

# Inferring population trends for the world's largest fish from mark–recapture estimates of survival

COREY J. A. BRADSHAW\*, HENRY F. MOLLET† and MARK G. MEEKAN‡

\*School for Environmental Research, Institute of Advanced Studies, Charles Darwin University, Darwin, Northern Territory 0909, Australia; †Moss Landing Marine Laboratories, Moss Landing, California 93950, USA; and ‡Australian Institute of Marine Science, PO Box 40197, Casuarina MC, Northern Territory 0811, Australia

## Summary

1. Precise estimates of demographic rates are key components of population models used to predict the effects of stochastic environmental processes, harvest scenarios and extinction probability.

2. We used a 12-year photographic identification library of whale sharks from Ningaloo Reef, Western Australia to construct Cormack–Jolly–Seber (CJS) model estimates of survival within a capture–mark–recapture (CMR) framework. Estimated survival rates, population structure and assumptions regarding age at maturity, longevity and reproduction frequency were combined in a series of age-classified Leslie matrices to infer the potential trajectory of the population.

3. Using data from 111 individuals, there was evidence for time variation in apparent survival ( $\phi$ ) and recapture probability ( $p$ ). The null model gave a  $\hat{\phi}$  of 0.825 (95% CI: 0.727–0.893) and  $\hat{p} = 0.184$  (95% CI: 0.121–0.271). The model-averaged annual  $\hat{\phi}$  ranged from 0.737 to 0.890. There was little evidence for a sex effect on survival.

4. Using standardized total length as a covariate in the CMR models indicated a size bias in  $\phi$ . Ignoring the effects of time, a 5-m shark has a  $\hat{\phi} = 0.59$  and a 9 m shark has  $\hat{\phi} = 0.81$ .

5. Of the 16 model combinations considered, 10 (63%) indicated a decreasing population ( $\lambda < 1$ ). For models based on age at first reproduction ( $\alpha$ ) of 13 years, the mean age of reproducing females at the stable age distribution ( $\bar{A}$ ) ranged from 15 to 23 years, which increased to 29–37 years when  $\alpha$  was assumed to be 25.

6. All model scenarios had higher total elasticities for non-reproductive female survival [ $E(s_{nr})$ ] compared to those for reproductive female survival [ $E(s_r)$ ].

7. Assuming relatively slow, but biologically realistic, vital rates ( $\alpha = 25$  and biennial reproduction) and size-biased survival probabilities, our results suggest that the Ningaloo Reef population of whale sharks is declining, although more reproductive data are clearly needed to confirm this conclusion. Combining relatively precise survival estimates from CMR studies with realistic assumptions of other vital rates provides a useful heuristic framework for determining the vulnerability of large oceanic predators for which few direct data exist.

*Key-words:* Australia, demography, Leslie matrix model, mark–recapture, Ningaloo Reef, *Rhincodon typus*, survival, vital rates, whale shark.

*Journal of Animal Ecology* (2007) **76**, 480–489

doi: 10.1111/j.1365-2656.2006.01201.x

## Introduction

Demographic data are useful for determining the effects of stochastic processes on abundance (Sibly & Hone

2002), the type and strength of regulation operating on a population (Sibly *et al.* 2005; Brook & Bradshaw 2006) and extinction risk faced by populations under various environmental scenarios (Fagan & Holmes 2006). However, demographic data alone cannot always divulge the mechanisms responsible for population trajectories, which is especially inconvenient when management actions are required to mitigate decline (McMahon *et al.* 2005). Population viability analyses (PVA) have

provided a means to examine the relative contributions of competing factors on rates of population change (Cochran & Ellner 1992; Caswell 2001), and have given useful heuristic direction in managing the processes threatening species of conservation concern (Brook *et al.* 2002). Despite this advance, most PVA models rely on detailed life history data (Ellner *et al.* 2002) and researchers are forced to make profligate assumptions when such data are missing or based on small samples. As such, the estimation of high-precision demographic parameters such as age- or stage-specific survival and fertility rates should be a major aim of any study attempting to elucidate the mechanisms driving population decline and persistence.

The world's largest fish, the whale shark (*Rhincodon typus* Smith 1828), is also one of the least-studied and poorly understood shark species. No data on survival rates are available, and the reproductive data that do exist are based on extremely small sample sizes (Joung *et al.* 1996; Colman 1997). Even basic parameters such as growth, age at first reproduction, longevity and population size are unknown for the majority of populations. However, some data exist for growth rates of captive juveniles (Chang, Leu & Fang 1997), size and age at first reproduction (Pai, Nandakumar & Telang 1983; Satyanarayana Rao 1986; Wintner 2000), size distributions (Pravin 2000; Meekan *et al.* 2006) and abundance estimates for particular aggregations (Heyman *et al.* 2001; Meekan *et al.* 2006).

The predictable aggregation of whale sharks that occurs each year from March to June at Ningaloo Reef, Western Australia (Taylor 1996; Wilson, Taylor & Pearce 2001) has been the site of a large and lucrative ecotourism industry where extensive photo-identification has been carried out over the last 15 years (Meekan *et al.* 2006). Recent studies have examined the potential to identify individuals over time using automated (Arzoumanian, Holmberg & Norman 2005) or manual (Meekan *et al.* 2006) approaches, with the mark–resight data used to predict the size of the super-population participating in the Ningaloo aggregation at 300–500 individuals (Meekan *et al.* 2006). The photo-identification data set can also be used within a capture–mark–recapture (CMR) modelling framework to estimate demographic parameters such as survival and capture probability.

Good estimates of whale shark demographic rates are essential components for assessing their conservation status. The species is listed as vulnerable according to World Conservation Union criteria (IUCN 2005) based on its rarity and reduction in catch rates in the regions where they are fished to supply meat throughout Asia (CITES 2002; IUCN 2005). Satellite tagging studies have verified that whale sharks attending the Ningaloo aggregation migrate regularly into South-east Asian waters (Wilson *et al.* 2006; J. Polovina *et al.* unpublished data), with anecdotal evidence suggesting that some tagged animals have fallen victim to fishing in this region (J. Polovina *et al.* unpublished data). Additionally,

Meekan *et al.* (2006) reported a decline in the proportion of large whale sharks seen between 1992 and 2004, which may indicate human-mediated changes in the age-class distribution of this population.

In this study we use the photo-identification database described in Meekan *et al.* (2006) to estimate apparent survival and capture probabilities for the Ningaloo Reef aggregation. We assess variation in survival over time, between the sexes and as a function of an individual's total length. These survival estimates and other available demographic data reported in the literature are then incorporated into a series of age-classified Leslie matrix population models to assess the long-term persistence probability of the aggregation. Our overall aim is to provide a heuristic assessment of the possible population trajectory given our mark–recapture estimates of survival probability for this aggregation. This general template can be used to derive information on population assessments when demographic, abundance and other key data are missing for species of conservation concern.

## Materials and methods

### STUDY AREA AND POPULATION

Our study was conducted at Ningaloo Reef (21°32'4" S, 114°6'0" E) off the coast of Exmouth in Western Australia from 1992 to 2004. Whale sharks aggregate predictably here from March to June each year (Taylor 1996; Wilson *et al.* 2001) and their presence supports a highly profitable ecotourism industry (Davis *et al.* 1997; Davis 1998). Observers have taken photographs of sharks attending this aggregation for over 12 years for the purposes of photo-identification (Arzoumanian *et al.* 2005; Meekan *et al.* 2006).

### DATA COLLECTION

A total of 581 photographs were taken of whale sharks between March and July from 1992 to 2004 (Meekan *et al.* 2006). Photographs were made using an underwater still camera or digital video camera while snorkelling with the animal. Still images of sharks were captured from videotape for analysis. Total length (*TL*: tip of snout to end of caudal fin) and dorsal fin height (*DIH*) were recorded using a measuring tape after animals were photographed. In cases where only *DIH* was measured, we used a previously established equation to predict *TL* (Meekan *et al.* 2006):

$$TL = 1.059 + 10.348 DIH$$

Animal gender was determined whenever possible by distinguishing males based on the presence of claspers on the pelvic fins (Taylor 1994). It was often difficult to discern claspers in relatively small (< 4 m *TL*) sharks, so those animals were recorded as indeterminate gender (Meekan *et al.* 2006).

## MARK–RECAPTURE ANALYSIS

We used Cormack–Jolly–Seber (CJS) capture–mark–recapture (CMR) models (Cormack 1964; Jolly 1965; Seber 1970) implemented in program MARK (White & Burnham 1999) to model apparent survival ( $\phi$ ) and recapture (resighting) probability ( $p$ ) of whale sharks participating in the Ningaloo Reef aggregation. Our primary interest was to estimate mean survival probability for inclusion into models projecting the population through time, so we endeavoured to assess variation in this parameter due to time and size effects. Estimates of  $\phi$  within a CMR framework confound mortality with permanent emigration from the population, so some underlying knowledge of population closure is required to assess the degree of potential bias associated with survival estimates. We have established previously that closed and open population models provided similar estimates of population size at the Ningaloo aggregation (Meekan *et al.* 2006). This suggests that the superpopulation is comprised of individuals that are not infrequent transients, but are those that attend the aggregation at least semiregularly. As such, we expect that the estimates of survival derived from the CMR provided reasonable parameters for inclusion into population models.

Our first analysis ignored the effects of size and sex and examined whether there was evidence for annual variation in  $\phi$  and  $p$  over the course of the study (1992–2004). Models were compared using an information-theoretical measure of model parsimony, Akaike's information criterion (AIC) (Akaike 1973; Burnham & Anderson 2002) and goodness-of-fit was assessed using the simulation procedures provided in program MARK (White & Burnham 1999). A second model set was constructed to incorporate the effects of sex and time (16 models considered). Two separate analyses were performed to determine whether there was a size- (length-) bias in survival using the estimates of total length. The first model set considered *size* as a categorical variable, where sharks  $< 8$  m were considered immature and those  $\geq 8$  m as mature (Colman 1997; see also below). This size-based grouping was applied only to the apparent survival parameter, with full time dependency considered for  $\phi$  and  $p$  (16 models). A potentially more sensitive assessment of the effects of size on survival used total length as a standardized covariate in a linear model to predict the logit of  $\phi$  (again, with the *time* effect considered for both  $\phi$  and  $p$ ). Here we examined the effects of total length as potentially altering both the intercept and slope of the linear model predicting logit( $\phi$ ) (12 models considered).

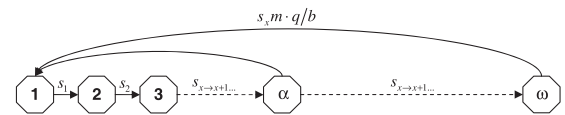
## POPULATION MODELS

To examine how our estimated survival probabilities altered population projections, we constructed a series of age-based Leslie matrix population models to examine the potential population trajectory (Caswell 2001).

Although we have now estimated many of the demographic rates necessary to parameterize population models such as population size, sex ratio, size distribution (Meekan *et al.* 2006) and survival (this study), many other parameters are unknown or based on few data. As such, we defined several model scenarios that examined different assumptions with respect to the least-known parameters.

## MODEL STRUCTURE

Although stage-classified models have been used to project shark populations through time (Frisk, Miller & Fogarty 2002; Mollet & Cailliet 2002; Otway, Bradshaw & Harcourt 2004), the relatively simple life history of elasmobranchs (i.e. sharks, rays and skates) coupled with the distorted elasticity patterns derived from stage-classified models (Mollet & Cailliet 2003) argue for the use of simpler age-classified Leslie matrix models for whale sharks. We constructed a simple, deterministic and density-independent Leslie matrix (birth-pulse, post-breeding design: Caswell 2001) for each of the model scenarios (described below) using the R package (R Development Core Team 2004) where the matrices were based on the general life cycle graph:



Here,  $s$  = the age-specific survival probability,  $x$  = age in years,  $\alpha$  = the age at primiparity,  $\omega$  = maximum age in years (longevity),  $m$  = litter size per female,  $q$  = pup sex ratio and  $b$  = adult female reproduction frequency. For biennial reproduction, we calculated the discounted fertilities for every second year after  $\alpha$  (i.e. setting the non-breeding years' discounted fertilities to 0).

## PARAMETER ESTIMATES AND ASSUMPTIONS

Whale sharks are live-bearers with an aplacental viviparous mode of development (Joung *et al.* 1996; Colman 1997). However, there is only one record of a captured female measuring approximately 11 m *TL* found to contain 300 embryos (Joung *et al.* 1996). There is no information available for the frequency of reproduction, with annual, biennial and possibly more infrequent reproduction possible. As such, the fertility parameter was calculated as the number of potential pups ( $m$ )  $\times$  the assumed pup sex ratio ( $q$ )  $0.5 \div$  the frequency of reproduction ( $b$ ) taking values of one or two (see model scenarios below).

Age at sexual maturity for females is thought to occur at  $> 8$ – $9$  m total length based on two female specimens of this size captured in Indian waters found to have immature ovaries (Pai *et al.* 1983; Satyanarayana Rao 1986). Colman (1997) therefore suggested that sexual maturity is reached at  $> 9$  m. We assumed that all

individuals  $\geq 8$  m were mature given the observed peak in the distribution of whale sharks at Ningaloo was 8 m (Meekan *et al.* 2006), which suggests an appearance in the seasonal aggregation of a particular (potentially) reproductive class relative to immatures. Additionally, growth rates (and hence length at sexual maturity) may be lower for animals regularly visiting the relatively cooler waters of Western Australia compared to India. Thus, based on our sample of individuals for which total length was known or estimated, the proportion of individuals that were mature ( $\geq 8$  m) was  $31 \div 108 = 0.29$ . However, a study of vertebral growth rings from stranded individuals recovered in South Africa (Wintner 2000) suggested that an immature 5.77 m (*TL*) female was 22 years old assuming annual growth rings (age not validated), although maturity could not be determined absolutely given the lack of mature animals to autopsy. None the less, we repeated all model scenarios where the duration of the immature stage was doubled (i.e. 24 years). No modification was made to overall longevity (see below) given that so few individuals remained after maximum age as to make little difference to the matrix outputs.

We used the von Bertalanffy growth function (von Bertalanffy 1938):

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt}$$

where  $L_t$  = predicted total length (m) at age  $t$  (in years),  $L_\infty$  = asymptotic maximum length,  $L_0$  = length at birth and  $k$  = a rate constant in units of reciprocal time. This growth equation has been shown to be suitable for many elasmobranch species (Aasen 1963; Cailliet *et al.* 1992; Van Dykhuizen & Mollet 1992; Gallucci, Taylor & Erzini 2006) and it can be used as a means to translate size-based estimates of survival to age-based probabilities and to estimate longevity. Pauly (2002) suggested that the rate constant ( $k$ ) for whale sharks was  $0.031 \text{ years}^{-1}$  with a corresponding longevity  $> 100$  years. This gives a first-year growth of 0.39 m, a value Pauly (2002) considered to be too large. The observed growth rate of young whale sharks in captivity was 0.81 m over 120 days (corresponding to 2.46 m annual growth) (Chang *et al.* 1997). We speculated and assumed that first-year growth in the wild was 0.80 (approximately twice that of Pauly 2002 and one-third the captive rate), yielding a von Bertalanffy rate constant  $k = 0.0637 \text{ years}^{-1}$ . Using a birth length ( $L_0$ ) of 0.58 m (Joung *et al.* 1996), maximum length ( $L_\infty$ ) = 13.7 (Compagno 1984) and assuming that maturity is reached at 8 m, this predicts age at maturity is approximately 13.0 years. Using a projected longevity of  $5 \log_e 2/k = 54$  years (Ricker 1979), which in this case equates to an individual achieving 97% of  $L_\infty$ , the duration of each stage is therefore 1 year for stage 1, 12 years for stage 2 (non-reproductive) and 41 years for stage 3 (reproductive). Finally, we set first-year survival to 0.5 based on the observed range of 0.38–0.65 for lemon sharks (*Negaprion brevirostris*; Gruber, de Marignac & Hoenig 2001)

and 0.37–0.82 for neonate black-tip sharks (*Carcharhinus limbatus*; Heupel & Simpfendorfer 2002). The paucity of juvenile survival data for almost all shark species prevents a more rigorous application of an evidence-based survival rate; however, we contend that given the balance of evidence, a first-year survival rate of 0.5 is a realistic mean for the heuristic purposes of inferring potential population trends.

The following sections outline various combinations of parameters and model assumptions to investigate the potential population trajectory using information derived from the CMR survival estimates. Model scenarios consider increasingly complex combinations of parameters under a deterministic framework only.

#### Model scenario 1

In this scenario we constructed a simple deterministic model incorporating the mean survival estimate from the CMR models described above. Here, we maintained the first-year survival rate at 0.5 and applied the mean CMR survival rate to the remaining age classes regardless of reproductive status (non-reproductive or reproductive). We assumed a maximum invariant litter size of 300 (Joung *et al.* 1996) and two reproduction frequencies: annual and biennial. No density-dependent feedback mechanisms were implemented. Finally, this deterministic scenario considered both short (12 years) and long (24 years) non-reproductive stage durations.

#### Model scenario 2

In this deterministic scenario we set the survival for the non-reproductive ages (years 1–12) to the mean probability of survival derived from the linear prediction based on total length over the size classes found at the Ningaloo Reef aggregation (4 to  $< 8$  m). The reproductive female ages (13+) survival rate was estimated similarly as the mean survival for the size classes considered to be reproductive at Ningaloo (8–10 m). All other parameters and assumptions were maintained as in scenario 1. Both short and long non-reproductive stage durations were examined.

#### Model scenario 3

This deterministic matrix included an incrementing survival up to the age of 13 years, after which time survival was held constant. Age-specific survival probabilities were calculated from combination of the total length, survival and von Bertalanffy growth relationships described above. Short and long non-reproductive stage durations were considered separately, as well as annual and biennial reproduction frequencies.

#### Model scenario 4

This matrix included incrementing survival up to the age of 25 years, with both non-reproductive stage durations



considered separately and annual and biennial reproduction frequencies.

#### ELASTICITIES OF $\lambda$ TO CHANGES IN MATRIX PARAMETERS

For each deterministic base matrix, we identified the most important demographic parameters influencing the rate of population change. This type of perturbation analysis is achieved by calculating the sensitivity of the dominant eigenvalue of a matrix to changes in its elements, where the sensitivity of matrix element  $a_{ij}$  is the local slope of  $\lambda$  as a function of  $a_{ij}$  (Caswell 2001). Elasticities (proportional sensitivities) were calculated for each matrix entry (survival, fertility) and summed to provide total elasticities for non-reproductive [ $E(s_{nr})$ ] and reproductive female survival [ $E(s_r)$ ], and adult fecundity [ $E(m)$ ]. This process requires taking into account the discounted fertilities (because survival is included in the first-row matrix entries in a post-breeding design) and then normalizing the elasticities for non-reproductive females, reproductive females and fertility so that they sum to 1 (Mollet & Cailliet 2003). We also calculated the mean age of reproducing females at the stable age distribution ( $\bar{A}$ ) for each matrix considered:

$$\bar{A} = \langle w, v \rangle$$

where  $w$  = left eigenvector of the matrix (age structure) and  $v$  = right eigenvector (reproductive values) when  $w_1 = v_1 = 1$  (Mollet & Cailliet 2003). Elasticities can then be calculated from  $\bar{A}$  (Mollet & Cailliet 2003):

$$E(m) = 1/(\bar{A} + 1)$$

$$E(s_{nr}) = (\alpha)/(\bar{A} + 1)$$

$$E(s_r) = (\bar{A} - \alpha)/(\bar{A} + 1)$$

In the case of biennial reproduction frequency, elasticities must be calculated differently because the projection interval does not agree with the reproductive cycle (Mollet & Cailliet 2003). Following the formulae in Appendix 1(b) of Mollet & Cailliet (2003),  $\bar{A}$  is adjusted to  $\bar{A}/2$  (i.e. in 2-year units),  $\alpha$  becomes  $(\alpha + 1)/2$ .

## Results

### SURVIVAL AND CAPTURE PROBABILITIES

The base CJS analysis estimating apparent survival ( $\phi$ ) and capture probability ( $p$ ) using data from 111 individual sharks demonstrated that the saturated model (time-variant  $\phi$  and  $p$ ) fitted the data reasonably well (probability of observing the model deviance as large = 0.464 based on 1000 iterations). Therefore, no adjustment to the AIC scores for over-dispersion ( $\hat{c}$ ) was required (White & Burnham 1999). The most parsimonious model had time-invariant  $\phi$  and  $p$  (Table 1); however, there was some evidence for time variation in both parameters

**Table 1.** Model ranking of Cormack–Jolly–Seber mark–recapture models estimating apparent survival ( $\phi$ ) and recapture probability ( $P$ ) for whale sharks participating in the Ningaloo Reef (Western Australia) aggregation from 1992 to 2004. Shown are the delta Akaike's information criteria ( $\Delta$ AIC), the AIC weight (AICwt), the number of parameters and the deviance for each model. A '(·)' denotes an invariant parameter, and '(t)' denotes a time-variant parameter

Model	$\Delta$ AIC	AICwt	Parameters	Deviance
$\phi(\cdot) p(\cdot)$	0.00	0.588	2	53.459
$\phi(t) p(\cdot)$	1.56	0.269	7	44.289
$\phi(\cdot) p(t)$	3.07	0.126	7	45.800
$\phi(t) p(t)$	7.11	0.017	10	43.015

**Table 2.** Time-variant model-averaged estimates of apparent survival ( $\hat{\phi}$ ) derived using Cormack–Jolly–Seber (CJS) mark–recapture models for whale sharks participating in the Ningaloo Reef (Western Australia) aggregation from 1992 to 2004. Also shown are the standard error (SE), unconditional SE and 95% confidence interval for each model-averaged estimate

Interval	$\hat{\phi}$	SE	Uncond.	
			SE	95% CI
1992–93	0.890	0.038	0.092	0.563–0.981
1993–94	0.890	0.038	0.092	0.563–0.981
1994–95	0.737	0.080	0.176	0.321–0.943
1995–96	0.863	0.124	0.139	0.386–0.984
1996–2003 (annual)	0.842	0.056	0.064	0.676–0.931
2003–04	0.773	–	–	–

based on AIC weights (Table 1). The null model gave an apparent annual survival of 0.825 (SE = 0.042; 95% CI: 0.727–0.893; CV = 5.1%) and capture probability of 0.184 (SE = 0.038; 95% CI: 0.121–0.271; CV = 20.7%). The model-averaged annual estimates of  $\phi$  are shown in Table 2 (range: 0.737–0.890).

### SEX DIFFERENCES IN SURVIVAL

There were 100 individuals of known sex in the database (81 males, 19 females). The saturated model with a *sex* effect in survival and capture probability fitted the data reasonably well (probability of observing the model deviance as large = 0.969 based on 1000 iterations). However, the top five models accounting for over 97% of the AIC weight had only a *time* effect on survival and no *sex* effect, suggesting that there were no survival differences between the sexes. There was some support for a sex effect on capture probability ( $\phi(t) p(\text{sex})$  model with AIC weight = 21.4%), but the model-averaged capture probability ranges for each sex overlapped (0.229–0.263 and 0.232–0.266 for males and females, respectively). As such, any possible sex bias in survival and recapture probabilities was ignored.

### SIZE DIFFERENCES IN SURVIVAL

There were size (total length) data for 75 individuals in the database (48 immature, 27 mature). Mean total

length was 7.2 m and ranged from 4.4 to 9.7 m. In the size-class analysis, the saturated model fitted the data reasonably well, although there was moderate evidence for a lack of fit to the data (probability of observing the model deviance as large = 0.052 based on 1000 iterations). The top four models (accounting for over 93% of the AIC weight) had only a time effect on survival, suggesting no support for size (categorical) differences in survival.

The analysis using standardized total length as a covariate in the models demonstrated, however, that there was a size bias in survival probability. The top four models all included a *length* and *time* effect on  $\phi$  and accounted for over 92% of the AIC weight. The most parsimonious model (AIC weight = 38%) indicated a common intercept and time-variant slopes for the *length* effect on survival, but the second model had identical weight (38%) and indicated both intercept and slopes were time-variant. Many of the parameters in the time-variant models were not estimable, so we chose to express the simpler relationship between length and  $\phi$  by ignoring the *time* effect. The linear model derived was:

$$\text{logit}(\hat{\phi}) = 0.966 + 0.388 \left( \frac{TL - \overline{TL}}{\hat{\sigma}_{TL}} \right)$$

where  $TL$  is the estimated length of a whale shark,  $\overline{TL}$  is the mean total length of all sharks in the sample (7.2 m) and  $\hat{\sigma}_{TL}$  is the standard deviation of total length from the sample (1.4 m). Thus, ignoring the effects of time, a 5-m shark has a predicted survival probability of 0.59 and a 9-m shark has a predicted survival probability of 0.81.

#### POPULATION MODELS

The results of the Leslie matrix projection models are presented in Table 3 (age at first reproduction,  $\alpha = 13$  years) and Table 4 ( $\alpha = 25$  years). Of the 16 model combinations considered, 10 (63%) indicated a decreasing population ( $\lambda < 1$ ). For models based on  $\alpha = 13$ , the mean age of reproducing females at the stable age distribution ( $\bar{A}$ ) ranged from 15 to 23 years (Table 3), which increased to 29–37 years when  $\alpha$  was increased to 25 (Table 4). In all model combinations considered,

**Table 3.** Matrix parameters calculated for each model scenario considered when age at first reproduction ( $\alpha$ ) = 13, for both annual and biennial reproduction frequencies. Shown are the dominant eigenvalue of the deterministic matrix ( $\lambda$ ), the stable stage distribution (SSD) for first-year (0–1 years), juvenile (1–12 years) and adult (13–54 years) sharks, respectively, the mean age of reproducing females at the stable stage distribution ( $\bar{A}$ ), the combined elasticities for non-reproductive [ $E(s_m)$ ] and reproductive [ $E(s_r)$ ] survival, the ratio of elasticities for reproductive to non-reproductive survival [ $E(s_r)/E(s_m)$ ] and the elasticity for fertility [ $E(m)$ ]

Scenario	Description	$\lambda$	SSD	$\bar{A}$	$E(s_m)$	$E(s_r)$	$E(s_r)/E(s_m)$	$E(m)$
Annual reproduction								
Scenario 1	Constant survival	1.2658	0.47, 0.53, 0.005	14.87	0.8191	0.1179	0.1440	0.0630
Scenario 2	Average length-based survival	1.0438	0.45, 0.54, 0.004	16.53	0.7412	0.2013	0.2713	0.0571
Scenario 3	Length-based survival to age 13	0.9500	0.60, 0.40, 0.005	17.12	0.7173	0.2275	0.3171	0.0552
Scenario 4	Length-based survival to age 25	0.9751	0.61, 0.39, 0.005	20.61	0.6015	0.3522	0.5855	0.0463
Biennial reproduction								
Scenario 1	Constant survival	1.2229	0.44, 0.55, 0.007	14.67	0.7798	0.1002	0.1285	0.1200
Scenario 2	Average length-based survival	1.0078	0.43, 0.57, 0.006	16.73	0.6940	0.1992	0.2870	0.1068
Scenario 3	Length-based survival to age 13	0.9177	0.58, 0.42, 0.008	17.52	0.6658	0.2317	0.3480	0.1024
Scenario 4	Length-based survival to age 25	0.9470	0.59, 0.40, 0.008	22.38	0.5332	0.3848	0.7218	0.0820

**Table 4.** Matrix parameters calculated for each model scenario considered when age at first reproduction ( $\alpha$ ) = 25, for both annual and biennial reproduction frequencies. Shown are the dominant eigenvalue of the deterministic matrix ( $\lambda$ ), the stable stage distribution (SSD) for first-year (0–1 years), juvenile (1–24 years) and adult (25–54 years) sharks, respectively, the mean age of reproducing females at the stable stage distribution ( $\bar{A}$ ), the combined elasticities for non-reproductive [ $E(s_m)$ ] and reproductive [ $E(s_r)$ ] survival, the ratio of elasticities for reproductive to non-reproductive survival [ $E(s_r)/E(s_m)$ ] and the elasticity for fertility [ $E(m)$ ]

Scenario	Description	$\lambda$	SSD	$\bar{A}$	$E(s_m)$	$E(s_r)$	$E(s_r)/E(s_r)$	$E(m)$
Annual reproduction								
Scenario 1	Constant survival	1.0508	0.31, 0.69, 0.003	28.63	0.8436	0.1223	0.1453	0.0337
Scenario 2	Average length-based survival	0.9432	0.38, 0.62, 0.003	30.91	0.7836	0.1851	0.2362	0.0313
Scenario 3	Length-based survival to age 13	0.8715	0.54, 0.44, 0.004	31.56	0.7679	0.2014	0.2623	0.0307
Scenario 4	Length-based survival to age 25	0.9352	0.58, 0.41, 0.004	35.45	0.6859	0.2867	0.4180	0.0274
Biennial reproduction								
Scenario 1	Constant survival	1.0295	0.29, 0.71, 0.004	28.55	0.8183	0.1162	0.1420	0.0655
Scenario 2	Average length-based survival	0.9244	0.36, 0.63, 0.005	31.20	0.7531	0.1867	0.2479	0.0602
Scenario 3	Length-based survival to age 13	0.8542	0.53, 0.47, 0.007	31.95	0.7364	0.2047	0.2780	0.0589
Scenario 4	Length-based survival to age 25	0.9178	0.57, 0.42, 0.008	36.23	0.6540	0.2937	0.4491	0.0523

the stable age distribution indicated a minority of reproductive females, but the dominance of first-year sharks or non-reproductive females varied according to particular combinations of vital rates and model assumptions. However, when survival rate was allowed to vary with age (length), the number of first-year sharks dominated the stable age distribution. All scenarios had higher total elasticities for non-reproductive female survival [ $E(s_{nr})$ ] compared to that for reproductive female survival [ $E(s_r)$ ] (Tables 3 and 4).  $E(m)$  was inferior to  $E(s_{nr})$  and  $E(s_r)$  in all cases.

## Discussion

The paucity of data describing the variation in vital rates in species of conservation concern is a common problem for ecological modellers (Boyce 1992; Morris & Doak 2002). Indeed, obtaining estimates of vital rates and their corresponding variances may be difficult or impossible for many species, especially for long-lived marine vertebrates (Caughley 1994; Heppell, Caswell & Crowder 2000). As such, generalizations for predicting population persistence derived from few data or based on allometric or species-specific ecological characteristics are often sought (Beissinger & Westphal 1998; Belovsky *et al.* 2004; Brook, Traill & Bradshaw 2006). Although heuristically useful (Brook *et al.* 2002), matrix population models lacking quantitatively derived vital rates are subject to many assumptions that are difficult to test or validate. In the case of the relatively poorly studied whale shark, we have provided the first estimates of survival rates based on mark-recapture data. These estimates, combined within a series of deterministic Leslie matrix models have permitted the first quantitative appraisal of the projected long-term trends of this vulnerable population.

Although caution must be exercised in interpreting our population matrices (see below), the variants of the age-classified Leslie matrix models using different estimates of non-reproductive female and reproductive female survival and stage duration demonstrate the importance of considering biologically plausible covariates in survival analyses, especially for long-lived and slow-growing species. For example, ignoring the important effect of total length (size) on estimates of survival led to the conclusion of population increase (i.e.  $\lambda > 1$ ), regardless of changes to age at first reproduction and frequency of reproduction. However, when we used the more parsimonious information-theoretical model predictions of length-varying survival, the importance of stage duration became much more apparent. With the shorter stage duration and age-specific survival estimates, most scenarios predicted a declining population ( $\lambda < 1$ ), and doubling the interval between reproductive events resulted in an increased rate of decline.

Many elasmobranchs have a reproductive cycle of two years (Cortés 2002) and a few species breed more infrequently, every 3 years (Mollet *et al.* 2000; Cortés 2002). Although the reproduction interval of whale

sharks is currently unknown, the precautionary principle for fisheries management (Caddy & Mahon 1995) suggests that assuming annual reproduction would be inappropriate for whale sharks. Reducing the breeding frequency further to once every 3 years, the estimates of  $\lambda$  under the most realistic scenario 4 (length-based survival to age 25) are further depressed to 0.9325 (age at first breeding = 13) and 0.9077 (age at first breeding = 25). Despite the severe lack of demographic data for this species (especially with respect to its reproductive capacity), the models that incorporated the most biologically realistic parameter estimates and assumptions support the conclusion of a declining population visiting Ningaloo Reef each year. However, this conclusion depends on some as yet untested assumptions. The duration of the non-reproductive stage and life span of the species are important determinants in the projections using length-varying estimates of survival. Of these two parameters, perhaps it is more tractable to collect information on growth rates that would verify the onset of reproduction.

The super-population of whale sharks participating in the Ningaloo Reef aggregation has been estimated at 300–500 individuals, of which approximately 16% were identified as female (74% male and 10% indeterminate gender) (Meekan *et al.* 2006). It should also be noted that pups and yearlings have never been observed at Ningaloo Reef, so pup production is likely to occur elsewhere. It is unknown whether the female component of the Ningaloo aggregation represents a small proportion of females that normally participate in a larger, sexually segregated female population that has yet to be identified. If there is an important sexual segregation of whale sharks, as has been documented for other elasmobranch species (Springer 1967; Klimley 1987; Sims, Nash & Morritt 2001; Sims 2006), then the small number of females observed at Ningaloo might not necessarily comprise the majority of the reproductively active females contributing new individuals to the aggregation. The embryo and juvenile sex ratio of many shark species does not depart from unity (Joung & Chen 1995; Chen, Liu & Chang 1997; Liu *et al.* 1999; Smale & Goosen 1999; Joung *et al.* 2005; Hazin *et al.* 2006), and Beckley *et al.* (1997) reported an equal sex ratio for stranded, immature whale sharks in South Africa. As such, we expect the low percentage (16%) of females at Ningaloo to be the result of sexual segregation, perhaps with many females within the super-population instead spending their time further north in Southeast Asian waters (Theberge & Dearden 2006), around the Indian coastline (Satyanarayana Rao 1986) or even in the vicinity of the Galápagos Islands (Stewart & Wilson 2005).

Our analyses also revealed some important aspects of the contribution of length- (and age-) specific survival rates to population rates of change. Elasticities from a mean matrix cannot by themselves predict accurately how  $\lambda$  fluctuates with variation in vital rates because of non-equality of change in these parameters, nonlinearities in their relationships to  $\lambda$  and differences in the coefficients of variation among matrix elements

(Mills, Doak & Wisdom 1999). Additionally, the reported elasticities were derived from deterministic matrices, which can be poor predictors of stochastic elasticities when the environment is extremely variable or includes catastrophic mortality events (Benton & Grant 1996). Although it has been shown previously that whale shark numbers at Ningaloo Reef fluctuate in response to environmental events such as El Niño–Southern Oscillation (ENSO; Wilson *et al.* 2001), we deliberately avoided using stochastic projections given the uncertainty associated with mean values of reproductive output, reproduction frequency and age at first reproduction.

With these caveats in mind, we found that the highest elasticities were for immature (i.e. non-reproductive) survival rates. This result agrees with reassessments of elasticities for most elasmobranch species (Mollet & Cailliet 2002, 2003). Even though others have suggested that elasmobranch population rates of change are more sensitive to adult (reproductive) survival (Colman 1997; Smith, Au & Show 1998; Walker 1998; Frisk, Miller & Fogarty 2001; Cortés 2002), the elasticities for many stage-classified models are calculated inappropriately (see Mollet & Cailliet 2003). When calculated correctly (and more easily) using age-classified Leslie matrix models, we found that immature female survival was a far more important determinant of the potential population rate of change for whale sharks; therefore, estimating this parameter precisely should be a prime area of research.

The limitation of producing robust estimates of the reproductive potential of whale sharks is problematic and may ultimately prevent the construction of reliable population viability analyses. There have been only nine 'juveniles' (0.55–0.93 total length) recorded for whale sharks (Colman 1997), some of which have been found in the stomach of other oceanic predators (blue shark *Prionace glauca* and blue marlin *Makaira mazara*) (Kukuyev 1996; Colman 1997). Nor have there ever been reports of individuals between 0.93 and 3.00 m total length, suggesting that there are either extremely high predation rates on small individuals or that reproduction occurs in the open ocean and is so dispersed that the probability of detecting young individuals is too low to quantify precisely. Another potential limitation is the probable density-related changes in vital rates used to parameterize the models, especially considering the pervasiveness of density dependence in nature (Brook & Bradshaw 2006). We deliberately avoided constructing hypothetical density-dependent relationships in our simple scenarios given the complete lack of associated data, but we acknowledge that persistence predictions and parameter elasticities are likely to vary with the inclusion of density dependence (Grant & Benton 2000; Drake 2005). However, future work on this aggregation and other whale shark populations should attempt to assess the degree to which vital rates are modified by density fluctuations. This may be achieved initially perhaps by examining the evidence for density dependence in phenomenological time series of relative abundance (e.g. sightings-per-unit-effort data; Brook & Bradshaw 2006).

Our analyses beg the following questions: (1) what is the state of the Ningaloo Reef whale shark population; and (2) can our analyses shed light on its persistence probability? Recent evidence from Ningaloo suggests that the population is comprised of a larger proportion of juveniles compared to previous decades (Meekan *et al.* 2006). However, severe declines have not been reported, so we believe that the real population trajectory lies somewhere between the extremes of our predictions. Additionally, an aggregation of juvenile whale sharks in nearby Thailand has declined recently by 96% (sightings per unit effort from 1992 to 2001) (Theberge & Dearden 2006). These observations, in combination with our results, lend credence to the hypothesis that the regional (Australasian) population of whale sharks is declining. As such, our results have several conservation implications for this and other large oceanic shark species. The wide dispersal range and sensitivity of population growth rates to minor variation in survival makes this species particularly vulnerable to anthropogenic sources of mortality (customary and commercial fishing). Non-reproductive whale sharks aggregating at Ningaloo travel long distances (1000 s km) to Southeast Asian waters (Wilson *et al.* 2006), where they are potentially susceptible to fishing pressure (Eckert *et al.* 2002; Polovina *et al.* unpublished data). The low population size (300–500 individuals; Meekan *et al.* 2006), the possibility of limited mixing (Wilson *et al.* 2006; Polovina *et al.* unpublished data) and the high elasticity of  $\lambda$  to non-reproductive female survival rates demonstrate the need for concerted conservation efforts to span national boundaries (Wilson *et al.* 2006).

The collection of mark–recapture databases for whale sharks has provided the first quantitative foundation for testing hypotheses regarding population persistence in one of the largest known aggregations of this species. Continued development of this database will be important for adjusting the predictions of matrix-based models, and will also provide a template for other large, oceanic marine vertebrates for which few demographic data exist. Our combination of standard CJS mark–recapture estimates of apparent survival and age-classified Leslie matrix models allowed us to assess the biological reality of the demographic rate estimates for whale sharks. In so doing, our study has highlighted the demographic processes that conservation practitioners should aim to maximize to increase the persistence probability of this, and other large elasmobranch species.

### Acknowledgements

We thank J. Polovina, S. Wilson, J. Stevens, B. Stewart and C. McLean for access to unpublished movement data, and R. Harcourt, D. Sims and an anonymous reviewer for helpful comments to improve the manuscript. We acknowledge the support of the whale shark ecotourism industry based in Exmouth and Coral Bay, Western Australia. We thank the West Australian Department of Environment and Conservation and BHP-Billiton for logistical and financial support.



## References

- Aasen, O. (1963) Length and growth of the porbeagle (*Lamna nasus*, Bonnaterre) in the North West Atlantic. *Reports on Norwegian Fishery and Marine Investigations*, **13**, 20–37.
- Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. In: *Proceedings of the Second International Symposium on Information Theory* (eds B.N. Petrov & F. Csaki), pp. 267–281. IEE Computer Society Press, Budapest, Hungary.
- Arzoumanian, Z., Holmberg, J. & Norman, B. (2005) An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. *Journal of Applied Ecology*, **42**, 999–1011.
- Beckley, L.E., Cliff, G., Smale, M.J. & Compagno, L.J.V. (1997) Recent strandings and sightings of whale sharks in South Africa. *Environmental Biology of Fishes*, **50**, 343–348.
- Beissinger, S.R. & Westphal, M.I. (1998) On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, **62**, 821–841.
- Belovsky, G.E., Botkin, D.B., Cowl, T.A., Cummins, K.W., Franklin, J.F., Hunter, M.L.J., Joern, A., Lindemayer, D.B., MacMahon, J.A., Margules, C.R. & Scott, J.M. (2004) Ten suggestions to strengthen the science of ecology. *Bioscience*, **54**, 345–351.
- Benton, T.G. & Grant, A. (1996) How to keep fit in the real world: elasticity analyses and selection pressures on life-histories in a variable environment. *American Naturalist*, **147**, 115–139.
- von Bertalanffy, L. (1938) A quantitative theory of organic growth. *Human Biology*, **10**, 181–213.
- Boyce, M.S. (1992) Population viability analysis. *Annual Review of Ecology and Systematics*, **23**, 481–506.
- Brook, B.W. & Bradshaw, C.J.A. (2006) Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology*, **87**, 1445–1451.
- Brook, B.W., Burgman, M.A., Akçakaya, H.R., O'Grady, J.J. & Frankham, R. (2002) Critiques of PVA ask the wrong questions: throwing the heuristic baby out with the numerical bath water. *Conservation Biology*, **16**, 262–263.
- Brook, B.W., Traill, L.W. & Bradshaw, C.J.A. (2006) Minimum viable population size and global extinction risk are unrelated. *Ecology Letters*, **9**, 375–382.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodal Inference: a Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York, USA.
- Caddy, J.F. & Mahon, R. (1995) *Reference Points for Fisheries Management*. Report no. 347. FAO Fisheries, Rome, Italy.
- 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.
- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd edn. Sinauer Associates, Inc., Sunderland.
- Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, **63**, 215–244.
- Chang, W.B., Leu, M.Y. & Fang, L.S. (1997) Embryos of the whale shark, *Rhincodon typus*: early growth and size distribution. *Copeia*, **1997** (2), 444–446.
- Chen, C.T., Liu, K.M. & Chang, Y.C. (1997) Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839) (Chondrichthyes: Alopiidae), in the northwestern Pacific. *Ichthyological Research*, **44**, 227–235.
- Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) (2002) CITES Appendix II nomination of the Whale Shark, *Rhincodon typus*. Proposal 12.35. *CITES Resolutions of the Conference of the Parties in Effect After the 12th Meeting, Santiago, Chile, 2002*.
- Cochran, M.E. & Ellner, S. (1992) Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecological Monographs*, **62**, 345–364.
- Colman, J.G. (1997) A review of the biology and ecology of the whale shark. *Journal of Fish Biology*, **51**, 1219–1234.
- Compagno, L.J.V. (1984) *Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 1. Hexanchiformes to Lamniforme. Food and Agriculture Organization (FAO) of the United Nations, Species Catalogue 5, Fisheries Synopsis*, **125** (4), 1–249.
- Cormack, R.M. (1964) Models for capture–recapture. *Biometrika*, **51**, 429–438.
- Cortés, E. (2002) Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation Biology*, **16**, 1048–1062.
- Davis, D. (1998) Whale shark tourism in Ningaloo Marine Park, Australia. *Anthrozoos*, **11**, 5–11.
- Davis, D., Banks, S., Birtles, A., Valentine, P. & Cuthill, M. (1997) Whale sharks in Ningaloo Marine Park – managing tourism in an Australian marine protected area. *Tourism Management*, **18**, 259–271.
- Drake, J.M. (2005) Density-dependent demographic variation determines extinction rate of experimental populations. *PLoS Biology*, **3**, e222.
- Eckert, S.A., Dolan, L.L., Kooyman, G.L., Perrin, W. & Rahman, R.A. (2002) Movements of whale sharks (*Rhincodon typus*) in South-east Asian waters as determined by satellite telemetry. *Journal of Zoology*, **257**, 111–115.
- Ellner, S.P., Fieberg, J., Ludwig, D. & Wilcox, C. (2002) Precision of population viability analysis. *Conservation Biology*, **16**, 258–261.
- Fagan, W.F. & Holmes, E.E. (2006) Quantifying the extinction vortex. *Ecology Letters*, **9**, 51–60.
- 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.
- Frisk, M.G., Miller, T.J. & Fogarty, M.J. (2002) The population dynamics of little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*: predicting exploitation limits using matrix analysis. *ICES Journal of Marine Science*, **59**, 576–586.
- Gallucci, V.F., Taylor, I.G. & Erzini, K. (2006) Conservation and management of exploited shark populations based on reproductive value. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 931–942.
- Grant, A. & Benton, T.G. (2000) Elasticity analysis for density-dependent populations in stochastic environments. *Ecology*, **81**, 680–693.
- Gruber, S.H., de Marignac, J.R. & Hoenig, J.M. (2001) Survival of juvenile lemon sharks (*Negaprion brevirostris*) at Bimini, Bahamas, estimated by mark-depletion experiments. *Transactions of the American Fisheries Society*, **130**, 376–384.
- Hazin, F.H.V., Fischer, A.F., Broadhurst, M.K., Veras, D., Oliveira, P.G. & Burgess, G.H. (2006) Notes on the reproduction of *Squalus megalops* off northeastern Brazil. *Fisheries Research*, **79**, 251–257.
- 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.
- Heupel, M.R. & Simpfendorfer, C.A. (2002) Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 624–632.
- Heyman, W.D., Graham, R.T., Kjerfve, B. & Johannes, R.E. (2001) Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series*, **215**, 275–282.
- International Union for the Conservation of Nature and Natural Resources (IUCN) (2005) *IUCN Red List of Threatened Species*. World Conservation Union, Gland, Switzerland. Available at: www.iucnredlist.org (accessed 1 June 2006).

- Jolly, G.M. (1965) Explicit estimates from mark–recapture data with both death and immigration–stochastic models. *Biometrika*, **52**, 225–247.
- Joung, S.J. & Chen, C.T. (1995) Reproduction in the sandbar shark, *Carcharhinus plumbeus*, in the waters off northeastern Taiwan. *Copeia*, **1995** (3), 659–665.
- Joung, S.J., Chen, C.T., Clark, E., Uchida, S. & Huang, W.Y.P. (1996) The whale shark, *Rhincodon typus*, is a livebearer – 300 embryos found in one megamamma supreme. *Environmental Biology of Fishes*, **46**, 219–223.
- Joung, S.J., Liao, Y.Y., Liu, K.M., Chen, C.T. & Leu, L.C. (2005) Age, growth, and reproduction of the spinner shark, *Carcharhinus brevipinna*, in the northeastern waters of Taiwan. *Zoological Studies*, **44**, 102–110.
- Klimley, A.P. (1987) The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes*, **18**, 27–40.
- Kukuyev, E.I. (1996) The new finds in recently born individuals of the whale shark *Rhincodon typus* (Rhincodontidae) in the Atlantic Ocean. *Journal of Ichthyology*, **36**, 203–205.
- Liu, K.M., Chen, C.T., Liao, T.H. & Joung, S.J. (1999) Age, growth, and reproduction of the pelagic thresher shark, *Alopias pelagicus* in the northwestern Pacific. *Copeia*, **1999** (1), 68–74.
- McMahon, C.R., Hindell, M.A., Burton, H.R. & Bester, M.N. (2005) Comparison of southern elephant seal populations, and observations of a population on a demographic knife-edge. *Marine Ecology Progress Series*, **283**, 273–283.
- Meekan, M.G., Bradshaw, C.J.A., Press, M., McLean, C., Richards, A., Quaschnick, S. & Taylor, J.G. (2006) Population size and structure of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Marine Ecology Progress Series*, **319**, 275–285.
- Mills, L.S., Doak, D.F. & Wisdom, M.J. (1999) Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology*, **13**, 815–829.
- 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.
- Mollet, H.F., Cailliet, G.M. (2003) Reply to comments by Miller *et al.* (2003) on Mollet and Cailliet (2002): confronting models with data. *Marine and Freshwater Research*, **54**, 739–744.
- Mollet, H.F., Cliff, G., Pratt, H.L. Jr & Stevens, J.D. (2000) Reproductive biology of the female shortfin mako, *Isurus oxyrinchus Rafinesque*, 1810, with comments on the embryonic development of lamnoids. *US National Marine Fisheries Service Fishery Bulletin*, **98**, 299–318.
- Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland, MA.
- Otway, N.M., Bradshaw, C.J.A. & Harcourt, R.G. (2004) Estimating the rate of quasi-extinction of the Australian grey nurse shark (*Carcharias taurus*) population using deterministic age- and stage-classified models. *Biological Conservation*, **119**, 341–350.
- Pai, M.V., Nandakumar, G. & Telang, K.Y. (1983) On a whale shark, *Rhincodon typus* Smith landed at Karwar, Karnataka. *Indian Journal of Fisheries*, **30**, 157–160.
- Pauly, D. (2002) Growth and mortality of the basking shark *Cetorhinus maximus* and their implications for whale shark *Rhincodon typus*. *Elasmobranch Biodiversity, Conservation and Management. Proceedings of an International Seminar and Workshop*. Sabah, Malaysia. (eds S.L. Fowler, T. Reid & F.A. Dipper). Occasional Papers of the IUCN Survival Commission no. 25. IUCN, Gland, Switzerland.
- Pravin, P. (2000) Whale shark in the Indian coast – need for conservation. *Current Science*, **79**, 310–315.
- R Development Core Team (2004) *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ricker, W.E. (1979) Growth rates and models. *Fish Physiology*, **8**, 677–743.
- Satyanarayana Rao, K. (1986) On the capture of whale sharks off Dakshina Kannada coast. *Marine Fisheries Information Service (India), Technical Extension Series*, **66**, 22–29.
- Seber, G.A.F. (1970) Estimating time-specific survival and reporting rates for adult birds from band returns. *Biometrika*, **57**, 313–318.
- Sibly, R.M., Barker, D., Denham, M.C., Hone, J. & Page, M. (2005) On the regulation of populations of mammals, birds, fish, and insects. *Science*, **309**, 607–610.
- Sibly, R.M. & Hone, J. (2002) Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, **357**, 1153–1170.
- Sims, D.W. (2006) Differences in habitat selection and reproductive strategies of male and female sharks. *Sexual Segregation of the Vertebrates: Ecology of the Two Sexes* (eds K.E. Ruckstuhl & P. Neuhaus), pp. 127–147. Cambridge University Press, Cambridge, UK.
- Sims, D.W., Nash, J.P. & Morritt, D. (2001) Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. *Marine Biology*, **139**, 1165–1175.
- Smale, M.J. & Goosen, A.J.J. (1999) Reproduction and feeding of spotted gully shark, *Triakis megalopterus*, off the Eastern Cape, South Africa. *Fishery Bulletin*, **97**, 987–998.
- 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. (1967) Social organisation of shark populations. *Sharks, Skates and Rays* (eds P.W. Gilbert, R.F. Mathewson & D.P. Rall), pp. 149–174. Johns Hopkins Press, Baltimore, MD.
- Stewart, B.S. & Wilson, S.G. (2005) Threatened fishes of the world: *Rhincodon typus* (Smith 1828) (Rhincodontidae). *Environmental Biology of Fishes*, **74**, 184–185.
- Taylor, G. (1994) *Whale Sharks*. Angus and Robertson Publishers, Sydney, Australia.
- Taylor, J.G. (1996) Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research*, **47**, 637–642.
- Theberge, M.M. & Dearden, P. (2006) Detecting a decline in whale shark *Rhincodon typus* sightings in the Andaman Sea, Thailand, using ecotourist operator-collected data. *Oryx*, **40**, 337–342.
- Van Dykhuizen, G. & Mollet, H.F. (1992) Growth, age estimation, and feeding of captive sevengill sharks, *Notorynchus cepedianus*, at the Monterey Bay Aquarium. *Australian Journal of Marine and Freshwater Research*, **43**, 297–318.
- 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.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46** (Suppl.), 120–138.
- Wilson, S.G., Polovina, J.J., Stewart, B.S. & Meekan, M.G. (2006) Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Marine Biology*, **148**, 1157–1166.
- Wilson, S.G., Taylor, J.G. & Pearce, A.F. (2001) The seasonal aggregation of whale sharks at Ningaloo reef, western Australia: currents, migrations and the El Niño/Southern oscillation. *Environmental Biology of Fishes*, **61**, 1–11.
- Wintner, S.P. (2000) Preliminary study of vertebral growth rings in the whale shark, *Rhincodon typus*, from the east coast of South Africa. *Environmental Biology of Fishes*, **59**, 441–451.