Quantifying maternal reproductive output of chondrichthyan fishes

For the live-bearing and egg-laying class of chondrichthyan fishes a three parameter logistic ‘maternity’ function with a variable upper asymptote, , 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 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 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 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.

# 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, Kaiser, and Reynolds 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, Miller, and Dulvy 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, Tobin, and Simpfendorfer 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, Gillanders, and Walker 2006; T. I. Walker 2007; Montealegre-Quijano et al. 2014). Finally, because female fecundity is low (usually 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 (I. G. 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.

## 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:

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

where and are the sizes or ages at which 50% and 95% of the maximum proportion of individuals () 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 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 (T. I. 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 (C. Huveneers et al. 2007; Rochowski et al. 2015; Fabian I. Trinnie et al. 2016) as well as those with annual or shorter reproductive cycles (F. I. Trinnie et al. 2009; Mejía‐Falla, Navia, and Cortés 2012; Harry, Tobin, and Simpfendorfer 2013; S. M. Taylor, Harry, and Bennett 2016). Techniques have been described for determining maternal output in asynchronously reproducing species (Braccini, Gillanders, and Walker 2006; Colonello et al. 2016), and maternity functions are also increasingly being used directly in shark and ray population assessments (SEDAR 2012, 2023; SEDAR 2017).

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. 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 (T. I. Walker 2005). Additionally, the use of a fixed value for , 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 (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.

## Revisiting the maternity function

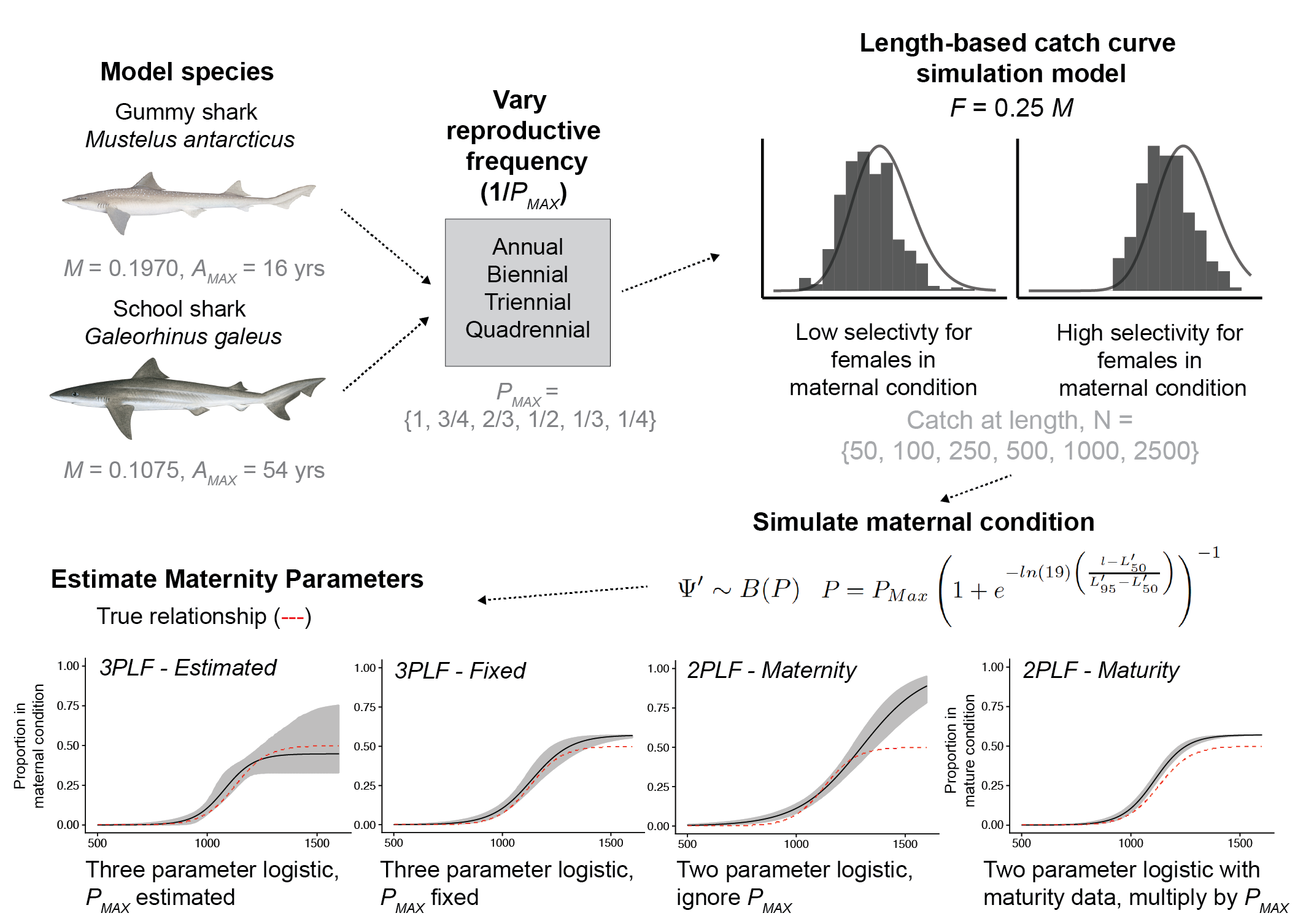
Wider use of maternity functions in studies of chondrichthyan reproductive biology is needed to improve calculation of reproductive capacity in the quantitative population assessments that are increasingly being used to support fisheries management and prioritize conservation actions (Cortés, Brooks, and Gedamke 2012). 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). Information on reproductive periodicity is contained within maternal data, however the existing approach of fixing 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 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.

# Methods

## 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).



Approach used to generate simulated data and test the performance of four methods for calculating maternity parameters.

## Simulation

### 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, Sandland, and Olsen 1979; Kirkwood and Walker 1986; Moulton, Walker, and Saddlier 1992; T. Walker 1992; A. E. Punt and Walker 1998; T. I. 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-based catch curve 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

where is asymptotic length, *K* is the growth coefficient and 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, , was calculated as

where and are the lower and upper limits of each 1cm length class, *k*. is the value of the normal probability density function at age for a given length, *l*,

where mean length, , was caclulated from the growth curve. The standard deviation, was not available for either species so was assumed to be directly proportional to length, with a constant of proportionality of 5% (Table 1), i.e. .

Growth in subsequent age classes was modelled using a length transition matrix (André E. Punt, Kennedy, and Frusher 1997; Hall et al. 2000), that represents the probability that a fish in length class, , will grow into length class, , over a specified time interval

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

where *l* is mean length, *f* is the specified normal distribution, and are the lower and upper limits of length class *j*, and is a vector of parameters.

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

where and 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

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

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

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

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.

Next, maturity-at-length data, , were randomly generated by simulating from a Bernoulli distribution, , where was given by the 2PLF:

This processe was then repeated to generate maternity-at-length data, , using the 3PLF:

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

### 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 asmyptote had (i.e.  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 , which must be subjectively chosen in the case of the 3PLF-fixed and the 2PLF-maturity. is ideally chosen based on detailed study of the ovarian and uterine cycles (T. I. Walker 2005), or alternatively based on the proportion of mature females observed to be in maternal condition during sampling (Baremore and Hale 2012; Harry, Tobin, and Simpfendorfer 2013; Fabian I. 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 in each simulation. was chosen as the proportion of females in maternal condition above a the length at which of females were mature, . In some cases this procedure failed due to there being no maternal females in the simulated data set meeting this criteria. If this occurred, was used, followed by , 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.

### Reproductive output

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

where and are the embryonic sex ratio and natural mortality rate (Table 1) and is the age-specific reproductive rate which incorporates (Xiao and Walker 2000).

### 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 and remained within specified bounds (). 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 , and . Bias was quantified using the mean relative error, and precision using the mean absolute relative error, . 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.

### 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 ( = 33 years) and slow growing species () 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; Piercy, Murie, and Gelsleichter 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 estimated and fixed at 0.5 and 0.33, respectively.

# Results

## Simulation study

Parameter estimation was generally straightforward; with sample sizes a success rate of was achieved in all scenarios (Figure 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 was always fixed at 1. In addition to convergence failures, 12 simulations also generated insufficient maternal data (zero or one maternal females in the simulated data), and were discarded.

Generally when using the 3PLF methods model performance declined as the periodicity of the reproductive cycle increased. The nature of this problem can be seen in the positive correlation between the and parameters whereby affects the magnitude and direction of bias in these parameters (Figure 2). With lower values of it was apparently more difficult for the model to separate the point of inflection in the logistic model and the upper asymptote. As true underlying decreased there was a greater potential for positive bias in (Figure 2).

![Bias (per cent relative error) in parameter estimates for \hat{L'_{50}} and \hat{P_{Max}} for 3PLF methods. Each point represents parameter estimates from one iteration of simulated data. Bias tended to increase as the true underlying P_{Max} decreased.](data:application/pdf;base64,)

Bias (per cent relative error) in parameter estimates for and for 3PLF methods. Each point represents parameter estimates from one iteration of simulated data. Bias tended to increase as the true underlying decreased.

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

![Precision (per cent absolute error) in parameter estimates of \hat{P_{Max}} for 3PLF methods. Large sample sizes were needed to accurately estimate \hat{P_{Max}} and precision decreased as the duration of the reproductive cycle increased](data:application/pdf;base64,)

Precision (per cent absolute error) in parameter estimates of for 3PLF methods. Large sample sizes were needed to accurately estimate and precision decreased as the duration of the reproductive cycle increased

While the 3PLF-fixed method was in some cases able to reduce bias at lower sample sizes, a trade off in the use of this method was poorer interval coverage (Figure 4, Figure S6). For most simulations, interval coverage for 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 and .

![Interval coverage for \hat{L'_{50}} for 3PLF methods (high selectivity scenarios). Figure shows the percentage of simulations where the true parameter value fell within the 50% bootstrap confidence interval.](data:application/pdf;base64,)

Interval coverage for for 3PLF methods (high selectivity scenarios). Figure shows the percentage of simulations where the true parameter value fell within the 50% bootstrap confidence interval.

Differences in life history and gear selectivity played an important role in the ability to obtain precise and unbiased maternity parameters. Certain combinations of variables in the simulated data resulted in captures of few females in maternal or immature condition making parameter estimation difficult (Figure S8, Figure S9). These effects were not necessarily consistent between species and seemed to reflect differences in the underlying population length structure. For example, in low selectivity scenarios for gummy sharks ~60% of individuals were immature compared to ~50% in the corresponding scenarios for school sharks (Figure S9). As decreased the proportion of maternal females in the analysis also decreased.

Overall, the 2PLF-maternity method performed the worst. Ignoring introduced a fixed bias in this parameter that increased in magnitude as reproductive periodicity increased (Figure S3). This manifested in an overestimation of that was exacerbated by gear selectivity effects (Figure S2). In contrast, using a maturity function to approximate the maternity function (2PLF-maturity method) resulted in relatively good performance. could usually be estimated with a higher precision than . For the gummy shark, where and were relatively similar, using the 2PLF-maturity method led to a constant underestimate of of approximately 2% and exceeding the performance of the 3PLF-methods at most sample sizes.

The effect of the different methods in ultimately calculating varied considerably and was also influenced by life history and selectivity characteristics. For school sharks, estimating , was the most effective way to minimize bias in most scenarios for the school shark (Figure 5, Figure S11). In contrast, using a fixed or substituting maturity parameters often led to better performance for the gummy shark (Figure 5, Figure S11).

![Performance of alternative maternity functions in minimising bias in calculations of R_0. The preferred method was that which minimised bias, |\text{relative error}| across 300 simulated datasets. Note 2PLF-maternity (Annual) scenarios were excluded for this comparison.](data:application/pdf;base64,)

Performance of alternative maternity functions in minimising bias in calculations of . The preferred method was that which minimised bias, across 300 simulated datasets. Note 2PLF-maternity (Annual) scenarios were excluded for this comparison.

Greater precision in calculating was achieved with the 3PLF methods, with the 3PLF-estimated method performing best in most scenarios tested (Figure 6, Figure S11). For gummy sharks the 3PLF-fixed method performed best at lower sample sizes and lower values of , consistent with decreasing performance of 3PLF methods as decreased (Figure 2, Figure 3).

![Performance of alternative maternity functions in accurately calculating R_0. The best performing method was that which minimised mean absolute error across 250 simulated datasets. Note 2PLF-maternity (Annual) scenarios were excluded for this comparison.](data:application/pdf;base64,)

Performance of alternative maternity functions in accurately calculating . The best performing method was that which minimised mean absolute error across 250 simulated datasets. Note 2PLF-maternity (Annual) scenarios were excluded for this comparison.

## 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 was 0.48 (Table 2). Despite having a sample size of > 600 mature females, the proportion of maternal individuals at length was still uncertain and was estimated to lie between 0.39 and 0.60 with 95% confidence. Comparison of 3PLF-fixed models with values of and showed much greater support for a biennial cycle ( = 14.15). The model with also outperformed the 3PLF-estimated method ( = 1.86). Given the fixed model had one fewer estimated parameters, both models had essentially the same level of support given the data (Burnham and Anderson 2002).

![Comparison of 3PLF-estimated and 3PLF-fixed methods used to estimate maternal parameters for sandbar shark, C. 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. P_{Max} was fixed at 0.5 in the lower panel](data:application/pdf;base64,)

Comparison of 3PLF-estimated and 3PLF-fixed methods used to estimate maternal parameters for sandbar shark, *C. plumbeus*, in the Gulf of Mexico and Western North Atlantic. Solid line is the expected proportion in maternal condition at length, . The grey shaded region denotes 95% confidence intervals based on bootstrap resampling. was fixed at 0.5 in the lower panel

# Discussion

Relatively few reproductive biology studies have used maternity functions to model maternal reproductive output in chondrichthyan fishes. Where they have been employed the approach has typically been to use a three parameter logistic function with a fixed, user-defined value for the upper asymptote, . Here we show that it is feasible to estimate from maternal data, in turn enabling statistical inferences on reproductive periodicity. Applying 3PLF models with estimated and fixed values of to simulated data showed that precision, bias, and confidence interval coverage often improved when was estimated. Using a fixed value for in some cases resulted in lower bias at low sample sizes. This study also demonstrated that recruitment can be overestimated when maturity data were used to approximate maternal data and if 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 to quantifying maternal reproductive output and future directions.

## 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 from data, but also identified some situations where it may be preferable to fix . In most scenarios sample sizes of at least 100 were needed for the 3PLF-estimated method to approach or exceed the performance of the 3PLF-fixed method. At sample sizes below this is therefore advisable to fix . Due to the decline in performance associated with longer reproductive cycles, larger sample sizes are desirable before attempting to estimate in species with a triennial or longer reproductive cycle.

While the estimation of maternity parameters in most simulations was possible, it was difficult to do so accurately. Outcomes of the simulation study suggested that samples sizes of would be needed to estimate with <10% MARE for a triennially reproducing species. This is a much larger error than is achievable from conventional logistic maturity analysis (Roa, Ernst, and Tapia 1999). In the case of the gummy shark this imprecision led to the 2PLF-maturity method performing comparably or better than the 3PLF methods in ultimately quantifying . Relatively wide confidence intervals were also obtained for in the empirical analysis for sandbar sharks, even with a sample size of > 1000. A similar sample size was used by Colonello *et al* (2016) to successfully estimate and maternity parameters for south Atlantic spiny dogfish. 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, Paesch, and Norbis 2010; Tribuzio and Kruse 2012).

In light of the data requirements suggested by this study, the current practice of using maturity parameters as a proxy for maternity parameters will likely still be the only option for numerous data-poor chondrichthyans. 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 is to . While several studies have shown these parameters to be similar (T. I. Walker 2007; Soto-López et al. 2018), is more frequently shifted to the right of (Braccini, Gillanders, and Walker 2006; Palacios-Hernández et al. 2020; Montealegre-Quijano et al. 2014; Colonello et al. 2016), and this length difference can equate to one or more years. For example, Harry *et al* (2013) found both spot-tail shark, *C. sorrah*, and Australian blacktip shark, *C. tilstoni*, began reproducing the year after reaching sexual maturity. Similarly, Fujiyama found to be 1.4 years older than 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 (effectively ignoring ) is likely to result in biased parameters and can also overestimate recruitment. While not widely used, this approach has been undertaken in several studies (Mejía‐Falla, Navia, and Cortés 2012; Baremore and Hale 2012; Baremore and Passerotti 2013; Rambahiniarison et al. 2018).

The success of any analysis using the 3PLF-estimated method, and its ability to outperform the 3PLF-fixed method, ultimately depends on the analyst choosing a suitable value for . In this study, the value for used in the fixed analyses was chosen based on the proportion of maternal females observed in the simulated data. The potential to introduce a greater level of bias in the analysis through the incorrect selection of should also be considered if using this approach.

## Empirical study

The empirical analysis carried out using data for the sandbar shark illustrates the potential for the 3PLF-estimated method to provide novel insights from maternal data. 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 longer at the population level. Reanalysis of these combined data sets using the 3PLF-estimated method, however, resulted in a maximum likelihood estimate of , more consistent with biennial cycle. Using AIC values to compare the relative plausibility of 3PLF-fixed models corresponding to biennial and triennial cycles also supported a biennial cycle.

This counter intuitive result may stem from the gradual attainment of asymptotic maternal status as a function of length. Maturity in sandbar sharks appears to occur over an extended period; and 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 may be reproducing less frequently, with the largest females potentially capable of reproducing biennially. Further work would be required to confirm this hypothesis, however, such an outcome would have implications for management of this stock; not only are larger females more fecund (Baremore and Hale 2012), they also reproduce more frequently. This implies removal of larger and older female sharks could have a disproportionately greater impact on population productivity.

## 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 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 .

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

More commonly, practitioners have chosen fixed values of the form , 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 that 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 from data avoids these decisions and enables uncertainty in this parameter to be included in subsequent population models.

Estimation of 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, *Rhinchodon 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 (Charlie 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 (Sulikowski et al. 2016).

A logical progression from estimating is the consideration of alternative functional forms for this parameter such as time- or space-varying or more complex length- or age-dependent forms. 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 potential to improve understanding reproductive strategies and is, many cases, of direct relevance to management.

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