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*

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 $\leqslant 50$ 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.
© 2004 Elsevier Ltd. All rights reserved.

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 resources to identify the major threatening processes (sensu Caughley, 1994) that reduce populations to the point where they are at risk of extinction. In contrast to many terrestrial species, marine species have traditionally been regarded as having high productivity and therefore, an inherent capacity to recover rapidly from severe depletion (Powles et al., 2000). However, several marine taxa have life-history and ecological characteristics that render them particularly vulnerable to anthropogenic impacts, whether through directed harvesting or indirect

---

* Corresponding author. Tel.: +61-3-6226-2644; fax: +61-3-6226-2745.
E-mail address: corey.bradshaw@utas.edu.au (C.J.A. Bradshaw).

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,
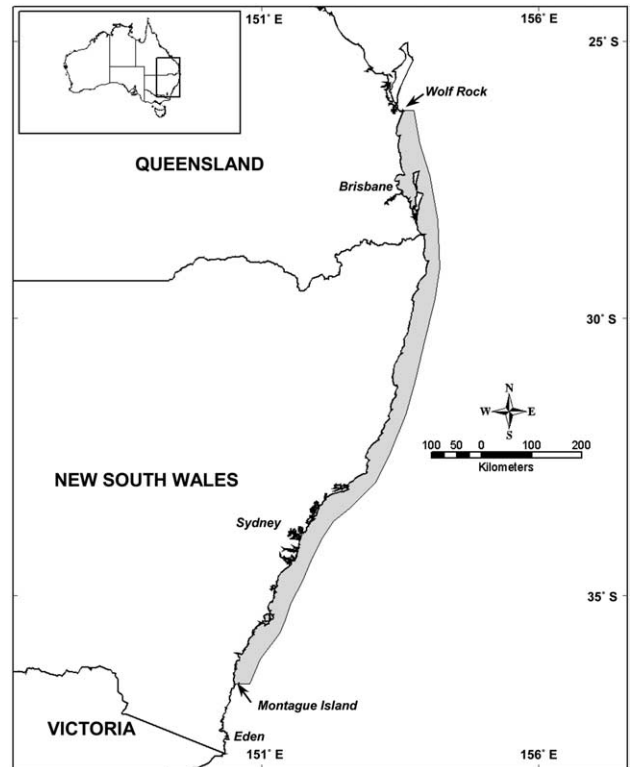

Fig. 1. Approximate distribution of grey nurse sharks (*Carcharias taurus*) in south-eastern Australian waters in 2002 (Otway et al., 2003).

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 game fishers (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
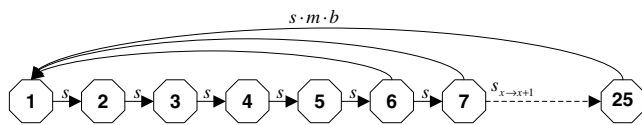
where s is the mean constant probability of survival from age x to $x + 1$, m is the number of female pups produced per breeding event, and b is the proportion of adult females breeding in any given year. The matrix entries were derived assuming a birth-pulse, pre-breeding design. Pups are born in August 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 $-\log_e(0.01)/\omega$. This assumes that 1.0% of the individuals remain at age ω (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 ⩾ 16.

Rounded minimum, likely and maximum population estimates were used as the total estimated $\hat{N}_1$ divided into each n_x 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 ($\hat{N}_{min}$) was taken to be 300 assuming that the 2001 survey accounted for approximately all animals (no missed individuals). The likely population size ($\hat{N}_{likely}$) was taken to be 1000 and assumes that only 30% of the population was sighted. Finally, we used $\hat{N}_{max} = 3000$ 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: $\hat{N}_{min} = 150$, $\hat{N}_{likely} = 500$ and $\hat{N}_{max} = 1500$. 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
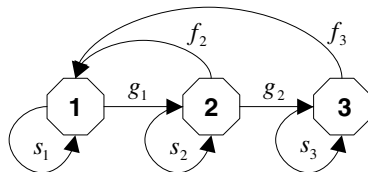
where s_i is the stage-specific survival probability for stage i, g_j is stage-specific transition (or 'growth') probabilities ($j = \{1, 2\}$) and $f_k = \sigma_k m_k b$ is stage-specific reproductive output of sexually mature females ($k = \{2, 3\}$). Therefore, the population projection matrix takes 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)

$$s_i = \sigma_i(1 - \gamma_i) \quad \text{and} \quad g_j = \sigma_i \gamma_i,$$

where σ_i is the probability of survival of an individual in stage i and γ_i is fraction of the individuals in stage i that graduate to stage $i + 1$ (Caswell, 2001; Mollet and Cailliet, 2002). Because data describing γ_i are sparse, we estimated γ_i using two different methods. First, we used the geometric distribution which assumes that γ_i is a constant, independent of the time spent in each stage. Here, $\hat{\gamma}_i = \overline{T}_i^{-1}$, where $\overline{T}_i$ 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)

$$\gamma_i = \frac{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - \left(\frac{\sigma_i}{\lambda}\right)^{T_i - 1}}{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - 1},$$

where λ 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 1
Calculation of stage-specific survival probabilities incorporating annual fisheries-related mortality (AFRM)

	Initial population size			N Alive after 1 year ($s = 0.8318$)		
Natural	$\hat{N}_1 = 150$	$\hat{N}_1 = 500$	$\hat{N}_1 = 1500$	$\hat{N}_2 = 125$	$\hat{N}_2 = 416$	$\hat{N}_2 = 1248$
Stage 1	25.5	85	255	21.2	70.7	212.1
Stage 2	99	330	990	82.3	274.5	823.4
Stage 3	25.5	85	255	21.2	70.7	212.1
AFRM	N Alive after 1 year			Modified s		
AFRM = 9	$\hat{N}_1 = 150$	$\hat{N}_1 = 500$	$\hat{N}_1 = 1500$	$\hat{N}_1 = 150$	$\hat{N}_1 = 500$	$\hat{N}_1 = 1500$
Stage 1 (−2)	19.2	68.7	210.1	0.7533	0.8082	0.8239
tage 2 (−7)	75.3	267.5	816.4	0.7611	0.8106	0.8247
AFRM = 18	$\hat{N}_1 = 150$	$\hat{N}_1 = 500$	$\hat{N}_1 = 1500$	$\hat{N}_1 = 150$	$\hat{N}_1 = 500$	$\hat{N}_1 = 1500$
Stage 1 (−4)	17.2	66.7	208.1	0.6749	0.7847	0.8161
Stage 2 (−18)	68.3	260.5	809.4	0.6904	0.7893	0.8176

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 σ_i are unknown, these parameters were estimated using an iterative technique similar to that used to estimate γ_i as described in Mollet and Cailliet (2002) and Caswell (2001). We set the dominant eigenvalue (λ) 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 γ_i described above, we used the Solver tool in an Excel (Microsoft Corporation) spreadsheet to vary σ_i and solve the matrix for λ by constraining $0 \leqslant \sigma_1 = \sigma_2 = \sigma_3 \leqslant 1$. 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://digi-lander.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 s_i by the number of females taken per length class per year and re-calculated λ_1 for each initial population size and level of fisheries-related mortality.

2.4. Quasi-extinction threshold

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

$$N_t = \hat{N}_1 e^{rt},$$

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

$$Q_t = \frac{\log_e\left(\frac{N_t}{\hat{N}_1}\right)}{\log_e \lambda},$$

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_t when they do not mimic the stable-age distribution.

2.5. Elasticities of λ_1 to changes in matrix parameters

Predicting the effects of changes in vital rates (perturbation analysis) to estimates of λ_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 λ considered as a func-

tion 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., σ_i, γ_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 λ by the same amount as fishing all the adult age classes (Mollet and Cailliet, 2002). The ratio of juvenile survival to fertility

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

$$\text{and } \frac{E(\sigma_1)}{E(f_2) + E(f_3)} \text{ (stage-classified)},$$

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 λ (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 (λ_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 $\hat{N}_1 = 150$, 533 females with $\hat{N}_1 = 500$ and 1599 females with $\hat{N}_1 = 1500$ after 25 years (i.e., approximately 7% increase). However, all populations achieved eventual quasi-extinction due to $\lambda_1 < 1$; therefore, times to quasi-extinction for $\hat{N}_1 = 150$, 500 and 1500 were 277, 582 and 859 years, respectively. Mean generation length ($\overline{A}$ 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., $\leqslant 50$ females) 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 σ_i for the geometric distribution and fixed stage durations models

Table 2
Predicted effects of fisheries-related mortality on age-classified matrix projections of the grey nurse shark population in south-eastern Australian waters

$\hat{N}_1$	s_{AFRM}		λ_1	$\hat{N}_{25}$	Q_t (years)
	Stage 1	Stage 2			
AFRM = 9 females					
150	0.7533	0.7611	0.9186	23	13
500	0.8082	0.8106	0.9728	302	84
1500	0.8239	0.8247	0.9883	1325	289
AFRM = 18 females					
150	0.6749	0.6904	0.8416	3	6
500	0.7847	0.7893	0.9496	169	45
1500	0.8161	0.8176	0.9806	1097	173

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); λ_1, dominant eigenvalue (population growth rate), $\hat{N}_{25}$, estimated population size after 25 years and Q_t, time (years) to quasi-extinction ($\leqslant 50$ females).

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 σ_i required setting $\lambda_1 = 0.9960$ (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 λ_1 to changes in matrix parameters

Elasticities of λ_1 to changes in the age-classified matrix entries were highest for survival (s) during the pre-breeding years (smallest length class, $\sum E(s_{1 \to 5}) = 0.4760$). The next highest elasticities were those for changes in survival of individuals within the medium-length class (0.3872) followed by females aged $\geqslant 16$ years (0.0416). Elasticities of λ_1 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 $\geqslant 16$ years (0.0135). For the stage-classified models, we estimated the sensitivities and elasticities of λ_1 to the matrix entries (s_i, g_i and f_i) and the lower-level parameters (σ_i, γ_i, m and b) for each stage-duration distribution used to estimate γ_i (Table 4). The stage-classified model indicated highest elasticities of λ_1 to changes in σ_2 (stage 2), followed by changes in σ_1 for the geometric model, and highest elasticities of λ_1 to changes in σ_1 (stage 1), followed by changes in σ_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 ~30–50% (stage-classified) increase in fertility for the population to return to its original λ.

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
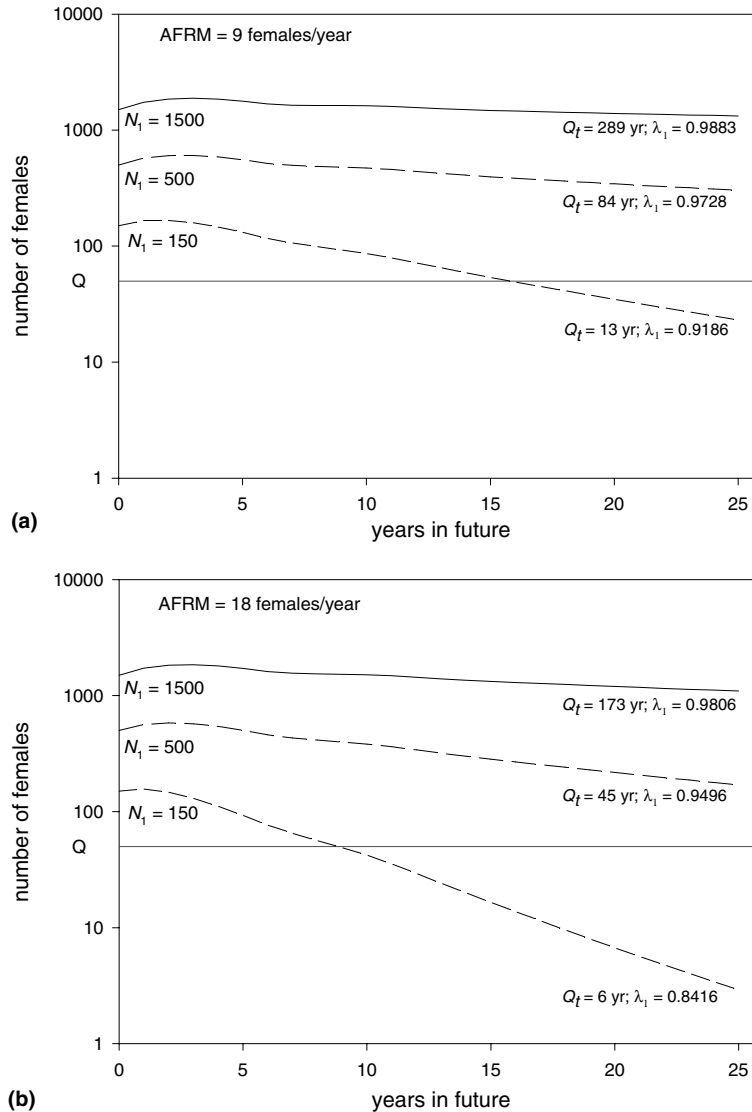
Fig. 2. Age-classified Leslie matrix projection of the south-eastern Australian grey nurse shark population for the three modelled initial population sizes ($N_1 = 150$, 500 and 1500) for 25 years from present. Two rates of additive fisheries-related mortality are incorporated into the projections: (a) 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 (λ_1) 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.

future. Under the realistic scenario of a population of ~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

Table 3
Predicted effects of fisheries-related mortality on stage-classified matrix projections

$\hat{N}_1$	s_1	s_2	λ_1	Q_t (years)
No AFRM				
Geometric distribution				
150	0.6552	0.7371	0.9961	277
500	idem	idem	idem	582
1500	idem	idem	idem	859
Fixed-duration				
150	0.7194	0.7993	0.9961	278
500	idem	idem	idem	582
1500	idem	idem	idem	859
AFRM = 9 females				
Geometric distribution				
150	0.5767	0.6664	0.9331	16
500	0.6316	0.7159	0.9767	98
1500	0.6473	0.7300	0.9896	324
Fixed-duration				
150	0.6410	0.7286	0.9302	15
500	0.6959	0.7781	0.9757	94
1500	0.7116	0.7923	0.9892	314
AFRM = 18 females				
Geometric distribution				
150	0.4983	0.5957	0.8768	8
500	0.6081	0.6946	0.9577	53
1500	0.6395	0.7229	0.9831	200
Fixed-duration				
150	0.5626	0.6579	0.8736	8
500	0.6724	0.7569	0.9558	51
1500	0.7038	0.7852	0.9825	192

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 ($s_2 = s_3$). With AFRM, the estimated in-stage probability (s_i) estimates, λ_1, and Q_t are shown ($^{geo}s_3 = \sigma_3(1 - \gamma_3) = 0.8190(1 - 0.1000) = 0.7371$ and $^{fix}s_3 = \sigma_3(1 - \gamma_3) = 0.8318(1 - 0.0390) = 0.7993$ are held constant for the geometric and fixed-duration distributions, respectively.)

Table 4
Stage-classified model elasticities (proportional sensitivities, E) of λ_1 to changes in matrix entries (s_i, g_i and f_i) and lower-level demographic parameters (σ_i, γ_i, m and b) using the geometric and fixed-stage duration distributions

Parameter	E (geometric)	E (fixed)
σ_1	**0.3799**	**0.5330**
σ_2	**0.5000**	**0.5250**
σ_3	0.1201	0.0617
γ_1	0.0675	0.0633
γ_2	−0.0099	−0.0025
γ_3	−0.0099	−0.0025
m	0.1300	0.1066
b	0.1300	0.1066
s_1	**0.2499**	**0.2773**
s_2	**0.3700**	**0.4331**
s_3	0.0889	0.0613
g_1	0.1300	0.1066
g_2	0.0312	0.0151
f_2	0.0988	0.0915
f_3	0.0312	0.0151

The highest and second-highest elasticities for lower-level parameters and matrix entries are shown in boldface.

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 $\cong 5$). 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 $\sim50\%$ 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* (Sminkey and Musick, 1996; Brewster-Geisz and Miller, 2000) and *Sphyrna 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).

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-

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).

References

Amorim, A.F., Arfelli, C.A., Fagundes, L., 1998. Pelagic elasmobranchs caught by longliners off southern Brazil during 1974–97: an overview. Marine and Freshwater Research 49, 621–632.

Bass, A.J., D'Aubrey, J.D., Kistnasamy, N. 1975. Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scaponorhynichidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. Investigational Report No. 39 of the Oceanographic Research Institute, Durban, pp. 6–16.

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., Doherty, P.A., 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science 299, 389–392.

Bigelow, H.B., Schroeder, W.C. 1948. Fishes of the western north Atlantic. Part 1. Lancelets, Cyclostomes and Sharks. Memoirs of the Sears Foundation for Marine Research, Yale University, pp. 59–546.

Branstetter, S. 1990. Early life history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. In: Pratt Jr., H.L., Gruber, S.H., Taniuchi, T. (Eds.), Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA National Marine Fisheries Service Tech. Rep. No. 90. pp. 17–28.

Branstetter, S., Musick, J.A., 1994. Age and growth estimates for the sand tiger in the northwestern Atlantic Ocean. Transactions of the American Fisheries Society 123, 242–254.

Brewster-Geisz, K.K., Miller, T.J., 2000. Management of the sandbar shark, *Carcharhinus plumbeus*: implications of a stage-based model. Fisheries Bulletin 98, 236–249.

Cailliet, G.M., 1992. Demography of the central California population of the leopard shark (*Triakis semifasciata*). Australian Journal of Marine and Freshwater Research 43, 183–193.

Cailliet, G.M., Mollet, H.F., Pittinger, G.G., Bedford, D., Ntanson, L.J., 1992. Growth and demography of the Pacific angel shark (*Squatina californica*), based upon tag returns off California. Australian Journal of Marine and Freshwater Research 43, 1313–1330.

Campana, S., Joyce, W., Marks, L., Harley, S. 2001. Analytical assessment of the porbeagle shark (*Lamna nasus*) population in the northwest Atlantic, with estimates of long-term sustainable yield. 2001/067. Canadian Stock Assessment Research Document, Ottawa, Canada, pp. 1-59.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer Associates Inc, Sunderland.

Caughley, G., 1994. Directions in conservation biology. Journal of Animal Ecology 63, 215–244.

Chiaramonte, G.E., 1998. Shark fisheries in Argentina. Marine and Freshwater Research 49, 601–609.

Compagno, L.J.V. 1984. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. Food and Agriculture Organization (FAO) of the United Nations Species Catalogue vol. 5, Fisheries Synopsis 125(4): 1–249, Rome.

Cortés, E., 1995. Demographic analysis of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, in the Gulf of Mexico. Fisheries Bulletin 93, 57–66.

Cortés, E., 2000. Life history patterns and correlation in sharks. Reviews in Fisheries Science 8, 299–344.

Cortés, E., 2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conservation Biology 16, 1048–1062.

Cortés, E., Parsons, G.R., 1996. Comparative demography of two populations of the bottenhead shark (*Sphyrna tiburo*). Canadian Journal of Fisheries and Aquatic Sciences 53, 709–718.

Cropp, B. 1964. Shark Hunters. Rigby, Adelaide.

Dudley, S.F.J., 1997. A comparison of the shark control programs of New South Wales and Queensland (Australia) and KwaZulu-Natal (South Africa). Ocean and Coastal Management 34, 1–27.

Frisk, M.G., Miller, T.J., Fogarty, M.J., 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. Canadian Journal of Fisheries and Aquatic Sciences 58, 969–981.

Gilmore, R.G., Dodrill, J.W., Linley, P.A., 1983. Reproduction and embyonic development of the sand tiger shark, *Odontaspis taurus* (Raffinesque). US National Marine Fisheries Service Fishery Bulletin 81, 201–225.

Harcourt, R.G., Gillings, M., Briscoe, D., Stow, A. 2003. Are east and west coast populations of the critically endangered grey nurse sharks (*Carcharias taurus*) genetically isolated? Final Report to Environment Australia. Environment Australia. Canberra, pp. 1–20.

Heppell, S.S., Caswell, H., Crowder, L.B., 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81, 654–665.

Heppell, S.S., Crowder, L.B., Menzel, T.R., 1999. Life table analysis of long-lived marine species with implications for conservation and management. In: Musick, J.A. (Ed.), Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals. American Fisheries Society, Bethesda, MD, pp. 137–146.

Horwood, J.W., Nichols, J.H., Milligan, S., 1998. Evaluation of closed areas for fish stock conservation. Journal of Applied Ecology 35, 893–903.

Kennelly, S.J., 1995. The issue of bycatch in Australia's demersal trawl fisheries. Reviews in Fish Biology and Fisheries 5, 213–234.

Krogh, M., 1994. Spatial, seasonal and biological analysis of sharks caught in the NSW Protective Beach Meshing programme. Australian Journal of Marine and Freshwater Research 45, 1087–1106.

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

Lucifora, L.O., Menni, R.C., Escalante, A.H., 2002. Reproductive ecology and abundance of the sand tiger, *Carcharias taurus*, from the southwestern Atlantic. ICES Journal of Marine Science 59, 553–561.

Marin, Y.H., Brum, F., Barea, L.C., Chocca, J.F., 1998. Incidental catch associated with swordfish longline fisheries in the south-west Atlantic Ocean. Marine and Freshwater Research 49, 633–640.

Mollet, H.F., Cailliet, G.M., 2002. Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. Marine and Freshwater Research 53, 503–516.

Otway, N.M., Burke, A.L., Morrison, N.S., Parker, P.C. 2003. Monitoring and identification of NSW critical habitat sites for conservation of grey nurse sharks. Final Report Series No. 47. NSW Fisheries Office of Conservation, Nelson Bay, NSW, p. 62.

Otway, N.M., Parker, P.C. 2000. The biology, ecology, distribution and abundance, and identification of marine protected areas for the conservation of threatened grey nurse sharks in south east Australian waters. Final Report Series No. 19. NSW Fisheries Office of Conservation, Sydney, NSW, p. 132.

Pepperell, J.G., 1992. Trends in the distribution, species composition and size of sharks caught by gamefish anglers off south-eastern Australia, 1961–1990. Australian Journal of Marine and Freshwater Research 43, 213–225.

Pollard, D.A., Lincoln-Smith, M.P., Smith, A.K., 1996. The biology and conservation status of the grey nurse shark (*Carcharias taurus*, Rafinesque 1810) in NSW, Australia. Aquatic Conservation of Marine and Freshwater Ecosystems 6, 1–20.

Powles, H., Bradford, M.J., Bradford, R.G., Doubleday, W.G., Innes, S., Levings, C.D., 2000. Assessing and protecting endangered marine species. ICES Journal of Marine Science 57, 669–676.

Reid, D., Krogh, M., 1992. Assessment of catches from protective shark meshing off NSW beaches between 1950 and 1990. Australian Journal of Marine and Freshwater Research 43, 283–296.

Russell, S.J. 1993. Shark bycatch in the northern Gulf of Mexico tuna longline fishery, 1989–1991, with observations on the nearshore directed shark fishery. In: Branstetter, S. (Ed.), Conservation Biology of Elasmobranchs. NOAA National Marine Fisheries Service Tech. Rep. No. 115. pp. 19–29.

Sadowsky, V., Arfelli, C.A., Amorim, A.F., Rodrigues, E.S., Oliveira, M.A.M. 1989. Aspectos sobre a biologia pesqueira da mangona, *Eugomphodus taurus*, capturada na região de Cannéia-SP (Abstract). IV Reunião do Grupo de Trabalho sobre Pesca e Pesquisa de Tubarões e Raias no Brasil (GTPPTRB), Tamarandé, Brazil, p. 20.

Saila, S.B. 1983. Importance and assessment of discards in commercial fisheries. FAO Fish Circular No. 765. Food and Agriculture Organization (FAO) of the United Nations, Rome, p. 62.

Schmid, T.H., Murru, F.L., McDonald, F., 1990. Feeding habits and growth rates of bull (*Carcharhinus leucas* (Valenciennes)), sandbar (*Carcharhinus plumbeus* (Nardo)), sandtiger (*Eugomophodus taurus* (Rafinesque)) and nurse (*Giglymostoma cirratum* (Bonnaterre)) sharks maintained in captivity. Journal of Aquariculture and Aquatic Sciences 5, 100–105.

Smale, M.J., 2002. Occurrence of *Carcharias taurus* in nursery areas of the Eastern and Western Cape, South Africa. Marine and Freshwater Research 53, 551–556.

Sminkey, T.R., Musick, J.A., 1996. Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic. Fisheries Bulletin 94, 341–347.

Smith, S.E., Au, D.W., Show, C., 1998. Intrinsic rebound potential of 26 species of Pacific sharks. Marine and Freshwater Research 49, 663–678.

Springer, S., 1948. Oviphagous embryos of the sand tiger shark, *Carcharias taurus*. Copeia 3, 153–157.

Stevens, J.D., 1992. Blue and mako shark by-catch in the Japanese longline fishery off south eastern Australia. Australian Journal of Marine and Freshwater Research 43, 227–236.

Walker, T.I., 1998. Can shark resources be harvested sustainably. A question revisited with a review of shark fisheries. Marine and Freshwater Research 49, 553–572.