



Original article

Predicting sustainable shark harvests when stock assessments are lacking

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Effective fisheries management generally requires reliable data describing the target species' life-history characteristics, the size of its harvested populations, and overall catch estimates, to set sustainable quotas and management regulations. However, stock assessments are often not available for long-lived marine species such as sharks, making predictions of the long-term population impacts of variable catch rates difficult. Fortunately, stage- or age-structured population models can assist if sufficient information exists to estimate survival and fertility rates. Using data collected from the bronze whaler (*Carcharhinus brachyurus*) fishery in South Australia as a case study, we estimated survival probabilities from life tables of harvested individuals, as well as calculated natural mortalities based on allometric predictions. Fertility data (litter size, proportion mature) from previous studies allowed us to build a fertility vector. Deterministic matrices built using estimates of life-table data or natural mortality (i.e. harvested-augmented and natural mortality) produced instantaneous rates of change of 0.006 and 0.025, respectively. Assuming an incrementing total catch at multiples of current rates, stochastic simulations suggest the relative rate of population decline starts to become precipitous around 25% beyond current harvest rates. This is supported by a sharp increase in weighted mean age of the population around 25% increase on current catches. If the catch is assumed to be proportional (i.e. a constant proportion of the previous year's population size), the relative r declines approximately linearly with incrementing harvest beyond the current rate. A global sensitivity analysis based on a Latin-hypercube sampling design of seven parameters revealed that variation in the survival estimates derived from the life tables was by far the dominant (boosted-regression tree relative influence score = 91.14%) determinant of model performance (measured as variation in the long-term average rate of population change r). While current harvest rates therefore appear to be sustainable, we recommend that fisheries-management authorities attempt to sample a broader size range of individuals (especially older animals) and pursue stock assessments. Our models provide a framework for assessing the relative susceptibility of long-lived fishes to harvest pressure when detailed stock data are missing.

Keywords: *Carcharhinus brachyurus*, chondrichthyan, demographic model, elasmobranch, global sensitivity analysis, Latin hypercube, sustainable fisheries, whaler shark

Introduction

As many commercially harvested populations of fish decline globally, there is increasing pressure to ascertain not only total stock size, but the rate at which fish can be caught without compromising long-term population resilience (Pauly *et al.*, 2002; Pauly *et al.*, 2005; Branch, 2008; Evans *et al.*, 2017). For many wide-ranging marine species in particular, the capacity to estimate stock size is limited by available funding and the enormous effort it can sometimes entail, so fisheries targeting these species often operate in something of an information vacuum. Sharks are of particular concern in this regard because many species have evolved life-history traits that make them more vulnerable to over-exploitation than most teleosts and other vertebrates (Field *et al.*, 2009; Dulvy *et al.*, 2014).

Largely as a result of this susceptibility and past over-exploitation, the conservation of sharks has seen increasing international attention in the form of multi-country signatories to conventions aiming to protect the most vulnerable species, such as the Convention on the International Trade of Endangered Species (CITES.org), and the Memorandum of Understanding on the Conservation of Migratory Sharks (www.cms.int). Further, many countries have devised national-scale management and conservation strategies to limit extinction risk of both harvested and non-target species (Lack and Sant, 2011). While the vulnerability of sharks to over-exploitation remains an issue for many species and populations, there are also many examples of shark populations that are harvested sustainably (Walker, 1998; Simpfendorfer and Dulvy, 2017). Yet, many challenges to ensure sustainable use of sharks and rays remain (Dulvy *et al.*, 2017).

Estimates of shark population size and/or biomass are difficult to obtain and hence, rare. Therefore, only a few shark species have had the detailed stock assessments required to model sustainable yields adequately (e.g. gummy and school sharks in Australia; blacktip sharks in the Gulf of Mexico; porbeagle sharks in Canada) (Walker, 1998; Southeast Data Assessment and Review, 2012b; Campana *et al.*, 2013). Most other shark fisheries are monitored using catch-per-unit-effort that attempts to signal when populations begin to decline. Alternatively, in some situations there is enough life-history information available to allow the construction of demographic models that aim to predict sustainable yields (McAuley *et al.*, 2007; Bradshaw *et al.*, 2013; Smart *et al.*, 2017).

One globally distributed species of shark is a good example of these management issues and the challenges of balancing commercial interests with conservation—the bronze whaler (*Carcharhinus brachyurus*), or copper shark. This large-bodied (up to 3 m total length), cosmopolitan species is primarily distributed in temperate coastal and neritic waters out to shallow maximum depths of ~ 100 m. Bronze whalers are commercially landed in South Africa, Australia, and New Zealand, with smaller targeted fisheries in Brazil, Uruguay, Argentina, Namibia, and the Mediterranean (Cliff and Dudley, 1992; Francis, 1998; Kroese and Sauer, 1999; Duffy and Gordon, 2003; Lucifora *et al.*, 2005; Jones, 2008; Rogers *et al.*, 2013).

In Australia, bronze whalers are targeted across their distribution from Port Macquarie (New South Wales) south to Perth (Western Australia) (McAuley *et al.*, 2007; Jones, 2008; Macbeth *et al.*, 2009; Fowler *et al.*, 2014). In South Australia, whaler sharks are an economically important component of the South Australian Marine Scale Fish fishery (Jones, 2008; Rogers *et al.*, 2013), a primarily owner-operated, multi-species industry, with most fishers targeting sharks with longlines and gillnets (Jones, 2008). South Australia has

a targeted *C. brachyurus* fishery that seasonally harvests both bronze whalers and dusky sharks (*C. obscurus*). The catch composition is dominated by bronze whalers (~80%; ~20% dusky sharks; although the dusky estimate was based on only a few, atypical shots and is probably not a representative sample) (Rogers *et al.*, 2013), with annual whaler shark catches averaging ~80 t since 1982–1983, and ~60 t since 2012–2013 (Jones, 2008; Fowler *et al.*, 2016). The low catch of *C. obscurus* means that we were obliged to focus solely on modelling *C. brachyurus*. A peak catch was recorded in 2009–2010, with a landed trunk weight of ~150 t (Fowler *et al.*, 2016). The catch composition consists mainly of juvenile sharks <1.5 m, which are targeted in the spring and summer months (September–April) (Rogers *et al.*, 2013), but small catches of large female sharks occurred in northern and southern Gulf St Vincent and southern Spencer Gulf over the same period (Jones, 2008).

For the South Australian population of *C. brachyurus*, which is considered a single management unit (Izzo *et al.*, 2016), there is currently no size or catch restrictions for whaler sharks, and individuals can be caught at any stage of their life history. Management strategies consist of gear restrictions, and catch-per-unit-effort trigger points monitored by fishery managers. For the recreational sector, management measures consist of spatial closures and daily catch limits. However, the effect of fishing mortality on this population is currently unknown and requires further assessments. We therefore constructed a stochastic matrix population model based on life-table and allometric estimates of survival, and fertility information collected from different populations. Using both constant- and proportional-catch scenarios, we projected populations for three generations to ascertain the influence of increasing harvest rates on the long-term mean instantaneous rate of population change (r), population size (N), and minimum population size (N_{\min}). We also investigated the effects on these parameters of imposing either minimum or maximum size limits on the catch.

Material and methods

Size frequency

The data sampled from the South Australian Marine Scalefish Fishery are described in detail in Drew *et al.* (2016); however, here, we summarise briefly the sampling protocol. Samples of *C. brachyurus* were collected between September 2009 and March 2014 using a combination of fisheries-dependent and -independent approaches. Most sharks were caught using floating longlines in the South Australian Marine Scalefish Fishery within the eastern Great Australian Bight and adjacent areas (West Coast, Spencer Gulf and Gulf St Vincent) (see Figure 1 in Drew *et al.* 2016), but some samples came from recreational fishers (mostly from northern Gulf St Vincent). Scientific longlines were also deployed in Gulf St Vincent using similar gear as for the commercial equipment. Sex was determined based on the presence of claspers in males. Length measurements were recorded to the nearest centimetre, including total length (L_T) and pre-caudal length (L_{PC}). Individuals' ages were determined based on counting the growth bands in vertebral sections (Drew *et al.*, 2016).

Length, age, weight relationships

We first established the relationship between total length (L_T) and age (years) for female *C. brachyurus* using parameters estimated for a three-parameter logistic growth model for female

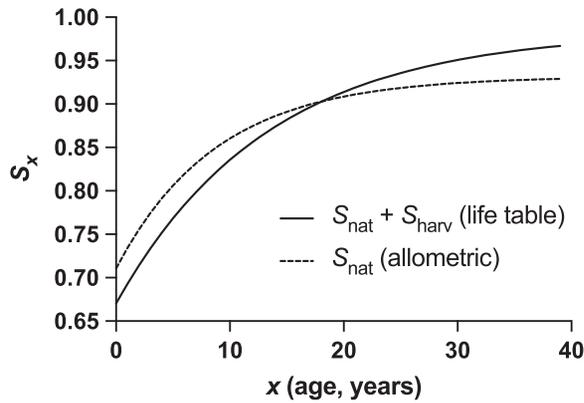


Figure 1. Predictive curves for age-specific (x , in years) survival of female bronze whalers (*Carcharias brachyurus*) based on life-table analysis (solid line), which includes both natural and fishing-related mortality, and for allometrically based predictions (dashed line).

sharks from the South Australian population (Drew *et al.*, 2016). Here, a female’s age (x) can be estimated as:

$$x = \frac{\log_e(L_T L_\infty) - \log_e(\alpha) - \log_e(L_\infty - L_T)}{k}$$

where L_∞ = asymptotic total length (308 cm), α = point of inflection for the logistic model (74), and k = the growth coefficient (0.146) (Drew *et al.*, 2016).

For age-specific estimates of natural mortality (M ; see below), we also had to estimate the relationship between precaudal length (L_{PC}) and L_T , as well as the relationship between L_{PC} and weight (W). We used the established *C. brachyurus* L_T - L_{PC} relationship from South Australia (Drew *et al.*, 2016) to calculate L_{PC} :

$$L_{PC} = \frac{L_T + 35.924}{1.364}$$

and then applied the previously estimated parameters for *C. brachyurus* in South Africa (Cliff and Dudley, 1992) to estimate wet weight (W_w) from L_{PC} :

$$W_w = 6.71 \times 10^{-6} (L_{PC})^{3.14}$$

Life-table analysis

We first calculated the frequency of harvested females (f_x) in each yearly age class (x) based on the above relationship. Life tables with small samples can give unrealistic estimates of final survival estimates because of incomplete sampling (especially of the older age classes), so some smoothing is generally required (Caughley, 1966; Caughley, 1977; Bradshaw *et al.*, 2013). First, we smoothed the logarithm of f_x using an exponential decay function of the form:

$$\log_e(f_x) = ae^{bx}$$

where $a = 5.628 (\pm 0.408 \text{ s.e.})$, and $b = -0.070 (\pm 0.009)$. We then calculated l_x (individuals surviving at the start of age x relative to l_1 ; with l_0 set to 1000 as is standard), d_x (mortality per year), q_x (age-specific mortality), and S_x (age-specific survival; $1 - q_x$) according

to standard life-table analysis (Caughley, 1977; Bradshaw *et al.*, 2013). However, S_x still gave biologically unrealistic (i.e. too low) estimates for some older age classes (> 15 years), so we additionally fitted an asymptotic logarithmic growth function to the relationship with x to produce a fitted S_x prediction:

$$S_x = S_{\max} (1 - be^{-kx})$$

where we fixed $S_{\max} = 0.944$ = the mean S of mature individuals ($x = 18-39$), $b = 0.319 (\pm 0.059)$, and $k = 0.075 (\pm 0.044)$. In this case, S_x includes both natural and fishing-related mortality (Figure 1).

Natural mortality

The life-table analysis estimates S_x from a harvested population, so they probably do not represent natural survival rates (S_{nat} ; i.e. from an unharvested population). To estimate natural mortality, we used existing relationships established for sharks. The first two are expected age-independent M_{nat} (natural mortality; where $S_{\text{nat}} = 1 - M_{\text{nat}}$) equations derived from estimated growth parameters:

$\log_e(M_{\text{nat}}) = -0.0066 - 0.279\log_e L_\infty + 0.6743\log_e k + 0.4643\log_e T$ (Pauly, 1980), where L_∞ and k are estimated from a three-parameter von Bertalanffy growth equation (457 cm and 0.034, respectively) (Drew *et al.*, 2016), and T = the average annual growth temperature (17 °C, the average sea surface temperature in Gulf St Vincent, South Australia) (Gaylard, 2004). The second age-independent estimate of M_{nat} was derived from:

$$M_{\text{nat}} = 1.6k$$

(Jensen, 1996).

We also calculated an age-variant S_{nat} based on an age-specific, dry-weight scaling factor:

$S_{\text{nat}} = e^{1.92(W_d)^{-0.25}}$ (Peterson and Wroblewski, 1984; Smart *et al.*, 2017), assuming $W_d = 0.2W_w$ (Cortés, 2002). However, in the absence of an objective way to combine the different natural mortality estimates, we took the mean of the two age-invariant S_{nat} and the asymptotic S_{nat} from the age-variant equation above and refitted the relationship using a three-parameter von Bertalanffy growth function of the form:

$$S_x = S_{\max} (1 - be^{-kx})$$

where in this case we set the S_{\max} to the mean of the two S_{nat} described above ($=0.866$), $b = 0.237 (\pm 0.0001)$, and $k = 0.113 (\pm 0.0002)$ (Figure 1).

Fertility

We estimated b_x , the proportion of mature females in each age class x , using data for the species from north Patagonia, Argentina (Lucifora *et al.*, 2005). Converting L_T to age (in years) as described above, we fitted a three-parameter sigmoidal model to the age-proportion mature relationship:

$$b_x = \frac{a}{1 + \left(\frac{x}{p}\right)^c}$$

where $a = 1.003 (\pm 0.005)$, $p = 14.350 (\pm 0.014)$, and $c = -39.603 (\pm 1.208)$. However, the youngest mature female observed in the

South Australian fishery had a $L_T = 271$ cm, which equates to ~ 16 years. Thus, we changed the p parameter in the age-proportion mature relationship above to 16 to reflect the regional catch data more closely (Figure 2).

To estimate age-variant litter size (B_x), we combined the 39 South African female *C. brachyurus* for which litter size and mother L_T were available (Cliff and Dudley, 1992) with the four available South Australian females with the same measurements (Drew et al., 2016). Converting L_T to age (in years x) as described above, we fitted both exponential growth ($B_x = ax^b$) and linear models ($B_x = a + bx$) to the combined dataset. The exponential had much more information-theoretic support than the linear (small-sample Akaike's information criterion weights: ~ 1 and ~ 0 , respectively), so we only used the exponential growth model to predict litter size, where $a = 1.960 (\pm 0.154)$, and $b = 0.388 (\pm 0.008)$ (Figure 3). Breeding frequency for *C. brachyurus* is probably biennial (Walter and Ebert, 1991; Cliff and Dudley, 1992). Thus, the final fertility vector was $0.5 \cdot 0.5b_x B_x$ (i.e. also halving litter size to model daughters only in this female-only model).

Maximum intrinsic rate of population increase

To estimate an independent maximum rate of population increase (r_{max})—a parameter useful in assessing extinction risk (Pardo et al., 2016)—we followed the updated r_{max} equation for chondrichthyans provided in Pardo et al. (2016) using the parameters estimated here for *C. brachyurus*. We solved r_{max} iteratively from the equation:

$$\sim \alpha = e^{r_{max} \alpha_{mat}} - p(e^{r_{max}})^{\alpha_{mat}-1}$$

where $\sim \alpha = l_{\alpha_{mat}} b$, $l_{\alpha_{mat}} = (e^{-M})^{\alpha_{mat}}$, b = mean female litter size for mature (16+ years) females = 2.53 (\sim fecundity), $M = 1/\omega$, $\omega = (\alpha_{max} + \alpha_{mat})/2 = (40 + 16)/2 = 28$, and $p = e^{-M}$ (Pardo et al., 2016).

Age-structured (Leslie) matrix model

We constructed a pre-breeding, 40 (i) \times 40 (j) element (ages 0 to 39, see below), Leslie projection matrix (\mathbf{M}) for females only, multiplying a population vector \mathbf{n} to estimate total population size and

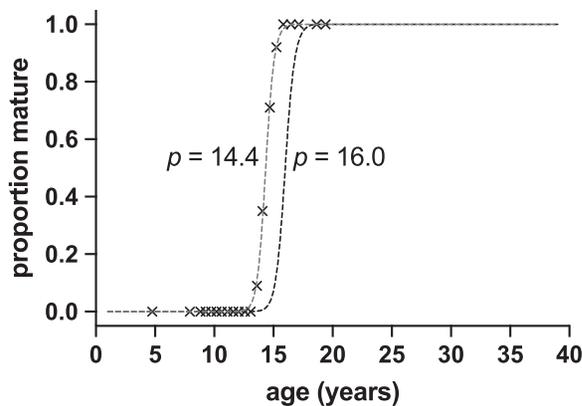


Figure 2. Three-parameter sigmoidal function fitted to the proportion of females mature (i.e. breeding) relative to age. However, the youngest mature female found in the South Australian fishery was 16 years; thus, we changed the b inflexion parameter to 16 years.

the instantaneous rate of population change ($\log_e (\sum_{x=0}^{\omega} \mathbf{n}_{t+1} / \sum_{x=0}^{\omega} \mathbf{n}_t)$, where ω = maximum longevity at each forecast time step (Caswell, 2001). We set $\omega = 39$ years according to data from the South Australian fishery (Drew et al., 2016). Fertilities (m_x) occupied the first row of the matrix, survival probabilities (S_x) occupied the sub-diagonal, and the final diagonal transition probability ($\mathbf{M}_{i,j}$) represented survival of the 39+ stage, which we set to zero. In fact, we created two, separate \mathbf{M} : one using S_x estimated from the catch data (\mathbf{M}_{harv} ; Supplementary Table S1), and one using our estimates of natural survival (S_{nat}) based on life-history traits (\mathbf{M}_{nat} ; Supplementary Table S2. We projected the \mathbf{Mn} combinations for three generations following IUCN Red List criteria (i.e. 78 years; see Results) to obtain changes in population size (IUCN, 2001). We also ignored the results from the first projected generation as a “burn-in” to allow the initial deterministic population vector (which is set arbitrarily because true population size is unknown) to stabilise to a density-dependent structure (Prowse et al., 2013) (see next section).

Compensatory density feedback and catastrophic mortality events

In the absence of measured compensatory density-feedback mechanisms in this species, we invoked a hypothetical reduction in the final fertility vector by arbitrarily defining a sub-unit multiplier (< 1) when the population increased above the starting size. For all simulations, we assumed that a tripling in population size invoked a 30% reduction (i.e. 0.7 fertility multiplier), with a linear change from 0 to 30% over the interval 1–3 N .

We also invoked a catastrophic die-off function in the simulations to account for the probability of catastrophic mortality events (C) scaling to generation length among vertebrates (Reed et al., 2003):

$$C = \frac{0.14}{G}$$

where G = mean generation time calculated from the deterministic matrix \mathbf{M} , which for the natural mortality matrix \mathbf{M}_{nat} was 26.1 years (Caswell, 2001). Once invoked at probability C for any

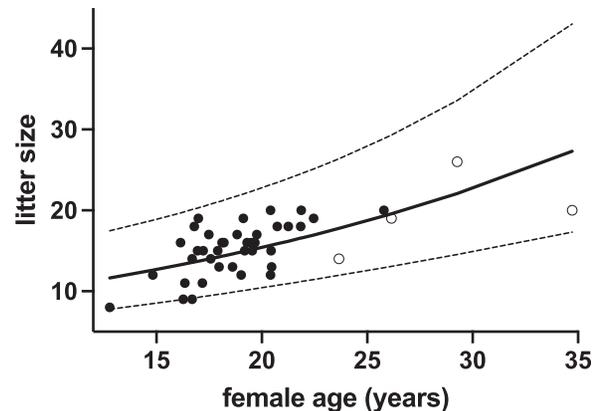


Figure 3. Relationship (mean: solid line; 95% confidence bounds: dashed lines) between age (years) and litter size. Full circles represent *C. brachyurus* data from South Africa (Cliff and Dudley, 1992), and open circles indicate the four, mature *C. brachyurus* females measured from South Australia (Drew et al., 2016).

iteration of the model, we halved the survival vector to induce a 50% mortality event for that year (e.g. Bradshaw *et al.*, 2013). This is based on the definition by Reed *et al.* (2003) that a catastrophe is “. . . any 1 yr peak-to-trough decline in estimated numbers of 50% or greater.”

Harvest projections

Given that we do not know (i) the proportion of the population that is being harvested, or (ii) the size of the total population, we assumed that an increasing harvest would eventually lead to population decline. We therefore took the age-variant proportional harvest data, and fitted a gamma-like peak model to estimate the proportional offtake per age class (O_x):

$$O_x = ax^k e^{-xc}$$

where $a=0.142 (\pm 0.015)$, $k=1.120 (\pm 0.221)$, and $c=0.419 (\pm 0.061)$. However, this fit produced $\hat{O}_0=0$, so we substituted the observed value at $O_0=0.508$ to emulate the observed data better (Supplementary Figure S1).

Assuming that the population is already below maximum growth rates due to current catch (see Results), we iterated the stochastic simulation through incrementing proportions of catch to the \mathbf{n} vector beyond the base \mathbf{M}_{harv} for both a constant catch (i.e. a value of 0.1 assumes a 10% increase above current harvest, 0.5 assumes a 50% increase, and 1.0 assumes a doubling of current catch) and a proportional catch (i.e. where the catch is a proportion of the previous year’s population size). However, given that the life table-based survival probabilities produced \mathbf{M} with a near-stable dominant eigenvalue ($\lambda = 1.006$; $r = 0.006$), any nominal increase in harvest rate would necessarily induce population declines. This result rests on the assumption that the survival probabilities produced by the life tables are accurate; however, the small sample size and inadequate sampling of individuals in the older age classes especially leads us to question this assumption. Therefore, we report the relative change in r with each incrementing harvest rate beyond the current instead of relying on the direct r values as indicative of the true biological potential of each scenario (i.e. all simulated scenarios are relative to the current state only).

For each of 1000 iterations of the three-generation projections within each harvest increment (iterated from 0 to 1.0 at increments of 0.1), we resampled the survival and fertility parameters to invoke demographic stochasticity. Here, we defined a function to estimate the shape parameters of a *beta* function, and then randomly *beta*-resampled each element of the survival vector for each year of the projection. For the fertility vector, we used a random Gaussian resampler for the a and b parameters of the fitted litter-size function (means and standard errors), and separately for the a , b parameters of the predicted proportional-maturity function. We also set the starting population vector at the arbitrarily set carrying capacity K (i.e. assuming that the population is at a density-feedback equilibrium; the actual value of the start population size is therefore arbitrary, but for all iterations we set K to 30 000 individuals). This does not necessarily produce a stable population size because population growth is still a possible outcome when the reduction on fertility does not produce negative r , but it does allow for changes in harvest to produce relative changes in population growth rate for comparison. Complete R

code (R Core Team, 2017) and data used for the scenario projections is available at github.com/cjabradshaw/WhalerSharkModel.

Size-limit scenarios

To simulate management scenarios based on size limits, we imposed a range of minimum age-at-first-capture thresholds, which translates to a minimum size limit that excludes juveniles from the catch. We iterated through ages 3–12 (which equates to ~ 100 – 199 cm T_L) as a minimum catch requirement, distributing the remaining proportional harvest among the remaining (older) ages according to the age-variant catch curve (Figure 4a). We applied these varying limit scenarios across all ranges of increasing harvest rate. We also applied a maximum size age limit that excludes adults and large juveniles, incrementing through ages 3–15 years, because maturity occurs at 16 years; this range equates to ~ 100 – 227 cm T_L) (Figure 4b).

Global sensitivity analysis

The complexity of the population model regarding the number of estimated and assumed parameters requires a “global” sensitivity analysis that varies many parameters simultaneously to provide robust sensitivity measures when nonlinear responses and interactions are present (Wainwright *et al.*, 2014; Prowse *et al.*, 2016). Following the approach outlined in Prowse *et al.* (2016), we designed a Latin-hypercube sampling protocol of the parameter space for the proportional harvest model based on the current

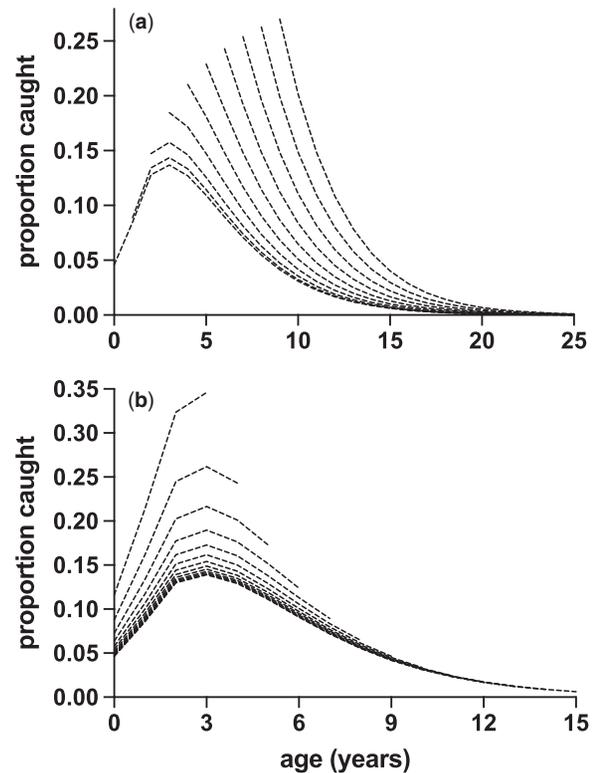


Figure 4. (a) Minimum-age catch ranges where the total catch becomes the area under the curve (always standardized to sum to 1) for increasing minimum-age thresholds from age 3 to 12 years. (b) Maximum-age catch ranges where the total catch becomes the area under the curve (always standardized to sum to 1) for increasing maximum-age thresholds from age 3 to 15 years.

population structure (i.e. \mathbf{M} with the life table-derived survival vector). We set the seven parameters we chose to investigate to be sampled from a uniform distribution as follows: (i) density-feedback multiplier on fertility between 0.5 and 0.9 (set in the original model arbitrarily to 0.7); (ii) inflexion point for age at maturity between 14 and 18 years (set in the original model to 16 years); (iii) modifier of total litter size (B_x), adding an integer between -3 and 3 to the age-specific litter-size vector; (iv) modifier of the vector of life-table survival estimates by -5 to $+5\%$; (v) modifier of the vector of natural survival estimates by -5 to $+5\%$; (vi) modifier of the catastrophe numerator from 0.1 to 0.2 (set to 0.14 in the original model); and (vii) change in the intensity of catastrophic die-offs as a multiplier on survival of between 0.25 and 0.75 (set to 0.5 in the original model).

For the Latin hypercube sampling, we set the simulation to run for 100 iterations each, with 1000 samples from the parameter space. The response variable was the mean long-term rate of population change (r) derived from each simulation. To test the effect of the parameter values on r , we applied a boosted-regression tree (Elith *et al.*, 2008) emulator implemented using the dismo R

library and its function *gbm.step* (Hijmans *et al.*, 2017), setting the error distribution family as Gaussian, the bag fraction to 0.75, the learning rate to 0.01, the tolerance to 0.0001, and the tree complexity to 2 (first-order interactions only considered). To assess the relative effect of each sampled parameter on r , we examined the boosted-regression tree metrics of relative influence (Prowse *et al.*, 2016).

Results

Deterministic matrix properties and r_{\max}

The base matrix \mathbf{M} using the life table-based survival vector produced a dominant eigenvalue $\lambda = 1.006$, which equates to an instantaneous rate of population change (r) = 0.006. With biennial breeding and an age of onset of maturity in females at 16 years, the ratio of the number of female offspring in year $t+1$ to the number born in the previous year (R_0) was 1.18, giving a mean generation time (G) of 27.4 years. In contrast, the natural-mortality \mathbf{M} produced $\lambda = 1.025$ ($r = 0.025$; $R_0 = 1.91$; $G = 26.1$), which supports the hypothesis that current harvest produced a

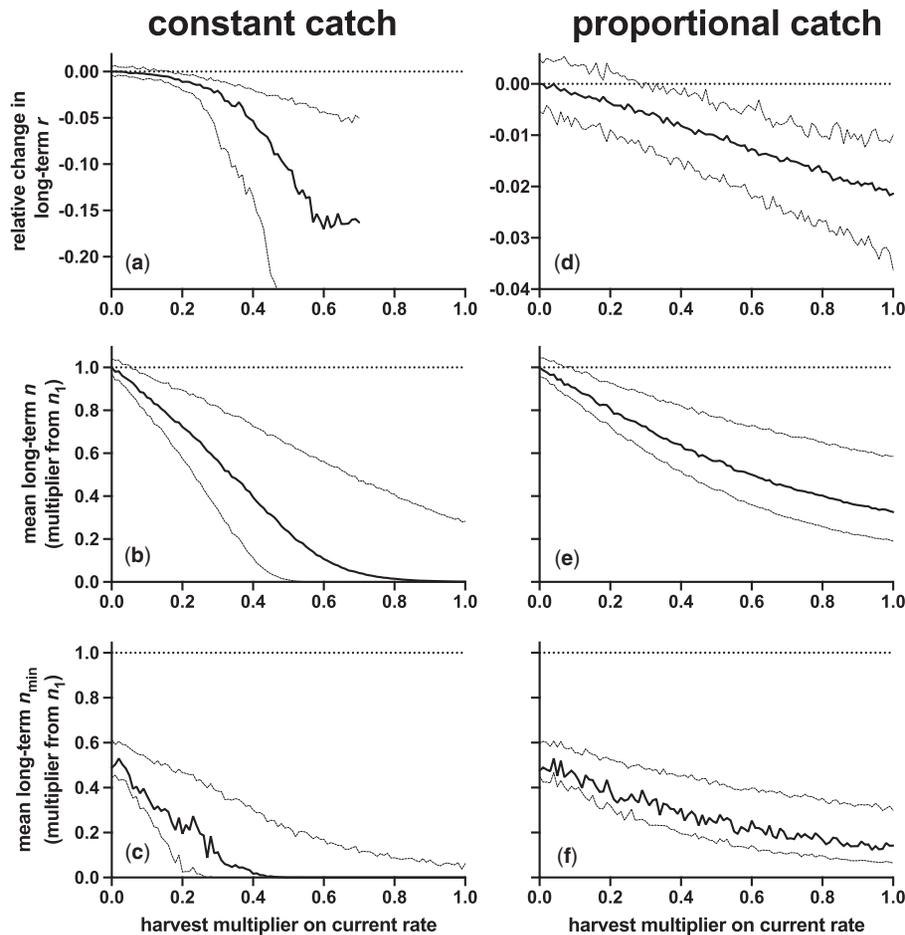


Figure 5. Harvest outcomes assuming a constant catch (left column) vs. a proportional catch (right column). Indicators include relative change in mean instantaneous rate of population change (r) including 95% confidence bounds (based on 1000 iterations of the model) (a, d), mean long-term population size (n , expressed as a multiplier of n_1) with 95% confidence bounds (b, e), and mean long-term minimum n (expressed as a multiplier of n_1) with 95% confidence bounds (c, f) relative to varying harvest rates. Harvest rates are expressed as a multiplier of current harvest (catch in time step 1 for constant catch, catch in time step $i - 1$ for proportional catch), such that 0.5 is equivalent to a 50% increase on current/previous annual harvest, and 1.0 means double current/previous annual harvest. All population projections are over the interval of three generations, with the first generation ignored.

population growth below its theoretical potential. We estimated the theoretical $r_{\max} = 0.170$ according to the parameter estimates used in constructing M .

Stochastic harvest projection

Assuming a starting population at density equilibrium (K), and incrementing the harvest beyond today's rate to double its current value, the stochastic projections suggest that at a constant catch (i.e. age-specific proportion caught $\times n_i$), the relative change in r starts to become strongly negative around 20–25% higher catch than today's annual rate (Figure 5a). With an additional 25% harvest increment, the mean long-term (three generations, or 82 years) population size is about 68% of the initial population size n_1 (Figure 5b), and the minimum population size (i.e. mean minimum possible over the stochastic projection window) is about 20% of the initial population size (Figure 5c). When the catch proportionally declines with population size (i.e. age-specific proportion caught $\times n_i$), relative r declines slowly and approximately linearly with incrementing harvest rates beyond the current (Figure 6d), but with some near-stabilization in mean and minimum long-term population size at high harvest rates (Figure 5e and f).

Given the dominance of juveniles in the current catch, the weighted-mean age and L_T of the final population (i.e. after three generations) increases markedly at about 25% beyond current rates for the constant-catch harvest (Figure 6a), but follows a modest downward trajectory with incrementing proportional catch rates (Figure 6b).

Size-limit scenarios

Applying a minimum-age or maximum-age (\sim -size) limit on the catch had little overall effect on the long-term rate of population change (r) (Supplementary Figure S2). While there was little effect of catch limits on r , the weighted-mean L_T of the final population varied somewhat with changes in minimum- or maximum-age limits (Figure 7). For minimum-age limits in particular, there was a non-linear effect of increasing minimum age on L_T at the highest harvest rates (Figure 7a and c).

Global sensitivity analysis

The boosted-regression tree emulator for the seven-dimension, Latin hypercube-sampled parameter space indicated that the dominant influence on model performance as measured by the long-term rate of population change (r) was the -5% to $+5\%$ modifier of the vector of survival estimates derived from the life tables (relative influence score = 95.54%). All other parameters had relative influence scores $< 3\%$ (Table 1). As an example of the effect of modifying the life-table survival estimates, we reset the survival vector to equivalent values of the natural survival from $x = 19$ to maximum age (i.e. beyond the intersection point of the two curves in Figure 1, the two curves become identical) and re-ran the proportional harvest model. This modification—essentially describing lower survival than currently estimated for older sharks—had little effect on the proportional harvest characteristics (cf. Figure 5d–f with Supplementary Figure S3). We also show in Supplementary Figure S4 the effects on n and r of including or excluding the catastrophic die-off probability in the stochastic projections.

Discussion

While it would be unwise to set harvest quotas for a shark fishery anywhere in the world based solely on stochastic population models, such approaches provide additional dimensions to the assessment of long-term population resilience to harvest. Worldwide, traditional fisheries management founded on the luxury of actual stock assessments has still had mixed success, with many fish populations still succumbing to over-exploitation despite adequate estimates of population size (Myers and Worm, 2003; Pauly et al., 2005). For commercially valuable sharks, their effective management is considerably more uncertain because of a near-complete lack of actual stock assessments, combined with the slow life histories of many species. In other words, the probability of over-exploiting shark populations in most fisheries is likely to be high relative to even large-bodied teleosts (Field et al., 2009; Dulvy et al., 2014; Simpfendorfer and Dulvy, 2017). As such, relying on simple management interventions such as gear restrictions and catch-per-unit-effort trigger points might underestimate the harvest impacts on any given population.

The longevity and slow breeding rates of many shark species, however, make them ideally suited to the application of matrix population models that can provide valuable information to fisheries managers. Indeed, such models are becoming more popular (e.g. Otway et al., 2004; McAuley et al., 2007; Bradshaw et al., 2013; Smart et al., 2017), but we argue that they are still probably an under-exploited tool in the fisheries-management toolbox that could be more frequently adopted in major shark fisheries (see also Au et al., 2015; Cortés et al., 2015; Cortés, 2016; Pardo et al., 2016). While all the parameters necessary to construct realistic demographic models of this type might not always be available, the basic ingredients normally are, or can be estimated

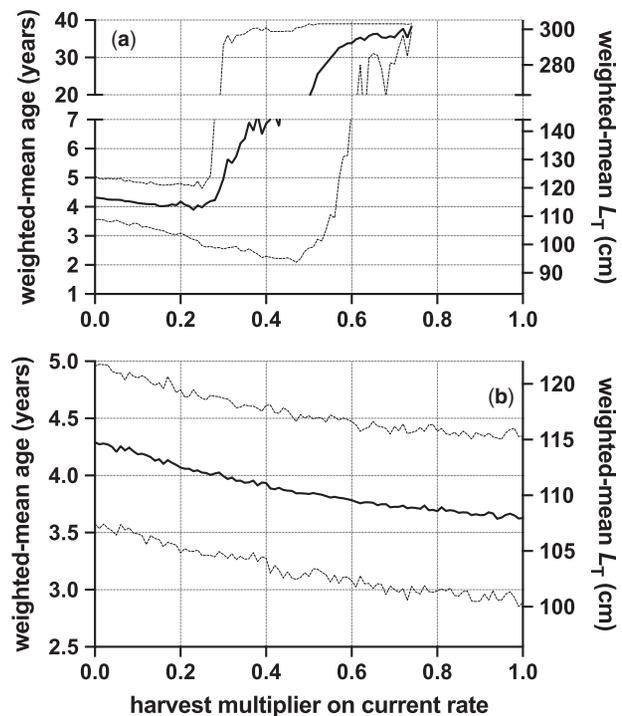


Figure 6. Trend in weighted mean age and total length (L_T) for the final projected population after three generations relative to constant (a) and proportional catch rate (b).

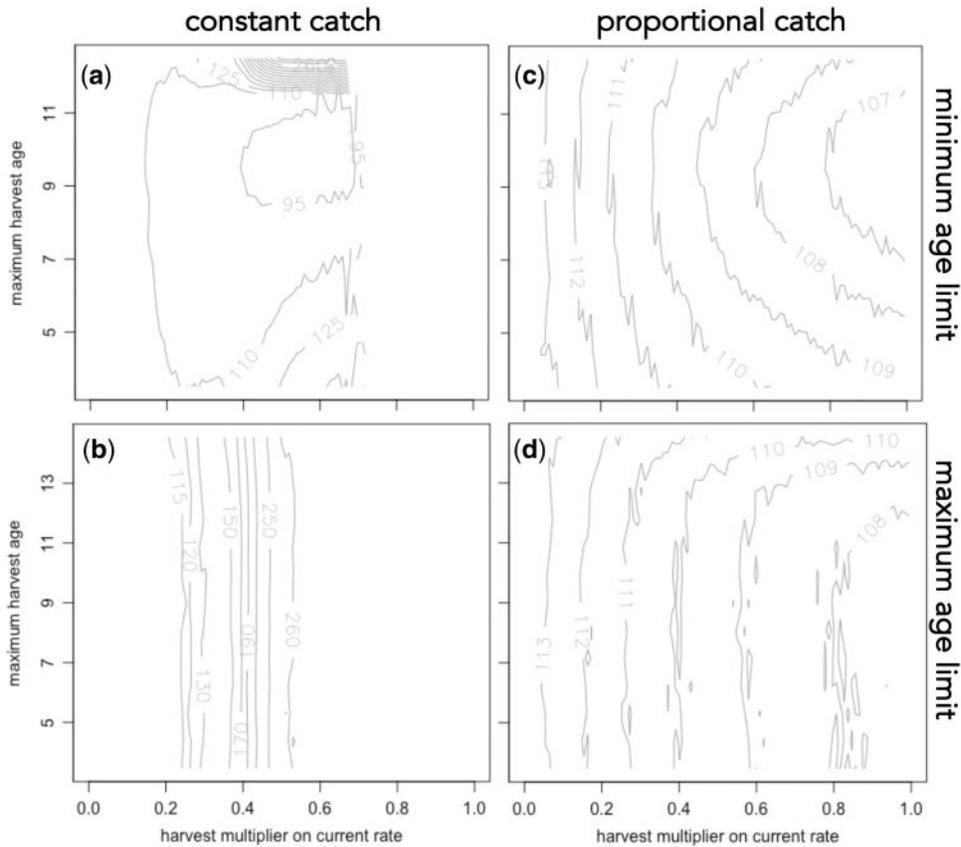


Figure 7. Change in mean long-term (three generations) weighted mean total length (L_T , in cm) of the final population for constant (left panels) and proportional catch (right panels) as a function of (top panels) minimum-age catch limit (from 3 to 12 years) or (bottom panels) maximum-age catch limit (from 3 to 15 years) and varying proportional harvest rates.

Table 1. Global sensitivity analysis: relative influence scores for the seven parameters sampled using a Latin-hypercube design (100 iterations of 1000 parameter samples) derived from the boosted-regression tree emulator.

Parameter	Sampled range	Relative influence (%)
Modifier of vector of survival estimates derived from life table	-5 to +5%	95.54
Modifier of litter size	-3 to +3 (integer)	2.74
Density-feedback fertility modifier	0.5-0.9	0.77
Catastrophe intensity survival modifier	0.25-0.75	0.58
Catastrophe numerator	0.1-0.2	0.24
Modifier of survival estimates derived from allometric relationships	-5 to +5%	0.10
Inflexion point for age at maturity	14-18 years (integer)	0.04

allometrically. Indeed, with a representative size-frequency distribution and a basic understanding of the species' reproduction schedule (including age-litter size and maturity details), even the most basic stochastic models can elucidate otherwise unknown elements of a species' potential susceptibility to over-exploitation, and our work outlines how this can be done. Such size-frequency distributions could be estimated from fisheries-dependent or -independent samples or market surveys, but only if large enough samples can be collected to represent the full range of individual sizes, and biases of size selectivity can be accounted for or avoided.

In the case of the example species we modelled here, our models suggest that the South Australia fishery's catch is potentially high enough to elicit population declines of *C. brachyurus* within

State waters, especially if total catches increase in the future. On the other hand, the lack of genetic structure across its distribution, means that there is probably some immigration within the greater meta-population that provides some resilience to over-exploitation. However, our global sensitivity analysis revealed that the most important parameters to estimate accurately for robust inference are estimates of survival from life tables. This means that adequate sampling across the size range of the population is essential, and was arguably insufficient in the case of South Australian *C. brachyurus* given the dominance of juveniles in the landed samples (Drew *et al.*, 2016). For this reason in particular, without a larger and more uniform sampling of all age classes with which to construct life tables, the true survival rates of the population at current harvest rates remain uncertain. Although

the constant harvest did not begin to drive relative r downwards until about a 20–25% increase on current harvest rates, we nonetheless recommend caution in concluding that the population could withstand such a sustained increase. The weighted mean age of the population increasing markedly around 25% additional harvest provides some validation that the population demonstrates some moderate resilience to increasing harvest rates. Should stock assessments for this population ever become feasible, the information would likely enhance the reliability of management quotas and other interventions.

A recent review (Simpfendorfer and Dulvy, 2017) showed that only 47 chondrichthyans (shark, batoids, and chimeras) have had stock assessments, and of those, 33 species are considered to be fished sustainably; this represents only a small percentage ($\sim 2.6\%$) of global shark diversity ($n = 1188$ species). That review also showed that while species with relatively low productivity—see estimates of various rates of population change (r , r_{\max} , and λ) (McAuley *et al.*, 2007; Dulvy *et al.*, 2008; Smith *et al.*, 2008; Romine *et al.*, 2009; Ward-Paige *et al.*, 2012; Liu *et al.*, 2015; Cortés, 2016)—can support sustainable fisheries (e.g. school sharks), no species with a maximum rate of population increase ($r_{\max} < 0.1$) were identified as sustainable. In our case, even though *C. brachyurus* is thought to grow slowly, reach maturity late (~ 16 years), and only reproduce every 2 years (Drew *et al.*, 2016), estimated r_{\max} was ~ 0.170 . This is higher than the $r_{\max} = 0.124$ estimated for *C. brachyurus* by Pardo *et al.* (2016), but they used a younger maximum age (34.5 years), an older age at maturity (20.9), and a smaller mean litter size (daughters) from mature females (4.2 vs. our 5.1). In comparison, fisheries for other large-bodied temperate or semi-temperate carcharhinid species with slow life-history traits (i.e. dusky shark and sandbar sharks) are listed as *rebuilding* (not sustainable, but fishing mortality is less than maximum sustainable yield mortality F_{MSY}) (Simpfendorfer and Dulvy, 2017). Catches for these species when declines occurred (~ 300 and 400 t year^{-1} for dusky and sandbar sharks, respectively) are, however, much greater than the $\sim 80 \text{ t}$ of *C. brachyurus* caught within the South Australian Marine Scalefish Fishery today (Southeast Data Assessment and Review, 2012a; McAuley *et al.*, 2014a, 2014b). Our independent estimate of r_{\max} suggests that our lack of confidence in the accuracy of the r derived from the life table-derived survival probabilities is probably justified.

In summary, a nuanced approach to shark fishery management when faced with data shortages can be achieved with the addition of age-structured population models such as the one we present here. With a growing body of literature now outlining how to estimate various life-history parameters for sharks, a routine application of sustainable-catch models invoking various model predictions embraces the concept of multi-model inference (Elliott and Brook, 2007) and increases the likelihood of making intelligent choices when setting harvest quotas or implementing other management strategies to ensure long-term sustainability of fished populations.

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designed and constructed the models; C.H. and M.D. collected some of the data; C.J.A.B. and C.H. led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

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