

# Quantifying maternal reproductive output of chondrichthyan fishes

Alastair V. Harry<sup>a</sup>, Ivy E. Baremore<sup>b</sup>, and Andrew N. Piercy<sup>c</sup>

<sup>a</sup>Fisheries & Agriculture Resource Management, Department of Primary Industries and Regional Development, 39 Northside Drive, Hillarys, 6025 WA, Australia; <sup>b</sup>MarAlliance, Roatán, Islas de la Bahía, Honduras; <sup>c</sup>College of Southern Maryland, La Plata, MD 20646, USA

Corresponding author: Alastair V. Harry (email: [alastair.harry@gmail.com](mailto:alastair.harry@gmail.com))

## Abstract

For the live-bearing and egg-laying class of chondrichthyan fishes a three parameter logistic ‘maternity’ function with a variable upper asymptote,  $P_{\text{Max}}$ , can be used to predict the average probability of a female giving birth or laying eggs in a season. Although fundamental to calculating the reproductive capacity of a population, few studies report maternity functions, with maturity functions often used as a proxy. Applying logistic models to simulated and empirical data showed that it was feasible to estimate  $P_{\text{Max}}$  from maternal data and that accuracy, bias, and confidence interval coverage often improved compared to when a fixed value was used. However, sample sizes of 100–200 maternal females were typically required for accurate estimation of  $P_{\text{Max}}$ . While maturity parameters could be estimated with greater accuracy, substituting them for maternity parameters overestimated lifetime reproductive output. Greater use of maternity functions has the potential to improve calculation of reproductive output in quantitative populations models. In addition to improvements in parameter estimation, this method involves fewer assumptions and enables statistical inferences to be made on frequency of reproduction.

**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 De-riso 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 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). The upper asymptote of the curve,  $\alpha$ , controls 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 De-riso 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:

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

where  $x_{50}$  and  $x_{95}$  are the sizes or ages at which 50% and 95% of the maximum proportion of individuals ( $P_{\text{Max}}$ ) 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 (nonmaternal/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 the two conditions are not always synonymous. For example, reproduction in the Australian population of school shark, *Galeorhinus galeus*, occurs triennially, such that approximately one third of mature females give birth annually and  $P_{\text{Max}} \approx 1/3$  (Walker 2005). Gestation lasts 20 months, and includes a protracted period of ovulation. Newly pregnant females are not considered to be in maternal condition until the year of pre-recruitment. Walker's (2005) definition is specific to species that reproduce during a single, well-defined period of the year, but the concept can be generalised to accommodate asynchronously reproducing species or those that reproduce more than once a year.

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

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

For practitioners that are aware of maternity functions, lack of information on implementation may also have discouraged use. Walker's (2005) approach to estimating parameters in the maternity function is difficult to reproduce, apparently due to the constraints of the proprietary statistical program first used to implement the analysis. Specifically, the method as described involves adjusting the raw data prior to parameter estimation and then weighting it during analysis (Walker 2005). Additionally, the use of a fixed value for  $P_{\text{Max}}$ , 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 chondrichthyans, 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  $P_{\text{Max}}$  in maternity functions prevents statistical inference from being made on these data. Changes to the way in which maternity functions are implemented may also contribute to quantifying uncertainty in reproductive frequency and help understand the temporal stability of reproductive cycles. To date only a single study on spiny dogfish, *Squalus acanthias*, has statistically estimated  $P_{\text{Max}}$  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 objective of providing guidance on implementation and appropriate use. To address this 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 maternity functions on calculations of lifetime reproductive output, and (3) outline strategies for making inferences on reproductive frequency from maternity data.

## 2. Materials and methods

### 2.1. Approach

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

### 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 pop-

ulations (Table 1) (Grant et al. 1979; Kirkwood and Walker 1986; Moulton et al. 1992; Walker 1992, 2005, 2007; Punt and Walker 1998). Both species are well-studied and were chosen to be representative of fast and slow chondrichthyan life history styles, respectively (Stevens 1999).

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

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

where  $L_{\infty}$  is the 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,  $\mu$ , was calculated from the growth curve. The standard deviation,  $\sigma$  was not available for either species so was assumed to be directly proportional to length, with a constant of proportionality of 5%, i.e.,  $\sigma = 0.05 \mu$ .

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

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

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

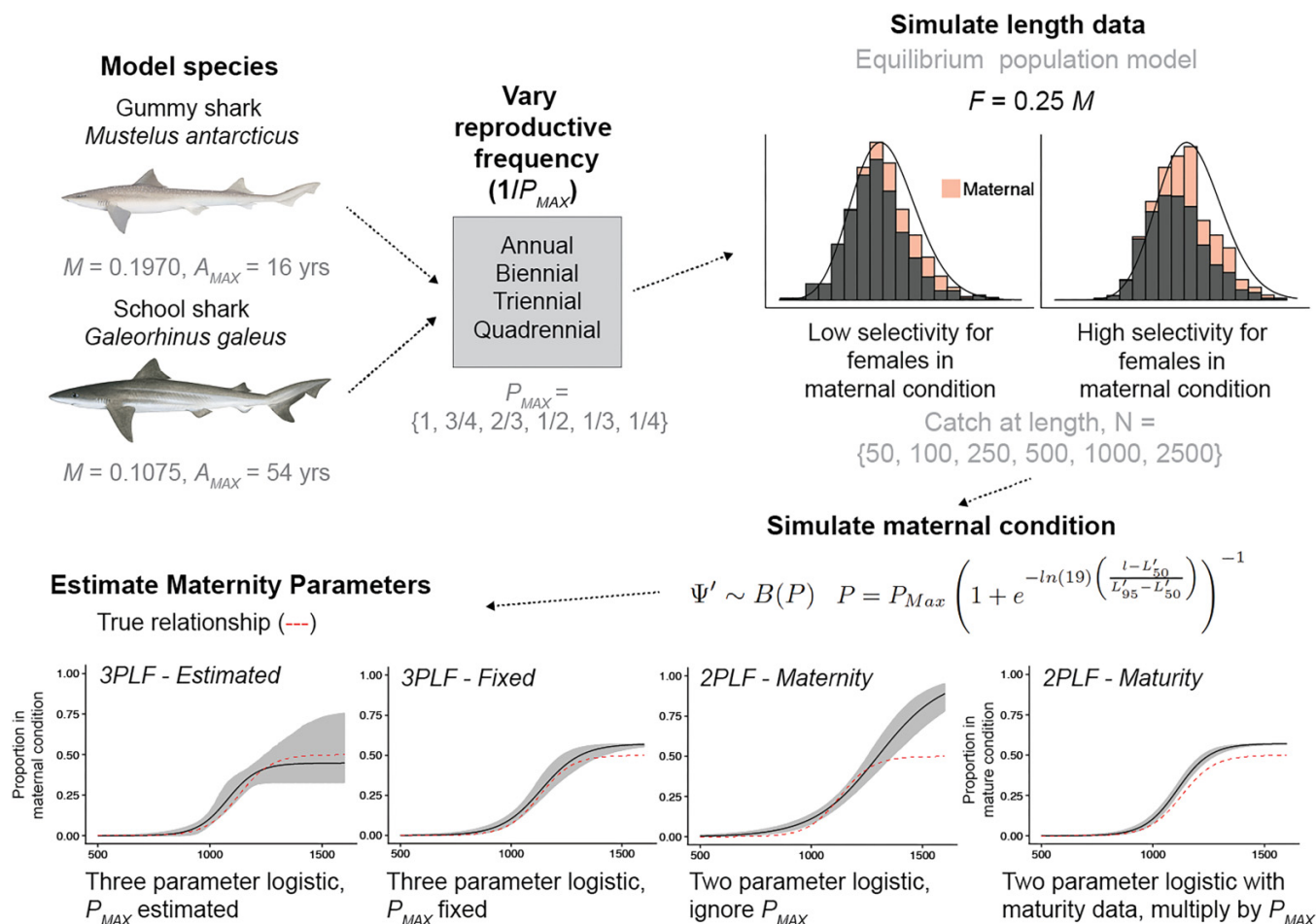
$$g_{k,j} = \begin{cases} \int_{l_k^-}^{l_k^+} f[\phi(l,j)] dl & \text{if } k = 1 \\ \int_{l_k^-}^{l_{k+1}^-} f[\phi(l,j)] dl & \text{if } k = 1 < k < n \\ \int_{l_k^-}^{\infty} f[\phi(l,j)] dl & \text{if } k = n \end{cases}$$

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

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



**Fig. 1.** Approach used to generate simulated data and test the performance of four methods for calculating maternity parameters. Illustrations R.Swainston/[www.anima.net.au](http://www.anima.net.au).



**Table 1.** Descriptions and values of parameters used in a simulation study to evaluate the performance of alternative methods for estimating maternity parameters.

Symbol	Description	School shark	Gummy shark
$L_{\infty}$	Asymptotic length (mm)	1618.3	2019
$K$	Growth coefficient (year <sup>-1</sup> )	0.16	0.086
$t_0$	Age at length 0 (years)	-1.2818	-3.01
$A_{Max}$	Maximum age	54	16
$L_{50}$	50 % maturity (mm)	1349	1253
$L_{95}$	95 % maturity (mm)	1502	1472
$L'_{50}$	50 % maternity (mm)	1421	1263
$L'_{95}$	95 % maternity (mm)	1488	1405
$\alpha$	Intercept (litter size)	-46	0.2804
$\beta$	Slope (litter size)	0.0491	0.00286
$R$	Sex ratio (M:F)	1	1
$\theta_1$	Selectivity parameter 1	192	184.3
$\theta_2$	Selectivity parameter 2	67595	29739
Mesh (low)	Gillnet mesh size (in)	7.05	6.08
Mesh (high)	Gillnet mesh size (in)	7.75	7.62

and Walker 1986; Punt and Walker 1998), where the selectivity of an individual in length class,  $l$  was given by

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

where  $\theta_1$  and  $\theta_2$  are estimated parameters (Kirkwood and Walker 1986). Two selectivity scenarios were simulated corresponding to low and high selectivity of the maternal component of the population. For consistency between species, gillnet mesh sizes were chosen that would result in peak relative selectivity occurring at the lengths equal to 25% and 75% of the population in maternal condition (Table 1).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

## 2.2.2. Estimation approaches

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

Only the 3PLF-estimated method involves statistically estimating  $P_{\text{Max}}$ , which must be subjectively chosen in the case of the 3PLF-fixed and the 2PLF-maturity.  $P_{\text{Max}}$  is ideally chosen based on detailed study of the ovarian and uterine cycles

(Walker 2005), or alternatively based on the proportion of mature females observed to be in maternal condition during sampling (Baremore and Hale 2012; Harry et al. 2013; Trinnie et al. 2016). For the purposes of the simulation, the timing and duration of the uterine and ovarian cycles were assumed to be unknown. The following procedure was used to 'guess' the fixed value of  $P_{\text{Max}}$  in each simulation.  $P_{\text{Max}}$  was chosen as the proportion of females in maternal condition above the length at which 99% of females 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:

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

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  $L'_{50}$ ,  $P_{\text{Max}}$  and  $R_0$ . Bias was quantified using the mean relative error,  $\text{MRE} = \text{mean}[(x_{\text{Estimated}} - x_{\text{True}})/x_{\text{True}}]$  and accuracy using the mean absolute relative error,  $\text{MARE} = \text{mean}[|(x_{\text{Estimated}} - x_{\text{True}})/x_{\text{True}}|]$ . 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.

## 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

( $A_{\text{Max}} = 33$  years) and slow growing species ( $K = 0.12 \text{ year}^{-1}$ ) 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 Musick 1995) and during the 2000s detailed studies of sandbar shark reproductive biology and growth were undertaken for stock assessment purposes (Baremore and Hale 2012; Hale and Baremore 2013; Piercy et al. 2016). In their study, Baremore and Hale (2012) estimated maternity parameters using the 2PLF-maternity method, weighting the final curve by 0.37 based on the proportion of pregnant females observed, most closely aligning with a triennial reproductive cycle. Piercy et al. (2016) did not estimate maternity parameters but also suggested that the average reproductive cycle was likely to be longer than two years based on examination of ovarian follicles. To examine relative support for either a biennial or triennial reproductive cycle, 3PLF-fixed models were fit with  $P_{\text{Max}}$  estimated and fixed at 0.5 and 0.33, respectively. Model performance was evaluated using Akaike information criteria (AIC).

## 3. Results

### 3.1. Simulation study

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

When using the 3PLF methods model performance typically declined as the periodicity of the reproductive cycle increased. This is seen in the positive correlation between  $\widehat{L}'_{50}$  and  $\widehat{P}_{\text{Max}}$ , whereby true underlying  $P_{\text{Max}}$  affected the magnitude and direction of bias in these parameters (Fig. 2). With lower values of  $P_{\text{Max}}$  it appeared to be more difficult for the model to separate the point of inflection in the logistic model and the upper asymptote. As true underlying  $P_{\text{Max}}$  decreased there was also a greater potential for positive bias in  $\widehat{P}_{\text{Max}}$ . Additionally, longer reproductive cycles resulted in fewer females in maternal condition, which was associated with larger bias (Fig. 2).

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

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

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

Overall, the 2PLF-maternity method performed the poorest. Ignoring  $P_{\text{Max}}$  introduced a fixed bias in this parameter that increased in magnitude as reproductive periodicity increased (Fig. S3). This manifested in an overestimation of  $L'_{50}$  that was exacerbated by gear selectivity effects (Fig. 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.

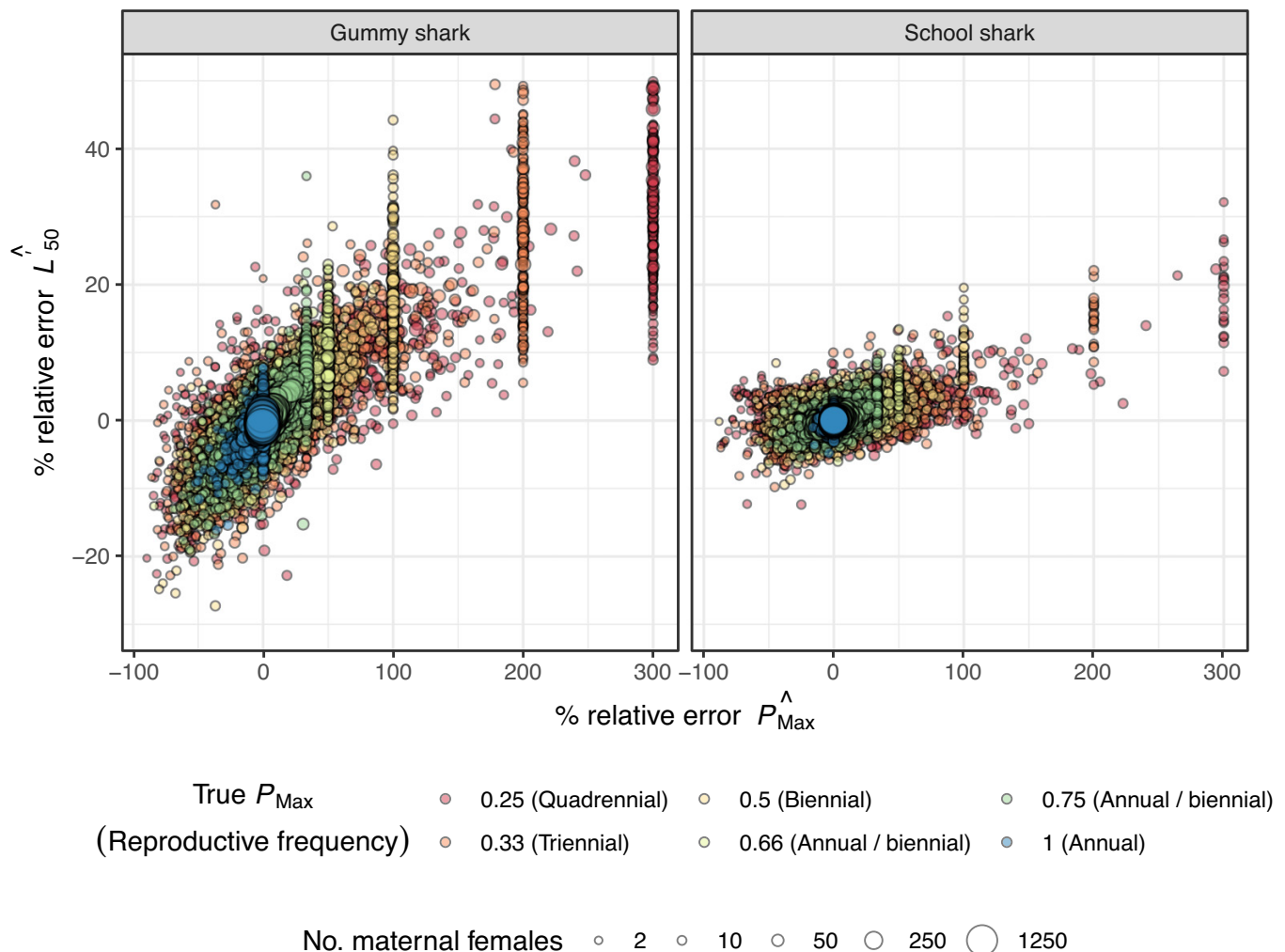
The effect of the different methods in ultimately calculating  $R_0$  varied considerably across the various scenarios. For school sharks, estimating  $P_{\text{Max}}$  was the most effective way to minimize bias in most scenarios (Fig. S10). Substituting maturity parameters (2PLF-maturity method) led 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% (Fig. 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 (Fig. S11). Using the 2PLF-maternity method for gummy sharks led to a median overestimate of  $R_0$  of 39% (Fig. 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 (Fig. 6 and Fig. S12). For gummy sharks the 3PLF-fixed method performed best at lower sample sizes and lower values of  $P_{\text{Max}}$ .

### 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  $\widehat{P}_{\text{Max}}$  was 0.48 (Table 2). Despite



**Fig. 2.** Bias (percent relative error) in parameter estimates for  $\hat{L}_{50}'$  and  $\hat{P}_{\text{Max}}$  for the three-parameter logistic regression function maternity function with  $P_{\text{Max}}$  estimated. Each point represents parameter estimates from one iteration of simulated data ( $n = 43\,129$ ), including all combinations of variables. Simulations with longer reproductive cycles and fewer maternal females were associated with higher bias in both  $\hat{L}_{50}'$  and  $\hat{P}_{\text{Max}}$ . Note: 42 data points were cropped to aid with data visualization (see Fig. S13 for uncropped figure).



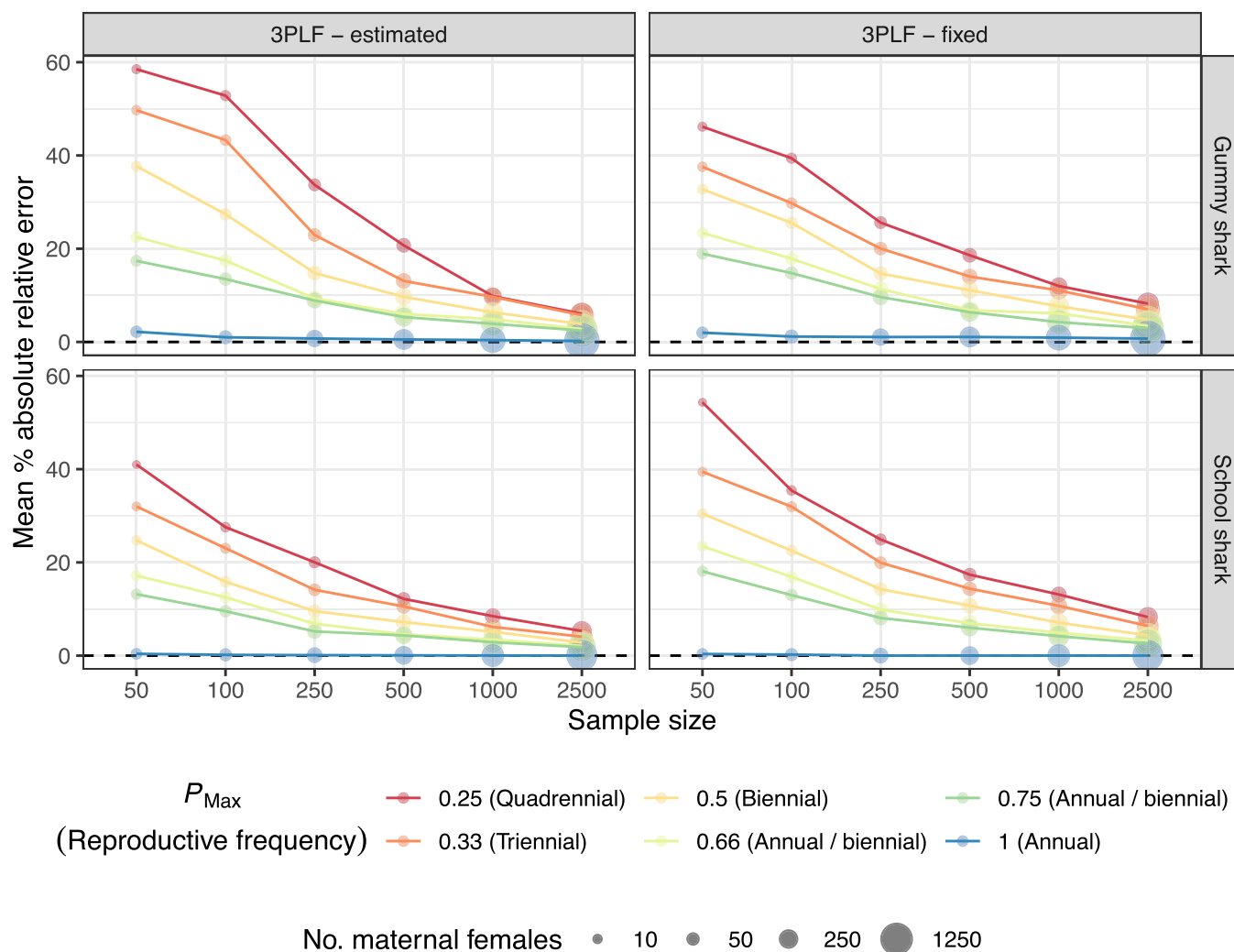
having a sample size of  $>600$  mature females, the proportion of maternal individuals at length was still uncertain and  $\hat{P}_{\text{Max}}$  was estimated to lie between 0.39 and 0.60 with 95% confidence (Figure 7). For 3PLF-fixed models a value of  $P_{\text{Max}} = 0.5$  was strongly supported ( $\Delta\text{AIC} = 14.15$ ) over the alternative fixed value of  $P_{\text{Max}} = 0.33$ . The model with  $P_{\text{Max}} = 0.5$  also outperformed the 3PLF-estimated method ( $\Delta\text{AIC} = 1.86$ ). Given the fixed model had one fewer estimated parameter, both models had essentially the same level of support given the data (Burnham and Anderson 2002).

## 4. Discussion

Relatively few reproductive biology studies have used maternity functions to model maternal reproductive output in chondrichthyan fishes. Where they have been employed the approach has typically been to use a three parameter logistic function with a fixed, user-defined value for the up-

per asymptote,  $P_{\text{Max}}$ . Here we show that it is feasible to estimate  $P_{\text{Max}}$  from maternal data, in turn enabling statistical inferences on reproductive periodicity. Applying 3PLF models with estimated and fixed values of  $P_{\text{Max}}$  to simulated data showed that accuracy, bias, and confidence interval coverage often improved when  $P_{\text{Max}}$  was estimated. Using a fixed value for  $P_{\text{Max}}$  in some cases reduced bias. Overall, however, relatively large sample sizes were needed to accurately estimate  $P_{\text{Max}}$ , particularly with longer reproductive cycles. This study also demonstrated that, in some cases, recruitment was overestimated when maturity data were used to approximate maternal data and inaccurate if  $P_{\text{Max}}$  was ignored when estimating maternity parameters. Based on these findings we outline considerations for practitioners using these methods and illustrate how they can provide novel insights into reproductive biology. We conclude by discussing the advantages of adopting this approach and future directions.

**Fig. 3.** Accuracy (percent absolute error) in parameter estimates of  $\hat{P}_{\text{Max}}$  for three-parameter logistic regression function methods with high maternal selectivity. Large sample sizes were needed to accurately estimate  $\hat{P}_{\text{Max}}$  and accuracy decreased as the duration of the reproductive cycle increased. Each point reflects a mean value from 300 simulated data sets. Point size denotes mean number of females in maternal condition at a given sample size.



#### 4.1. Implementing maternity functions

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

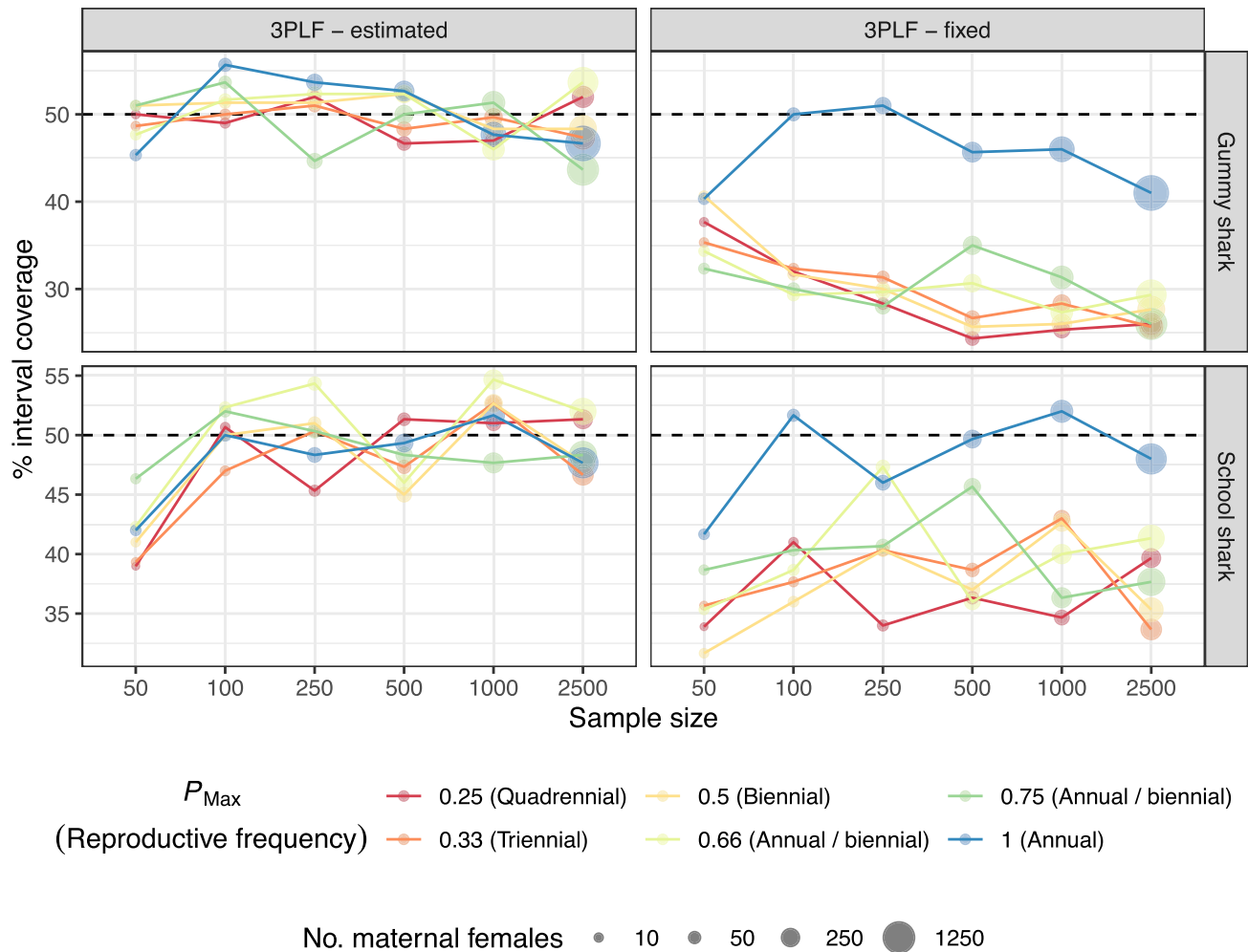
ues of  $P_{\text{Max}}$  and maternity parameters for south Atlantic spiny dogfish.

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

Together, these results suggest that data requirements of the 3PLF analyses may be prohibitively large for many chondrichthyans and therefore best suited to use on commercially captured species where large sample sizes can be obtained (Oddone et al. 2010; Tribuzio and Kruse 2012). For smaller samples sizes, placing a prior or penalty on  $P_{\text{Max}}$



**Fig. 4.** Confidence interval coverage for  $\hat{L}'_{50}$  for three-parameter logistic regression function methods with high maternal selectivity. Figure shows the percentage of simulations ( $n = 300$ ) where the true parameter value fell within the 50% bootstrap confidence interval. Point size denotes mean number of females in maternal condition at a given sample size.



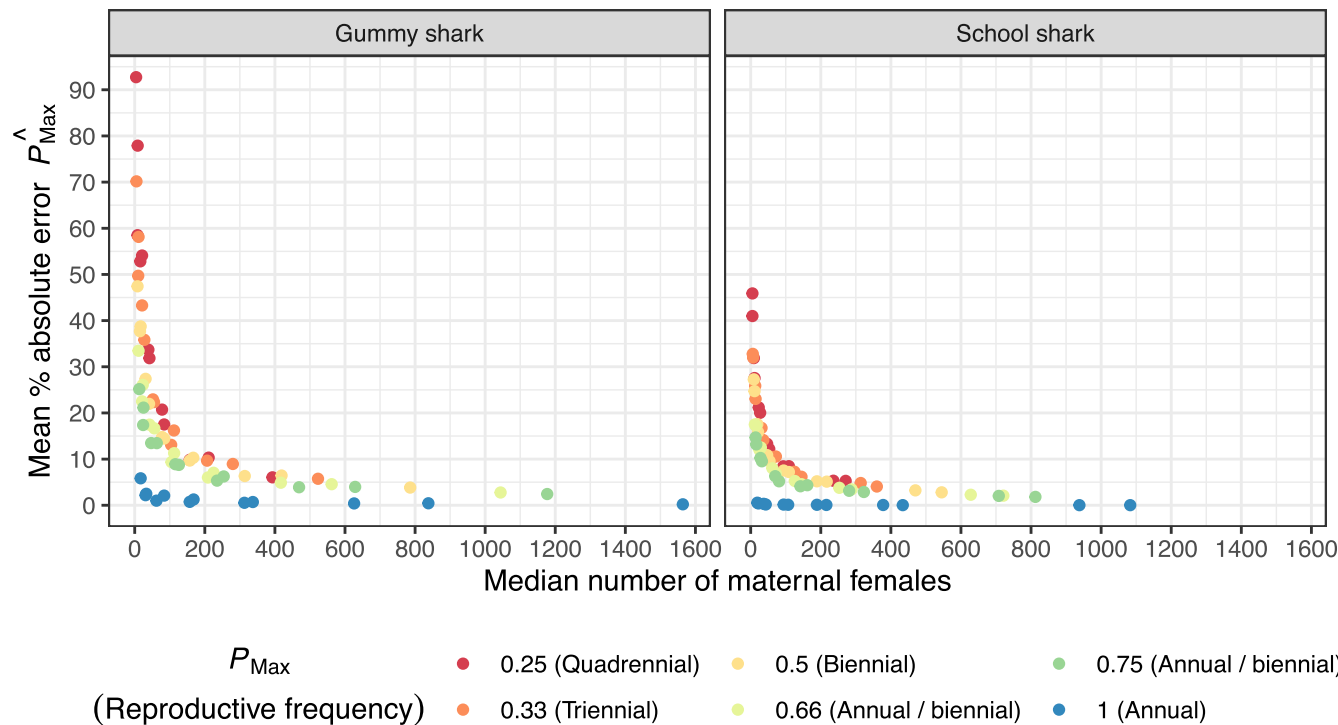
may also help overcome issues of parameter inaccuracy, enabling existing information about reproductive periodicity to be incorporated from other populations or closely-related species (Smart and Grammer 2021). Information on length at maturity, which is likely to be relatively easier to estimate, may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

For data-poor chondrichthyan species, or where data on pregnant females are sparse or unattainable, the current practice of using maturity parameters as a proxy for maternity parameters will likely still be the only option. From this perspective, the outperformance of the 3PLF-methods by the 2PLF-methods for the gummy shark in several simulations is encouraging. However, the extent to which maturity parameters can provide a good approximation of maternity parameters may be species-specific, depending on how close  $L_{50}$  is to  $L'_{50}$ . While several studies have shown these parameters to be similar (Walker 2007; Soto-López et al. 2018),  $L'_{50}$  is more frequently shifted to the right of  $L_{50}$  (Braccini

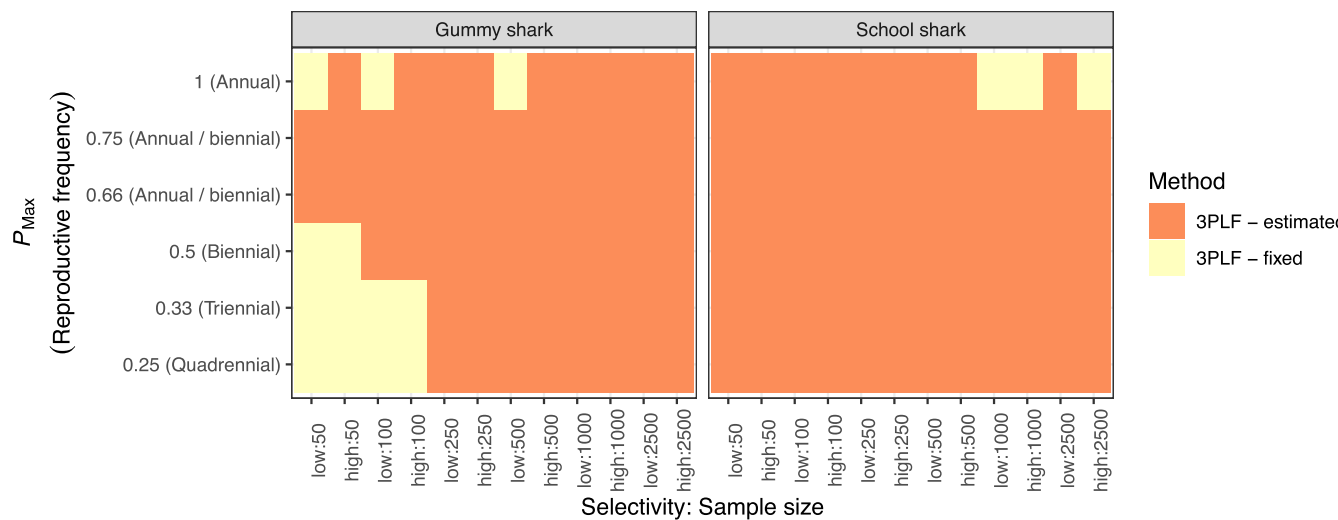
et al. 2006; Montealegre-Quijano et al. 2014; Colonello et al. 2016; Palacios-Hernández et al. 2020), and this length difference can equate to one or more years. For example, Harry et al. (2013) found both spot-tail shark, *Carcharhinus sorrah*, and Australian blacktip shark, *Carcharhinus tilstoni*, began reproducing the year after reaching sexual maturity. Similarly, Fujinami et al. (2017) found  $A'_{50}$  to be 1.4 years older than  $A_{50}$  in blue sharks.

More research is needed to understand the relationship between size at maturity and maternity and variability within and among taxa. In general, this study confirms Walker's (2005) assertion that the common practice of weighting the maturity curve by the frequency of parturition overestimates recruitment. This study also confirms that fitting a 2PLF to maternal data when  $P_{Max} < 1$  (effectively ignoring  $P_{Max}$ ) is likely to result in biased parameters and can also overestimate recruitment. While not widely used, this approach has been undertaken in several studies (Baremore and Hale 2012; Mejía Falla et al. 2012; Baremore and Passerotti 2013; Rambahiniarison et al. 2018).

**Fig. 5.** Accuracy (percent absolute error) in parameter estimates of  $\widehat{P}_{\text{Max}}$  for the three-parameter logistic regression function - estimated method as a function of number of maternal females. Each point reflects a value from 300 simulated data sets.



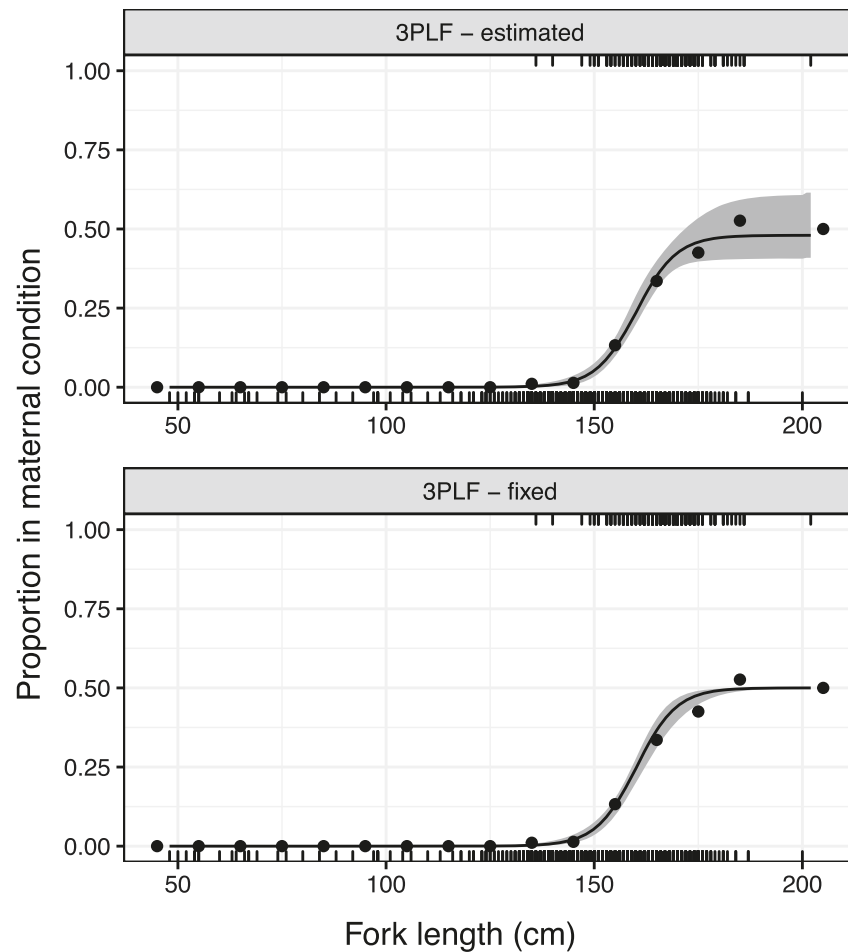
**Fig. 6.** Performance of four alternative maternity functions in accurately calculating  $R_0$ . The best performing method was that which minimised mean absolute error across 300 simulated datasets. Note two-parameter logistic regression function-maternity (Annual) scenarios were excluded for this comparison.



**Table 2.** Parameter estimates and model selection criteria for three parameter logistic functions (3PLF) fit to empirical data for western North Atlantic sandbar sharks. \* Denotes fixed values of parameters used.

Method	$\widehat{P}_{\text{Max}}$	$\widehat{L}_{50}^{\prime}$ (cm)	$\widehat{L}_{95}^{\prime}$ (cm)	AIC	$\Delta_i$	$w_i$
3PLF—fixed	0.5*	161 (159–163)	176 (171–181)	833.91	0.00	71.63
3PLF—estimated	0.48 (0.392–0.611)	160 (157–164)	174 (167–183)	835.77	1.86	28.31
3PLF—fixed	0.333*	156 (155–158)	167 (163–171)	848.06	14.15	0.06

**Fig. 7.** Comparison of three-parameter logistic regression function-estimated and 3PLF-fixed methods used to estimate maternal parameters for sandbar shark, *Carcharhinus plumbeus*, in the Gulf of Mexico and western North Atlantic. Solid line is the expected proportion in maternal condition at length,  $\Psi(l)$ . The grey shaded region denotes 95% confidence intervals based on bootstrap resampling. Black points show proportion in maternal condition in 10cm length intervals. Marginal rug plots denote raw data that models were fit to.  $P_{\text{Max}}$  was fixed at 0.5 in the lower panel.



## 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  $P_{\text{Max}}$ . 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  $\hat{P}_{\text{Max}} = 0.48$ , 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  $P_{\text{Max}} = 0.5$  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 146 and 176 cm—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, while larger sharks may ultimately be capable of reproducing biennially. Given that few females appear to attain this size ([Hale and Baremore 2013](#)), the modal reproductive frequency is still likely at least triennial within the population. 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  $P_{\text{Max}}$  within a maternity function transforms it from a nuisance parameter to one of direct inferential interest that can be seen as a valuable output of the modelling process itself. In addition to the potential benefits of using this method to improve estimation of maternal parameters, there are also a range of other advantages that arise from estimating  $P_{\text{Max}}$ .

One benefit of this approach is that it reduces the need for subjective modelling assumptions relating to  $P_{\text{Max}}$ . Such assumptions can have important implications for population modelling. For example, due to uncertainty in temporal and spatial frequency of reproduction in sparsely-spotted stingarees, *Urolophus paucimaculatus*, Trinnie et al. (2014) estimated maternity parameters for 10 plausible scenarios. In stock assessment of western North Atlantic sandbar sharks a breeding frequency of 2.5 years was assumed to account for uncertainty in the duration of the reproductive cycle (SEDAR 2017).

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

Estimation of  $P_{\text{Max}}$  using the 3PLF-estimated method may also be a means to resolving the longstanding question of reproductive frequency in some rare and threatened chondrichthyans. White sharks, *Carcharodon carcharias*, and whale shark, *Rhincodon typus*, are two examples of intensively studied species where only fragmentary observations of female reproductive biology exist (Joung et al. 1996; Sato et al. 2016). In both species lack of data on reproductive frequency is a major impediment to population modelling and the development of management strategies (Huveneers et al. 2018; Bowlby and Gibson 2020). With many of these populations the focus of ongoing monitoring, non lethal methods for assessing maternal state may eventually provide a way of collecting sufficient data for estimation of  $P_{\text{Max}}$  (Sulikowski et al. 2016).

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

tential to improve understanding reproductive strategies and is, in many cases, of direct relevance to management.

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### Data availability

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

## Author information

### Author ORCIDs

Alastair V. Harry <https://orcid.org/0000-0002-9905-7909>

### Author contributions

Conceptualization: AH

Data curation: AH, IEB, ANP

Formal analysis: AH

Investigation: IEB, ANP

Methodology: AH

Validation: IEB, ANP

Visualization: AH

Writing – original draft: AH

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## Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2024-0031>.

## References

- Baremore, I.E., and Hale, L.F. 2012. Reproduction of the sandbar shark in the Western North Atlantic Ocean and Gulf of Mexico. *Mar. Coast. Fish.* **4**(1): 560–572. doi:[10.1080/19425120.2012.700904](https://doi.org/10.1080/19425120.2012.700904).
- Baremore, I.E., and Passerotti, M.S. 2013. Reproduction of the blacktip shark in the Gulf of Mexico. *Mar. Coast. Fish.* **5**(1): 127–138. doi:[10.1080/19425120.2012.758204](https://doi.org/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*). *Eco. Evol.* **10**(11): 4990–5000. doi:[10.1002/ece3.6252](https://doi.org/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.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. 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](https://doi.org/10.1111/jfb.12940).
- Cortés, 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](https://doi.org/10.1016/S0165-7836(98)00183-0).
- Cortés, E., Brooks, E.N., and Gedamke, T. 2012. Population dynamics, demography, and stock assessment. In *Biology of sharks and their relatives*, 2nd ed. Edited by J.C. Carrier, J.A. Musick and M.R. Heithaus. CRC Press, New York. pp. 453–86.
- Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortés, E., Domingo, A., et al. 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **18**: 459–482.
- Feldheim, K.A., Gruber, S.H., DiBattista, J.D., Babcock, E.A., Kessel, S.T., Hendry, A.P., et al. 2014. Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. *Mol. Ecol.* **23**(1): 110–117. doi:[10.1111/mec.12583](https://doi.org/10.1111/mec.12583).
- Frisk, M.G., Miller, T.J., and Dulvy, N.K. 2005. Life histories and vulnerability to exploitation of elasmobranchs: Inferences from elasticity, perturbation and phylogenetic analyses. *J. Northwest Atl. Fish. Sci.* **35**: 27–45. doi:[10.2960/J.v35.m514](https://doi.org/10.2960/J.v35.m514).
- Fujinami, Y., Semba, Y., Okamoto, H., Ohshimo, S., and Tanaka, S. 2017. Reproductive biology of the blue shark (*Prionace glauca*) in the western North Pacific Ocean. *Mar. Freshwater Res.* **68**(11): 2018–2027. doi:[10.1071/MF16101](https://doi.org/10.1071/MF16101).
- Grant, C., Sandland, R., and Olsen, A. 1979. Estimation of growth, mortality and yield per recruit of the Australian school shark, *Galeorhinus australis* (Macleay), from tag recoveries. *Mar. Freshwater Res.* **30**(5): 625–637. doi:[10.1071/MF9790625](https://doi.org/10.1071/MF9790625).
- Hale, L.F., and Baremore, I.E. 2013. Age and Growth of the sandbar shark (*Carcharhinus plumbeus*) from the Northern Gulf of Mexico and the Western North Atlantic Ocean. *Gulf Mex. Sci.* **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](https://doi.org/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.* **72**: 693–708. doi:[10.1071/MF20120](https://doi.org/10.1071/MF20120).
- Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment. In *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.
- Huveneers, C., Apps, K., Becerril-García, E.E., Bruce, B., Butcher, P.A., Carlisle, A.B., et al. 2018. Future research directions on the “Elusive” white shark. *Front. Mar. Sci.* **5**: 455. doi:[10.3389/fmars.2018.00455](https://doi.org/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](https://doi.org/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*, is a livebearer: 300 embryos found in one “megamamma” supreme. *Environ. Biol. Fish.* **46**(3): 219–223. doi:[10.1007/BF00004997](https://doi.org/10.1007/BF00004997).
- King, M. 2007. Fisheries biology, assessment and management. Blackwell Publishing, Oxford.
- Kirkwood, G.P., and Walker, T.I. 1986. Gill net mesh selectivities for gummy shark, *Mustelus antarcticus* Gunther, taken in southeastern Australian waters. *Aust. J. Mar. Fresh. Res.* **37**: 689–697.
- Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., and Bell, B.M. 2016. TMB: automatic differentiation and laplace approximation. *J. Stat. Softw.* **70**(5): 1–21. doi:[10.18637/jss.v070.i05](https://doi.org/10.18637/jss.v070.i05).
- Mejia Falla, P.A., Navia, A.F., and Cortés, E. 2012. Reproductive variables of *Urotrygon rogersi* (Batoidea: Urotrygonidae): A species with a triannual reproductive cycle in the eastern tropical Pacific Ocean. *J. Fish Biol.* **80**(5): 1246–1266. doi:[10.1111/j.1095-8649.2012.03237.x](https://doi.org/10.1111/j.1095-8649.2012.03237.x).
- Mollet, H.F., and Cailliet, G.M. 2002. Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. *Mar. Freshwater Res.* **53**: 503–516.
- Montealegre-Quijano, S., Cardoso, A.T.C., Silva, R.Z., Kinas, P.G., and Vooren, C.M. 2014. Sexual development, size at maturity, size at maternity and fecundity of the blue shark *Prionace glauca* (Linnaeus, 1758) in the Southwest Atlantic. *Fish. Res.* **160**: 18–32. doi:[10.1016/j.fishres.2014.03.003](https://doi.org/10.1016/j.fishres.2014.03.003).
- Motulsky, H., and Christopoulos, A. 2004. Fitting models to biological data using linear and nonlinear regression: a practical guide to curve fitting. Oxford University Press, San Diego.
- Moulton, P.L., Walker, T.I., and Saddler, S.R. 1992. Age and growth-studies of gummy shark, *Mustelus antarcticus* Gunther, and school shark, *Galeorhinus galeus* (Linnaeus), from Southern Australian waters. *Aust. J. Mar. Fresh. Res.* **43**: 1241–1267. doi:[10.1071/MF9921241](https://doi.org/10.1071/MF9921241).
- Natanson, L.J., Deacy, B.M., Joyce, W., and Sulikowski, J. 2019. Presence of a resting population of female porbeagles (*Lamna nasus*), indicating a biennial reproductive cycle, in the western North Atlantic Ocean. *Fish. Bull.* **117**.
- Nosal, A.P., Cartamil, D.P., Ammann, A.J., Bellquist, L.F., Ben-Aderet, N.J., Blinckow, K.M., et al. 2021. Triennial migration and philopatry in the critically endangered soupfin shark *Galeorhinus galeus*. *J. Appl. Ecol.* **58**(8): 1570–1582. doi:[10.1111/1365-2664.13848](https://doi.org/10.1111/1365-2664.13848).
- Oddone, M.C., Paesch, L., and Norbis, W. 2010. Size structure, abundance and preliminary information on the reproductive parameters of the shortspine spurdog (*Squalus mitsukurini*) in the argentinean-uruguayan common fishing zone from the mid-1990s. *J. Northw. Atl. Fish. Sci.* **43**: 13–26. doi:[10.2960/j.v43.m662](https://doi.org/10.2960/j.v43.m662).
- 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](https://doi.org/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](https://doi.org/10.1111/jfb.12945).
- Punt, A.E., Kennedy, R.B., and Frusher, S.D. 1997. Estimating the size-transition matrix for Tasmanian rock lobster, *Jaanus edwardsii*. *Mar. Freshwater Res.* **48**(8): 981–992. doi:[10.1071/MF97017](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](https://doi.org/10.1071/MF96101).

- Quinn, I.I., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York, NY.
- R Core Team. 2022. R: a language and environment for statistical computing. Vienna, Austria. Available from <https://www.R-project.org/> [accessed January 2022].
- Rambahiniarison, J.M., Lamoste, M.J., Rohner, C.A., Murray, R., Snow, S., Labaja, J., et al. 2018. Life history, growth, and reproductive biology of four mobulid species in the Bohol Sea, Philippines. *Front. Mar. Sci.* **5**: 269. doi:[10.3389/fmars.2018.00269](https://doi.org/10.3389/fmars.2018.00269).
- Rigby, C., and Simpfendorfer, C.A. 2015. Patterns in life history traits of deep-water chondrichthyans. *Deep Sea Res. Part II*, **115**: 30–40. doi:[10.1016/j.dsr2.2013.09.004](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. Bull.* **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](https://doi.org/10.1111/jfb.12593).
- Rudd, M.B., and Thorson, J.T. 2018. Accounting for variable recruitment and fishing mortality in length-based 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. *Biol. Open*, **5**(9): 1211–1215. doi:[10.1242/bio.017939](https://doi.org/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.
- Smart, J.J., and Grammer, G.L. 2021. Modernising fish and shark growth curves with Bayesian length-at-age models. *Plos One*, **16**(2): 1–21. doi:[10.1371/journal.pone.0246734](https://doi.org/10.1371/journal.pone.0246734).
- Sminkey, T.R., and Musick, J.A. 1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia*, **1995**(4): 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.
- Swenson, J.D., Brooks, E.N., Kacev, D., Boyd, C., Kinney, M.J., Marcy-Quay, B., et al. 2024. Accounting for unobserved population dynamics and aging error in close-kin mark-recapture assessments. *Ecol. Evol.*, **14**(2): e10854. doi:[10.1002/ece3.10854](https://doi.org/10.1002/ece3.10854).
- 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:[10.1016/j.fishres.2012.04.018](https://doi.org/10.1016/j.fishres.2012.04.018).
- Taylor, S.M., Harry, A.V., and Bennett, M.B. 2016. Living on the edge: latitudinal variations in the reproductive biology of two coastal species of sharks. *J. Fish Biol.* **89**(5): 2399–2418. doi:[10.1111/jfb.13126](https://doi.org/10.1111/jfb.13126).
- Tribuzio, C.A., and Kruse, G.H. 2012. Life history characteristics of a lightly exploited stock of *Squalus suckleyi*. *J. Fish Biol.* **80**(5): 1159–1180. doi:[10.1111/j.1095-8649.2012.03241.x](https://doi.org/10.1111/j.1095-8649.2012.03241.x).
- Trinnie, F.I., Walker, T.I., Jones, P.L., and Laurenson, L.J. 2009. Reproductive biology of the eastern shovelnose stingaree *Trygonoptera imitata* from south-eastern Australia. *Mar. Freshwater Res.* **60**: 845–860.
- Trinnie, F.I., Walker, T.I., Jones, P.L., and Laurenson, L.J. 2014. Regional differences in the reproductive parameters of the sparsely-spotted stingaree, *Urolophus paucimaculatus*, from south-eastern Australia. *Mar. Freshwater Res.* **65**(11): 943. doi:[10.1071/mf13275](https://doi.org/10.1071/mf13275).
- Trinnie, F.I., Walker, T.I., Jones, P.L., and Laurenson, L.J. 2016. Reproductive cycle of *Urolophus cruciatus* in south-eastern Australia: does the species exhibit obligate or facultative diapause? *Mar. Biol.* **163**(1): 226. doi:[10.1007/s00227-016-2976-x](https://doi.org/10.1007/s00227-016-2976-x).
- Walker, T. 1992. Fishery simulation model for sharks applied to the Gummy Shark, *Mustelus antarcticus* Gunther, from southern Australian waters. *Mar. Freshwater Res.* **43**(1): 195–212. doi:[10.1071/MF9920195](https://doi.org/10.1071/MF9920195).
- Walker, T.I. 2005. Reproduction in fisheries science. In *Reproductive biology and phylogeny of Chondrichthyes: Sharks, batoids, and chimaeras*. Edited by W.C. Hamlett. Science Publishers Inc., Enfield. pp. 81–127.
- Walker, T.I. 2007. Spatial and temporal variation in the reproductive biology of gummy shark *Mustelus antarcticus* (Chondrichthyes : Triakidae) harvested off southern Australia. *Mar. Freshwater Res.* **58**: 67–97. doi:[10.1071/MF06074](https://doi.org/10.1071/MF06074).
- Winton, M.V., Wuenschel, M.J., and McBride, R.S. 2014. Investigating spatial variation and temperature effects on maturity of female winter flounder (*Pseudopleuronectes americanus*) using generalized additive models. *Can. J. Fish. Aquat. Sci.* **71**(9): 1279–1290. doi:[10.1139/cjfas-2013-0617](https://doi.org/10.1139/cjfas-2013-0617).
- Xiao, Y.S., and Walker, T.I. 2000. Demographic analysis of gummy shark (*Mustelus antarcticus*) and school shark (*Galeorhinus galeus*) off southern Australia by applying a generalized Lotka equation and its dual equation. *Can. J. Fish. Aquat. Sci.* **57**: 214–222. doi:[10.1139/f99-224](https://doi.org/10.1139/f99-224).
- Zuur, A., Ieno, E.N., and Smith, G.M. 2007. Analyzing ecological data. New York, NY.