Estimating the rate of quasi-extinction of the Australian grey nurse shark (*Carcharias taurus*) population using deterministic age- and stage-classified models

Nicholas M. Otway a, Corey J.A. Bradshaw b,*, Robert G. Harcourt c

a New South Wales Fisheries, Port Stephens Fisheries Centre, Private Bag 1, Nelson Bay, NSW 2315, Australia
b Antarctic Wildlife Research Unit, School of Zoology, University of Tasmania, Private Bag 05, Hobart, Tasmania 7001, Australia
c Marine Mammal Research Group, Graduate School of the Environment, Macquarie University, Sydney, NSW 2109, Australia

Received 16 June 2003; received in revised form 24 November 2003; accepted 26 November 2003

Abstract

Grey nurse sharks off the east coast of Australia are listed nationally as “critically endangered” under Schedule 1 of the Environmental Protection and Biodiversity Conservation Act (1999) and may number no more than 300 in New South Wales and southern Queensland waters. They are an inshore, coastal dwelling species and were severely depleted by spearfishing in the 1960s. The population has continued to decline despite protection since 1984. Their life history (long-lived to 25+ years), late maturation (6–8 years), low fecundity (maximum 2 live young biennially), specific habitat requirements, limited inshore distribution, and small population size render them particularly vulnerable to extinction. We estimated the time to quasi-extinction (years elapsed for the population to consist of ≤ 50 females) for the grey nurse shark population off the east coast of Australia based on current estimates of abundance and known anthropogenic rates of mortality. Estimated minimum population size was 300 as of 2002, and minimum anthropogenic mortality assessed from recovered carcasses was 12/year of which 75% were females. We modelled time to quasi-extinction using deterministic age- and stage-classified models for worst-, likely and best-case scenarios. Population size was estimated at 300 (worst), 1000 (likely) and 3000 (best). Anthropogenic mortality was added to the model assuming either all carcasses are being recovered (best), or conservatively, that only 50% are reported (realistic). Depending on model structure, if all carcasses are being reported, quasi-extinction times for worst-, likely and best-case scenarios range from 13 to 16 years, 84–98 years and 289–324 years, respectively. If under-reporting is occurring, time to quasi-extinction ranges from 6 to 8 years, 45–53 years and 173–200 years, respectively. In all scenarios modelled the grey nurse shark population will decline if no further steps are taken to remove anthropogenic sources of mortality. Because estimates of quasi-extinction rate depend on initial population size, and sensitivity analysis revealed that population rate of change was most sensitive to changes in the survival probability of the smallest length classes, obtaining precise estimates of abundance and annual survival of young females is critical.

Keywords: Grey nurse shark; *Carcharias taurus*; Leslie matrix models; Survival; Endangered; South-eastern Australia; Elasticities; Fisheries-related mortality

1. Introduction

Protection of endangered species is an important component of conservation activities at national and international levels. Hence, conservation and resource-management agencies often devote considerable re-
impacts such as by-catch (Saila, 1983; Stevens, 1992; Russell, 1993; Kennelly, 1995; Marin et al., 1998; Baum et al., 2003) or loss of habitat (Powles et al., 2000). Long-lived animals with low reproductive rates such as sharks and marine mammals exhibit low productivity and therefore, have poor recovery potential (Smith et al., 1998; Walker, 1998; Frisk et al., 2001; Cortés, 2002). Moreover, slow rates of recovery are exacerbated in species with specific habitat requirements and localised distributions because immigration from non-exploited populations is probably limited (Walker, 1998).

The grey nurse shark (*Carcharias taurus*), also known as the sand tiger shark (USA) or ragged-tooth shark (South Africa), grows to approximately 3 m in length and is a coastal inshore species with a once widespread, but disjunct distribution (Compagno, 1984). In recent times, grey nurse sharks have only been seen or caught in the waters off the eastern USA (Russell, 1993), Brazil (Sadowsky et al., 1989; Amorim et al., 1998), Uruguay (Marin et al., 1998), Argentina (Chiaramonte, 1998; Lucifora et al., 2002), South Africa (Smale, 2002) and on the western and eastern coasts of Australia (Last and Stevens, 1994). The species inhabits the continental shelf down to 190 m, but is most commonly found in aggregations in sandy or gravel-filled gutters, or in rocky caves around inshore rocky reefs and islands in depths of 10–40 m (Compagno, 1984; Pollard et al., 1996; Otway and Parker, 2000; Smale, 2002; Otway et al., 2003). Grey nurse sharks feed on a wide range of bony fishes (e.g., Carangids and Sciaenids – Bass et al., 1975; Schmid et al., 1990; Otway et al., 2003; N. Otway, unpublished data), elasmobranchs (e.g., juvenile dusky sharks, *Carcharhinus obscurus* – Branstetter, 1990), cephalopods and occasionally crustaceans (Bigelow and Schroeder, 1948; Compagno, 1984). The reproductive biology of the grey nurse shark has been well documented in the eastern waters of the USA (Springer, 1948; Gilmore et al., 1983; Branstetter and Musick, 1994). First reproduction occurs at 6–8 years and two pups are born biennially following intra-uterine cannibalistic and oviphagous phases (Springer, 1948; Gilmore et al., 1983; Branstetter and Musick, 1994; Smith et al., 1998). It is also a long-lived species with maximum ages estimated at approximately 25 years (Cortés, 2000; Mollet and Cailliet, 2002).

Prior to 1998, only sparse data were available describing the spatial and temporal patterns of abundance of grey nurse sharks along the eastern coast of Australia (Pepperell, 1992; Reid and Krogh, 1992; Krogh, 1994; Dudley, 1997). More recently, the population size of grey nurse sharks was estimated from 10 diving surveys covering southern Queensland and New South Wales (hereafter referred to as south-eastern Australian) waters (Fig. 1; Otway et al., 2003). An average of 57 sites sampled per survey yielded a maximum estimate of 292 grey nurse sharks in total in May/June 2001. Moreover, grey nurse sharks were absent from an average of 64% of the sites sampled over the ten surveys spanning 2.5 years (Otway et al., 2003). This contrasts with surveys done in the early 1960s when at least 30 individuals were observed at each of these now-unoccupied sites (Cropp, 1964; N. Otway, unpublished data). Although it is not possible to estimate the population size from the 1960s due to a disjoint and incomplete sampling effort, it appears that numbers have declined substantially since that time. This decline is mirrored by the temporal reduction in catches of grey nurse sharks over the past 50 years by gamefishers (Pepperell, 1992) and in the New South Wales shark-meshing program (Pollard et al., 1996; Otway and Parker, 2000). Accordingly, grey nurse sharks on the east coast of Australia are now listed nationally as “critically endangered” under Schedule 1 of the Environmental Protection and Biodiversity Conservation Act (1999).

In the absence of reliable demographic data for local populations, simple deterministic models can be useful tools for the management of endangered species (Caswell, 2001). In particular, such models provide estimates of the effects of anthropogenic perturbations on species already nearing the threshold of extinction. For populations at possible risk of extinction, such as the grey nurse shark in south-eastern Australia, these models can provide insight into the potential conse-
quences of threatening processes and highlight the urgency with which management authorities need to act. In this paper, we used life-history parameters obtained from the literature and estimated rates of anthropogenic mortality from an ongoing research program (Otway and Parker, 2000; Otway et al., 2003) to construct age- and stage-classified deterministic population projection matrices. We assess the rate of quasi-extinction by evaluating the impact of fisheries-related mortality on changes in population growth and provide recommendations to stem the decline.

2. Methods

2.1. Age-classified Leslie matrix model

We first constructed a simple, deterministic and density-independent Leslie matrix model to project the grey nurse shark population through time (Caswell, 2001). We chose to use a density-independent model given that we believed it would be unlikely that the small population size at present would elicit a measurable feedback on the population’s vital rates. We used MATLAB software to define a twenty-five-year age-classified model shown below as a life-cycle graph

where \( s \) is the mean constant probability of survival from age \( x \) to \( x+1 \), \( m \) is the number of female pups produced per breeding event, and \( b \) is the proportion of adult females breeding in any given year. The matrix entries were derived assuming a birth-pulse, pre-breeding design. Pups are born in August and early September (Otway and Parker, 2000; Otway et al., 2003) and first-year mortality is incorporated into the fertility coefficients (Caswell, 2001).

Deterministic parameter estimates were assumed to remain constant because of the absence of age-specific data on vital rates and were derived as follows: \( s \) was estimated as a function of maximum lifespan (\( \omega = 25 \) years) taken from Mollet and Cailliet (2002)

\[
s = e^{-M} = 0.8318,
\]

where \( M \), the natural mortality rate, was taken as \(-\log_{10}(0.01)/\omega\). This assumes that 1.0% of the individuals remain at age \( \omega \) (Cortés, 2000; Campana et al., 2001; Mollet and Cailliet, 2002). Fecundity was estimated as the product of \( m = 1 \) (equivalent to one female pup per breeding event) and \( b = 0.5 \) (adult females breed biennially – Branstetter and Musick, 1994; Mollet and Cailliet, 2002). Ages from 1 to 5 corresponded to the smallest length class defined by Otway et al. (2003) at <2 m length. These were determined using the estimates for minimum growth rates for \( C. taurus \) assuming birth length of 1.0 m (Branstetter and Musick, 1994). This growth rate produced an estimated minimum age of first breeding for \( C. taurus \) of 6 years, which coincides with estimates of age at first breeding used elsewhere (e.g., Smith et al., 1998; Cortés, 2000; Mollet and Cailliet, 2002). Subsequently, ages from 6 to 15 corresponded to the medium length class (2–3 m), and the largest length class (>3 m – Otway et al., 2003) corresponded to ages \( \geq 16 \).

Rounded minimum, likely and maximum population estimates were used as the total estimated \( N_1 \) divided into each \( n \) class to create the initial population vectors \([n_1, n_2, \ldots, n_{25}]\). These estimates were based on minimum estimates of population size from Otway et al. (2003). Minimum population size (\( N_{\text{min}} \)) was taken to be 300 assuming that the 2001 survey accounted for approximately all animals (no missed individuals). The likely population size (\( N_{\text{likely}} \)) was taken to be 1000 and assumes that only 30% of the population was sighted. Finally, we used \( N_{\text{max}} = 3000 \) individuals assuming that the true population size was an order of magnitude larger than the number of individuals sighted in the 2001 survey. Assuming an equal sex ratio for all age classes, the numbers of females modelled were thus: \( N_{\text{min}} = 150 \), \( N_{\text{likely}} = 500 \) and \( N_{\text{max}} = 1500 \). We used the proportion of females in each of the three length classes (<2, 2–3, >3 m) sampled during the breeding season (Survey 8 – Otway et al., 2003) to divide the female population size into the respective starting vector for each age class. Here, 0.17 of the females belonged to the length class <2 m, 0.66 to the 2–3 m length class, and 0.17 to the largest length class. We allocated a uniform number of initial females per age class in each of the length classes based on these proportions.

2.2. Additive fisheries-related mortality

The current estimate for the minimum number of adult grey nurse sharks taken by commercial and recreational fishers in south-eastern Australia is approximately one individual per month based on 12 individuals reported killed between October 2001 and September 2002 (Otway et al., 2003). Of those 12, nine were females belonging to the two smallest length classes (two in the smallest class and seven in the medium-length class – Otway et al., 2003). To model the potential effects of this additional mortality, we assumed completely additive (i.e., non-compensatory) mortality on the ‘natural’ deterministic matrix for the minimum fisheries-related take (nine females per year) by modifying survival in the two smallest length classes accordingly.
Thus, with the additional non-natural mortality in the two smallest length classes due to fishing, it was necessary to modify the survival probabilities for the ages corresponding to each of these length classes. Using the value of $s$ calculated for natural mortality above, we calculated the number of individual females remaining in each length class after one year based on the three initial population sizes and the corresponding initial population vectors. The addition of 2 (in the smallest length class) and 7 (in the medium-length class) additional mortalities resulted in modified annual survival probabilities for each initial population size (Table 1). Additionally, we used a second estimate of fisheries-related mortality assuming 50% under-reporting by fishers (i.e., 18 adult females killed per year). Here, the survival probabilities for the smallest and medium-length categories were modified by 4 and 14 additional fisheries-related mortalities, respectively (Table 1).

2.3. Stage-classified model

Because the age-classified model assumed a uniform distribution of the possible ages within the three length classes measured for grey nurse sharks (Otway et al., 2003), a stage-classified model for a birth-pulse population was used (Caswell, 2001; Mollet and Cailliet, 2002). Three stages were defined as small-, medium- and large-length, and this resulted in a life-cycle graph of the form

\[
\begin{align*}
1 & \quad g_1 & \quad 2 & \quad g_2 & \quad 3 \\
& \quad s_1 & & \quad s_2 & \quad s_3 \\
& \quad f_2 & & \quad f_3 &
\end{align*}
\]

where $s_i$ is the stage-specific survival probability for stage $i$, $g_j$ is stage-specific transition (or ‘growth’) probabilities ($j = \{1, 2\}$) and $f_k = a_k m b$ is stage-specific reproductive output of sexually mature females ($k = \{2, 3\}$). Therefore, the population projection matrix takes the form

\[
\begin{bmatrix}
s_1 & f_2 & f_3 \\
g_1 & s_2 & 0 \\
0 & g_2 & s_3
\end{bmatrix}.
\]

To estimate the matrix parameters we used the formulae presented by Caswell (2001) to separate the processes of survival ($s$) and stage transition ($g$, or growth) $s_i = \sigma_i(1 - \gamma_i)$ and $g_j = \sigma_i \gamma_j$, where $\sigma_i$ is the probability of survival of an individual in stage $i$ and $\gamma_j$ is the fraction of the individuals in stage $i$ that graduate to stage $i+1$ (Caswell, 2001; Mollet and Cailliet, 2002). Because data describing $\gamma_j$ are sparse, we estimated $\gamma_j$ using two different methods. First, we used the geometric distribution which assumes that $\gamma_j$ is a constant, independent of the time spent in each stage. Here, $\gamma_j = \bar{T}_i$, where $\bar{T}_i$ is the mean duration of stage $i$, meaning that during each time interval a fixed fraction of the individuals must grow to the next stage (Caswell, 2001; Mollet and Cailliet, 2002). Second, we used the fixed stage duration distribution so that (Caswell, 2001)

\[
\gamma_j = \frac{(\lambda_i - 1)}{(\lambda_i - 1)}
\]

where $\lambda$ was set to the dominant eigenvalue for the age-classified matrix (see below). This means that the time spent in stage $i$ is fixed before graduating to stage $i+1$ (i.e., the probability of graduating to the next stage is not constant and depends on the age distribution within a stage – Caswell, 2001).

<table>
<thead>
<tr>
<th>Initial population size</th>
<th>$N$ Alive after 1 year ($s = 0.8318$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Natural</strong></td>
<td></td>
</tr>
<tr>
<td>$N_1 = 150$</td>
<td>$N_2 = 125$</td>
</tr>
<tr>
<td>Stage 1</td>
<td>$N_3 = 21.2$</td>
</tr>
<tr>
<td>Stage 2</td>
<td></td>
</tr>
<tr>
<td>Stage 3</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>AFRM = 9</strong></th>
<th>$N$ Alive after 1 year</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N_1 = 150$</td>
<td>$N_2 = 1248$</td>
</tr>
<tr>
<td>Stage 1 (−2)</td>
<td></td>
</tr>
<tr>
<td>Stage 2 (−7)</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>AFRM = 18</strong></th>
<th>$N$ Alive after 1 year</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N_1 = 150$</td>
<td>$N_2 = 1500$</td>
</tr>
<tr>
<td>Stage 1 (−4)</td>
<td></td>
</tr>
<tr>
<td>Stage 2 (−18)</td>
<td></td>
</tr>
</tbody>
</table>

The first section of the table shows the size of the initial population vector (females) relative to stages 1, 2 and 3 (length classes <2, 2–3 and >3 m, respectively) and the number of females alive after 1 year using the natural (constant) annual survival probability = 0.8318 (no production of new individuals). The second part of the table shows the number of females alive after 1 year with additive AFRM at two levels: nine and 18 females killed per year (divided by stage) and the corresponding modified estimates of annual survival probability ($s$) used in the projection matrices. Note that $s_3$ remains constant at 0.8318 because of no recorded AFRM within stage 3.
Because the values of $\sigma_i$ are unknown, these parameters were estimated using an iterative technique similar to that used to estimate $\gamma_i$ as described in Mollet and Cailliet (2002) and Caswell (2001). We set the dominant eigenvalue ($\lambda$) equal to that for the ‘natural’ (i.e., no fisheries-related mortality) population as determined by the age-classified matrix and, using the values of $\gamma_i$ described above, we used the freeware add-in spreadsheet to vary $\sigma_i$ and solve the matrix for $\lambda$ by constraining $0 \leq \sigma_1 = \sigma_2 = \sigma_3 \leq 1$. Matrix operations were done in Excel using the freeware add-in ‘Matrix and Linear Algebra for Excel V. 1.4’ (L. Volpi; available from: http://digilander.libero.it/foxes/SoftwareDownload.htm).

The matrices for fishing-related mortality were adjusted in a manner similar to that used in the stage-classified model. Here, we adjusted $\xi$ by the number of females taken per length class per year and re-calculated $\lambda_1$ for each initial population size and level of fisheries-related mortality.

2.4. Quasi-extinction threshold

We defined quasi-extinction ($Q_1$) for the south-eastern Australian population as the number of years required to reduce the population to $\leq 50$ females (breeding and non-breeding females). We derived the formula to estimate $Q_1$ by solving the Malthusian model of exponential population growth

$$N_t = \tilde{N}_1 e^{\lambda t},$$

for $t$. Here, $t$ is the time to quasi-extinction ($Q_1$), $N_t$ is the set threshold final population size (50 females), $\tilde{N}_1$ is initial population size and $r$ is the instantaneous rate of exponential population change. Thus, solving for $Q_1$ gives the formula

$$Q_1 = -\frac{\log_e \left( \frac{\tilde{N}_1}{N_t} \right)}{\log_e \lambda},$$

where $\log_e \lambda = r$. This relationship assumes that the initial population vector has a stable-age distribution, so the assumed age distribution of individuals relative to length class at $t = 0$ will bias the estimate of $Q_1$ when they do not mimic the stable-age distribution.

2.5. Elasticities of $\lambda_1$ to changes in matrix parameters

Predicting the effects of changes in vital rates (perturbation analysis) to estimates of $\lambda_1$ is an important step in managing endangered species because it identifies the most important parameters influencing the decline. Calculating the sensitivity of the dominant eigenvalue of a matrix model to changes in matrix elements provides information in this regard. Here, sensitivity of a matrix element $a_{ij}$ is the local slope of $\lambda$ considered as a function of $a_{ij}$ (Caswell, 2001). For the age-classified model, we calculated sensitivity and elasticity (proportional sensitivity) matrices in MATLAB by calculating the right and left eigenvectors of the projection matrices (see Caswell, 2001).

For the stage-classified matrices, we also calculated elasticities of the dominant eigenvalue to changes in matrix entries (i.e., $s_i$, $g_j$, and $f_k$) and lower-level parameters used to calculate matrix entries (i.e., $\gamma_i$, $\sigma_i$, $m$ and $b$). For the lower-level parameters, we calculated the first derivatives of each transition element to each lower-level parameter, and then multiplied these by the sensitivity of the corresponding transition element summed over all transition elements (Caswell, 2001). Because sensitivity values are comparable only for matrix entries on the same scale, we report only elasticities (proportional sensitivities) for each parameter.

We also calculated the elasticity ratios of adult survival to fertility for the age-classified model as

$$\frac{E(s_2) + E(s_3)}{E(f_2) + E(f_3)},$$

where $E$ is the elasticity of a parameter. For the stage-classified models, the ratio was calculated as

$$\frac{E(\sigma_2) + E(\sigma_3)}{E(f_2) + E(f_3)}.$$ 

The value of the ratio is the approximate number of juvenile age classes that, if fished, would reduce $\lambda$ by the same amount as fishing all the adult age classes (Mollet and Cailliet, 2002). The ratio of juvenile survival to fertility

$$\frac{E(s_1)}{E(f_2) + E(f_3)} \text{ (age-classified)}$$

and

$$\frac{E(\gamma_1)}{E(f_2) + E(f_3)} \text{ (stage-classified)},$$

indicates the factor (number of times) by which fertility would have to increase to compensate for a given per cent reduction in juvenile survival for the population to return to its original $\lambda$ (Heppell et al., 1999; Cortés, 2002).

3. Results

3.1. Age-classified matrix projections without fisheries-related mortality

The parameter estimates used produced a dominant eigenvalue ($\lambda_1 = 0.9960$), which is equivalent to an exponential rate of change ($r = \log_e(\lambda_1) = -0.0040$). Thus, natural mortality estimates and stable, biennial production of one female pup per breeding female leads to near-stability of the population with a small intrinsic rate of population decline. After an initial increase in population size during the first 5 years projected, the
population declined slowly. This equates to a population of 160 females with \( N_t = 150, 533 \) females with \( N_t = 500 \) and 1599 females with \( N_t = 1500 \) after 25 years (i.e., approximately 7\% increase). However, all populations achieved eventual quasi-extinction due to \( \lambda_t < 1 \); therefore, times to quasi-extinction for \( N_t = 150, 500 \) and 1500 were 277, 582 and 859 years, respectively. Mean generation length (\( T \) is average age of the parents of the offspring produced by a population at the stable age distribution – Caswell, 2001) was 10.5 years. The stable stage distribution calculated from the right eigenvector of the age-classified matrix was 0.6006 for the smallest length class (ages 1–5), 0.3429 for the medium-length class (ages 6–15) and 0.0565 for the large-length class (ages 16–25).

3.2. Age-classified matrix projections with fisheries-related mortality

The addition of the minimum and maximum fisheries-related mortality per year to the deterministic projections resulted in increased rates of population decline (Table 2: Fig. 2). The worst-scenario projection (i.e., lowest initial population size = 150 females and highest fisheries-related mortality = 18 females per year) resulted in a quasi-extinction of the south-eastern Australian population (i.e., \( N_t = 50 \)) within 6 years (Table 2). However, the likely scenario (i.e., initial population size = 500 females and a fisheries-related mortality of 18 females per year) indicated that the population would achieve quasi-extinction within 45 years.

3.3. Stage-classified matrix projections

The iterative process used to calculate \( \sigma_i \) for the geometric distribution and fixed stage durations models resulted in \( \sigma_1 = \sigma_2 = \sigma_3 = 0.8190 \) (geometric) and \( \sigma_1 = \sigma_2 = \sigma_3 = 0.8318 \) (fixed stage durations). Because the estimates of \( \sigma_i \) required setting \( \lambda_t = 0.9960 \) (age-classified matrix dominant eigenvalue), there was no difference to the age-classified matrix in the population projections without fisheries-related mortality. The addition of fisheries-related mortality did produce slightly different results to the age-classified model. The worst-case scenario projection (i.e., lowest initial population size = 150 females and highest fisheries-related mortality = 18 adult females per year) resulted in a quasi-extinction of the population within 8 years (Table 3). The likely scenario (i.e., initial population size = 500 females and a fisheries-related mortality of 18 females per year) indicated that the population would be quasi-extinct in 51–53 years.

3.4. Elasticities of \( \lambda_t \) to changes in matrix parameters

Elasticities of \( \lambda_t \) to changes in the age-classified matrix entries were highest for survival (\( s \)) during the pre-breeding years (smallest length class, \( \sum E(s_{1-5}) = 0.4760 \)). The next highest elasticities were those for changes in survival of individuals within the medium-length class (0.3872) followed by females aged \( \geq 16 \) years (0.0416). Elasticities of \( \lambda_t \) to changes in fecundity (\( b \cdot s \cdot m \)) were generally lower than those for \( s \); the highest was for the medium-length class females (0.0817), followed by those for females aged \( \geq 16 \) years (0.0135). For the stage-classified models, we estimated the sensitivities and elasticities of \( \lambda_t \) to the matrix entries (\( s_i \), \( g_i \) and \( f_i \)) and the lower-level parameters (\( \sigma_i \), \( \gamma_i \), \( m \) and \( b \)) for each stage-duration distribution used to estimate \( \gamma_i \) (Table 4). The stage-classified model indicated highest elasticities of \( \lambda_t \) to changes in \( s_2 \) (stage 2), followed by changes in \( \sigma_1 \) for the geometric model, and highest elasticities of \( \lambda_t \) to changes in \( \sigma_1 \) (stage 1), followed by changes in \( \sigma_2 \) for the fixed stage durations model (Table 4). The elasticity ratios of adult survival to fertility were 4.5 for the age-classified model, and 4.7 and 5.5 for the geometric and fixed stage duration stage-classified models, respectively. The elasticity ratios of juvenile survival to fertility were 5.0, 2.9 and 5.0, respectively. These indicate that a 10\% reduction in juvenile survival would have to be compensated by a 50\% (age-classified) or \( \sim 30–50\% \) (stage-classified) increase in fertility for the population to return to its original \( \lambda \).

4. Discussion

The likely estimates of population size and additive fisheries-related mortality for the grey nurse shark in south-eastern Australian waters indicate that the species is likely to become quasi-extinct within the foreseeable

---

Table 2

Predicted effects of fisheries-related mortality on age-classified matrix projections of the grey nurse shark population in south-eastern Australian waters

<table>
<thead>
<tr>
<th>( N_t )</th>
<th>( s_{AFRM} )</th>
<th>( \lambda_t )</th>
<th>( N_{25} )</th>
<th>( \bar{Q} ) (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>150 females</td>
<td>0.7533</td>
<td>0.7611</td>
<td>0.9186</td>
<td>23</td>
</tr>
<tr>
<td>500 females</td>
<td>0.8082</td>
<td>0.8106</td>
<td>0.9728</td>
<td>302</td>
</tr>
<tr>
<td>1500 females</td>
<td>0.8239</td>
<td>0.8247</td>
<td>0.9883</td>
<td>1325</td>
</tr>
<tr>
<td>150 females</td>
<td>0.6749</td>
<td>0.6904</td>
<td>0.8416</td>
<td>3</td>
</tr>
<tr>
<td>500 females</td>
<td>0.7847</td>
<td>0.7893</td>
<td>0.9496</td>
<td>169</td>
</tr>
<tr>
<td>1500 females</td>
<td>0.8161</td>
<td>0.8176</td>
<td>0.9806</td>
<td>1097</td>
</tr>
</tbody>
</table>

AFRM, annual fisheries-related mortality; \( s_{AFRM} \), AFRM annual survival probability relative to length class (from Table 1; \( s \) for stage 3 held constant at 0.8318); \( \lambda_t \), dominant eigenvalue (population growth rate), \( N_{25} \), estimated population size after 25 years and \( \bar{Q} \), time (years) to quasi-extinction (\( \leq 50 \) females).
future. Under the realistic scenario of a population of \( \sim 1000 \) individuals and a conservative under-reporting rate in fisheries-related mortality of 50%, our models suggest that the species could achieve quasi-extinction within as little as 45 years. The use of simple, deterministic Leslie matrix models provided insight into the severity of the species’ endangered status, and identified life-history parameters requiring the highest accuracy of estimation for effective management of the species’ recovery and long-term conservation. Indeed, accurate estimates of stage-specific survival will provide more accurate predictions of population change in future modelling exercises.

Otway et al. (2003) demonstrated that the incidence of hooking grey nurse sharks in south-eastern Australian waters was seven times greater with lighter gear used by recreational fishers (hook and nylon line) than it was using commercial gear (hook with steel trace). This observation is of particular concern because the use of this lighter gear results in a higher incidence of capture and death of smaller-sized sharks given their relative ease of handling. Our models demonstrated that the population decline was most sensitive to changes in the survival probability of the two smallest length classes. Because the fisheries-catch data indicate that most individuals are caught within these two smaller length classes, accurate estimates of stage-specific survival will provide more accurate predictions of population change in future modelling exercises.

Fig. 2. Age-classified Leslie matrix projection of the south-eastern Australian grey nurse shark population for the three modelled initial population sizes (\( N_1 = 150, 500 \) and 1500) for 25 years from present. Two rates of additive fisheries-related mortality are incorporated into the projections: (a) nine females taken per year (two from the smallest size class, seven from the medium-size class) and (b) assuming a 50% under-reporting of sharks taken per year (i.e., 18 females). Time to quasi-extinction (\( Q_t \)) and the rate of population change (\( \lambda \)) are given for each projection. Note that the estimation of \( Q_t \) assumes a stable-age distribution; therefore, the slight initial increase in population size after \( t = 0 \) for each projection results in values of \( Q_t \) that are marginally greater at \( n = 50 \) females.
fixed-duration distributions, respectively.)

The rate of potential quasi-extinction for grey nurse sharks is, of course, entirely dependent on accurate estimates of population size, annual survival and dispersal capability. The impact of the relatively conspicuous fisheries-related mortality depends on a better under-

classes, we suggest that a reduction of fishing-related mortality in these classes would provide the most effective means of reducing the rate of decline of this species in south-eastern Australia. Some caution should be exercised with this interpretation because elasticities alone may still provide an incomplete guide to management and conservation efforts given the potential for complex interactions among age classes (Heppell et al., 2000; Cortés, 2002). However, the deviation of the observed distribution of individuals within each length class from that predicted using the stable-age distribution from the age-classified matrix suggests that the under-representation of juveniles may be the result of elevated juvenile mortality.

Our conclusions agree with previous attempts at modelling *C. taurus* or other carcharhinid populations elsewhere (Heppell et al., 1999; Cortés, 2002; Mollet and Cailliet, 2002). Using both age- and stage-classified models, Mollet and Cailliet (2002) demonstrated that fishing all the juvenile age-classes would have the same effect on population growth rate as fishing all the adult classes (elasticity ratio of adult survival to fertility ≥ 5).

In our models, these elasticity ratios were similar (4.7–5.5). Mollet and Cailliet (2002) also determined that a 10% decrease in juvenile or adult survival would require ~50% increase in fertility for the population to return to its original λ. Our results for the age-classified and fixed stage duration models agree with this value, although the geometric stage-classified models suggested the value was closer to 30%. However, it is worth noting that given the obligatory intra-uterine cannibalistic phase observed for *C. taurus*, increases in fertility must be driven by increases in survival because pup production cannot exceed 2 pups biennially.

Juvenile survival has also been identified as a major contributing factor to population growth in many different shark species: *Triakis semifasciata* and *Squatina californica* (Cailliet, 1992; Cailliet et al., 1992; Heppell et al., 1999), *Rhizoprionodon terraenovae* (Cortés, 1995), *Carcharhinus plumbeus* (Smirnoff and Musick, 1992; Brewster-Geisz and Miller, 2000) and *Sphyra tiburo* (Cortés and Parsons, 1996). Hence, managing activities that reduce mortality during the earlier stages of shark life history has important implications for the long-term conservation of many long-lived species around the world (see Cortés, 1995; Walker, 1998; Baum et al., 2003 for examples).

Friction of the potentially quasi-extinction for grey nurse sharks is, of course, entirely dependent on accurate estimates of population size, annual survival and dispersal capability. The impact of the relatively conspicuous fisheries-related mortality depends on a better under-

---

### Table 3

Predicted effects of fisheries-related mortality on stage-classified matrix projections

<table>
<thead>
<tr>
<th>Stages</th>
<th>s1</th>
<th>s2</th>
<th>λ1</th>
<th>Q1 (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No AFRM Geometric distribution</td>
<td>150</td>
<td>0.6552</td>
<td>0.7371</td>
<td>0.9961</td>
</tr>
<tr>
<td>500</td>
<td>idem</td>
<td>idem</td>
<td>idem</td>
<td>582</td>
</tr>
<tr>
<td>1500</td>
<td>idem</td>
<td>idem</td>
<td>idem</td>
<td>859</td>
</tr>
<tr>
<td>Fixed-duration</td>
<td>150</td>
<td>0.7194</td>
<td>0.7993</td>
<td>0.9961</td>
</tr>
<tr>
<td>500</td>
<td>idem</td>
<td>idem</td>
<td>idem</td>
<td>582</td>
</tr>
<tr>
<td>1500</td>
<td>idem</td>
<td>idem</td>
<td>idem</td>
<td>859</td>
</tr>
<tr>
<td>AFRM = 9 females Geometric distribution</td>
<td>150</td>
<td>0.5767</td>
<td>0.6664</td>
<td>0.9331</td>
</tr>
<tr>
<td>500</td>
<td>0.6316</td>
<td>0.7159</td>
<td>0.9767</td>
<td>98</td>
</tr>
<tr>
<td>1500</td>
<td>0.6473</td>
<td>0.7300</td>
<td>0.9896</td>
<td>324</td>
</tr>
<tr>
<td>Fixed-duration</td>
<td>150</td>
<td>0.6410</td>
<td>0.7286</td>
<td>0.9302</td>
</tr>
<tr>
<td>500</td>
<td>0.6959</td>
<td>0.7781</td>
<td>0.9757</td>
<td>94</td>
</tr>
<tr>
<td>1500</td>
<td>0.7116</td>
<td>0.7923</td>
<td>0.9892</td>
<td>314</td>
</tr>
<tr>
<td>AFRM = 18 females Geometric distribution</td>
<td>150</td>
<td>0.4983</td>
<td>0.5957</td>
<td>0.8768</td>
</tr>
<tr>
<td>500</td>
<td>0.6081</td>
<td>0.6946</td>
<td>0.9577</td>
<td>53</td>
</tr>
<tr>
<td>1500</td>
<td>0.6395</td>
<td>0.7229</td>
<td>0.9831</td>
<td>200</td>
</tr>
<tr>
<td>Fixed-duration</td>
<td>150</td>
<td>0.5626</td>
<td>0.6579</td>
<td>0.8736</td>
</tr>
<tr>
<td>500</td>
<td>0.6724</td>
<td>0.7569</td>
<td>0.9558</td>
<td>51</td>
</tr>
<tr>
<td>1500</td>
<td>0.7038</td>
<td>0.7852</td>
<td>0.9825</td>
<td>192</td>
</tr>
</tbody>
</table>

*Shown first are the parameters used for the no-fishing scenario and the prediction times to quasi-extinction using the geometric and fixed-duration distributions (s2 = s3). With AFRM, the estimated in-stage probability (Pi) estimates, λ1, and Q1 are shown (*k*/C0 = 3.0190(1 – γ1) = 0.7371 and *f*/C0 = 3.0381(1 – 0.0390) = 0.7993 are held constant for the geometric and fixed-duration distributions, respectively.*

### Table 4

Stage-classified model elasticities (proportional sensitivities, E) of λ1 to changes in matrix entries (s1, g1, and f1) and lower-level demographic parameters (a1, g1, m and b) using the geometric and fixed-stage duration distributions

<table>
<thead>
<tr>
<th>Parameter</th>
<th>E (geometric)</th>
<th>E (fixed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>s1</td>
<td>0.3799</td>
<td>0.5350</td>
</tr>
<tr>
<td>s2</td>
<td>0.5000</td>
<td>0.5250</td>
</tr>
<tr>
<td>s3</td>
<td>0.6575</td>
<td>0.6633</td>
</tr>
<tr>
<td>s4</td>
<td>-0.0999</td>
<td>-0.0025</td>
</tr>
<tr>
<td>s5</td>
<td>-0.0999</td>
<td>-0.0025</td>
</tr>
<tr>
<td>m</td>
<td>0.1300</td>
<td>0.1066</td>
</tr>
<tr>
<td>b</td>
<td>0.1300</td>
<td>0.1066</td>
</tr>
<tr>
<td>s1</td>
<td>0.2499</td>
<td>0.2773</td>
</tr>
<tr>
<td>s2</td>
<td>0.3700</td>
<td>0.4331</td>
</tr>
<tr>
<td>s3</td>
<td>0.0889</td>
<td>0.0613</td>
</tr>
<tr>
<td>s4</td>
<td>0.1300</td>
<td>0.1066</td>
</tr>
<tr>
<td>s5</td>
<td>0.0312</td>
<td>0.0151</td>
</tr>
<tr>
<td>f1</td>
<td>0.0988</td>
<td>0.0915</td>
</tr>
<tr>
<td>f2</td>
<td>0.0312</td>
<td>0.0151</td>
</tr>
</tbody>
</table>

The highest and second-highest elasticities for lower-level parameters and matrix entries are shown in boldface.
standing of the abundance and life history of this species. The most-recent minimum estimates place the south-eastern Australian population at approximately 300 individuals (Otway et al., 2003); however, it is still unclear what proportion of the population may have been missed during the survey. Re-sightings of tagged individuals (N. Otway and A. Burke, unpublished data) have yielded annual resighting rates of 83% (20 out of 24 marked individuals resighted), suggesting that the true population size is likely to be <1000 individuals. Although preliminary data suggest that the south-eastern Australian population appears to be derived from a single maternal lineage (Harcourt et al., 2003), and individuals have been observed travelling in excess of 800 km (N. Otway, unpublished data), the spatial structure of disjunct sub-populations should be incorporated into future models. Additionally, once information on variance in life-history parameters becomes available, future models should incorporate this uncertainty to allow for the effects of environmental stochasticity.

Nonetheless, the estimates of population size and the realistic values of annual survival used in our models indicate that the precautionary principle for conservation must be implemented immediately. Grey nurse sharks off the east coast of Australia do not appear to have the capacity to recover unless anthropogenic mortality is eliminated. Indeed, many large-bodied elasmobranchs have low potential intrinsic rates of population growth and ‘rebound’ potential (Smith et al., 1998; Frisk et al., 2001) due to slow maturation and low fecundity. Therefore, as suggested here, additional mortality, even at apparently low levels, can reduce population growth to values of $\lambda < 1.0$ and cause potentially catastrophic reductions in population size within relatively short time frames (e.g., decades – Baum et al., 2003). We suggest that effective management of this species can only be achieved by the removal of all fishing-related mortality from important habitat areas within south-eastern Australian waters. We also recommend that the exclusion of fishing from these areas should be accompanied by a reduction in overall fishing rates to prevent the possibility of merely displacing fishing activity (Horwood et al., 1998; Baum et al., 2003).

Acknowledgements

This research has been done with funding from NSW Fisheries and Environment Australia (via the Natural Heritage Trust). We thank B. Creese, J. Scandol, S. Kennelly and two anonymous referees for their constructive comments on the manuscript. We are grateful to C. Bland and K. Bown of the NSW Fisheries library for the time spent obtaining some of the references, and A. Burke for her dedication and assistance in the field and laboratory. Finally, we thank the many scuba divers for their assistance with various aspects of this research.

References


Last, P.R., Stevens, J.D., 1994. Sharks and Rays of Australia. CSIRO Division of Fisheries, Melbourne, Australia.


Schmid, T.H., Murr, F.L., McDonald, F., 1990. Feeding habits and growth rates of bull (Carcharhinus leucas (Valencienniens)), sandbar (Carcharhinus plumbeus (Nardo)), sandtiger (Eugomphodus taurus (Rafinesque)) and nurse (Gilgomyostoma cirratum (Bonnatere)) sharks maintained in captivity. Journal of Aquaculture and Aquatic Sciences 5, 100–105.


