# Estimated Maturity Ogives for Data-limited Sharks

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# Introduction

Sharks and rays form one of the ocean’s oldest and most diverse vertebrate lineages (Dulvy et al., 2014), and have long provided economic social and cultural benefits to people in many countries (Dulvy et al., 2017). Yet intensifying exploitation of these species in recent decades (Davidson et al., 2016) has resulted in population declines or even collapses in multiple regions (Baum et al., 2003; Ferretti et al., 2008; Lam and Sadovy De Mitcheson, 2011) and across habitat types (Dulvy et al., 2008; MacNeil et al., 2020).

Despite growing global concern for the future of elasmobranchs, few populations are subject to formal stock assessments (Cortés et al., 2012; Simpfendorfer and Dulvy, 2017). Shark and ray species are often taken as bycatch, or form relatively low-value fisheries which do not merit the investment necessary for data-intensive assessments (Cortés et al., 2006; FAO, 2008). Fisheries-dependent data is frequently unreliable, with catch figures misallocated or unreported (Clarke et al., 2006; Fischer, 2015). Elasmobranchs are therefore more often assessed using risk-based methods which use life history traits to estimate, for example, species rebound potential (Au et al., 2015) or intrinsic sensitivity to fishing (Reynolds et al., 2005).

Within elasmobranchs there is variability in data availability; although fishery-independent data tends to be more reliable compared to fishery-dependent data (Brooks et al., 2010), there are still many knowledge gaps in the life history of sharks, partly because they are so difficult to age (Frisk et al., 2001). Parameters which have not been directly observed can be estimated, however, using empirically demonstrated relationships (Thorson et al., 2017) also dulvy & forrest 2010. Life history traits interrelate in predictable ways because of the evolutionary constraints imposed by energy acquisition and use (Charnov, 1993); and the nature of these relationships has been well documented for fish and for sharks in particular (Cortés, 2000; Frisk et al., 2001). Thus, information can be stolen from better studied species and donated to data-limited species using a so-called ‘robin hood approach’ (Kacev et al., 2017).

Unstructured risk-based methods require data collected at the species or population level, rather than subdivided by age, and have the advantage of relying on simpler assumptions as well as having greater availability of information (Pardo et al., 2018). Most elasmobranch population models use unstructured demographic rates because of data limitations (Cortés et al., 2012). However, access to age-structured demographic information opens up a whole new suite of methods, which can, for example, produce reliable biomass reference points (Cortés and Brooks, 2018) or identify life stages which are more vulnerable to fishing (Mollet and Cailliet, 2002).

The age when fish reach maturity is a key life history characteristic used to calculate maximum population growth rate (Rmax), which in turn is central to describing population dynamics, establishing biological reference points and estimating the long term effects of mortality (Myers et al., 1999). As such, many studies have been dedicated to estimating Rmax (also referred to as extinction risk, or reproductive rate at low population size) in sharks and rays (Hutchings et al., 2012; Pardo et al., 2018; Reynolds et al., 2005). Age at maturity is often expressed as a single parameter, a50, which is the age at which 50% of a population reaches maturity (cite?). Even in studies which require age-structured data, the assumption is often made that all females mature at the same moment (knife-edge maturity) rather than fitting maturity data to an ogive (Cortés et al., 2012).

In this paper, we attempt to advance the field of elasmobranch risk-based assessment by predicting age-structured maturity data for less-studied species. We use Bayesian Hierarchical modelling to first describe the relationship of existing maturity ogives to other life history traits, and then predict new ogives for an additional suite of species. We limited our study to the family Carcharhinidae, a speciose family with both well-studied and data-limited members, in order to limit phylogenetically derived variation. Our predicted ogives can be used in future work to assess status of elasmobranchs which are in serious need of improved management but have been impossible to assess in the past.

# Methods

Part 1: Data Collection

1. Age-structured maturity data
   1. Stock assessments
   2. Papers
2. Trait covariates
   1. How chose candidate traits – papers describing relationships between shark or fish maturity and related factors.
      1. Most (all?) studies examining the relationship between life history traits look at unstructured data, therefore there were no papers explicitly measuring how S varies with other traits. However since S is a measure of how quickly species reach maturity, we assumed that traits related to individual growth (such as k) would be likely to help describe S
   2. How collected candidate traits
      1. fishbase
      2. shark traits
      3. shark refs
      4. google scholar
      5. fill in from closely related species (life history is phylogenetically constrained so that closely related species will have more similar parameters than distantly related species (Frisk et al., 2005)). Shark stock assessments often borrow data from similar species/use species complexes because there is not enough species-specific data available (NMFS, 2006)

how matched traits and maturity ogives

how chose traits – if more than one estimate of trait for same area, take average (as was done in Frisk 2001)

Part 2: Modelling

We developed a Bayesian hierarchical model to quantify the relationship between Carcharhinid maturity ogives and candidate life history variables at the family and at the stock scale. Maturity ogives are specified by two variables *a50* and *s* (equation 1), where *a* isage, *a50* is the age at which 50% of a population of sharks achieves sexual maturity, and *s* describes the steepness of the ogive (ref).

Both response variables were described using Normal distributions and were estimated simultaneously as two levels within the same model. The distribution of *a50* values were defined by a mean *Ga50* and a standard deviation Ϭa50 (equation 2). *Ga50* was described as a Uniform distribution and allowed to vary between 0 and 30, as the range of known Carcharhinid ages at maturity are 1 and 21 (FishBase2020). Ϭa50 was described using an Exponential distribution decaying from 1.

The distribution of steepness values was defined by a mean *Gs* and a standard deviation *Ϭs* (equation 6). The mean values of *S* where described using a Uniform distribution and allowed to vary between 0.01 and 10, meaning all curves must describe an increasing % maturity as age increases but can do so at different rates.

Covariates were applied at the level of *Ga50* and *Gs* as shown in equations 9 and 10.

Xx Life history traits were initially related to a50 and S because of previous research investigating various relationships between shark growth and other aspects of ecology and life history (go into more detail here, run through the papers cited in list of model params).

Explain how initial list of covariates was refined down to final list

* + - * + Ran a series of model versions
        + Removed covariates with no effect
        + Ran models with S and a50 separately

Summary table of input data? With candidate and chosen covariates, sources for mat data

The outcome space defined by these prior distributions combined with age-structured maturity data and related life history traits was sampled using a Hamiltonian Markov Chain Monte Carlo sampler. Modelling was carried out in Python using the PyMC3 package. Model performance was assessed by looking at convergence (Gelman-Ruben’s R-hat statistic), and through examining posterior traces for full exploration of the potential outcome space. Model fit was evaluated using Widely Acceptable Information Criterion (WAIC) and by plotting observed maturity values against the posterior distribution of maturity ogives.

Part 3: Predicted Ogives:

* Describe prediction method
* Describe process of assessing results
* Use Pardo et al 2018 to justify use of mean/median values for life history traits in prediction dataset. There is uncertainty around maximum age etc for shark species but generally this does not change the median value of calculated parameters such as Rmax (Pardo et al., 2018)

# Results

### Part 1: discuss model performance

* Maybe put a table of parameters, model versions with different parameters, WAIC values

Chart

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### Part 2: talk about effect of covariates

The forest plot (figure x) shows the relative direction and magnitude of the effect of each explanatory variable on a50 and on S, that is how much does each covariate affect a50 or S given the variation already explained by the other covariates. Offspring size and interbirth interval both had a positive effect on a50, revealing that species which produce larger offspring and which reproduce less frequently are likely to mature later than species producing smaller offspring on a yearly basis. Depth, trophic level, and maximum age also had a positive effect on a50. Species producing larger litters were likely to mature later than species with smaller litters, although this effect was not as clear because some of the posterior effect size distribution fell below 0. Similarly, maximum length was likely to have a positive effect on a50, although the size and direction of this influence is less certain as the distribution is wider than for other covariates and some of it falls below 0.

Chart, box and whisker chart

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Von Bertalanffy’s growth parameter K had a strongly positive effect on S, meaning that species which grow more rapidly are likely to have a steeper maturity curve. Maximum age also had a slightly positive effect. Conversely, the model showed trophic level to have a negative relationship with S, such that species which are higher on the food chain mature more gradually than those lower down.

Chart

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Chart

Description automatically generatedPart 3: predicted a50s and ogives

* Talk about performance of prediction script – why some species were able to predict more precisely than others (smaller range of values)
* Talk about species where observed a50 is outside the range of predicted a50. What traits probably contributed to this happening,
* Remember to take out or mark the species from the model input data

Chart, scatter chart

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* One more figure about out-of-sample species where the model fails?

# Discussion

1. Effects of covariates on a50

litter size (fecundity): species with larger litters mature later than species with smaller litters, which at first sounds counterintuitive because a life history theory would dictate smaller litters for longer-lived species, but actually this make sense because the model also includes maximum length. Once body size is accounted for, the effect of litter size is actually positive (take 2 sharks that are the same size, the one with the larger litter will mature later). A similar result was seen in Cortes 2000 (Cortés, 2000) where the relationship between litter size and offspring size reversed once maternal body size was accounted for.

interbirth interval (fecundity): the positive relationship between a50 and interbirth interval makes sense again because species which mature later usually have a large body size (Cortés, 2000; Holden, 1974) and therefore exhibit lower fecundity (Frisk et al., 2001; Jennings and Kaiser, 1998).

offspring size: Cortes 2000 finds there is a negative relationship between offspring size and number of pups (more pups = smaller individuals) when body size is accounted for. When not accounted for, there is a positive relationship between offspring size and number of pups.

amax: maximum age positively related to age at maturity throughout literature (Cortés, 2000; Frisk et al., 2001; Thorson et al., 2017), so results are consistent with previous work. Max age is perhaps the most direct determinant of age at maturity (not mediate through other characteristics) which is why the effect size is larger than all the other covariates.

trophic: trophic position is closely related to body size (Pauly et al., 1998) which is why a50 covariates with trophic level. Our results confirm this.

lmax: Body size is positively related to age at maturity in previous studies (Frisk et al., 2001; Jennings and Kaiser, 1998) and is here as well

depth: Species inhabiting deeper water usually have higher age of maturity, as a function of higher maximum age (García et al., 2008)

temp: Age at maturity decreases with increasing temperature (Myers and Mertz, 1997)

1. Effect of covariates on S

Repro: All the covariates that directly describe reproduction (litter size, interbirth interval, and offspring size) do not have an effect on K. Expected to have at least a slight negative relationship reflecting the tradeoff between reproduction and growth, but no effects observed.

K: K and S are both expressions of individual growth rate, so it makes sense that they are k is a good determinant of K

Amax: age is related to growth rate K in previous studies (Cortés, 2000; Frisk et al., 2001)

Lmax: Age is related to K (Cortes, Frisk) which is related to body size (Frisk et al., 2001; Jennings and Kaiser, 1998), so based on existing research it would make sense for S to decrease with increasing body size. However there was a very weak relationship in our model, indicating either that the relationship is too indirect to show up in the model results or the variation between carcharhinid species is too little

Trophic level: Trophic level is related to body size

* Talk about the idea that the S covs should be more related to growth than reproduction. K had a strong effect so that makes sense. Both growth and timing of maturity have to do with body size so it makes sense that rophic level has some effect, although it’s indirect. Maximum age again is indirectly related to S because sharks which reach higher max are usually larger, which in turn means they have a slower growth rate, but since this connection is mediated through two other traits it makes sense that the effect is so much larger for a50 than for S.
* Why is it that a50 is easier to predict than s? S has less variation than a50. Available covariates have more to do with reproduction than growth

Shape of S is dtaken from existing models which may have made unknwon assumptinos about the shape, not reflecting real biological variation. That’s why variation in s in our dataset is limited and why it is not explained well by most of the covariates

General comments:

Our model results as a whole reflect current thinking on life history as a balancing act between reproduction and growth, an idea first expounded in the 1950s by Beverton and Holt (Beverton & Holt 1959) and further developed with different species groups and larger datasets (Cortés, 2000; Thorson et al., 2017). The ratio between natural mortality and growth (M/K) is a Life History Invariant (LHI) which remains constant within taxonomic families, and necessitates a tradeoff between longevity and growth (Frisk et al., 2001). All of the covariate relationships with a50 and with S reflect some aspect of this essential biological reality, that energy is limited and therefore can be allocated only to a limited number of functions (Charnov 1993). Closely related species share similar life history traits because of their shared evolutionary history (Kindsvater et al., 2016), and sharks are generally characterised as species which prioritise longevity over growth. But there is still variation within families (Thorson et al., 2017), in the case of family Carcharinidae there is actually quite a lot of variation which means that the different species, though closely related, deserve individual attention and potentially different fisheries management strategies (Kindsvater et al., 2016; Simpfendorfer and Dulvy, 2017)

1. Predicted ogives

* Compare results to other predictive exercises: Frisk 2001, Thorson 2017, Holden 1974
* Why some of the out of sample results don’t work – what traits do tigers have e.g.g that make them hard to predict? and what does this tell us about the potential usefulness of this prediction exercise for future applications to other species?
* Talk about species with predicted ogives, what kinds of management improvements could be realised with this data

1. Implications of current study for shark conservation and management
2. Suggestions for further work

# Supplementary

Possible maturity ogives described by the null model and priors were visualised using prior predictive simulation (figure 1)

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Describe covariate choice for models

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Covariate** | **a50** | **Justification** | **S** | **Justification** |
| age\_max | x | Maximum age positively related to age at maturity (Frisk et al 2001, Cortes 2000) | x | Maximum age negatively related to growth rate K (Frisk et al 2001, Cortes 2000) |
| depth\_ave | x | Preferred depth positively related to age at maturity (Garcia et al 2008) | x | Preferred depth positively related to maximum age (Garcia et al 2008), maximum age negatively related to K (Frisk et al 2001, Cortes 2000) |
| growth\_coeff\_k | x | K negatively related to age at maturity (Frisk 2001) | x | both K and S are expressions of the speed of individual growth |
| habitat | x | Habitat related to age at maturity (Garcia et al 2008) |  |  |
| interbirth\_interval | x | Interbirth interval is part of fecundity, which relates to body size (Holden 1974, Cortes 2000), which in turn relates to a50 (Frisk et al 2001, Jennings 1998) |  |  |
| litter\_size | x | Litter size is part of fecundity, which relates to body size (Holden 1974, Cortes 2000), which in turn relates to a50 (Frisk et al 2001, Jennings 1998) |  |  |
| offspring\_size\_mm | x | Offspring size is positively related to maternal body size (Cortes 2000), which is positively related to a50 (Frisk et al 2001, Jennings 1998) |  |  |
| temp\_pref | x | Age at maturity decreases with increasing temperature (Myers & Mertz 1997) | x | Growth rate increases with higher temperatures (Myers & Mertz 1997) |
| trophic\_level | x | Trophic level is positively related to body size (Pauly et al 1998), and body size is positively related to a50 (Frisk et al 2001, Jennings et al 1998) | x | Trophic level is positively related to body size (Pauly et al 1998), which is related to maximum age (Frisk et al 2001) and thence to growth rate (Frisk et al 2001, Cortes 2000) |
| linf | x | Body size is positively related to age at maturity (Frisk et al 2001, Jennings 1998) | x | Body size is positively related to maximum age (Frisk et al 2001, Jennings 1998), which is related to growth rate K (Frisk et al 2001, Cortes 2000) |
| lmax | x | Body size is positively related to age at maturity (Frisk et al 2001, Jennings 1998) | x | Body size is positively related to maximum age (Frisk et al 2001, Jennings 1998), which is related to growth rate K (Frisk et al 2001, Cortes 2000) |

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Figures

Tables