{Max} and maternity parameters for south Atlantic spiny

336   dogfish. These results suggest that data requirements of the 3PLF analyses may be prohibitively large for

337   many chondrichthyans and therefore best suited to use on commercially captured species where large sample

338   sizes can be obtained (Oddone et al. 2010, Tribuzio and Kruse 2012).

15

339   In light of the data requirements suggested by this study, the current practice of using maturity parameters as

340   a proxy for maternity parameters will likely still be the only option for numerous data-poor chondrichthyans.

341   From this perspective, the outperformance of the 3PLF-methods by the 2PLF-methods for the gummy shark

342   in several simulations is encouraging. However, the extent to which maturity parameters can provide a good

343   approximation of maternity parameters may be species-specific, depending on how close L_{50} is to L'_{50}. While

344   several studies have shown these parameters to be similar (Walker 2007, Soto-López et al. 2018), L'_{50} is more

345   frequently shifted to the right of L_{50} (Braccini et al. 2006, Montealegre-Quijano et al. 2014, Colonello et

346   al. 2016, Palacios-Hernández et al. 2020), and this length difference can equate to one or more years. For

347   example, Harry *et al* (2013) found both spot-tail shark, *C. sorrah*, and Australian blacktip shark, *C. tilstoni*,

348   began reproducing the year after reaching sexual maturity. Similarly, Fujiyama found A'_{50} to be 1.4 years

349   older than A_{50} in blue sharks.

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

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

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

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

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

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

356   2013, Rambahiniarison et al. 2018).

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

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

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

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

361   also be considered if using this approach.

16

4.2 Empirical study

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

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

4.3 Advantages and future directions

Despite the simplicity of the 3PLF-estimated method, it nonetheless represents a conceptual shift for chondrichthyan reproductive and population biology. Until now reproductive periodicity has largely been determined qualitatively from observations of female reproductive biology or inferred based on circumstantial evidence. Using the 3PLF-estimated method to estimate P_{Max} within a maternity function transforms it

17

387 from a nuisance parameter to one of direct inferential interest that can be seen as a valuable output of the

388 modelling process itself. In addition to the potential benefits of using this method to improve estimation of

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

390 One benefit of this approach is that it that it reduces the need for subjective modelling assumptions relating

391 to P_{Max}. Such assumptions can have important implications for population modelling. For example, to

392 account for uncertainty in temporal and spatial frequency of reproduction in sparsely-spotted stingarees,

393 *Urolophus paucimaculatus*, Trinnie *et al* (2014) estimated maternity parameters for ten plausible scenarios. In

394 stock assessment of western North Atlantic sandbar sharks a breeding frequency of 2.5 years was assumed to

395 account for uncertainty in the duration of the reproductive cycle (SEDAR 2017).

396 More commonly, practitioners have chosen fixed values of the form $P_{Max} = 1/n$, where n is the apparent

397 duration of the reproductive cycle in years. This process also has the potential to introduce bias if a small

398 proportion of females reproduce more or less frequently that the larger population. Long-term study of

399 offspring from genetically profiled lemon sharks, *Negaprion brevirostris*, confirmed that most individuals

400 reproduced biennially, but also revealed some cases of triennial reproduction (Feldheim et al. 2014). Statistical

401 estimation of P_{Max} from data avoids these decisions and enables uncertainty in this parameter to be included

402 in subsequent population models.

403 Estimation of P_{Max} using the 3PLF-estimated method may also be a means to resolving the longstanding

404 question of reproductive frequency in some rare and threatened chondrichthyans. White sharks, *Carcharodon*

405 *carcharias*, and whale shark, *Rhinchodon typus*,are two examples of intensively studied species where only

406 fragmentary observations of female reproductive biology exist (Joung et al. 1996, Sato et al. 2016). In

407 both species lack of data on reproductive frequency is a major impediment to population modelling and

408 the development of management strategies (Huveneers et al. 2018, Bowlby and Gibson 2020). With many

409 of these populations the focus of ongoing monitoring, non-lethal methods for assessing maternal state may

410 eventually provide a way of collecting sufficient data for estimation of P_{Max} (Sulikowski et al. 2016).

411 A logical progression from estimating P_{Max} is the consideration of alternative functional forms for this

412 parameter such as time- or space-varying P_{Max} or more complex length- or age-dependent forms. Despite

18

the diverse range of reproductive modes found in chondrichthyan fishes, the current, limited knowledge of maternal investment has typically investigated variables such as litter size and pup condition (Hussey et al. 2010). Little is known about how reproductive frequency varies as a function of size or age, in response to environmental effects, or at changing population densities. Better understanding of these factors has the potential to improve understanding reproductive strategies and is, many cases, of direct relevance to management.

5   Acknowledgements

References

10 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: 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.

19

436   Colonello, J.H., Cortés, F., Belleggia, M., and Massa, A.M. 2016. Reproductive and population parameters

437   of spiny dogfish *Squalus acanthias* in the south-western Atlantic Ocean. J. Fish Biol. **88**(5): 1758–1775. doi:

438   10.1111/jfb.12940.

439   Cortes, E. 1998. Demographic analysis as an aid in shark stock assessment and management. Fish. Res. **39**:

440   199–208. doi: 10.1016/S0165-7836(98)00183-0.

441   Cortés, E., Brooks, E.N., and Gedamke, T. 2012. Population dynamics, demography, and stock assessment.

442   *In* Biology of Sharks and Their Relatives, Second Edition. *Edited by* J.C. Carrier, J.A. Musick, and M.R.

443   Heithaus. CRC Press, New York. pp. 453–86.

444   Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortes, E., Domingo, A., Fordham, S., Fowler, S.,

445   Francis, M.P., Gibson, C., Martínez, J., Musick, J.A., Soldo, A., Stevens, J.D., and Valenti, S. 2008. You can

446   swim but you can't hide: The global status and conservation of oceanic pelagic sharks and rays. Aquatic

447   Conservation: Marine and Freshwater Ecosystems.

448   Feldheim, K.A., Gruber, S.H., DiBattista, J.D., Babcock, E.A., Kessel, S.T., Hendry, A.P., Pikitch, E.K., Ash-

449   ley, M.V., and Chapman, D.D. 2014. Two decades of genetic profiling yields first evidence of natal philopatry

450   and long-term fidelity to parturition sites in sharks. Mol. Ecol. **23**(1): 110–117. doi: 10.1111/mec.12583.

451   Frisk, M.G., Miller, T.J., and Dulvy, N.K. 2005. Life histories and vulnerability to exploitation of elasmo-

452   branchs: Inferences from elasticity, pertubation and phylogenetic analyses. Journal of Northwest Atlantic

453   Fishery Science **35**: 27–45. doi: 10.2960/J.v35.m514.

454   Fujinami, Y., Semba, Y., Okamoto, H., Ohshimo, S., and Tanaka, S. 2017. Reproductive biology of the

455   blue shark (*Prionace glauca*) in the western North Pacific Ocean. Mar. Freshwater Res. **68**(11): 2018–2027.

456   Available from https://doi.org/10.1071/MF16101.

457   Grant, C., Sandland, R., and Olsen, A. 1979. Estimation of growth, mortality and yeild per recruit of the

458   Australian school shark, *Galeorhinus australis* (Macleay), from tag recoveries. Mar. Freshwater Res. **30**(5):

459   625–637. doi: 10.1071/MF9790625.

460   Hale, L.F., and Baremore, I.E. 2013. Age and Growth of the Sandbar Shark (*Carcharhinus plumbeus*) from

461   the Northern Gulf of Mexico and the Western North Atlantic Ocean. Gulf of Mexico Science **1**(2): 28–39.

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

Harry, A.V., Tobin, A.J., and Simpfendorfer, C.A. 2013. Age, growth and reproductive biology of the 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.

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: 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., Wcisel, 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.

21

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

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

490   is a livebearer: 300 embryos found in one "megamamma" supreme. Environ. Biol. Fish. **46**(3): 219–223. doi:

491   10.1007/BF00004997.

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

493   Kirkwood, G.P., and Walker, T.I. 1986. Gill net mesh selectivities for gummy shark, *Mustelus antarcticus*

494   Gunther, taken in southeastern Australian waters. Aust. J. Mar. Fresh. Res. **37**: 689–697.

495   Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., and Bell, B.M. 2016. TMB: Automatic Differentiation

496   and Laplace Approximation. J. Stat. Softw. **70**(5): 1–21. doi: 10.18637/jss.v070.i05.

497   Mejía-Falla, P.A., Navia, A.F., and Cortés, E. 2012. Reproductive variables of *Urotrygon rogersi* (Batoidea:

498   Urotrygonidae): A species with a triannual reproductive cycle in the eastern tropical Pacific Ocean. J. Fish

499   Biol. **80**(5): 1246–1266. doi: 10.1111/j.1095-8649.2012.03237.x.

500   Mollet, H.F., and Cailliet, G.M. 2002. Comparative population demography of elasmobranchs using life

501   history tables, Leslie matrices and stage-based matrix models. Mar. Freshwater Res. **53**: 503–516.

502   Montealegre-Quijano, S., Cardoso, A.T.C., Silva, R.Z., Kinas, P.G., and Vooren, C.M. 2014. Sexual

503   development, size at maturity, size at maternity and fecundity of the blue shark *Prionace glauca* (Linnaeus,

504   1758) in the Southwest Atlantic. Fish. Res. **160**: 18–32. doi: https://doi.org/10.1016/j.fishres.2014.03.003.

505   Motulsky, H., and Christopoulos, A. 2004. Fitting models to biological data using linear and nonlinear

506   regression: A practical guide to curve fitting. Oxford University Press, San Diego.

507   Moulton, P.L., Walker, T.I., and Saddlier, S.R. 1992. Age and growth-studies of gummy shark, *Mustelus*

508   *antarcticus* Gunther, and school shark, *Galeorhinus galeus*(Linnaeus), from Southern Australian waters. Aust.

509   J. Mar. Fresh. Res. **43**: 1241–1267. doi: 10.1071/MF9921241.

510   Oddone, M.C., Paesch, L., and Norbis, W. 2010. Size structure, abundance and preliminary information on

511   the reproductive parameters of the shortspine spurdog (*Squalus mitsukurii*) in the Argentinean-Uruguayan

512   common fishing zone from the mid–1990s.

22

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

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

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

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

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

R Core Team. 2018. R: A Language and Environment for Statistical Computing. Vienna, Austria. Available from https://www.R-project.org/.

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

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

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

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

Rudd, M.B., and Thorson, J.T. 2018. Accounting for variable recruitment and fishing mortality in length-based

23

stock assessments for data-limited fisheries. Can. J. Fish. Aquat. Sci. **75**(7): 1019–1035.

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

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

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

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

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

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

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

Stevens, J.D. 1999. Variable resilience to fishing pressure in two sharks: The significance of different ecological and life history parameters. Am. Fish. S. S. **23**: 11–15.

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

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

24

562 Taylor, S.M., Harry, A.V., and Bennett, M.B. 2016. Living on the edge: Latitudinal variations in the

563 reproductive biology of two coastal species of sharks. J. Fish Biol. **89**(5): 2399–2418. doi: 10.1111/jfb.13126.

564 Tribuzio, C.A., and Kruse, G.H. 2012. Life history characteristics of a lightly exploited stock of *Squalus*

565 *suckleyi*. J. Fish Biol. **80**(5): 1159–1180. doi: 10.1111/j.1095-8649.2012.03241.x.

566 Trinnie, F.I., Walker, T.I., Jones, P.L., and Laurenson, L.J. 2009. Reproductive biology of the eastern

567 shovelnose stingaree *Trygonoptera imitata* from south-eastern Australia. Mar. Freshwater Res. **60**: 845–860.

568 Trinnie, F.I., Walker, T.I., Jones, P.L., and Laurenson, L.J. 2016. Reproductive cycle of *Urolophus cruciatus*

569 in south-eastern Australia: Does the species exhibit obligate or facultative diapause? Mar. Biol. **163**(11):

570 226. doi: 10.1007/s00227-016-2976-x.

571 Walker, T. 1992. Fishery simulation model for sharks applied to the Gummy Shark, *Mustelus antarcticus*

572 Gunther, from Southern Australian waters. Mar. Freshwater Res. **43**(1): 195–212. Available from

573 https://doi.org/10.1071/MF9920195.

574 Walker, T.I. 2005. Reproduction in fisheries science. *In* Reproductive biology and phylogeny of Chon-

575 drichthyans: Sharks, batoids, and chimaeras. *Edited by* W.C. Hamlett. Science Publishers Inc., Enfield. pp.

576 81–127.

577 Walker, T.I. 2007. Spatial and temporal variation in the reproductive biology of gummy shark *Mustelus*

578 *antarcticus* (Chondrichthyes : Triakidae) harvested off southern Australia. Mar. Freshwater Res. **58**: 67–97.

579 doi: 10.1071/MF06074.

580 Xiao, Y.S., and Walker, T.I. 2000. Demographic analysis of gummy shark (*Mustelus antarcticus*) and school

581 shark (*Galeorhinus galeus*) off southern Australia by applying a generalized Lotka equation and its dual

582 equation. Can. J. Fish. Aquat. Sci. **57**: 214–222. doi: 10.1139/f99-224.

583 Zuur, A., Ieno, E.N., and Smith, G.M. 2007. Analyzing ecological data. Springer Science & Business Media,

584 New York, NY.