Quantifying the known unknowns: estimating maximum intrinsic rate of population increase in the face of uncertainty

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Abstract

Scientists are often called upon to provide advice on the consequences of exploiting data-poor and potentially threatened sharks and rays. For species lacking detailed biological information, sensitivity to overfishing is often estimated using simple models that depend upon life history parameters. Yet, there has been little exploration of the degree to which uncertainty in life history parameters can influence demographic parameter estimates and therefore fisheries management options. We estimate the maximum intrinsic rate of population increase (r_{max}) for ten coastal carcharhiniform shark populations using an unstructured life history model that explicitly accounts for uncertainty in life history parameters. We also seek to understand which parameters most influenced the estimate of r_{max}. The median r_{max} estimate proved to be robust to the propagation of uncertainty of life history parameters when that uncertainty is symmetric around the parameters' point estimates, but accounting for uncertainty can lead to a wide range of plausible r_{max} estimates for any given species. While natural mortality M can considerably impact r_{max} estimates when its uncertainty is high it is very difficult to estimate this parameter directly, hence we focused on the two directly estimated parameters: age at maturity α_{mat} and annual reproductive output b. Uncertainty in age at maturity values was low, yet it still resulted in moderate uncertainty in r_{max} estimates. The model was particularly sensitive to uncertainty in annual reproductive output as b approached values of less than 5 female offspring per year, which is not unusual for large elasmobranchs and marine mammals. Furthermore, at very low b values (<1), there is a threshold that results in implausible r_{max} estimates when both M and α_{mat} are high. Managers and policy makers should be careful to restrict mortality on species with very low annual reproductive output <2 females per year. We recommend elasmobranch biologists to measure frequency distributions of litter sizes (rather than just a range) and age at maturity, as well as improving estimates of natural mortality of data-poor elasmobranchs.

Keywords: Bycatch, Carcharhinus, Chondrichthyes, Elasmobranchii, reference points, risk assessment, demography

1 Introduction

Many marine megafauna and predator populations are declining globally and are at increasing risk of local and regional extinction (Fowler *et al.*, 2005; Christensen *et al.*, 2014; Dulvy *et al.*, 2017). Sharks, rays, and chimaeras (class Chondrichthyes) play a complex role as marine predators, hence there is concern for potential indirect impacts of predator declines on marine ecosystems (Kitchell *et al.*, 2002; Heithaus *et al.*, 2008; Heupel *et al.*, 2014). They are often large-bodied, long-lived, late-maturing and produce few offspring (Compagno, 1990; Musick, 1999). Consequently, they tend to have low intrinsic rates of population increase and weak compensatory density dependence in juvenile survival (Compagno, 1990; Musick, 1999; Forrest and Walters, 2009); traits which make them less able to withstand over-exploitation (Kindsvater *et al.*, 2016).

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There are relatively few stock-assessed elasmobranch species (Simpfendorfer and Dulvy, 2017) even though they can be directly targeted (Jaiteh *et al.*, 2016, 2017) and are also caught as bycatch in longline fisheries targeting large finfish, coastal gill-net, and trawl fisheries (Kitchell *et al.*, 2002; Ellis *et al.*, 2005). Despite the large catch and high commercial value of elasmobranchs, our understanding of species-specific catches is poor because many species are not directly targeted (Stevens, 2000) but are considered valuable bycatch. Hence, accurate information on population trends is lacking for most species. These challenges to understanding sustainability of elasmobranch fisheries and using precautionary approaches for their management are compounded further by multi-species fisheries and poor species-specific monitoring (Barker and Schluessel, 2005; Lack and Sant, 2009; Dulvy *et al.*, 2017).

Many countries have recently adopted policy regulations that require them to assess fisheries according to an Ecosystem-Based Management (EBM) approach (Jennings and Rice, 2011; Rogers *et al.*, 2007). The EBM approach requires, among other things, the identification of safe ecological limits for bycatch species (Hobday *et al.*, 2011; Salomon and Holm-Müller, 2013). These species, which lack detailed stock assessments and are not the focus of targeted commercial extraction, are usually understudied, resulting in a dearth of information on their biology and demography. As such, the usual data-intensive stock assessment methods are not applicable for a large diversity of bycatch, which has led to a recent increase in the development of tools for the assessment of data-poor species (Brooks *et al.*, 2010).

Identifying which life history traits affect resilience to a range of fishing pressures is crucial for averting over-exploitation or extinction of data-poor species (Reynolds, 2003; Kindsvater *et al.*, 2016). Life history traits are interrelated due to the evolutionary constraints imposed by energy acquisition and processing (Law, 1979; Charnov, 1993). Some of these relationships, widely known as Beverton-Holt dimensionless ratios, can be used to predict other life history parameters and tied to population dynamics, albeit with considerable uncertainty (Dulvy and Forrest, 2010). The link between life histories and demography allows the use of life history traits to quantify a species' intrinsic sensitivity (Frisk *et al.*, 2001; Dulvy *et al.*, 2004; Reynolds *et al.*, 2005), which encompasses biological traits that, in conjunction with exposure to threatening processes, determine their vulnerability or extinction risk (Reynolds, 2003; Dulvy and Kindsvater, 2017). For example, age- and stage-structured models have been used to estimate the intrinsic sensitivity of numerous shark and ray species (e.g. Cortés, 2002; Mollet and Cailliet, 2002; Simpfendorfer, 2005). Such models depend heavily on age- and stage-specific estimates of growth, natural mortality and reproductive output, but such detailed information is often lacking for most elasmobranchs, particularly natural mortality (Miller *et al.*, 2003; Gedamke *et al.*, 2007). Alternatively, unstructured models do not require age- or stage-specific life history estimates and instead use single trait estimates. Unstructured models have the advantage of relying on simple assumptions on how fertility or survival may vary with age or stage, and have been used to estimate relative intrinsic sensitivity for numerous data-poor elasmobranch species (Smith *et al.*, 1998; García *et al.*, 2008; Simpfendorfer and Kyne, 2009).

Recently, there has been increasing awareness of the importance of considering multiple sources of uncertainty in demographic parameter estimation and risk assessment (Simpfendorfer *et al.*, 2011; Cortés *et al.*, 2014; Jaiteh *et al.*, 2016). In addition, demographic modelling frameworks quantify the degree of caution that should be exercised for their sustainable management and can have major implications for the conservation of species (Caswell *et al.*, 1998; Cortés, 2002; Cortés *et al.*, 2014). The two main sources of uncertainty that can be easily accounted for in a modelling framework are measurement error (or trait error), stemming from uncertainty in the empirical estimation of a life history parameter (Harwood and Stokes, 2003; Quiroz *et al.*, 2010), and coefficient error, which is derived from the uncertainty in the values of the coefficients of a model (Quiroz *et al.*, 2010, e.g., uncertainty around the intercept of a linear model, see). While multiple sources of uncertainty can be readily accounted for in stock assessments, this has not happened to the same extent in data-poor situations, particularly in commonly used unstructured models (for a recent example see Jaiteh *et al.*, 2016).

In this study, we use an unstructured derivation of the Euler-Lotka demographic model, which estimates the maximum intrinsic rate of population increase r_{max} (Myers *et al.*, 1997; Pardo *et al.*, 2016; Cortés, 2016). We address how measurement error in life history traits affects (1) uncertainty in productivity estimates, and (2) sensitivity of these estimates to uncertainty in each trait. We examine model performance under the estimated uncertainty of each required life history parameter for ten populations of comparatively well-studied ground sharks (order Carcharhiniformes) found in the Gulf of Mexico and northwest Atlantic Ocean. We selected these species as they are well studied and there is relatively good life history information for them. Specifically, we calculate uncertainty in r_{max} estimates through Monte Carlo resampling from probability distributions of the three input parameters required in the model: annual reproductive output, age at maturity, and instantaneous natural mortality. To assess sensitivity, we also compare models that only include uncertainty from individual life history traits.

2 Methods

[Figure 1 about here.]

We used a Monte Carlo simulation model (Fig. 1) based on published information on the biology of a species to iteratively estimate maximum intrinsic rate of population increase r_{max} using a derivation of the Euler-Lotka model (Cortés, 2016; Pardo *et al.*, 2016). The model starts with the data required (Values for age at maturity α_{mat}, maximum age α_{max}, litter size l, and breeding interval i ("Data" section in Fig. 1), which are then used to define probability distributions for each parameter (except breeding interval whose value is fixed, see "Probability distributions" in Fig. 1). Values for age at maturity, maximum age, and litter size are then drawn from these distributions (see "Parameters drawn" in Fig. 1), and used to estimate natural mortality M and annual reproductive output b (see "Model inputs" section), which in turn are required to obtain an estimate of r_{max} (blue box in Fig. 1). The drawing of parameters from distributions is repeated 20,000 times to obtain 20,000 r_{max} estimates (see inner loop in Fig. 1). Finally, we repeat the whole process after replacing the probability distributions of each parameter with a fixed value to assess the sensitivity of the model to uncertainty in α_{mat}, b, and M (see outer loop in Fig. 1). We apply this model to ten populations of ground sharks (order Carcharhiniformes) to examine how the uncertainty in traits underlies uncertainty in r_{max}.

2.1 Life history data

The population-specific life history information required for this simulation model consists of age at maturity (range of years), maximum age (in years), ranges of litter size (in number of female pups), and breeding interval (in years) (Table 1, Fig. 1 "Data" section).

[Table 1 about here.]

The annual reproductive output of females (b) was calculated as $b = 0.5 * l/i$, where l is litter size (in numbers of males and females) and i is breeding interval (in years). Annual reproductive output estimates were derived from uniform distributions constrained by the minimum and maximum litter sizes published in the literature. This was necessary because empirical distributions of litter sizes are lacking for most elasmobranchs. We assumed a sex ratio of 1:1 to calculate numbers of females only per litter. Age at maturity (α_{mat}) estimates were derived from uniform distributions constrained between the minimum and maximum ages at maturity published in the literature (Table 1).

Instantaneous natural mortality M was estimated using the reciprocal of average lifespan ($M = {}^{1}\!/\!_{\omega}$), with average lifespan ω defined as the midpoint between age at maturity and maximum age ($\omega = \frac{\alpha_{mat}+\alpha_{max}}{2}$), for rationale see Pardo *et al.* (2016). Given that we obtained a distribution of age at maturity values for each population (see above), we used this uncertainty in age at maturity as the basis to estimate uncertainty in M, thus uncertainty of M was iteratively estimated using the same age at maturity distribution described above. Uncertainty in instantaneous natural mortality M had very little influence on r_{max} compared to the effect of uncertainty in age at maturity α_{mat} and annual reproductive output b; however, this is an artifact of the constrained range of M values produced by our estimation method. When accounting for uncertainty in natural mortality using the reciprocal of lifespan equation, we only included uncertainty in age at maturity as it is difficult to set a plausible range for maximum age. These narrow estimates of M (see Fig. S2d in Supplementary Materials) resulted in uncertainty in M having a very small effect on r_{max} estimates (see Results). We could increase the degree of uncertainty in M estimates, yet this increase would be arbitrary. We explored an alternative scenario where we arbitrarily increase uncertainty in our M estimate and as expected, its importance on r_{max} estimates increased considerably (see "Alternative scenario with a more uncertain M" in Supplementary Materials). The effect of uncertainty in M on r_{max} estimates will depend on the M estimator used and the degree of uncertainty associated with it (Then *et al.*, 2015). Because of the difficulties of specifying an adequate level of uncertainty in M as well as how resource intensive it would be to obtain better estimates of M, we focus our analysis on the effects of including uncertainty in the other parameters required to estimate r_{max}: α_{mat} and b.

2.2 Estimating r_{max}

We estimated the maximum intrinsic rate of population increase r_{max}, which in theory, occurs at low population sizes (i.e., in the absence of density dependence) whereupon it is equivalent to the fishing mortality required to drive a population to extinction F_{ext} (Dulvy *et al.*, 2004; Gedamke *et al.*, 2007; Cortés *et al.*, 2014). These two metrics are equivalent because, in order for a species to become extinct from fishing, fishing mortality needs to be to equal or exceed the maximum population growth rate ($F_{ext} \geq r_{max}$). Unlike previous estimates of r_{max} for chondrichthyans (García *et al.*, 2008; Dulvy *et al.*, 2014b), this equation accounts for juvenile mortality which has been previously overlooked (Pardo *et al.*, 2016; Cortés, 2016)

$$l_{\alpha_{mat}} b = e^{r_{max} \alpha_{mat}} - e^{-M} (e^{r_{max}})^{\alpha_{mat}-1} \tag{1}$$

where $l_{\alpha_{mat}}$ is survival to maturity in the absence of fishing and is calculated as $l_{\alpha_{mat}} = (e^{-M})^{\alpha_{mat}}$. Because $l_{\alpha_{mat}}$ is derived from M and α_{mat} we did not examine the effect of uncertainty in $l_{\alpha_{mat}}$ independently. Equation 1 is equivalent to equation 8 in (Myers and Mertz, 1998) which assumes age at selectivity (i.e., age at which they begin to be captured) is 1. We used Monte Carlo simulation to propagate uncertainty of input parameters. We drew parameters from their respective distributions iteratively 20,000 times, and solved for r_{max} (inner loop in Fig. 1)

We calculated two metrics that quantify uncertainty in the estimation of r_{max}. We first calculated the range between the 2.5% and 97.5% quantiles, which encompasses 95% of the r_{max} values in each distribution and we refer to as the 95% quantile interval. In order to compare variation for parameters of different magnitudes, we also calculated a coefficient of variation (CV, %) by dividing the mean by the standard deviation of each distribution.

2.3 Model sensitivity

To assess how uncertainty in each parameter affected estimated of r_{max}, we repeated the Monte Carlo simulation for each of the seven possible model combinations with uncertainty in: (i) only b, (ii) only α_{mat}, (iii) only M, (iv) $b + \alpha_{mat}$, (v) $b + M$, (vi) $\alpha_{mat} + M$, and (vii) a full model of $b + \alpha_{mat} + M$ (Fig. 1g).

In order to visualise the parameter space of r_{max} values created by ranges of α_{mat}, b, and M, we created two-dimensional contour plots, showing r_{max} estimates along gradients of α_{mat} and b, plotted separately for three levels of M: low $M = 0.05$ year^{-1}, medium $M = 0.1$ year^{-1}, and high $M = 0.2$ year^{-1}. We chose these three values of M as they span the natural mortality values we estimated for the ten shark populations examined.

All models were built in R version 3.2.4 (R Core Team, 2016). The r_{max} equation was solved using the `nlminb` optimisation function by minimising the sum of squared differences.

3 Results

3.1 Estimation of r_{max} and comparison of uncertainty in input parameters

The median r_{max} estimates were robust to uncertainty in all populations examined likely due to the symmetric uncertainty in the underlying parameters. As expected, uncertainty in r_{max} estimates varied considerably among species as a result of uncertainty in the underlying traits (Fig. 2).

Estimates of r_{max} are most sensitive to uncertainty in annual reproductive output b (Fig. 2). This is particularly pronounced in the least fecund species (Fig. 3b), that is, those with ranges of annual reproductive output b less than 5 such as the Finetooth Shark *C. isodon* ($b = 2.7$; Fig. 2b) and Blacknose Shark *C. acronotus* ($b = 1.8$; Fig. 2c) as these species had larger differences in coefficients of variation between b and α_{mat} (Table 2).

[Figure 2 about here.]

[Figure 3 about here.]

By focusing on the Atlantic Sharpnose Shark *R. terraenovae* we see that the uncertainty r_{max} values for a model only incorporating uncertainty in b is approximately twice as great as those in the model only incorporating uncertainty in α_{mat} (Fig. 2i).

For this species the coefficient of variation (CV) in r_{max} estimates is 32% when only accounting for uncertainty in b compared to 10% when only accounting for uncertainty in α_{mat} (Table 2). While the ranges of plausible age at maturity values were low for all ten populations examined when compared with variation in the other traits (see Fig. 2b in Supplementary Materials), they still resulted in considerable uncertainty in r_{max} estimates (Fig. 2). Furthermore, CVs of r_{max} estimates were moderately higher in species with lower estimates of α_{mat}, which are often thought to be relatively resilient to fishing, than those with higher α_{mat} estimates (Fig. 3a). The CV of r_{max} estimates increased as average b values of decreased (Fig. 3b). The species in the lower left corner of Fig. 3b that have low b values but do not have high variability in r_{max} CV are *C. leucas* and *C. brevipinna*; these species have the highest minimum litter sizes among those with low b values (see Table 1). Thus, CV is reduced as parameter draws of litter size are very constrained and never below six, which result in b estimates that are also constrained (hence low CV in r_{max} estimates) but that never approximate zero.

For all ten populations, the full model incorporating all uncertainties ($b + \alpha_{mat} + M$) had a slightly smaller CV than the $\alpha_{mat} + b$ model due to the close correlation between α_{mat} and M (Table 2). This same pattern exists when comparing models with just α_{mat} versus $\alpha_{mat} + M$.

Accounting for uncertainty in life history parameters is important: theoretical biological reference points based on the 2.5% quantile of r_{max} (equivalent to F_{ext}) were on average 60% lower when all sources of uncertainty were accounted for than when the deterministic model was used (Fig. 4).

[Figure 4 about here.]

[Table 2 about here.]

3.2 Model sensitivity

The interactive effects of annual reproductive output and age at maturity on r_{max} are nonlinear and vary based on the values of natural mortality (M = 0.05, 0.1, 0.2 year^{-1}; Fig. 5). Overall, r_{max} drops steeply at low b values regardless of α_{mat} or M (bottom left corner of all plots in Fig. 5). At medium to high values of annual reproductive output, the estimate of r_{max} becomes increasingly sensitive to variation in age at maturity. With increasing M values, there are increasing combinations of α_{mat} and b values that result in implausible r_{max} values ($r_{max} \leq 0$; red areas in Fig. 5b & c). This "implausibility" threshold is particularly apparent when natural mortality M is less than 0.2 year^{-1}, b is very low ($b < 1$), and α_{mat} is over 5 years (Fig. 5b & c). Nonetheless, it is highly unlikely that any species have this combination of life histories.

[Figure 5 about here.]

4 Discussion

The availability of simple methods for estimating key population parameters has opened the door to comparative risk assessment of a wider range of bycatch species (Stobutzki *et al.*, 2002; Hobday *et al.*, 2011; Dulvy *et al.*, 2014a). One such simple method is the Euler-Lotka approach to estimating the maximum intrinsic rate of population increase using point estimates of three life history traits (García *et al.*, 2008; Hutchings *et al.*, 2012; Dulvy *et al.*, 2014a). However, all life history parameters are estimated with some associated uncertainty. Here, we show that the degree of uncertainty in life history parameters has a considerable effect on the distribution of the resulting range of maximum intrinsic rate of population increase, but little effect on median values. Fully propagating the uncertainty in natural mortality M, age at maturity α_{mat}, and annual reproductive output b, increased the coefficient of variation of r_{max} values by between 11 and 46% (Table 2). These findings have important implications for the use of r_{max} estimates to set fishing limits for sharks and other data-poor species (Fig. 5). Acknowledging the level of uncertainty associated with estimates is crucial when using the precautionary approach, as the degree of risk associated with specific management practices can be estimated (Harwood and Stokes, 2003; Artelle *et al.*, 2013).

As we have shown, r_{max} is particularly sensitive to differences in annual reproductive output, particularly for species with very low annual reproductive output ($b < 5$ females per year; Fig. 3b). That demography is influenced by fecundity of the least fecund species is apparent from some demographic models, but it depends on how reproductive output is parameterised. Our finding is consistent with that of more data-intensive age-structured models. For example, an age-structured model of dogsharks (order Squaliformes) revealed that biological reference points can be strongly influenced by their low fecundity (Forrest and Walters, 2009). In contrast, we caution that another commonly used unstructured model—the rebound potential model (Au and Smith, 1997)—is agnostic to annual reproductive output as the values of b on both sides of the equation cancel out and hence are not considered mathematically in this model (Au *et al.*, 2015). This difference in the implementation of annual reproductive output (b) between two superficially similar unstructured models may help explain differences in species' sensitivity between these methods. For example, Ward-Paige *et al.* (2013) used the rebound potential model to compare the sensitivity of manta rays (*Mobula spp.*) to that of other elasmobranchs. They found that manta rays were intermediate in sensitivity (r), are more similar to Spinner Shark (*Carcharhinus brevipinna*) or Silky Shark (*C. falciformis*). However, when the very low annual reproductive output of manta rays is accounted for using r_{max}, they were found to have one of the lowest population growth rates r_{max} observed in chondrichthyans (Dulvy *et al.*, 2014a). The annual reproductive output of manta rays is highly uncertain, but with the potential of skipped mating, reproductive output may be as low as one female pup every second or third year (Couturier *et al.*, 2012; Marshall and Bennett, 2010), resulting in r_{max} varying from 0.089 to 0.139 year^{-1} (Dulvy *et al.*, 2014a). Being aware of major differences in the implementation of annual reproductive output in different models is important when choosing the model best suited to the research question.

We show that the highest demographic uncertainty occurred in species with very low annual reproductive outputs—less than five female pups per year. Many elasmobranchs have this reproductive rate (Cortés, 2000). Nonetheless, we reached this conclusion based on assuming a uniform distribution of litter sizes, but they are unlikely to be uniform in the real world. For us to explore the validity of this assumption requires a better understanding of the empirical distribution of litter sizes. By having more accurate distributions of litter size, the uncertainty in annual reproductive output b is likely to decrease, and thus result in more accurate estimates of r_{max}. Hence, we urge biologists to report frequency distributions of individual litter sizes: choosing adequate distributions based on empirical data will result in reduced uncertainty in annual reproductive output. As we have shown in our study, this has considerable downstream effects in the uncertainty of r_{max} estimates.

The updated model for estimating r_{max} includes juvenile survival which is derived from adult natural mortality M (Pardo *et al.*, 2016). Yet, because of the known trade-off between offspring size and litter size (Smith and Fretwell, 1974; Hussey *et al.*, 2010), the least fecund species often have the largest offspring. As is typical for marine fishes, such larger offspring will likely have a greater survival probability than the smaller offspring of species with r_{max} among species. An example of this can be illustrated by comparing the Spinner Shark (*C. brevipinna*) with the Scalloped Hammerhead (*S. lewini*). The Spinner Shark litter size ranges between 3–15 individuals born between 60 and 80 cm in length, while the Scalloped Hammerhead has a larger litter size ranging between 13–41 individuals but which are born smaller, between 45 and 50 cm in length (Last and Stevens, 2009). Spinner Sharks likely have lower young-of-year survival rates than Scalloped Hammerheads, resulting in a higher survival to maturity and thus higher r_{max} estimates than those from our study. Additionally, local-scale differences in habitat have also been shown to relate with M (Heupel and Simpfendorfer, 2011). Nuances in relation to differential juvenile mortality among species are not accounted for in our model but should be the focus of further study.

Natural mortality is one of the most important parameters in fisheries modelling but one of the hardest to estimate (Pope, 1975; Vetter, 1988; Kenchington, 2014). Our estimates of r_{max} are relatively insensitive to uncertainty in M for shark-like life histories (Figs. 2) because of the method we used for accounting for uncertainty in M. For example, the CV of r_{max} estimates for *R. terraenovae* is 1% when accounting for uncertainty in only M yet it increases to 31.5% if only uncertainty in annual reproductive output is taken into account (Table 2). Our finding is similar to Au *et al.* (2015), who showed that

M had only a minor role in the estimation of rebound potential when compared with α_{mat}. However, as natural mortality is a difficult parameter to estimate it is unrealistic for its uncertainty to be narrowly constrained as it was with our method. This begs the question of how to assess how much uncertainty in M is “enough” or “too much”.

Furthermore, there is considerable debate as to which empirical model should be used to estimate natural mortality M (Hewitt and Hoenig, 2005; Quiroz *et al.*, 2010; Then *et al.*, 2015). Here, we used the reciprocal of average lifespan; however, other methods, such as Chen and Watanabe (1989) and Peterson and Wroblewski (1984), have been used as they provide varying values of M through ontogeny as required for age-structured demographic modelling (Pardo *et al.*, 2012). We note the differences in r_{max} estimates in our study compared to Cortés (2016) arise because Cortés uses the minimum estimate of a range of mortality estimators, whereas we use one simple method for consistency and transparency.

Improving natural mortality estimates, and identifying the best indirect estimator, would require the use of data-intensive methods such as extensive catch data to analyse catch curves, mark recapture experiments, virtual population analyses (VPA), or even fully integrated stock assessments (Kenchington, 2014; Sippel *et al.*, 2017). Therefore, research efforts on data-poor species might be better spent improving on life history estimates of the other parameters age at maturity and annual reproductive output. Further increasing uncertainty in natural mortality (by an arbitrary amount) does increase uncertainty in r_{max} (see Supplementary Materials). While in our study M is relatively unimportant, more complex age- and stage-structured models consistently show that juvenile mortality has important contributions to population growth rate (Cortés, 2002; Frisk *et al.*, 2005) and realized recovery potential (Hutchings and Kuparinen, 2017). This difference in importance of M needs to be borne in mind when comparing across demographic model types.

While age-dependent mortality estimates are needed for matrix models, only average natural mortality values (and the uncertainty around them) are needed for unstructured models. Natural mortality estimates in which correlation of parameters can be accounted for (e.g., Pauly, 1980) reduced uncertainty of estimates and their error when applied to elasmobranchs (Quiroz *et al.*, 2010). A recent study by Then *et al.* (2015) suggests that the Pauly (1980) mortality model should not be used, and instead a new variant that eliminates temperature from the equation is preferred. Regardless, our results showing the effect of uncertainty in age at maturity and annual reproductive output on r_{max} estimates are likely to be robust to the choice of natural mortality estimator used.

We show that accounting for uncertainty in trait estimates is important as it can lead to much more conservative estimates of fishing limits than if uncertainty is ignored. Incorporating uncertainty also considerably increased the potential range of maximum population growth rate r_{max} estimates in these relatively well-studied sharks. Furthermore, we urge managers and policy makers to focus on restricting mortality in species with annual reproductive outputs <2 females per year, particularly if this mortality occurs among younger age classes. For data-limited species, we recommend incorporating all sources of uncertainty in life history parameters, especially when lacking directly-estimated life history parameters. This uncertainty in r_{max} can be reduced by understanding the correlation in life history parameters, and we encourage researchers studying chondrichthyan reproductive biology to report distributions of litter sizes and offspring sizes as to reduce uncertainty in these parameter distributions and thus better quantify known uncertainty in demographic productivity models.

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Table 1: Values and sources of life history parameters used to estimate r_{max} for the ten populations studied. Note that annual reproductive output b is not obtained directly from the literature but is estimated from litter size and breeding interval.

Species	Litter size min	Litter size max	Breeding interval	Mean b	Age at mat. min	Age at mat. max	Max. age	Source
Carcharhinus acronotus	1	6	2.0	1.8	4.0	5.0	19.2	Driggers *et al.* (2004a,b); Barreto *et al.* (2011); Branstetter (1990)
Carcharhinus brevipinna	6	10	2.0	4.0	7.0	8.0	16.0	Cortés (2002); Branstetter (1987a)
Carcharhinus isodon	2	6	1.5	2.7	3.3	5.3	8.0	Castro (1993); Carlson *et al.* (2003); Driggers and Hoffmayer (2009)
Carcharhinus leucas	6	12	2.0	4.5	17.0	19.0	31.0	Branstetter (1990); Cliff and Dudley (1991); Cortés (2002); Branstetter and Stiles (1987)
Rhizoprionodon terraenovae	1	12	1.0	6.5	2.8	3.9	9.0	Parsons (1983); Bigelow and Schroeder (1948); Branstetter (1987b); Parsons (1985)
Sphyrna lewini	12	38	1.0	25.0	13.0	15.0	36.0	Branstetter (1987c); Drew *et al.* (2015); Stevens and Lyle (1989); Cortés (2002)
Sphyrna mokarran	13	42	2.0	13.8	7.4	9.5	31.7	Harry *et al.* (2011); Compagno (1984); Stevens and Lyle (1989); Last and Stevens (2009)
Sphyrna tiburo	3	15	1.0	9.0	2.9	4.0	7.5	Lombardi-Carlson *et al.* (2003); Cortés (2002)
Carcharhinus limbatus ATL	2	10	2.0	3.0	5.7	7.7	21.6	Carlson *et al.* (2006); Branstetter (1990); Castro (1996)
Carcharhinus limbatus GULF	2	10	2.0	3.0	4.7	6.7	14.4	Carlson *et al.* (2006); Branstetter (1990); Castro (1996)

Table 2: Coefficients of variation (CV) in r_{max} estimates of seven models with varying levels of uncertainty in age at maturity, natural mortality and annual reproductive output for the ten shark populations examined. Means, medians and standard deviations are also presented for the full model which accounts for uncertainty in all three parameters.

	Model Coefficient of Variation (CV, %)							$b + \alpha_{mat} + M$ (Full) Model		
Species	b	α_{mat}	M	$b + \alpha_{mat}$	$b + M$	$\alpha_{mat} + M$	$b + \alpha_{mat} + M$	Mean	Median	St.Dev
Carcharhinus isodon	25.0	16.4	4.1	30.0	25.4	12.3	27.9	0.197	0.188	0.061
Carcharhinus limbatus GULF	25.2	10.2	1.4	27.3	25.2	8.8	26.8	0.195	0.195	0.015
Rhizoprionodon terraenovae	31.5	9.6	1.0	33.1	31.6	8.7	32.8	0.185	0.185	0.052
Carcharhinus limbatus ATL	21.8	7.9	0.7	23.2	21.8	7.2	23.0	0.112	0.112	0.009
Carcharhinus acronotus	31.9	5.5	0.5	32.5	31.9	4.9	32.4	0.428	0.405	0.133
Carcharhinus brevipinna	7.1	3.9	0.5	8.1	7.1	3.4	7.8	0.240	0.239	0.021
Carcharhinus leucas	7.4	3.3	0.4	8.1	7.4	2.8	7.9	0.316	0.315	0.037
Sphyrna tiburo	21.0	9.8	1.1	23.2	21.0	8.7	22.8	0.462	0.453	0.103
Sphyrna mokarran	9.7	6.6	0.2	11.7	9.7	6.4	11.6	0.202	0.197	0.045
Sphyrna lewini	7.9	4.0	0.2	8.8	7.9	3.8	8.7	0.204	0.199	0.053

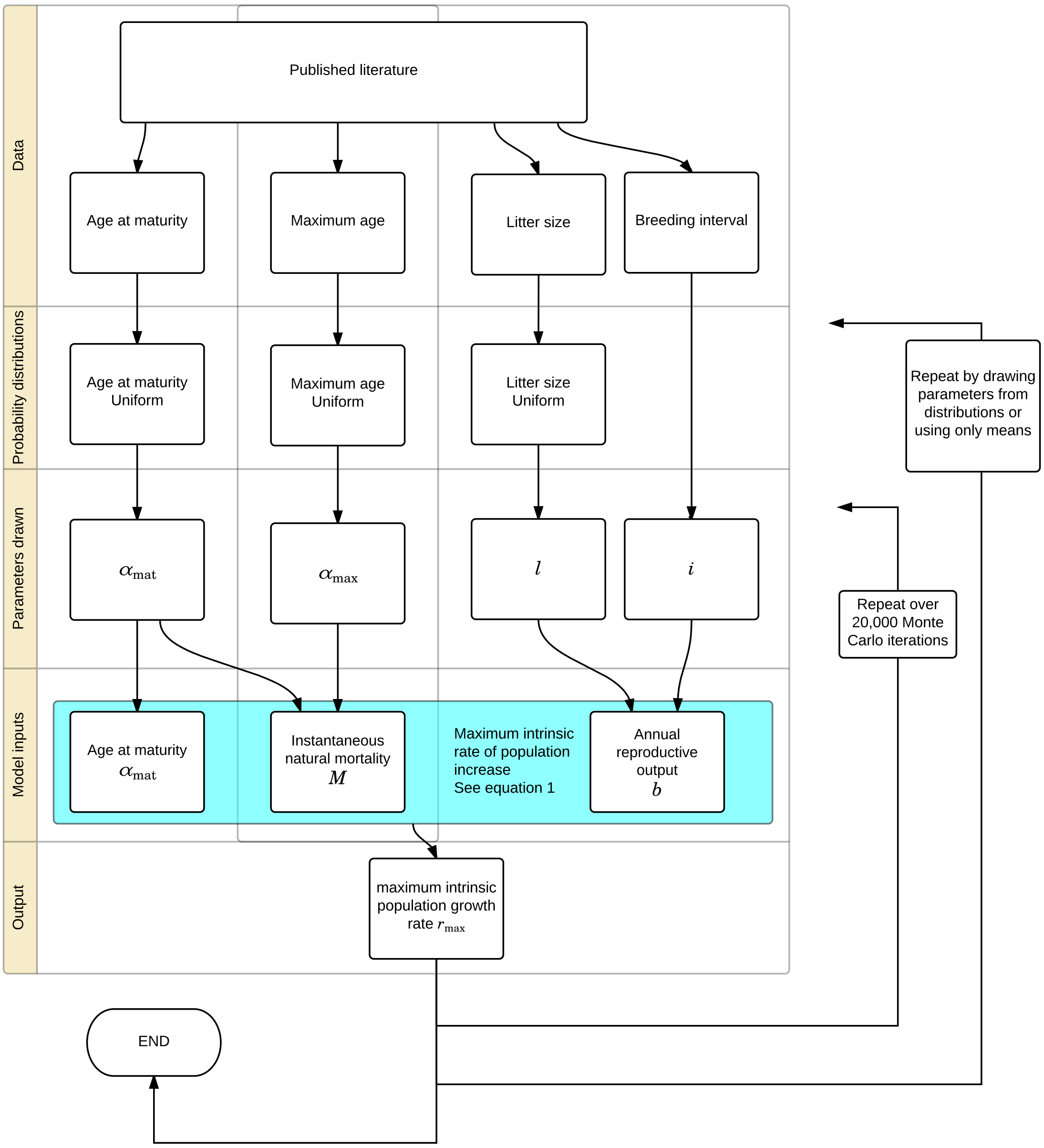

Figure 1: Flow chart illustrating the structure of the Monte Carlo simulation model used in this study. The model starts with the data required (Values for age at maturity α_{mat}, maximum age α_{max}, litter size l, and breeding interval i), which are then used to define probability distributions for each parameter (except breeding interval whose value is fixed). Values for age at maturity, maximum age, and litter size are then drawn from these distributions, and used to estimate natural mortality M and annual reproductive output b, which in turn are required to obtain an estimate of maximum intrinsic rate of population increase r_{max}. The drawing of parameters from distributions is repeated 20,000 times to obtain 20,000 r_{max} estimates. Finally, we replace the probability distributions of each parameter with a fixed value to assess the sensitivity of the model to uncertainty.

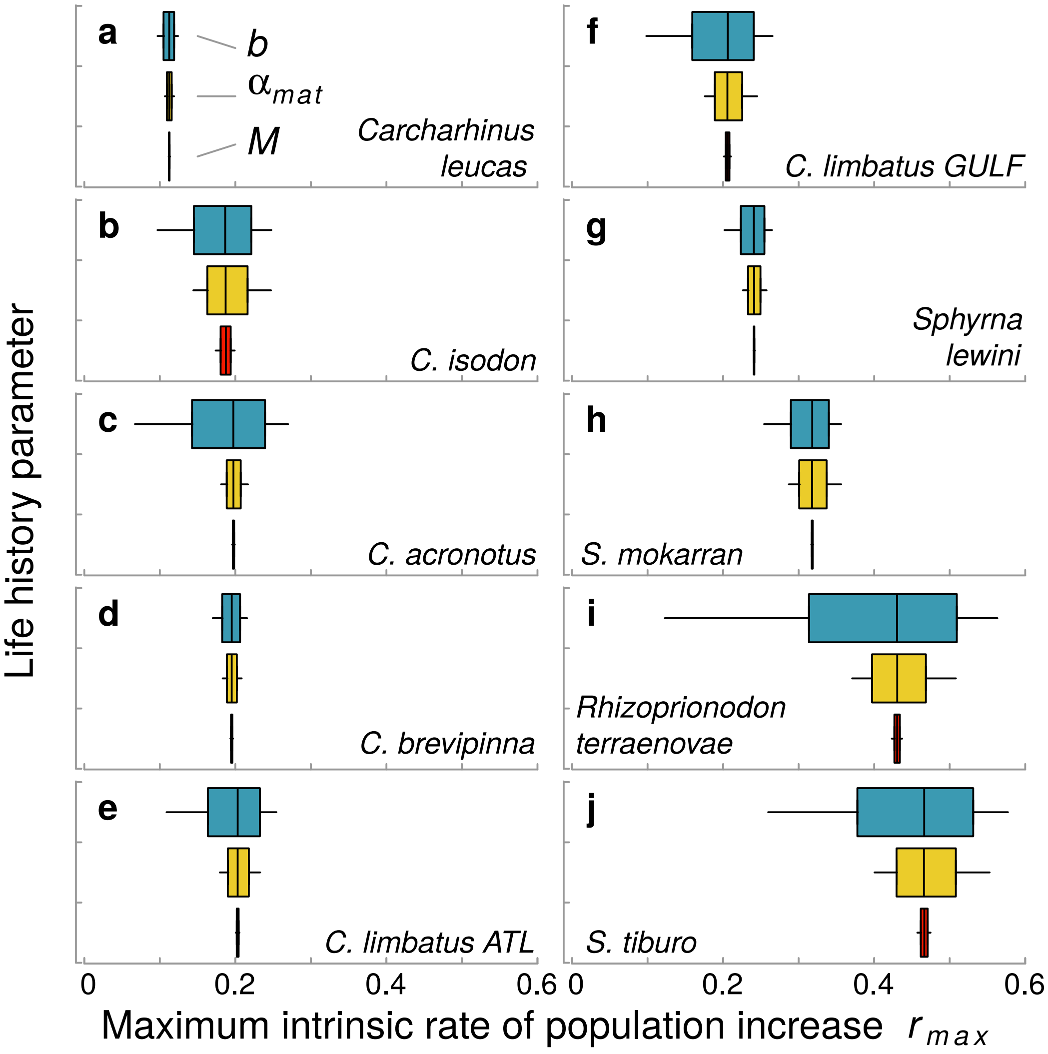

Figure 2: Predicted values of maximum intrinsic rate of increase r_{max} for ten different shark populations when including uncertainty in annual reproductive output b (blue box plots), age at maturity α_{mat} (yellow box plots), and natural mortality M (red box plots). Boxes indicate median, 25% and 75% quantiles, while the lines encompass 95% of the values (2.5% and 97.5% quantiles).

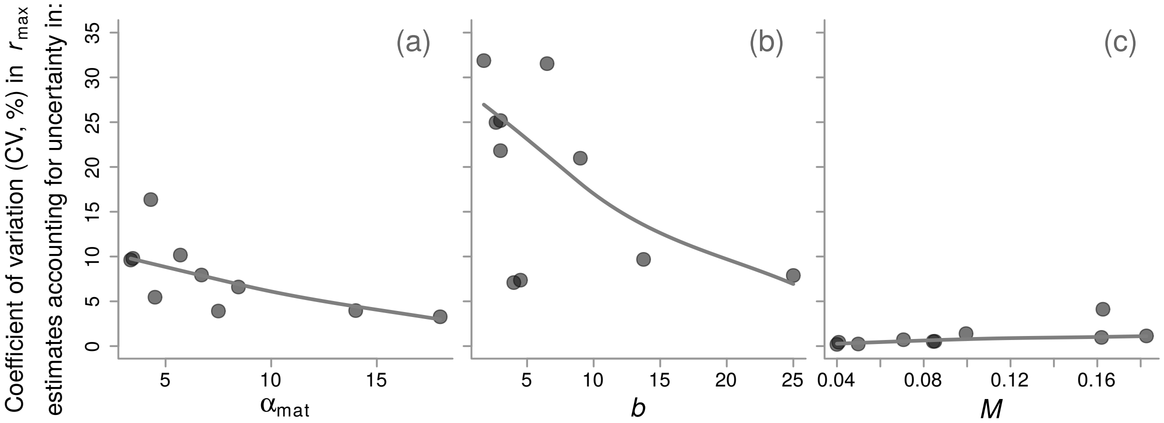

Figure 3: Coefficient of variation (CV, %) in r_{max} estimates for ten different shark populations when accounting for uncertainty in (a) age at maturity α_{mat}, (b) annual reproductive output b, and (c) natural mortality M, plotted against the median values of the respective life history parameter. Lines are loess-smoothed curves.

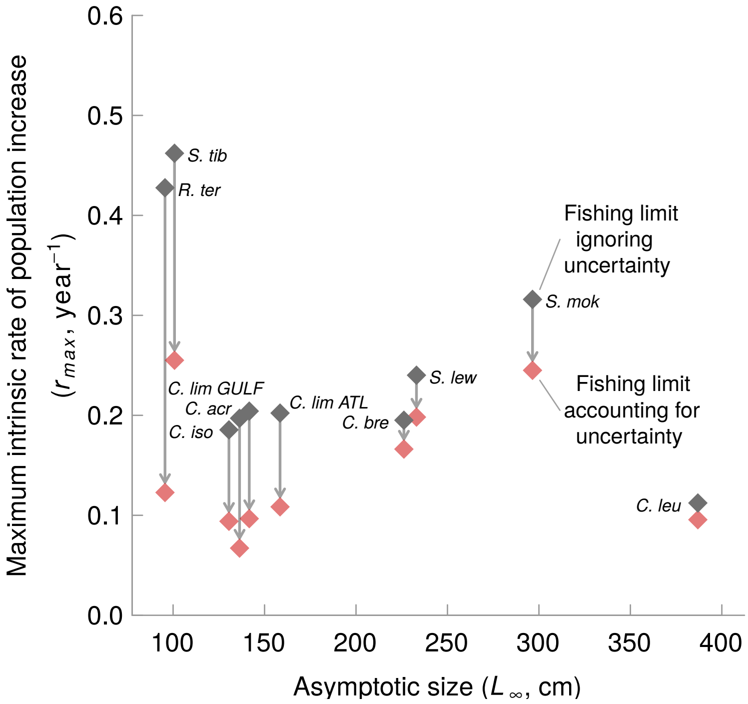

Figure 4: Comparison of potential fishing limits based on r_{max} when estimated with no uncertainty accounted for (grey diamonds) and when accounting for uncertainty from all sources in the model (using 2.5% quantile, red diamonds). Points were slightly jittered horizontally to avoid overlap. Note that r_{max} is equivalent to F_{ext}, i.e. the point at which fishing mortality is equal to the maximum rate of population increase.

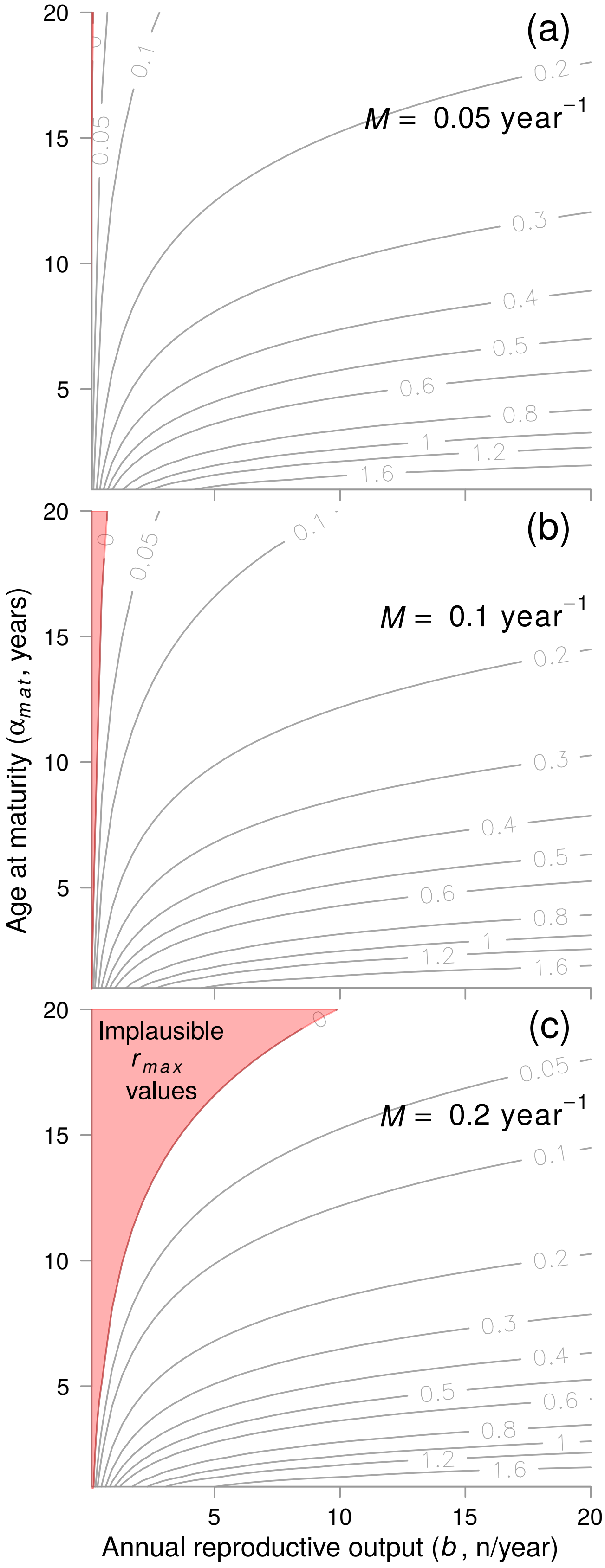

Figure 5: Contour plots of r_{max} values for varying ranges of age at maturity α_{mat} and annual reproductive output b, with values of instantaneous natural mortality M set as (a) low (0.05 year^{-1}), (b) medium (0.1 year^{-1}, and (c) high (0.2 year^{-1}).