Life-history traits inform on population trends when assessing the conservation status of a declining tiger shark population

Christopher J. Brown [1]
George Roff [2]

1. Australian Rivers Institute, Griffith University, 170 Kessels Road, Nathan, Queensland, 4111, Australia
2. School of Biological Sciences, University of Queensland, QLD 4072, Australia.

Abstract

1. The assessment of the conservation status of wide ranging species depends on estimates of the magnitude of their population trends. The accuracy of global trend estimates will depend on how many locations within a species range are sampled and where in the range population size is sampled.

2. We ask how the spatial extent of sampling within a species range interacts with non-linear patterns in long-term trends to affect estimates of decline in the tiger sharks (*Galeocerdo cuvier*) population on the east coast of Australia. We use Bayesian random effects models to estimate long-term population trends. We compare estimates of trends where we use all data spanning 11.5 degrees of latitude to estimates that used spatial subsets of the data. We also introduce a method to that uses prior information on species life-history to inform on the expected level of population variation.

3. As more regions were included in the model the trend estimates converged towards an overall decline of 65% over three generations. Trends estimated from data only from northern regions underestimated the regional decline, trends estimated from data only from southern regions overestimated the regional decline. When a subset of regions were modelled, rather than the full data-set, the estimated trend depended on the choice of the Bayesian prior for population variation. The prior informed by life-history traits performed well, a prior incorrectly informed by life-history traits of a much slower growing shark species performed poorly.

Synthesis and applications The rate of decline in tiger sharks is consistent with a listing East Coast Australia tiger sharks as endangered under local legislation. Monitoring programs that aim to estimate population trends should attempt to cover the extremes and mid-points of a population's range. Life-history information can be used to inform priors for population variation and may give more accurate estimates of trends that can be justified in debates about red listing of threatened species, particularly when sampling is limited.

Keywords: Bayesian model, informed prior, migratory species, IUCN red list, megafauna

Introduction

Determining the status of species threatened by human activities is important for evaluating the success of conservation actions and when considering the investment of funds in further actions (Rodrigues et al. 2006). A species' status is often defined on the basis of trends in population size (Conservation of Nature Species Survival Commission 2001). For instance, Great Hammerhead Sharks (*Sphyrna mokarran*) were listed as critically endangered on the International Union for the Conservation of Nature (IUCN) Red List in parts of the Atlantic and Indian Oceans, partly on the basis of an >80% population decline over the past three generations (Camhi et al. 2009). The performance of management actions aimed at averting decline should also be assessed by monitoring population trends (e.g. Ward-Paige et al. 2012). Monitoring data will be most useful when it covers sufficient spatial and temporal scales to estimate trends accurately with respect to the IUCN criteria for red listing.

Accurate estimates of the magnitude of a population change may be confounded by short-term and localised variability in abundance, or masked by measurement errors (Gaston & McArdle 1994). When sampling does not cover the entire range of a mobile organism, migration into and out of the sampling area may also bias local measurements of population trends (Forney 2000). Our ability to observe a species may also vary place to place because of environmental variation, for instance, catch indicators of tiger shark (*Galeocerdo cuvier*) abundance vary interannually with temperature (Payne et al. 2018). This issue is likely to be worsened where sampling of abundances is limited to few locations within a species' broader range, because fewer sites are more likely to exhibit random variations that do not reflect a global trend (Forney 2000). The precision to which a population trend can be determined will therefore depend on the spatial extent of sampling.

Appropriately formulated statistical models can separate short-term noise from important trends. Linear and log-linear models have been popular approaches for estimating the magnitude of population change (Dudley & Simpfendorfer 2006; e.g. Baum & Blanchard 2010; Keith et al. 2015; Knape 2016). Linear models provide a simple phenomological explanation of population change, but may miss non-linear changes, or be unduly influenced by short-term temporal 'outliers' (Fewster et al. 2000; Knape 2016). Non-linear statistical models, like smoothing splines, are another popular phenomological approach, because they smooth over short-term deviations in abundance to capture longer-term non-linear trends (Fewster et al. 2000; Forney 2000; Knape 2016). A choice must then be made in the modelling about the degree of smoothing. The choice about smoothing is usually made ad-hoc based on sample size or the level of smoothing is fitted empirically, however both approaches can lead to over-fitting and biased inferences on trends (Knape 2016). A model's fit to time-series data can also be controlled by using process models that explicitly account for species life-history traits. Process models can be effective at discerning short-term noise from longer term trends driven by population dynamics (e.g. Wilson et al. 2011; Rueda-Cediel et al. 2018), but accurate estimation of population parameters can be difficult if the population trend exhibits a 'one-way-trip' (Szuwalski & Thorson 2017). 'One-way-

trips' will be common in species data that is being analysed for extinction risk. Process models, such as those used to model trends in fished populations (e.g. Maunder et al. 2006), also make additional assumptions that can lead to biased reporting of trends (Edgar et al. n.d.). What we need is an approach that takes strength from both the phenomological and process based approaches to obtain accurate estimates of population trends in the face of monitoring data that is limited in geographic and temporal extent.

Here we apply Bayesian random-effects models to fit trends to population declines. The Bayesian framework allows us to use a species' life-history traits as prior information that controls the level of smoothing in the fitted trend line. Inclusion of life-history information can improve the estimation of population trends, and may be particularly beneficial for overcoming the deficiency of monitoring data for many potentially threatened species (Kindsvater et al. 2018). The approach is thus a hybrid that blends phenomological description of trends with ecological processes that inform the smoothing. We use simulations to explore the accuracy of fitted trends for species with a range of population growth rates.

As a case-study we model data on the tiger shark population on the east coast of Australia. Tiger shark abundance is declining on the east coast of Australia (Holmes et al. 2012; Roff et al. 2018). We use data from the Queensland Shark Control Program (QSCP) a unique spatially replicated annual time-series of shark catch and effort that covers 1962-2017. Specifically we aim to determine using the tiger shark data (A) how the choice of prior influences the models' ability to detect a long-term trend in relative abundance; and (B) whether the appropriate choice of a prior can give a more accurate estimate of the large-scale trend when sampling is constrained to fewer regions.

Methods

Case-study

We analysed the decline in shark catch per unit effort in the Queensland Shark Control Program (QSCP, Kidston et al. 1992). The QSCP was instigated in 1962 at several sites around south-east Queensland, and has since been expanded to 11 regions across 1760km of coastline, ranging from the tropics (16.7^{o}S) to sub-tropical areas (28.2^{o}S, Figure 1). The QSCP uses a series of baited drumlines and mesh nets to capture sharks. The nets and drumlines are checked by contractors 15-20 days of each month, who also record the length and taxonomic identity of captured sharks. A previous analysis that analysed this same data-set found declines in four major groups of sharks caught in the QSCP, and declines were consistent across regions, suggesting a common trend across the eastern coast of Australia in these shark groups (Roff et al. 2018).

Our aim here was to explore the impact of model choice and the spatial extent of data on estimates of declines, so we focus this new analysis on a single species, tiger sharks. Tiger shark catch per unit effort (CPUE) was previously shown to have declined from historical values by 75% between 1962 and 2017 (Roff et al. 2018). We focus on tiger sharks because: (1) they are reliably identified due to their distinctive body stripes (Fig 1b), so there is less concern about misidentification of this species by contractors working on the

QSCP than with other species (Holmes et al. 2012; Roff et al. 2018); (2) there are extensive catch records for this species, providing sufficient data for us to analyse the effect of using data from a sub-set of regions; (3) the trend in tiger shark CPUE was previously shown to be non-linear (Roff et al. 2018), making tiger sharks a useful test-case for exploring the impact of non-linear trends on estimates of decline.

For inclusion in the IUCN red list, populations must exhibit observed, estimated, inferred or suspected population size reductions over the last 10 years, or over three generations (Conservation of Nature Species Survival Commission 2001). Many regional agencies also apply the IUCN red listing criteria to determine if a species should be listed locally, for instance the state of Queensland and Australia both apply the red list criteria for regional listing of threatened species (Committee n.d.; Environment & Protection n.d.). Analysis of sharks caught in the QSCP indicate an estimated age at 50% of maturity (A50) for female sharks of 10-13 years (Holmes et al. 2015). Based on this criteria, we analysed the QSCP dataset of 11 regions for trends in tiger shark catches between two time periods: three generations which was 1984 to 2017; and the longer term trend over 1970 to 2017. 1970 was the earliest year shared by all sites in used in the regional subsets.

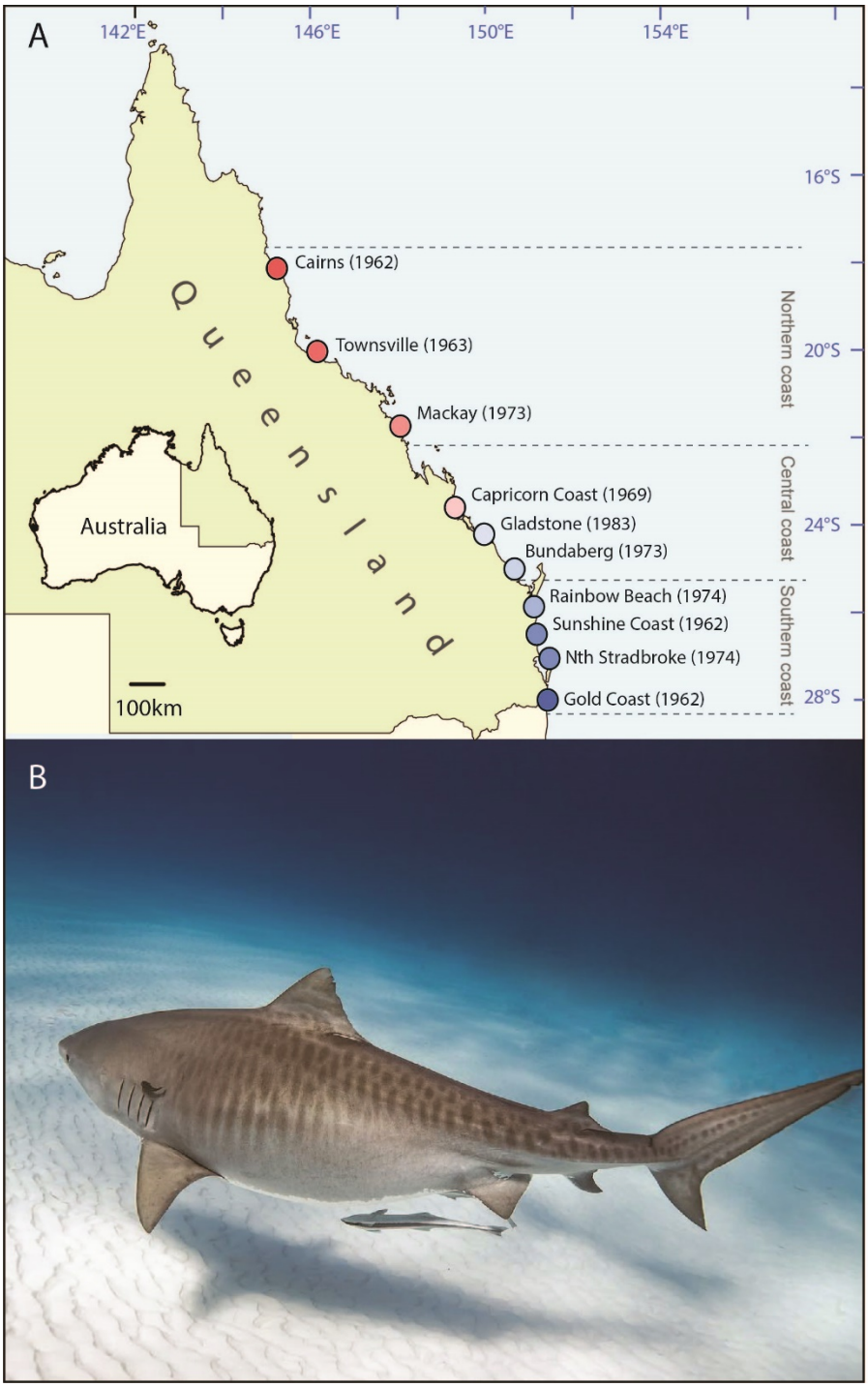

Figure 1 A) Map of the study region, showing major regions, first year of shark program sizes and scaling of sites from north to south, B) mature female *Galeocerdo cuvier* (~3m length) showing characteristic vertical striping pattern. Photo credit: Juan Oliphant

Model

We used Bayesian random effects models to fit non-linear trend lines to tiger shark CPUE patterns. The model of the count of shark catch for each region, gear type and year ($y_{i,g,t}$) was as follows:

$$y_{i,g,t} \sim nbinom(\mu_{i,g,t}, \theta)$$

Where θ was the scale parameter of the negative binomial distribution and $\mu_{i,g,t}$ was the expected abundance. The expectation was specified:

$$ln(\mu_{i,g,t}) = \alpha + \beta x_{i,g,t} + b_i + z_t + E_{i,g,t}$$

Where α was a global intercept, β was the additive effect of mesh nets, $x_{i,g,t}$ was an indicator variable for nets (=1) or drumlines (=0), b_i was an independent, normally distributed random effect of region, with standard deviation $sigma_b$, z_t was a latent second order random walk, with standard deviation σ_{RW2} (e.g. Rue & Held 2005):

$$z_t - 2z_{t+1} + z_{t+2} \sim norm(0, \sigma_{RW2})$$

The term $E_{i,g,t}$ was an offset term that accounted for variation in the number of drum lines and nets across time and regions. This model is similar to that used in Roff et al. (2018), except that we ignored site level variation by summing over drum/net sites within a region.

We specified prior distributions for the parameters α, β and the hyper-parameters θ, $sigma_b$ and σ_{RW2}. For α and β we used broad normal priors with mean zero. These are the defaults in the software we used (Martins et al. 2013). For σ_b we also used the default that is a weakly informative loggamma prior with parameters 1 and 1e-5. For θ we used the penalized complexity prior with one parameter. We set this parameter to a value of 7 based on a simulation study (Supplementary material). The penalized complexity prior will shrink the negative binomial distribution toward a poisson distribution if there is not strong evidence for over-dispersion ($\sigma^2 >> \mu$) (Simpson et al. 2017). Using weakly informative priors means computations are more efficient and avoids overfitting the data to the variance parameters (Simpson et al. 2017). Finally, we refitted models with several different priors for σ_{RW2}, as is explained below. To peform Bayesian computation we used the programming package INLA (Integrated Nested Laplace Approximation) (Rue et al. 2009, 2017) as implemented in the R programming environment (INLA version 17.06.20; R version 3.4.4; Martins et al. 2013; Team & others 2018).

Prior choice for the standard deviation of the random walk

We used prior information on the annual potential for variation in tiger shark population abundance to select the level of smoothing for the random walk model of CPUE (Simpson et al. 2017). The level of smoothing in the trend line can be controlled by varying the prior for the standard deviation of the random walk. A prior that has greater density close to a standard deviation of zero will shrink the trend toward a constant line. We could use prior information on variation in abundance, because the standard deviation of a random walk has a direct interpretation in terms of population growth. For the exponential population

model $N_t = N_{t-1}e^{(r_t t)}$, where r_t is an annually varying instantaneous growth rate and is sampled from a normal distribution, the standard deviation of a (logged) random walk will equal the standard deviation of r (σ_r). Thus, we can inform the prior for the random walk based on the maximum expected yearly population change for tiger sharks. For this application we use a second order random walk, because it gave better smoothing properties (it smooths over single year deviations) and is analogous to the smoothers used in generalized additive models (Rue & Held 2005). The standard deviation for the second order random walk ($\sigma_{RW2} = sd(N_t - 2N_{t+1} + N_{t+2}) \forall t < T - 2$) will equal $\sigma_r\sqrt{2}$. In applying this approach to CPUE data, we assumed that CPUE was proportional to population abundance.

Given that tiger sharks are large predators with relatively late age at maturity (estimated at 10-13 years by Holmes et al. (2015)), a low fecundity and a high adult survival rate (Cortés 2002), we assumed that the finite growth rate represents the near maximum rate of negative or positive annual change in the population. Therefore, we choose the prior such that there was only a 0.025 probability of a standard deviation greater than a prior estimate of r. We obtained an estimate of the maximum annual instantaneous growth rate by applying the corrected Lotka-Euler equation to *G. cuvier* life-history parameters (Cortés 2016; Pardo et al. 2016). We used life-history parameters from the local region where possible (Supplementary information). The estimate of the instantaneous rate of increase for Pacific tiger sharks was 0.24, which is consistent with previous estimates from the Atlantic (Cortés 2016; Pardo et al. 2016).

We used a penalized complexity prior for precision of the random walk (= 1/variance) with parameters U and α where $pr(\sigma_{RW2} > U) = \alpha$ (Simpson et al. 2017). As our best estimate, we used $U = ln(1.26)$ and $alpha = 0.025$ to capture the low probability of population changes greater than the maximum potential growth rate. The prior has a high density near a standard deviation of zero, but also a long tail that can capture large magnitude events (Figure 2). The model of the random walk is symmetrical, so the prior reflects the probability of both CPUE increases and decreases. Decreases could be expected to be much greater than *r* if they are caused by high mortality. The penalized complexity can accommodate large mortality events provided they result in sustained changes to CPUE. For instance, a sudden decline in CPUE would be smoothed over if the population immediately recovered the next year, which might be indicative of a temporary migration. Whereas, we would expect a sudden decline that was caused by overfishing to result in a sustained decline in CPUE, such sustained changes would be captured by the model.

We compare results from the best-guess prior with three other priors. The first was the INLA default prior (a loggamma with parameters (1, 1E-5)). The second and third were penalized complexity priors parameterised to represent a very slow growing shark species ($U = log(1.01)$) and a very fast growing shark species ($U = log(1.66)$) (Cortés 2002). We also tried 'traditional' broad gamma priors (e.g. the gamma(0.01, 0.01) prior) that have a high probability density at very high variances, however we have not included those results here because we found that they caused significant issues with model estimation. Such priors are now eschewed by statisticians, because they allow for unrealistically high variance (e.g. Simpson et al. 2017).

In the INLA implementation we set the 'scale.model' option equals 'TRUE' to ensure the value provided for σ_{RW2} was interpreted as the marginal standard deviation. We also set 'constr' equals 'FALSE' to remove the sum to zero constraint.

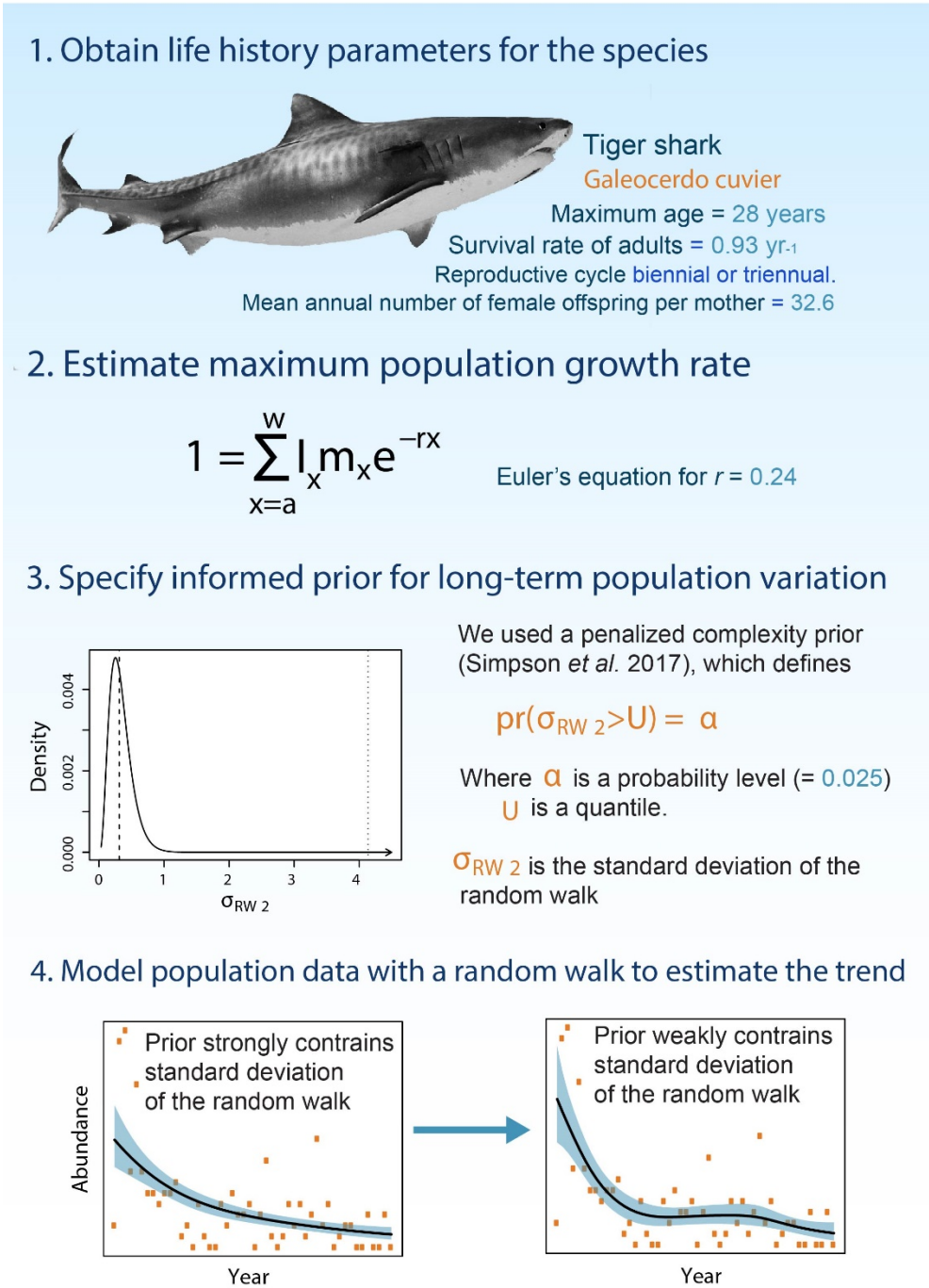

Figure 2 The approach for using life-history information to inform on trends in population modelling. From Cortes 2002

Analyses

To explore the impact of prior choice on species with a range of life-history traits, we initially ran a simulation study, where we simulated random walks and then fit models to the simulated data. We included a bias in the simulated random walk so the population declined on average by 2.5% each year. We simulated the biased random walks that covered the range of shark species population growth rates with simulations for values of $exp(\sigma_r)$ = 1.01, 1.34 and 1.66 (Cortés 2002). For each trend and life-history type we simulated 20 replicate time-series of 30 years. Annual observations were then sampled from a negative binomial distribution with an expectation equal to the random walk value in each year and a dispersion (size) parameter = 2, to generate overdispersed counts. We repeated these analyses drawing observation errors from a poisson distribution. We assumed effort was fixed over time and initial CPUE was set at 10 (approx. mean for tiger sharks). For each time-series we fitted three models with different penalized complexity priors: $\sigma_r w$ = ln(1.01), ln(1.34) and ln(1.66). In total we simulated 120 random time-series, fitting a total of 360 models. Each set of model fits was evaluated by: (1) the product of the likelihood of the true (simulated) mean given the fitted marginal probability distributions in each year and; (2) using the predictive ordinate (Held et al. 2010).

For the tiger shark data we explore the impact of the extent of sampling and prior choice on estimates of decline over the time periods 1970 to 2017 and 1984 to 2017. We fit models to 60 subsamples of the data and different prior specifications. We performed a factorial set of analyses crossing the four prior densities for σ_{RW2} with subsets of the number of regions included in the model fitting. We included 15 subsets of the set of 11 regions. The 15 subsets were a factorial cross of 1, 3, 6 and 9 regions by a selection of regions that included the northern-most regions, middle latitude regions, southern-most regions, and regions equally dispersed across the full extent of the dataset (fig. 1). For the subsets, we chose regions that had the most complete time-series. We also ran all priors for the complete set of 11 regions.

We compared results from models with the different priors and different numbers of regions for their predictions of the magnitude of the population decline across two time-periods. Comparisons were made to the 11 region model with the life-history prior as our best-estimate. The % magnitude of population decline from the reference year was calculated as $-100(1 - z_{2017}/z_0)$ where z_{2017} was the value of the smoother in the most recent year and z_0 was its value at the reference year (1970 or 1984). We used INLA's 'lincomb' feature to calculate the marginal posterior distribution of the % decline statistic. We then compared scenarios for their median values and 95% credible intervals.

We also compared results for the tiger sharks by fitting a Generalized Additive Mixed Model (GAMM) with maximum likelihood methods and cross validation (with the R package mgcv, version 1.8-23 Wood 2017). The GAMM was fit with random effects by regions (for sub-samples with >1 region) and a thin plates smoothing spline applied to year. The maximum degrees of freedom was set to either 1/3 the number of years (as recommended by Fewster et al. (2000)), or chosen with cross-validation (Wood 2017).

Results

The simulation study to test the ability of different priors to fit population trends indicated that model fits were a more accurate representation of the true mean for slower growing species when compared to fast-growing species (Fig 3). Slow growing species had less variability overall, so it was easier to detect the simulated trend. For slow growing species, the fit was equally accurate for any prior. For species with medium and fast growth rates, fits were more accurate with either medium or fast priors, when compared to the slow prior (Fig. 3). Interestingly, the predictive ordinate, a standard in-sample evaluation measure did not detect any differences in the accuracy of fits by different priors (Fig S2). In general, fits to the model with poisson errors, rather than over-dispersed negative binomial errors, were more accurate (Fig 3, S2).

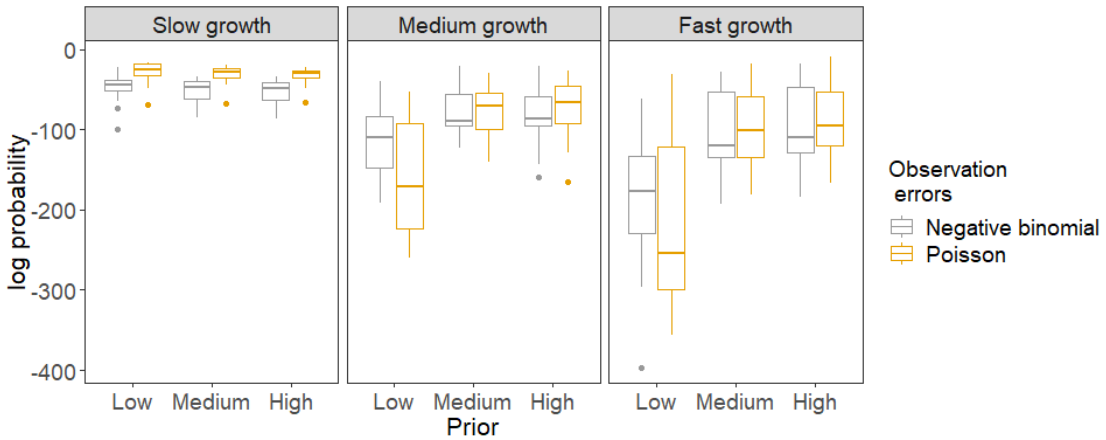

Figure 3 Results from simulation study for the log probability of the true simulated mean across all sample years given the results of the fitted model. Horizontal axes give the different priors, the panels show results from models fitted to time-series data simulated for species with different life-history traits. Higher (less negative values) indicate the model performed better at recovering the true trend. Boxes give the inter-quartile range and the horizontal bar gives the mean value. Vertical error bars extend no more than 1.5xIQR.

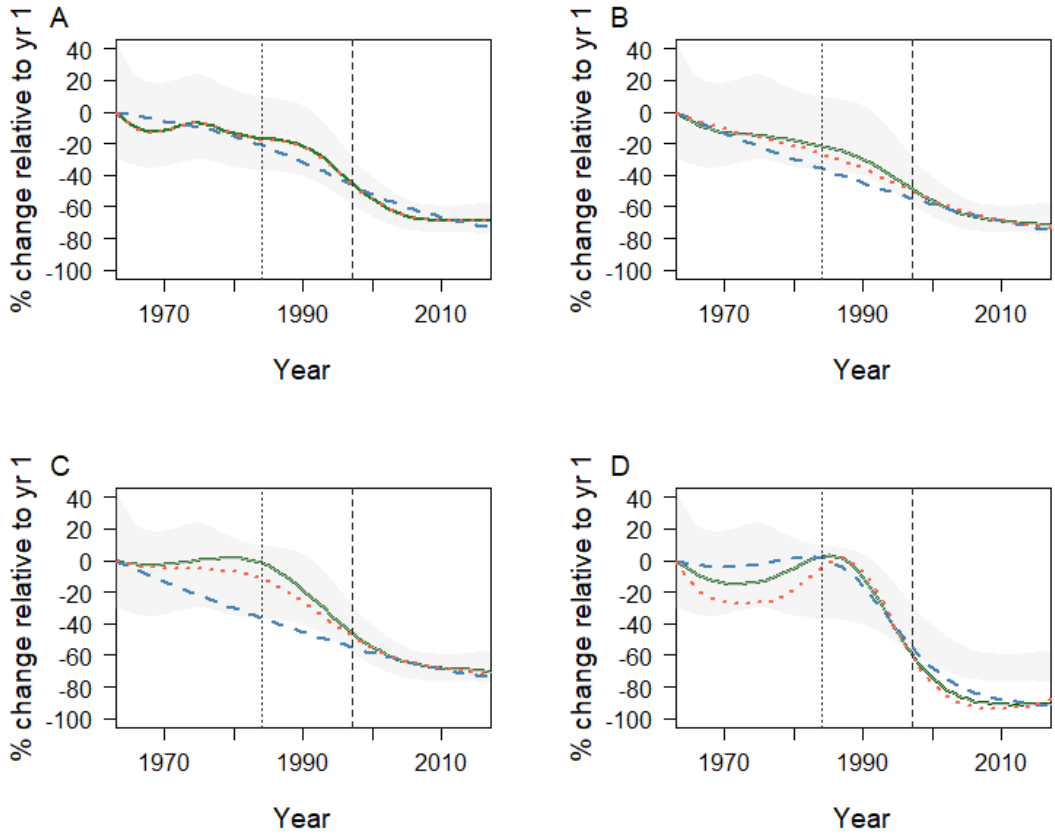

Fig 4 Examples of non-linear trends fitted to the tiger shark data. Models fitted to all regions (A), and 6 and 3 extreme-latitude regions (B, C), and just the southern most region (Gold Coast) (D). Lines show the fitted values for the random walk with 95% C.I.s (shading) for the life-history prior (solid), slow life history prior (dashed) and INLA default prior (dotted, orange). For comparison the 95% C.I.s for model fitted to all data with the life-history prior is included as the shaded polygon.

For tiger sharks the magnitude of decline over three generations was reasonably accurate with any prior (Fig 4, Fig 5). The slow prior tended to under-estimate non-linearities in the trend (e.g. Fig 4), but this did not matter for the long-term estimation of the decline, which was quite strong. The slow prior tended to have the poorest coverage of the true magnitude when there were only 1-6 regions included. The slow prior was also more confident about the magnitude of the trend (narrower credible intervals, Fig 5). Results were similar when estimating declines over 1970 - 2017 (Fig S4). It is notable that INLA's default prior gave similar results to the prior informed by life-history traits (Fig 5).

With a greater number of regions the estimate of decline became more accurate. Subsets with southern regions tended to overestimate the trend, whereas subsets with middle and northern regions tended to underestimate the trend (Fig. 5). Data subsets that mixed extreme north and south regions were more accurate than data subsets just of north or south regions, because the different rates of the trends balanced out. A generalized additive mixed model fitted using maximum likelihood methods showed a similar pattern to the

Bayesian model of convergence of trend estimates as more regions were added, and greater declines estimated if data were taken from southern regions when compared to data taken from northern regions (Fig S5). The GAMM had similar results for either standard setting for its degrees of freedom.

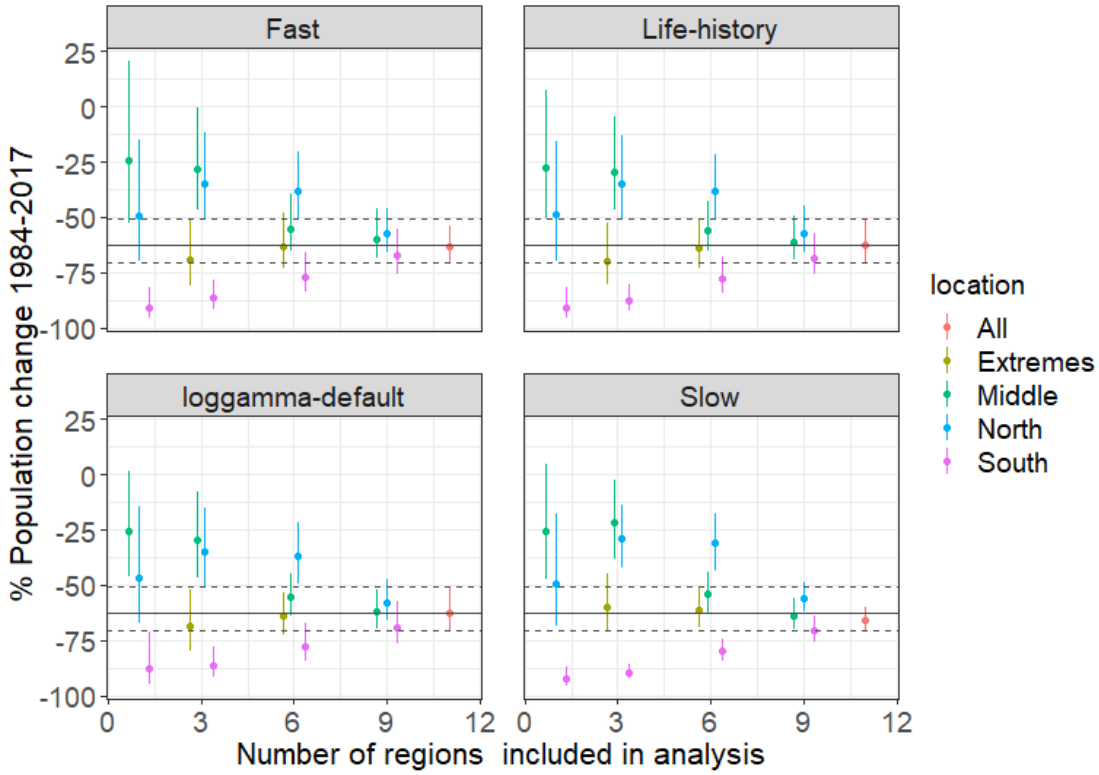

Fig 5 Estimated magnitudes of decline for the each prior (panels) and each scenario for subsets of regions (coloured points) over 3 generations (1984-2017). Points give median estimates and bars give 95% C.I.s. For comparison, the black and dashed lines give the median and 95% C.I.s for the life-history prior fitted to data for all regions.

Discussion

Important statistics for informing on the status of threatened species and the effectiveness of management interventions are estimates of the magnitude of population change (Rodrigues et al. 2006). We found the accuracy of population change estimates can be improved by using fitting non-linear trends where the level of smoothing is informed with life-history traits and, that greater spatial replication of time-series can improve the reliability of estimates. Accurate estimates of population change for wide-ranging species are therefore best based on sampling that covers a full range of sites. However, spatially extensive sampling can expensive and not all species will have spatially extensive time-series available for assessing trends (Kindsvater et al. 2018). We additionally found that using prior information on life-history traits to set the degree of smoothing in trends can help to establish more robust estimates of decline by smoothing over short-term, site-specific deviations in population size.

We introduced a method for using prior information in Bayesian models to inform on the degree of non-linearity in population trends. The method may help to overcome some of the short-comings of analysing abundance indices with purely descriptive statistical models (Maunder et al. 2006), by enabling the inclusion of information on species life-history. The results for the three generation decline were similar for all priors, except the prior for a slow growing species. The generalized additive model also estimated a similar rate of decline as the Bayesian model. The convergence in estimates across these different methods occurred because the tiger sharks CPUE data had a strong trend. Where patterns in the data are strong, the prior will be less influential (e.g. Kindsvater et al. 2018).

Despite the consistencies in trend estimates across the different methods, we still advocate using prior information to inform on population variability for several reasons. The informed prior gave estimates closer to the global trend when subsets of the data were used. It is also powerful that we can tune the level of smoothing in the Bayesian model for a species life-history. The control of smoothing in generalized additive models is not based on species life-history. The choice of smoothing for generalized additive models must instead be made by evaluating smoothing against the data at hand, or with reference to prior simulation studies that are often from very different organisms (Fewster et al. 2000; Knape 2016). In our simulations the predictive ordinate (an in-sample evaluation measure) performed poorly in that it did not distinguish among different priors, even though the out-of-sample measures clearly indicated some priors had superior accuracy for estimating trends. This suggests that using the in-sample measure to may lead to overfitting of the smoothing splines. We suggest that a-priori decisions about smoothing will provide more accurate trend estimates. Informed priors may also be more easily justified than choices about smoothing made with reference to other organisms. Defensible parameter choices are important when model results may be contested when governments make potentially contentious decisions about the status of populations (e.g. Edgar et al. n.d.).

When life-history traits are uncertain we suggest using a penalized complexity prior that allows for greater variation (and non-linearity) in the long-term trend. Our simulations study suggested that priors that allow for higher variance gave more accurate results than priors that restricted variance. However, the decision to allow for overestimation of variance may not be safe if a different prior distribution other than the penalized complexity priors was used. For instance, very flat priors that give equal prior weighting to low and high temporal variances can perform very poorly, because they overweight the probability of very high variability (Simpson et al. 2017). The shape of the penalized complexity prior was specifically designed to allow the data to speak for themselves when trends are strong, but to shrink estimates towards no trend when the data are weak or noisy (Simpson et al. 2017). Our results add further support to usefulness of penalized complexity priors for applied problems.

An avenue that requires further research is the utility of our method for partitioning long-term trends from short-term variation across many species with a broader range of life-history types. We expect our approach will work best when short-term variation in abundance, such as that caused by temporary migrations, is much more variable than long-term trends. For very fast growing species, such as those with maturity ages of <1 year, a statistical model fitted to annual data may confound real population trends with short-term

deviations. Classification errors for IUCN red list status tend to be greater for species with fast population growth than species with slow population growth (Rueda-Cediel et al. 2018). For instance, the results of our simulation study were most accurate for slow growing species, whereas accuracy was more variable for fast growing species. Our model could still be effective if the temporal resolution of sampling was increased (e.g. with sub-annual data). A further improvement to the model would be to specify a prior that gives population declines more probability than population increases. Rapid declines in population abundance tend to be more common than rapid increases (Anderson et al. 2017), because the processes that cause declines, like overfishing, often operate on a much faster time-scale than reproduction and population recovery.

Widespread declines of large sharks are occurring throughout the world's oceans (Baum & Myers 2004; e.g. Ferretti et al. 2008; Roff et al. 2018). Tiger sharks are targeted by numerous fisheries and are caught as bycatch at a global scale (see Simpfendorfer (2009) for a concise review). At a global scale, changes in tiger shark populations are variable: Comparisons of surveys between the 1950's and 1990's indicate no substantial change in catch rates in the Gulf of Mexico (Baum & Myers 2004), while analysis of data from recent decades indicate declines in tiger shark populations by 65% since the mid 1980's in the Northwest Atlantic (Baum et al. 2003). The conservation status of tiger sharks globally escalated from "Lower Risk/near threatened" under the IUCN listing to "Near Threatened" in 2005 (Simpfendorfer 2009). The current global population trend is unknown, although the relatively high growth and reproductive rates (Cortés 2002; Holmes et al. 2015) means that tiger sharks are not considered at high risk of extinction (Simpfendorfer 2009).

In Australia, tiger sharks are caught as bycatch in commercial fisheries (Macbeth & Macbeth 2009) and are considered the principal target of shark fishing tournaments (Stevens 1984, Park & others 2007)). In northern New South Wales (NSW) commercial shark fisheries, tiger sharks represent the fifth highest species (5.9% of total catch, Macbeth & Macbeth 2009) and in Queensland, represent 17.4% of recreational shark catch (Stevens 1984). Few long-term records of abundance exist in Australia, although a similar (but less pronounced) downward trend in abundance has been observed in the monitoring of gamefish sports fishing between 1993-2005 (Park & others 2007). Declines in tiger shark catches in shark nets in NSW over the past two decades, coinciding with a significant decrease in the number of large (>3.0m) individuals has been attributed to increased fishing pressure in temperate waters in NSW (Reid et al. 2011), and the average size of tiger sharks caught in the Queensland Shark Control Program has declined from 2.72m to 2.15m over the past five decades (Roff et al. 2018). A point of contention for listing tiger sharks may be the quality of the QSCP effort data - which is collected by contractors working to clear nets and drumlines, not by independent scientific observers. Catch per unit effort data can also be a biased indicator of abundance trends (Maunder et al. 2006). Our proposed statistical method cannot improve the quality of the data, however it may help smooth over temporal and regional variability in trends by estimating the long-term trend that is consistent across regions. If the QSCP catch records accurately reflect the population's trend, the decline of 65% over three generations suggests that the conservation status of the East Coast Australian population of tiger sharks should be escalated to Endangered under Queensland's threatened species legislation (IUCN Criteria

A2, >50% decline over three generations). Tiger sharks may also warrant listing under national legislation, because genetic studies indicate the east coast population is part of a well mixed Indo-Pacific population (Holmes et al. 2017).

We considered how estimates of population trends for wide-ranging species depend both on the spatial extent of data and the model used to partition short-term variation from long-term trends in population size. We found that the choice of model and the spatial extent of sampling interact to effect population trends. Informing priors with life-history information could improve the accuracy of estimates, particularly when sampling was constrained to fewer regions across a species range. Informed priors provide theoretical grounds for choosing the level of smoothing to apply to population trends modelling that is defensible on the basis of a species ecology. The trends estimated here suggest that tiger sharks should be listed as a threatened species under Australian state and possibly national legislation.

Acknowledgements

Use of the Shark Control Program data is by courtesy of the State of Queensland, Australia through the Department of Agriculture and Fisheries. We thank Juan Oliphant for the tiger shark photographs. CJB was supported by a Discovery Early Career Researcher Award (DE160101207) from the Australian Research Council. CJB wishes to thank TB for his patience through numerous drafts.

Literature cited

Anderson SC, Branch TA, Cooper AB, Dulvy NK. 2017. Black-swan events in animal populations. Proceedings of the National Academy of Sciences **114**:3252–3257. National Acad Sciences.

Baum JK, Blanchard W. 2010. Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data. Fisheries Research **102**:229–239. Elsevier.

Baum JK, Myers RA. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecology Letters **7**:135–145. Wiley Online Library.

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science **299**:389–392. American Association for the Advancement of Science.

Camhi MD, Valenti S, Fordham S, Fowler S, Gibson C. 2009. The conservation status of pelagic sharks and rays: Report of the IUCN shark specialist group pelagic shark red list workshop. IUCN Species Survival Commission Shark Specialist Group. Newbury, UK. x+ 78p.

Committee TSS. (n.d.). Guidelines for assessing the conservation status of native species according to the environment protection and biodiversity conservation act 1999 and environment protection and biodiversity conservation regulations 2000.

http://www.environment.gov.au/biodiversity/threatened/nominations/forms-and-guidelines; Australian Government, Department of Environment; Energy.

Conservation of Nature Species Survival Commission IU for. 2001. IUCN Red List categories and criteria. Version 3.1. https://www.iucn.org/content/iucn-red-list-categories-and-criteria-version-31; IUCN, Gland, Switzerland.

Cortés E. 2002. Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. Conservation Biology **16**:1048–1062. Wiley Online Library.

Cortés E. 2016. Perspectives on the intrinsic rate of population growth. Methods in Ecology and Evolution **7**:1136–1145. Wiley Online Library.

Dudley SF, Simpfendorfer CA. 2006. Population status of 14 shark species caught in the protective gillnets off KwaZulu–Natal beaches, South Africa, 1978–2003. Marine and Freshwater Research **57**:225–240. CSIRO.

Edgar GJ, Ward TJ, Stuart-Smith RD. (n.d.). Rapid declines across Australian fishery stocks indicate global sustainability targets will not be achieved without an expanded network of "no-fishing" reserves. Aquatic Conservation: Marine and Freshwater Ecosystems. Wiley Online Library.

Environment QGD of, Protection H. (n.d.). Threatened species. https://www.ehp.qld.gov.au/wildlife/threatened-species/.

Ferretti F, Myers RA, Serena F, Lotze HK. 2008. Loss of large predatory sharks from the Mediterranean Sea. Conservation Biology **22**:952–964. Wiley Online Library.

Fewster RM, Buckland ST, Siriwardena GM, Baillie SR, Wilson JD. 2000. Analysis of population trends for farmland birds using generalized additive models. Ecology **81**:1970–1984. Wiley Online Library.

Forney KA. 2000. Environmental models of cetacean abundance: Reducing uncertainty in population trends. Conservation Biology **14**:1271–1286. Wiley Online Library.

Gaston KJ, McArdle BH. 1994. The temporal variability of animal abundances: Measures, methods and patterns. Phil. Trans. R. Soc. Lond. B **345**:335–358. The Royal Society.

Held L, Schrödle B, Rue H. 2010. Posterior and cross-validatory predictive checks: A comparison of MCMC and INLA. Pages 91–110 in Statistical modelling and regression structures. Springer.

Holmes BJ, Peddemors VM, Gutteridge AN, Geraghty PT, Chan RW, Tibbetts IR, Bennett MB. 2015. Age and growth of the tiger shark *Galeocerdo cuvier* off the east coast of Australia. Journal of Fish Biology **87**:422–448. Wiley Online Library.

Holmes BJ, Sumpton WD, Mayer DG, Tibbetts IR, Neil DT, Bennett MB. 2012. Declining trends in annual catch rates of the tiger shark (*Galeocerdo cuvier*) in Queensland, Australia. Fisheries Research **129**:38–45. Elsevier.

Holmes BJ, Williams SM, Otway NM, Nielsen EE, Maher SL, Bennett MB, Ovenden JR. 2017. Population structure and connectivity of tiger sharks *(Galeocerdo cuvier)* across the Indo-Pacific Ocean basin. Royal Society Open Science **4**:170309. The Royal Society.

Keith D et al. 2015. Temporal correlations in population trends: Conservation implications from time-series analysis of diverse animal taxa. Biological Conservation **192**:247–257. Elsevier.

Kidston W, Dwyer K, Buhk A, Waldock J, Anderson G. 1992. Review of the operation and maintenance of shark meshing equipment in Queensland waters: Report of the Committee of Inquiry. Queensland Department of Primary Industries: Brisbane.

Kindsvater HK, Dulvy NK, Horswill C, Juan-Jordá M-J, Mangel M, Matthiopoulos J. 2018. Overcoming the data crisis in biodiversity conservation. Trends in Ecology & Evolution. Elsevier.

Knape J. 2016. Decomposing trends in Swedish bird populations using generalized additive mixed models. Journal of Applied Ecology **53**:1852–1861. Wiley Online Library.

Macbeth WG, Macbeth WG. 2009. Observer-based study of targeted commercial fishing for large shark species in waters off northern New South Wales. Cronulla Fisheries Research Centre of Excellence. Industry; Investment NSW.

Martins TG, Simpson D, Lindgren F, Rue H. 2013. Bayesian computing with INLA: New features. Computational Statistics & Data Analysis **67**:68–83. Elsevier.

Maunder MN, Sibert JR, Fonteneau A, Hampton J, Kleiber P, Harley SJ. 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. ICES Journal of Marine Science **63**:1373–1385. Oxford University Press.

Pardo SA, Kindsvater HK, Reynolds JD, Dulvy NK. 2016. Maximum intrinsic rate of population increase in sharks, rays, and chimaeras: The importance of survival to maturity. Canadian journal of fisheries and aquatic sciences **73**:1159–1163. NRC Research Press.

Park T, others. 2007. NSW gamefish tournament monitoring-angling research tournament monitoring program. NSW Department of Primary Industries-Fisheries Final Report Series. NSW Department of Primary Industries.

Payne NL et al. 2018. Combining abundance and performance data reveals how temperature regulates coastal occurrences and activity of a roaming apex predator. Global Change Biology **24**:1884–1893. Wiley Online Library.

Reid D, Robbins W, Peddemors V. 2011. Decadal trends in shark catches and effort from the New South Wales, Australia, shark meshing program 1950–2010. Marine and Freshwater Research **62**:676–693. CSIRO.

Rodrigues AS, Pilgrim JD, Lamoreux JF, Hoffmann M, Brooks TM. 2006. The value of the IUCN Red List for conservation. Trends in Ecology & Evolution **21**:71–76. Elsevier.

Roff G, Brown C, Priest M, Mumby P. 2018. Rapid decline of coastal apex shark populations over the past half century. in review **0**:0–0.

Rue H, Held L. 2005. Gaussian Markov random fields: Theory and applications. CRC press.

Rue H, Martino S, Chopin N. 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society: Series B (Statistical Methodology) **71**:319–392. Wiley Online Library.

Rue H, Riebler A, Sørbye SH, Illian JB, Simpson DP, Lindgren FK. 2017. Bayesian computing with INLA: A review. Annual Review of Statistics and Its Application **4**:395–421. Annual Reviews.

Rueda-Cediel P, Anderson KE, Regan TJ, Regan HM. 2018. Effects of uncertainty and variability on population declines and IUCN Red List classifications. Conservation Biology. Wiley Online Library.

Simpfendorfer C. 2009. *Galeocerdo cuvier*. The IUCN Red List of Threatened Species 2009.

Simpson D, Rue H, Riebler A, Martins TG, Sørbye SH, others. 2017. Penalising model component complexity: A principled, practical approach to constructing priors. Statistical Science **32**:1–28. Institute of Mathematical Statistics.

Stevens J. 1984. Biological observations on sharks caught by sport fisherman of New South Wales. Marine and Freshwater Research **35**:573–590. CSIRO.

Szuwalski CS, Thorson JT. 2017. Global fishery dynamics are poorly predicted by classical models. Fish and Fisheries **18**:1085–1095. Wiley Online Library.

Team RC, others. 2018. R: A language and environment for statistical computing. Vienna, Austria.

Ward-Paige C, Keith D, Worm B, Lotze HK. 2012. Recovery potential and conservation options for elasmobranchs. Journal of Fish Biology **80**:1844–1869. Wiley Online Library.

Wilson HB, Kendall BE, Possingham HP. 2011. Variability in population abundance and the classification of extinction risk. Conservation Biology **25**:747–757. Wiley Online Library.

Wood SN. 2017. Generalized additive models: An introduction with R. Chapman; Hall/CRC.