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

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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 standardised catch of tiger sharks (*Galeocerdo cuvier*) in a shark control program 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

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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 64% 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 informing the investment of conservation funds (Rodrigues et al. 2006). A species' status is often defined on the basis of trends in population size (Conservation of Nature Species

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Survival Commission 2001). For instance, some Great Hammerhead Shark populations (*Sphyrna mokarran*) were listed as critically endangered on the International Union for the Conservation of Nature (IUCN) Red List, 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.

Accurate estimates of the magnitude of a population change may be confounded by short-term and localised variation in abundance, or masked by measurement errors (Gaston & McArdle 1994). Migration into and out of the sampling area may also bias local abundance measurements of mobile species (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 inter-annually 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 the population's true trend (Forney 2000). The precision of population trend estimates 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 trend analysis (e.g. Dudley & Simpfendorfer 2006; Baum & Blanchard 2010; Keith et al. 2015; Knape 2016). Linear models provide a simple phenomological model of trends, but may miss non-linear

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changes and be 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. This choice is usually made based on sample size (Fewster et al. 2000) or the level of smoothing is fitted empirically with a method like generalized cross validation (Wood 2006). However, empirical approaches to smoothing 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 (Kindsvater et al. 2018; Sköld & Knape 2018). 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 also make additional assumptions that can lead to biased reporting of trends (Edgar et al. 2018). 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.

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Here we apply Bayesian random-effects models to fit trends to population declines. We use a species' life-history traits as Bayesian prior information to control 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 modelled multi-decadal trends in a declining tiger shark population from the east coast of Australia (Holmes et al. 2012; Roff et al. 2018). The data are from the Queensland Shark Control Program (QSCP) a unique spatially replicated annual time-series of shark catch and effort that covers 1962-2017. We aimed to determine (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 temporal variation 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°S) to sub-tropical areas (28.2°S, Figure

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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 of 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). This included a 75% decline in tiger sharks between 1962 and 2017 (Roff et al. 2018). Effort data in the form of total number of nets and drumlines was reconstructed using historical records from contractor's logbooks between 1962-2017. Historical effort records account for seasonal lifting of gear and swapping of gear between beaches during seasons to avoid bycatch of turtles and whales, and annual effort was adjusted to reflect these changes (Roff et al. 2018). Where catch records were unclear or uncertainty existed regarding number of drumlines or nets, beaches were excluded from the analysis (Roff et al. 2018). Since the early 1990's, drumlines and net types have been standardised across the program (Sumpton et al. 2010).

A recent analysis of the QSCP data found declines in four major groups of sharks across regions, suggesting a common trend across the eastern coast of Australia in these shark groups (Roff et al. 2018). Here, we explore the impact of model choice and the spatial extent of data on estimates of tiger shark declines. We focus on tiger sharks because: (1) they are reliably identified due to their distinctive body stripes (Fig 1b) (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) they may be of conservation concern because the previous found declines of ~75% between

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1962 and 2017 (Roff et al. 2018) and (4) the declines were non-linear, 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 local listing of species, including the state of Queensland and Australia (Committee 2019; Environment & Heritage Protection 2019). 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 used in the regional subsets.

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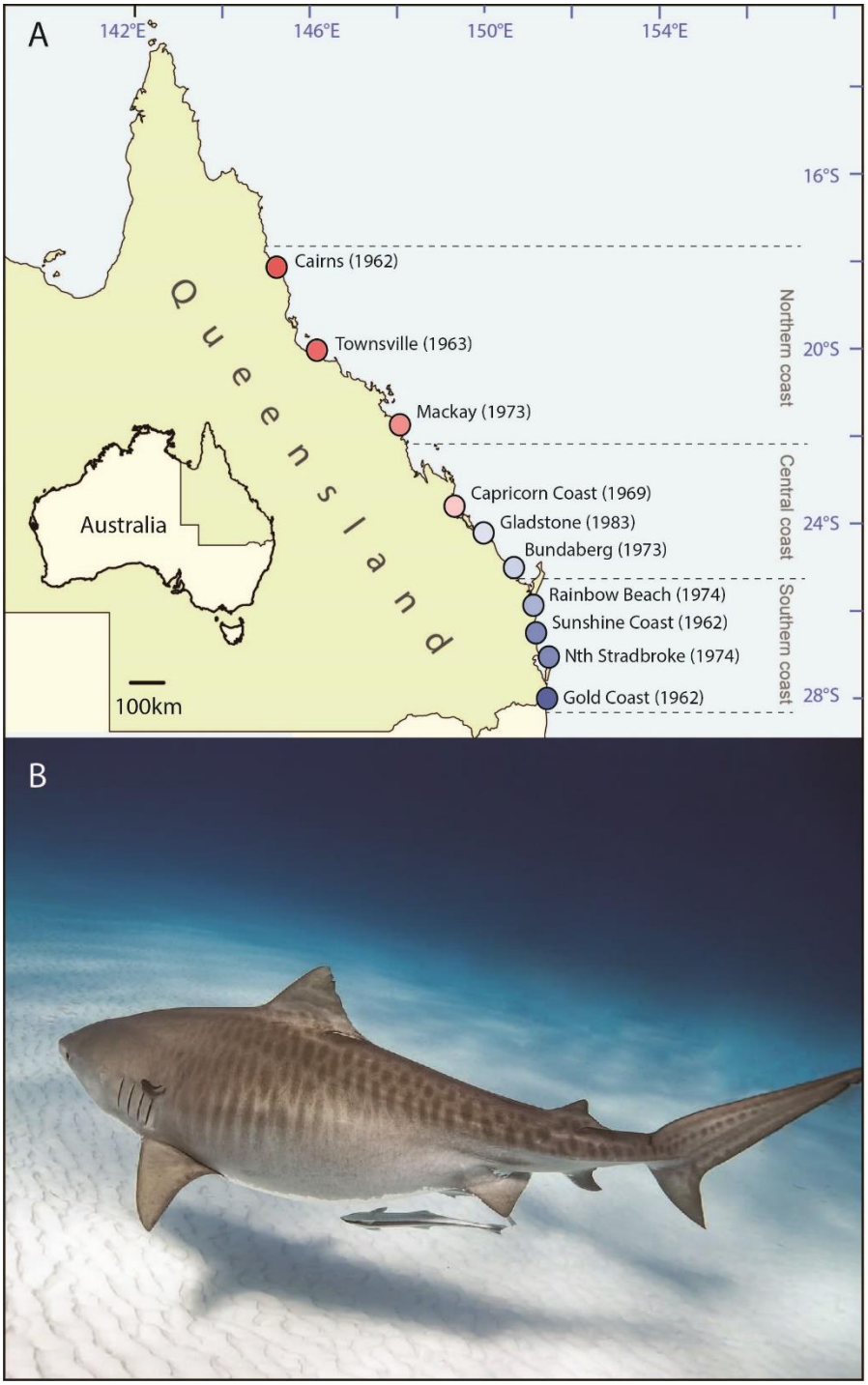

Figure 1 A) Map of the study region, showing major regions, first year of shark program sizes and scaling of sites from north to south, B) mature female *Galeocerdo cuvier* (~3m length) showing characteristic vertical striping pattern. Photo credit: Juan Oliphant

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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 $sigma_b$. Gear and region effects were included to help control for differences in catches in different location by different gear types (e.g. Holmes et al. 2012). z_t was a latent first order random walk, with standard deviation σ_{RW1} (e.g. Rue & Held 2005):

$$z_{t+1} - z_t \sim norm(0, \sigma_{RW1})$$

The random walk allows for non-linear trends in abundance with time, but will shrink toward a flat line for small values of σ_{RW1}. 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.

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We specified prior distributions for the parameters α, β and the hyper-parameters θ, $sigma_b$ and σ_{RW1}. 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_{RW1}, 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; R Core Team 2018).

Prior choice for the standard deviation of the random walk

The prior for the standard deviation of the random walk controls the level of smoothing in the trend line. A prior that has greater density closer to a smaller standard deviation will shrink the trend toward a constant line. We used life-history information on the annual potential for variation in tiger shark abundance to inform the prior for the random walk (Simpson et al. 2017). The standard deviation of a random walk has a direct interpretation in terms of population growth: For the exponential population model $N_t = N_{t-1}e^{r_t}$, where r_t is an annually varying instantaneous growth rate and is sampled from a normal

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distribution, the standard deviation of a (logged) random walk will equal the standard deviation of r ($\sigma_{RW1} = \sigma_r$). In applying this approach to CPUE data, we assumed that CPUE was proportional to population abundance.

One potential pitfall of the above approach is that normally distributed values of r_t imply the same probability of increases as decreases, thus, a prior constrained by population growth may also limit our ability to observe large population declines. To overcome this problem we used a penalized complexity prior for precision of the variance of the random walk (Simpson et al. 2017). The penalized complexity prior had a high density near a standard deviation of zero, but also a long tail (Figure 2). The long tail accommodates the possibility of rapid declines 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, but we explore this assumption below.

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 instantaneous growth rate represents the near maximum rate of negative or positive annual change in the population. Therefore, we choose the penalized complexity prior such that there was only a 0.025 probability of a standard deviation greater than a prior estimate of r for tiger sharks. The exact probability level of 0.025 is arbitrary, but the probability should be small enough that annual changes larger than r are

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unlikely. The penalized complexity prior combined with the normally distributed random walk meant the probability of $r_t > r_{max}$ (or $r_t < -r_{max}$) was 0.016.

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 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) however 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 'FALSE' to ensure the value provided for σ_{RW1} was interpreted as the marginal standard deviation. We also set 'constr' equals 'FALSE' to remove the sum to zero constraint.

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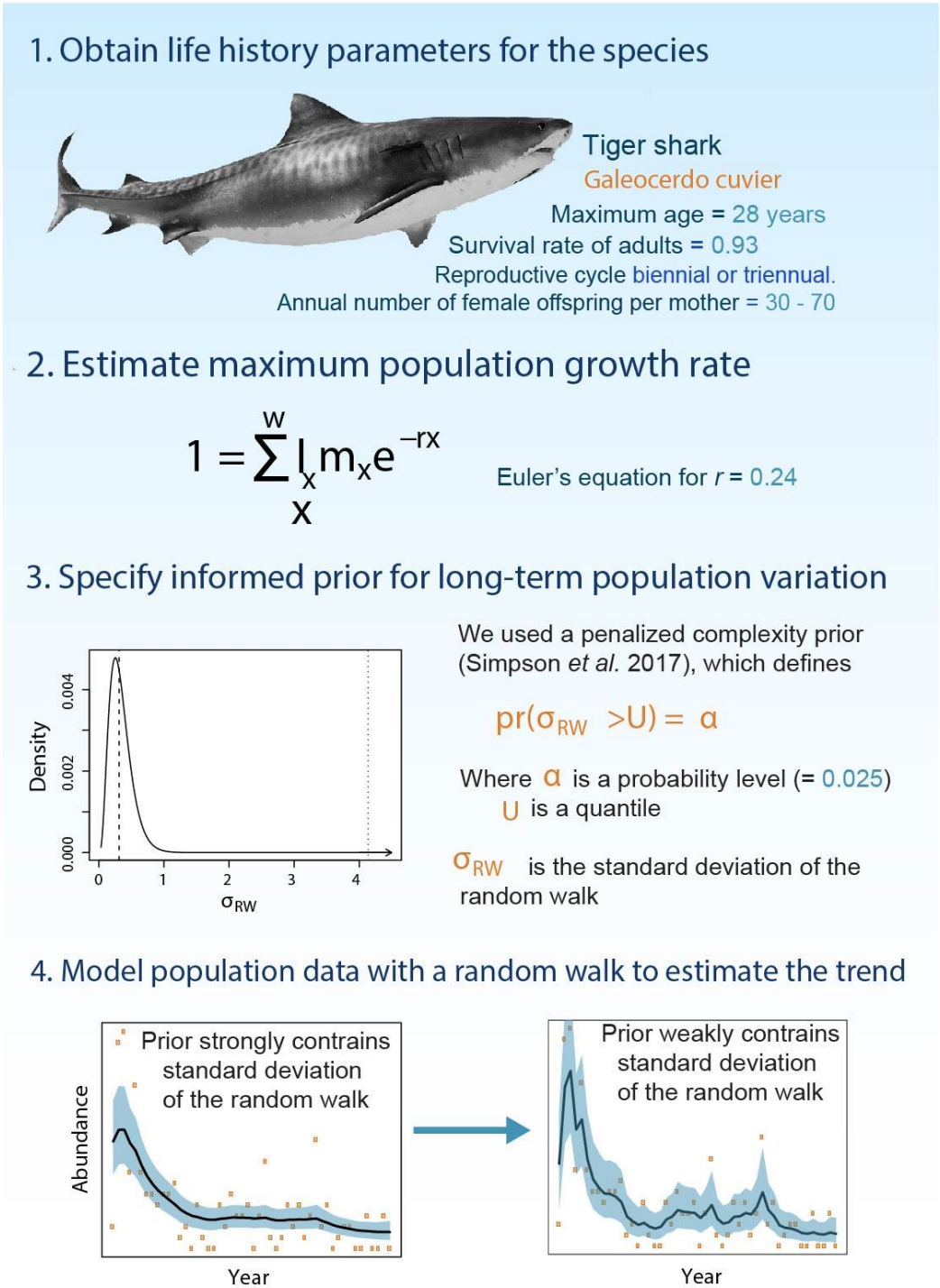

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228 **Figure 2** The approach for using life-history information to inform on trends in population

229 modelling. From Cortes 2002

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Analyses

We initially ran a simulation study to explore the impact of prior choice on estimation for species with a range of life-history traits. We simulated random walks and then fit models to the simulated data. We simulated drifting random walks (with an average decline of 2.5% per year) 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 negative binomial models with different penalized complexity priors: σ_{rw} = 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).

We also studied the ability of different priors and models to detect sudden sustained population crashes. In these simulations we used the same priors and observation errors as above and an initial CPUE of 50. We created time-series where the mean abundance was stable for 27 years, then collapsed in the 28th year to one of four values (12.5%, 25% or

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50%). Models were fitted with random walks and either three or six years of post-decline observations (see Supplementary material).

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 time-series drawn from different subsets of all regions and different prior specifications. We performed a factorial set of analyses crossing the four prior densities for σ_{RW1} 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 crossed with a selection of regions grouped into: (A) the northern-most regions, (B) middle latitude regions, (C) southern-most regions and, (D) 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 all tiger shark model fits 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

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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 plate smoothing spline applied to year. The maximum degrees of freedom was set to either 1/3 the number of years (Fewster et al. 2000), or chosen with cross-validation (Wood 2017).

Results

The simulation study 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 all species, 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 slightly more accurate (Fig 3, S2).

The simulation study of a sudden rapid decline showed that the faster priors were more likely to detect a sudden decline in CPUE (Fig S3). With the slow prior, the model estimated probability of a decline was always near 0.5. The models fitted to observations that were negatively binomially distributed were less sensitive to the decline than if the data were Poisson distributed. For instance, the probability of detecting a sudden decline with medium or fast priors was near one when data were Poisson distributed for any magnitude of decline and length of post-decline data. When data were negative binomially distributed the probability of decline was estimated to be between 0.55 and 0.88 for three years of post-decline data and between 0.6 and 0.9 for six years of post-decline data (Fig S3).

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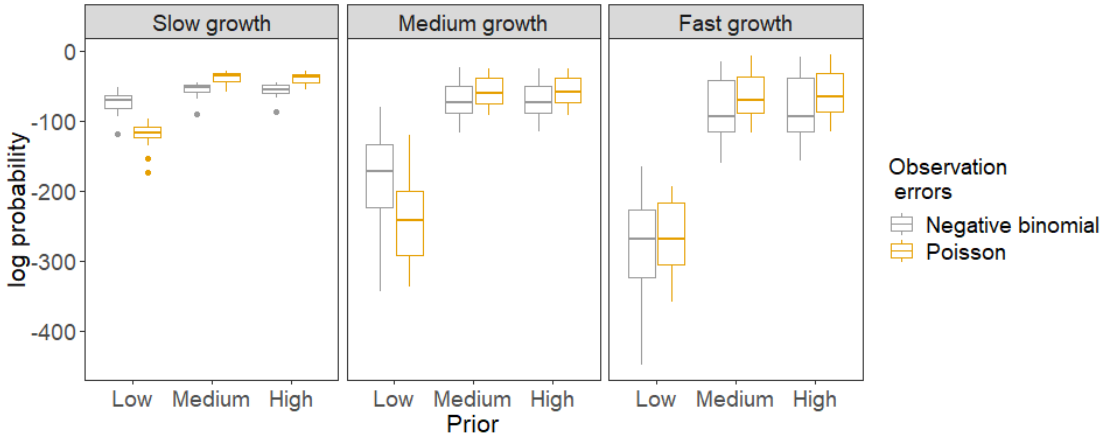

Figure 3 Results from simulation study for the log probability of the true simulated mean across all sample years given the results of the fitted model. Horizontal axes give the different priors, the panels show results from models fitted to time-series data simulated for species with different life-history 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.

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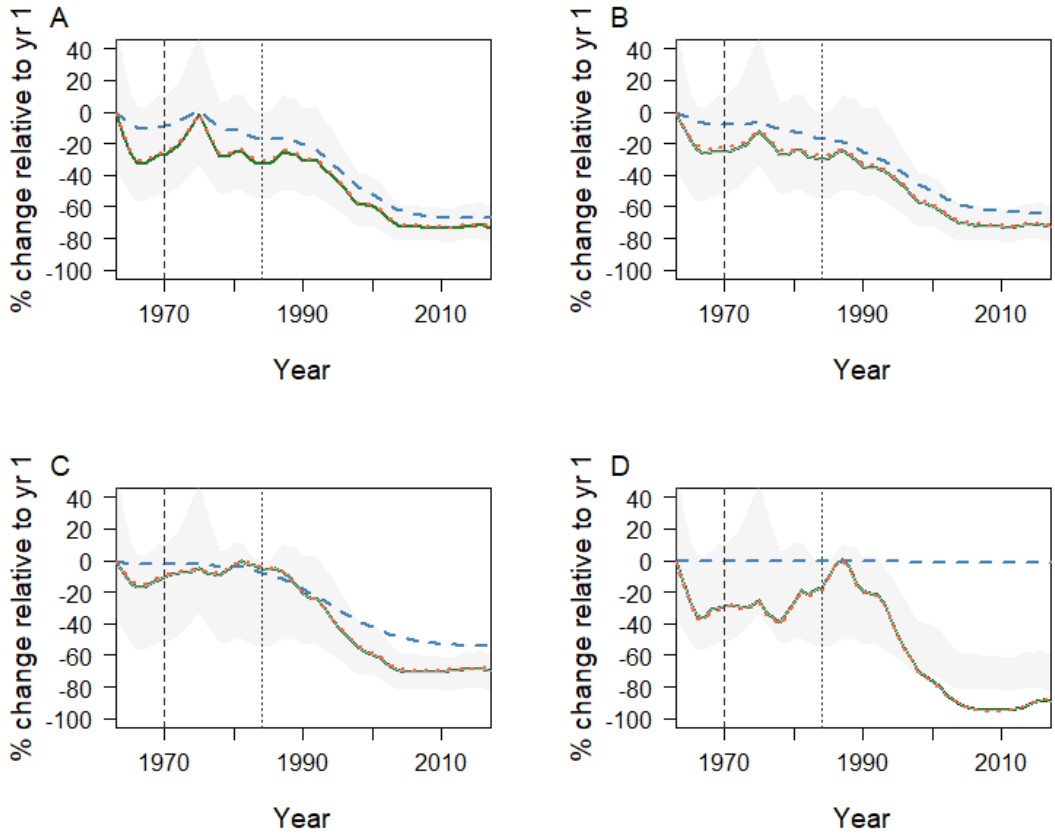

Fig 4 Examples of non-linear trends fitted to the tiger shark data. Models fitted to all regions (A), and 6 and 3 extreme-latitude regions (B, C), and just the southern-most region (Gold Coast) (D). Lines show the fitted values for the random walk with 95% C.I.s (shading) for the life-history prior (solid), 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 and data from six or more regions (Fig 4, Fig 5). The slow prior tended to under-estimate non-linearities in the trend and shrunk back to no trend when there were only data for 1-3 regions (Fig 4D, Fig 5). The slow prior also tended to have the poorest

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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 converged to 64%. Subsets with southern regions tended to overestimate the decline, whereas subsets with middle and northern regions tended to underestimate the decline (Fig. 5). Data subsets that mixed extreme north and south regions were closer to the 64% decline than data subsets just of north or south regions. There was a notable spike in abundance during the 1970s predicted by the model that used all regions and the life-history prior (Fig 4A), which was not present in subsets of the data (Fig 4B-D).

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.

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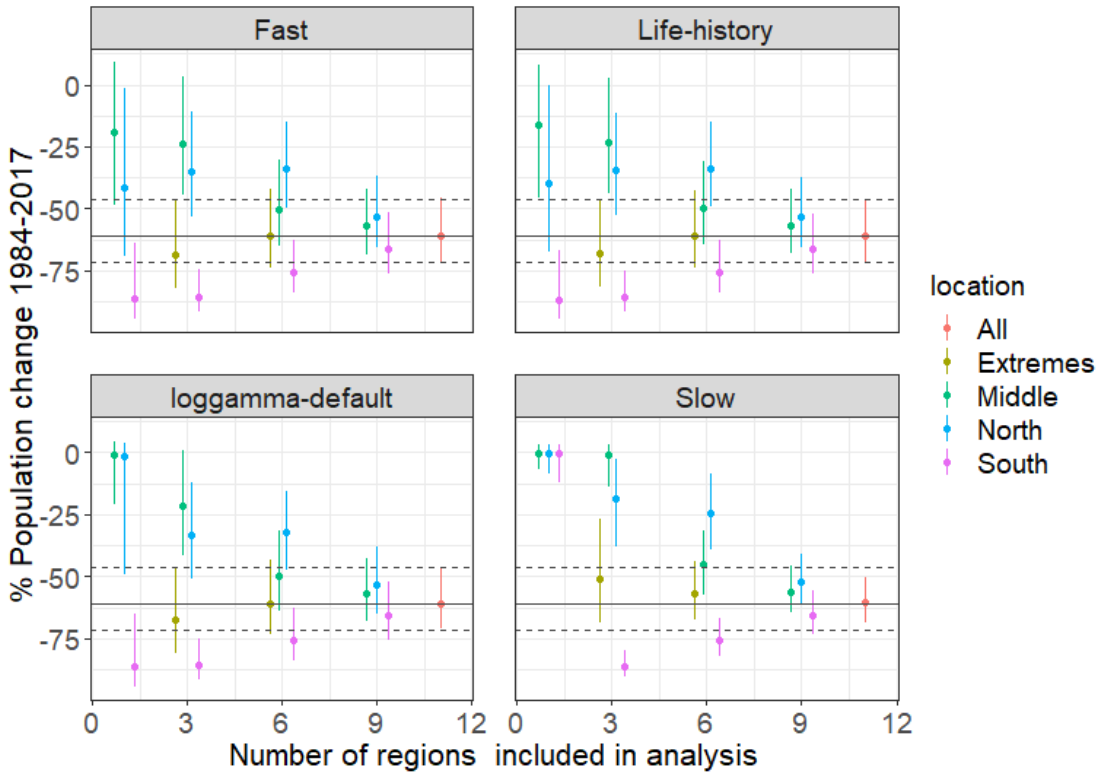

Fig 5 Estimated magnitudes of decline for the each prior (panels) and each scenario for subsets of regions (coloured points) over 3 generations (1984-2017). Points give median estimates and bars give 95% C.I.s. For comparison, the black and dashed lines give the median and 95% C.I.s for the life-history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

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therefore best based on sampling that covers a large part of their range. However, spatially extensive sampling can be 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 can help to establish more robust estimates of decline by smoothing over short-term and local deviations in population size.

We introduced a method for using Bayesian priors to inform on the degree of non-linearity in population trends. The method may help to overcome some of biases that come from analysing abundance indices with purely descriptive statistical models (Maunder et al. 2006). For instance, models that limit population growth by life-history parameters can overcome biased trends that resulted from change in detection probability of cryptic species (Sköld & Knape 2018). The results for the three generation decline were similar for all priors, so long as all sites were included in the analysis. 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. 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. Life-history does not figure into the choice of smoothing for generalized additive models, which instead be made by evaluating smoothing against the data at hand, or with reference

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to 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. This suggests that using the in-sample measures 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, such as when governments make potentially contentious decisions about the status of populations (e.g. Edgar et al. 2018).

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 (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 testing the utility of the new method across many species with a broader range of life-history types. We expect the approach will work

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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. The random walk 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 allows for greater population declines 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. An alternative would be to use a more complex model, like the Gompertz, that allows for a hard upper limit on population increases (Sköld & Knape 2018). Our simulation study of rapid declines suggested that the random walk with penalized complexity prior can still detect rapid declines in abundance, because its long probability tail does allow for rare but rapid changes in abundance. Conservation management must balance the risk of missing a true decline against the chance of false alarm. A next step therefore, would be to apply Bayesian decision analysis to optimise models for the balance between the cost of missed detection and the cost of false alarms.

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The decline of tiger sharks we observed is consistent with a decline in large sharks throughout the world's oceans (e.g. Baum & Myers 2004; Ferretti et al. 2008; Roff et al. 2018). The current global population trend for tiger sharks is unknown, although there is considerable variation across different oceans, with some regions showing no change (Baum & Myers 2004) and others large declines (Baum et al. 2003). Overall, their 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). The conservation status of tiger sharks globally escalated from "Lower Risk/near threatened" under the IUCN listing to "Near Threatened" in 2005 (Simpfendorfer 2009).

Tiger sharks may warrant listing as Endangered under state and national threatened species legislation (IUCN Criteria A2, >50% decline over three generations). The trend we observed in Queensland may be part of a broader scale trend. Genetic studies indicate the east coast population is part of a well mixed Indo-Pacific population (Holmes et al. 2017). Further, in nearby New South Wales tiger shark catches have also declined, a decline that has been attributed to increased fishing pressure in temperate waters (Reid et al. 2011). While our study does not cover the entire Indo-Pacific population, the large spatial extent of the current study (11 regions across 1760km of coastline) plus declines in adjacent NSW nearly 1000km south (Reid et al. 2011) likely reflects a large scale regional trend spanning 18° in latitude across tropical and temperate coastlines of eastern Australia. While the inclusion of time-series data from throughout Indo-Pacific would strengthen evidence for a whole of population decline, long-term datasets spanning multiple generations are largely absent for adjacent regions in the Pacific.

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While some uncertainty exists in the historical data used here, data collection was standardized in the QSCP in the early 1990's. This implies trends in recent decades when declines have been observed are robust (see Roff et al. (2018) for discussion). Our proposed statistical method may also help smooth over temporal and regional variability in trends by estimating the long-term trend that is consistent across regions, and by controlling for differences in gear type.

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 when modelling population trends. The trends estimated here, while dependent on the quality of the CPUE data, suggest that tiger sharks should be listed as a threatened species under Australian state and possibly national legislation.

Authors contributions

CB and JR conceived of the manuscript idea and designed the study. JR obtained the data, performed quality control and conducted initial analyses. CB conducted the modelling. CB and JR created the figures and wrote the manuscript.

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