More analytical bite in estimating targets for shark harvest

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ABSTRACT: The typically slow life histories of sharks make them susceptible to overexploitation. However, this characteristic also means that shark populations are more amenable to mark-recapture estimation of vital rates and to population viability analysis, compared to many teleost (bony) fishes. We applied this novel approach to inform fisheries management for 2 shark species (*Carcharhinus tilstoni* and *C. sorrah*) in northern Australia. We calculated survival estimates based on a current mark-recapture study and age-frequency distributions from historical catch data, and used these along with other estimates of vital rates to construct an individual-based population viability analysis (using VORTEX software). We estimated total current mortality (natural and fishing-related) from tagging data using Brownie models (mean ± SE: 0.532 ± 0.097 and 0.487 ± 0.136) and recapture rate (fisheries-related mortality) (0.023 ± 0.005 and 0.008 ± 0.003) for *C. tilstoni* and *C. sorrah*, respectively. Based on historical age-at-length and age-frequency data, mean survival across ages after historical overexploitation was similar for both species (~0.43, or ~0.33 as an age frequency-weighted mean). After correcting for capture-related mortality and permanent emigration, VORTEX population projections including incrementing simulated harvest suggest that the current rates of harvest of both species result in population trajectories that are approximately stable (20 yr predicted average rate of population change $r \cong 0$), but this is complicated by a variable contribution of the slower-reproducing species *C. limbatus* within the black-tip shark complex (*C. limbatus* is commonly misidentified as *C. tilstoni* in the fishery). VORTEX projections also clearly indicated that the fishery was overexploited in the past. Using multiple datasets and an individual-based modelling framework to estimate harvest limits for a commercial fishery provides novel insights into management. This is especially pertinent to shark populations given the relative tractability of marking and recovering individuals and the inherent susceptibility of shark populations to overexploitation.

KEY WORDS: Harvest · Fisheries · Survival · Life table · Demography · VORTEX · *Carcharhinus tilstoni* · *Carcharhinus sorrah* · *Carcharhinus limbatus*

INTRODUCTION

The increasing global demand for protein has fuelled a push to increase fisheries production, despite the generally poor track record of sustainable management for many fisheries worldwide (Jackson et al. 2001, Roberts 2002, Field et al. 2009b). Marine fisheries in particular have poor histories of sustainability, either due to a lack of evidence-based management, poor enforcement or

both (Beddington et al. 2007). Exploitation beyond commercial viability, then abandonment, often ensue, with the industry ultimately forced to seek profitable resources elsewhere (Berkes et al. 2006). One essential element required to break this boom-and-bust cycle of over-exploitation is to have access to comprehensive life history, demographic and eco-system data with which managers can estimate and impose realistic upper limits to harvest (Beddington et al. 2007). Compared to most terrestrial species managed for harvest, fisheries have the disadvantage of often having to rely on simple measures of size structure from which to estimate maximum allowable harvest limits (Walters & Martell 2004). Without access to information on other components of the life history and ecology of fishes, there is substantial risk of overestimating safe harvest limits (Walters & Maguire 1996).

It is axiomatic that one of the most efficient ways to estimate demographic parameters is to mark individuals for later recapture (White & Burnham 1999, Walters & Martell 2004): data from which mark-recapture models can been developed to estimate *inter alia* survival, recapture and dispersal probabilities. Once such basic information is available, population projection models incorporating demographic rates, sex ratios, density-feedback functions, dispersal rates, inbreeding depression, disease dynamics and catastrophes can be developed (e.g. Bradshaw et al. 2012, Prowse et al. 2013). The application of realistic management scenarios to these baseline population models can then provide estimates of the most efficient means to control invasive species (McMahon et al. 2010), promote the recovery of threatened species (Brook et al. 2000), manage disease outbreaks (Bradshaw et al. 2012) or sustainably harvest commercially important species that are susceptible to range retractions from climate change (Traill et al. 2010a).

In the context of commercial fisheries, however, such population projection models are rarely developed because of the difficulty of obtaining the necessary parameter estimates. However, one taxon of harvested fish that is potentially amenable to mark-recapture applications and the development of population projection models is sharks, mainly because of their relatively slow (conservative) life histories (Field et al. 2009b), low densities and capacity to support durable external tags (Stevens et al. 2000). However, these same characteristics mean that sharks are also particularly vulnerable to over-exploitation given their lower rebound potential relative to many teleosts (Field et al. 2009b).

The global catch of chondrichthyans (including sharks, rays and chimaeras) has increased over time, with annual catches from 1996 to 2004 exceeding 800 000 t (FAO 2012). It is also likely that catches might in reality be up to 4 times higher based on estimates derived from the number of shark fins found during market surveys (Clarke et al. 2006). Despite regional declines and overexploitation (Field et al. 2009b), sustainable and economically viable shark and ray fisheries can be maintained if carefully managed, especially for relatively productive species (Walker 1998) such as gummy (*Mustelus antarcticus*) and blue sharks (*Prionace glauca*). That said, most industrial shark fisheries remain unmanaged, with the exception of those based in a few countries such as Australia, New Zealand, Canada and the USA (Fowler et al. 2005).

Using both historical and modern data from a shark fishery in northern Australia (Field et al. 2012), our objectives here were to apply population projection models to determine whether current fisheries for 2 commercially exploited shark species are not resulting in population declines (i.e. estimated long-term population change does not differ statistically from zero). Our first approach was to estimate survival rates for the 2 species using 2 independent methods: from age-frequency data collected following an intensive period of fishing in the 1970s and early 1980s, and from a recent (2006 to 2009) mark-recapture study (Field et al. 2012). Using these survival rates combined with other life history information, we constructed a series of individual-based population models in VORTEX (Bradshaw et al. 2012) to estimate the population growth rate under various scenarios of harvest rate. Our main hypothesis was that harvest-induced mortality from the historical fishery was unsustainable (i.e. resulted in population declines) and that the lower harvest rates of the present do not result in long-term population decline.

MATERIALS AND METHODS

Tagging

As part of the Northern Territory Offshore Net and Line Fishery monitoring and tagging program, we identified, measured, marked with 2 visible plastic tags (Superflexi Rototag, Dalton ID Systems) and released commercially caught (n = 1141) black-tip *Carcharinus tilstoni* and (n = 850) spot-tail sharks *C. sorrah* from September 2006 to September 2010 (Field et al. 2012). We attached the external yellow

tags towards the base of the first dorsal fin, using special applicators through a pre-punched hole. The external surface of each tag bore an individual, indelible identification number and the inside had a return address and reward message. Commercial vessels caught sharks using 165 mm (6 inch) mesh commercial gillnet. Only those sharks we were able to remove quickly and that showed no signs of trauma or capture stress were tagged and released, similar to those classified as in 'good' condition by Stevens et al. (2000).

To enhance recoveries, we publicised the tagging program through the media, fishing publications, fishery offices and domestic commercial and recreational fishing companies. We informed commercial fishing skippers about the program at fisheries advisory meetings and through the Northern Territory Seafood Council correspondence and by fishery technicians, who motivated skippers and crew when periodically monitoring fishing activities aboard these vessels, and during wharf-side visits. We asked fishers to retain captured sharks whole, with the tags in place when possible, or to provide the tag numbers, date and location of their recoveries. Sharks caught in the fishery are only landed in Darwin and Karumba ports, so there was a high probability of tag discovery. In addition to our constant motivation effort with the few operators in the fishery (typically 5 active at any given time), these shark species are rarely captured in other commercial and recreational fisheries; we are thus confident that most recaptured sharks had their tags returned and thus could be included in the final dataset. We do acknowledge however that without additional attempts to estimate reporting rates (e.g. via seeding experiments), this is based on feedback from liaison rather than quantitative experimentation.

Brownie mark-recapture survival models

We used the mark-recapture data to create recovery tables as input files for program MARK (White & Burnham 1999) to estimate apparent survival (S) and recovery probabilities (f) based on Brownie recovery-only models (Brownie et al. 1985). The model set we used included constant and time-variant survival and recovery parameters; we had insufficient returns to estimate age-specific parameters. The input data for each species contained adult and juve-

Table 1. *Carcharinus tilstoni* and *C. sorrah*. Process of mortality correction to estimate natural mortalities. $\hat{S}$ = estimated apparent survival (±SE); $\hat{f}$ = tag recovery rate (±SE); e = rate of permanent emigration; M_{cap} = capture-related mortality; M_{nat} = natural mortality (±SE). All rates expressed annually (i.e. probability per year)

	$\hat{S}$	$\hat{f}$	e	M_{cap}	M_{nat}
C. tilstoni	0.468 ± 0.097	0.023 ± 0.005	0.027	0.2	0.31 ± 0.10
C. sorrah	0.513 ± 0.136	0.008 ± 0.003	0.034	0.2	0.27 ± 0.14

nile releases. We combined recoveries into one group because recapture/recovery rates were low (see 'Results'). We ranked models using an information-theoretic measure of Kullback-Leibler information loss to assign relative strengths of evidence to each of the different competing models (Burnham & Anderson 2002, 2004): Akaike's information criterion corrected for small sample sizes (AIC$_c$). We ran parametric goodness-of-fit tests within MARK to test whether Cormack-Jolly-Seber model assumptions were met. To accommodate lack of fit, we estimated the amount of overdispersion and corrected for the extra-binomial variation in the data by the variance inflation factor $\hat{c}$ (Lebreton et al. 1992) to adjust the deviance in the calculation of the AIC$_c$ to a quasi-likelihood AIC$_c$ (QAIC$_c$) and parameter standard errors (Lebreton et al. 1992).

The resulting S estimates represented the cumulative effect of several sources of mortality and bias: natural mortality, fishing-related mortality, capture-related mortality, permanent emigration (e, probability per year) and tag loss. The estimation of natural (i.e. with other sources and biases removed) mortality rates necessary for the population projection models required several steps (Table 1). We endeavoured to estimate the most plausible modern natural mortality rates to project the current population forward 20 yr (3 to 4 generations for these species, a realistic temporal scale of management given longevities of 19 and 12 yr for *Carcharinus tilstoni* and *C. sorrah*, respectively) to examine the effect of variable harvest rates (H) on long-term rate of population change (r; often used interchangeably with population rate of 'growth' particularly when r is positive) (see modelling section below). Because apparent S from the Brownie mark-recapture models include (the unknown contribution of) e, and they are likely to be underestimated because of capture-related mortality, the former bias can be accounted for partially via estimates of long-distance migration. Recapture of tagged sharks indicates that most movements are <50 km, and only a small proportion (*C. tilstoni*:

0.027; *C. sorrah*: 0.034) move offshore beyond the range of current fishery operations (Stevens et al. 2000). We therefore corrected the Brownie survival estimates by dividing apparent survival by $1 - e$.

The next source of potential overestimated natural mortality was perhaps the largest: mortality arising from the capture process itself. Due to a higher amount of stress and physical damage, sharks caught in gillnets have substantially lower S than animals caught with hand lines (Stevens et al. 2000). Although we endeavoured to tag only those individuals in the best post-capture condition, there was undoubtedly substantial mortality induced by capture. Capture mortality from hand lines can be as high as 5 to 10% (Stevens et al. 2000); we therefore conservatively assumed that it would be double this maximum mortality rate when gill nets were employed to capture sharks for tagging. Consequently, we subtracted 0.2 from e in the calculation of corrected S described above. Finally, we subtracted f from the corrected mortality $(1 - S)$ value to provide the most biologically realistic natural mortality rate estimates for inclusion in the population projection models. Although substantial tag loss can result in a study failing to identify marked individuals and producing a downward bias in survival estimates, earlier work in northern Australia has shown that the probability of losing both tags is so small as to be negligible (0.000625 yr^{-1}) (Stevens et al. 2000). For this reason, we ignored this potential source of bias.

Life table analysis

Life tables characterise the survival properties of cohorts and provide important insights into a population's probability of long-term persistence under various ecological and management scenarios (Caughley 1977, Sinclair et al. 2006). In addition to assuming that the population is stable, the accuracy of this method is contingent on an unbiased sampling protocol. Although the Taiwanese fishery operating in northern Australia in the 1970s and 1980s caught sharks using nylon-monofilament gillnets (stretched mesh 145 to 190 mm), and there was a possibility that catch selectivity excluded sharks of extremely large size, Stevens & Wiley (1986) noted that the gillnets captured individuals of the complete size range for these species (birth size to maximum known length). Consequently, we are confident that the life tables we constructed from the age-frequency data were representative over most age classes for these species, so survival estimates arising were also reason-ably realistic. We also note that if only the largest (≈oldest) members of the populations are underrepresented, then this is likely to introduce relatively little error into the analysis.

We first estimated age frequency from the Taiwanese length-frequency data by sex-specific algorithms relating shark length (L, cm) and age (A, yr) (Davenport & Stevens 1988):

$$A = \left(\frac{-1}{G}\right)\log_e\left[1 - \left(\frac{L}{L\infty}\right)\right] + t_0 \qquad (1)$$

where G is a rate (yr^{-1}), and $t_0 = -2.6$ yr, $L_\infty = 165$ cm, $G = 0.19$ yr^{-1} for males, and $t_0 = -2.8$ yr, $L_\infty = 194.2$ cm, $G = 0.14$ yr^{-1} for female *Carcharinus tilstoni*; and $t_0 = -0.6$ yr, $L_\infty = 98.4$ cm, $G = 1.17$ yr^{-1} and $t_0 = -1.9$ yr, $L_\infty = 123.9$ cm, $G = 0.34$ yr^{-1} for *C. sorrah* males and females, respectively. We did not apply the life-table analysis to the current fishery catch data because of insufficient samples obtained across all age lengths and the bimodal distribution apparent in the length-frequency plots (Field et al. 2012). The possible reasons for bimodality are discussed in Field et al. (2012).

We used Caughley's 'Method 6' (Caughley 1977) to analyse the life tables we constructed from the age-frequency data. Method 6 is used for populations with a stable age distribution, known rates of increase and an annual birth pulse so that distinct cohorts are recognisable as is the case in some larger shark species (e.g. McAuley et al. 2007, Heupel & Simpfendorfer 2011). Here, the proportion of individuals surviving at the start of Age x, l_x, is: $l_x = n_x e^{rx}/n_0$, where n_x = the number observed in age class x to $x+1$ and n_0 = the number of births estimated from the fertility data. We determined age-specific female fertility (m_x, daughters per female) using the number of mature females throughout the population and proportion of females at birth for *Carcharinus tilstoni* and *C. sorrah* (46 and 50%, respectively) (Stevens & Wiley 1986). This information summarised l_x, mortality (d_x, probably per year), and m_x up to the maximum observed age of 7 yr for sharks in the fished sample (although this does not represent maximum longevity for either species; see population projection model description below). In the absence of any published information on population status we recalculated S based on 3 different finite population growth rates: $\lambda = 0.9$, 1.0 and 1.1 to determine the sensitivity of the mortality estimates to assumptions associated with rate of population change (cf. McMahon et al. 2011); variation in survival using these different values was negligible (data not shown), so we defaulted to the assumption of $\lambda = 1.0$.

Age-frequency distributions estimated from wild animals typically do not decrease at constant rates or smoothly (since a single cohort is not being followed), which can lead to negative estimates of mortality that are biologically implausible (Caughley 1966, 1977). Accordingly, we smoothed the observed age frequency data (Caughley 1966) into an adjusted age frequency (F_x, no. of ind.). We applied the most common smoothing algorithm — the log-polynomial regression of the form $\log g_x = a + bx + c^2x + d^3x$ …. Given that it is rare for the log-polynomial fitted to an age distribution from Age 1 to extend beyond the quadratic term (x^2) (Caughley 1966, 1977), we smoothed (F_x) our raw frequencies (f_x) using the quadratic form. We assessed the relative support of the quadratic smoothing relative to a linear smoothing model using AIC_c (Burnham & Anderson 2002).

Given that the age-frequency data used to estimate mortality rates were collected immediately following a period of intense harvest by the Taiwanese, we consider the derived estimates to represent maximum total mortality rates. These estimates are then useful for comparison to modern rates obtained from the mark-recapture data to determine the relative effect of vastly different harvest rates on the population trajectory.

Individual-based population models

We used program VORTEX (www.vortex9.org/vortex.html) to construct species-specific (*Carcharinus tilstoni* and *C. sorrah*) population models parameterised using the corrected mortality estimates from the Brownie models and other demographic information (including number of pups produced, age at first breeding, breeding intervals, longevity and population carrying capacity). VORTEX is an individual-based age- and sex-structured stochastic simulation (Miller & Lacy 2004) of the dynamics of small populations and the extinction process (Lacy 2000). VORTEX models population dynamics as discrete, sequential events that occur according to probabilities set by the user, stepping through life-cycle events of an organism. The simulation of the population is then iterated repeatedly to generate a fate distribution. For a detailed description of the software and its applications, see Lacy (2000), Miller & Lacy (2004) and Bradshaw et al. (2012).

The species-specific demographic information we used to parameterise the VORTEX models was as follows: for *Carcharinus tilstoni*, longevity was 19 yr with age at primiparity set to 3 yr (1.05 to 1.20 m total

length [TL]) for both sexes (Stevens & Wiley 1986, J. Stevens unpubl. data). The proportion of females breeding at Age 3 was ~50%, rising to 70% at Age 4 (1.30 to 1.35 m) and 90% for ages ≥5 (Stevens & Wiley 1986, Davenport & Stevens 1988). Litter size ranged from 1 to 6 pups ($\bar{x} = 3.0$, SD = 1.0), and there was a slight male bias in the neonate sex ratios (54% male) (Stevens & Wiley 1986). *C. sorrah* has a faster life history; longevity is only 12 yr and age at primiparity is 2 yr (0.95 to 1.00 m TL) for females (age at sexual maturity is 1 yr for males). The proportion of primiparous females breeding is 50%, rising to 93% for older animals (Stevens & Wiley 1986). Litter sizes are slightly higher than in *C. tilstoni*, ranging from 1 to 8 pups per annual breeding cycle ($\bar{x} = 3.1$, SD = 1.1).

To simulate die-offs (e.g. arising from disease, severe weather such as cyclones, Bradshaw et al. 2012), we invoked the observed relationship between generation length (4.6 and 3.4 yr for *Carcharinus tilstoni* and *C. sorrah*, respectively) and the occurrence of catastrophes for vertebrates (Reed et al. 2003). When a catastrophe occurred, survival decreased by 50% for that year. Although the choice of a catastrophe's severity is somewhat arbitrary, we based our choice on the definition by Reed et al. (2003): a catastrophe was "… any 1 yr peak-to-trough decline in estimated numbers of 50% or greater. Regardless, the value is not overly important to the final results because we were estimating long-term *r* rather than extinction risk per se. The application of a catastrophe function is important when the data used to derive vital rate estimates do not span a large number of the organism's generations, such that *S* could be over-estimated over longer time scales (thus increasing the risk of setting total allowable catch quotas, or total effort for a fishery, too high).

Viviparous sharks are generally thought to be limited by space for embryo development (Cortés 2002, Carlson & Baremore 2003), and captive sharks generally increase growth rates when food availability rises (Cortés & Gruber 1994). Gruber et al. (2001) found that juvenile lemon shark *Negaprion brevirostris* survival declined with increasing population abundance, and Punt & Walker (1998) hypothesized that the natural mortality rate of school shark *Galeorhinus galeus* pups was density-dependent. There is also good empirical evidence that reduced densities of Atlantic sharpnose *Rhizoprionodon terraenovae*, sandbar *Carcharhinus plumbeus* and porbeagle *Lamna nasus* sharks increase juvenile growth rate and lower age at primiparity (α) (Sminkey & Musick 1995, Carlson & Baremore 2003, Cassoff et al. 2007). For *L. nasus*, a reduction in age at maturity from 8 to

7 yr (males), and from 19 to 14 yr (females) occurred as densities declined by 75 to 80% (Cassoff et al. 2007).

VORTEX has limited capacity to alter α, or the rate of transition between age classes (Lacy & Kreeger 1992). Thus, we opted to emulate density feedback (sensu Herrando-Pérez et al. 2012) in the model parameters by (1) reducing fertility as the population approached carrying capacity (K, no. of ind., set using a stock reduction analysis; see below); this mimics an increase in the age of primiparity as the population approaches K, and (2) by applying a 'ceiling' density function as a proxy for compensatory density feedback in adult survival. First, we set a density-feedback function where fertility declines gradually to a value 0.2 below the maximum age-specific value at K (Bradshaw et al. 2012). Second, K is implemented as a ceiling where the population grows without restriction (proportion of females breeding excepted) to this level, but where individuals are randomly removed from the population if the total population size exceeds K in the simulation (Bradshaw et al. 2012). While ceiling density models tend to overestimate extinction risk (Traill et al. 2007), our aim was to compare the relative population trends among different harvest rates and not extinction risk per se.

To provide a realistic, approximate scale for the VORTEX simulations (initial population size, N_0, and K), we took unfished population sizes estimated for *Carcharinus tilstoni* and *C. sorrah* from deterministic stock reduction analyses (Kimura & Tagart 1982, Kimura et al. 1984). These estimates of stock size were developed during preliminary analyses for subsequent assessments of the fisheries for black-tip sharks in northern Australia (Grubert et al. 2013) using stochastic stock reduction analyses (Walters et al. 2006). These produced total population estimates of $N_0 = 1.7 \times 10^{11}$, $K = 3.17 \times 10^{11}$ for *C. tilstoni*; and $N_0 = 2.4 \times 10^{10}$, $K = 1.04 \times 10^{11}$ for *C. sorrah*, which we reduced to $N_0 = 1700$, $K = 3170$ and $N_0 = 240$, $K = 1040$ for *C. tilstoni* and *C. sorrah*, respectively for the VORTEX runs to reduce computation time (cf. Bradshaw et al. 2012). The size of the population in this context is not our principal concern; 'true' population size estimates are not essential for running comparative population projections if the goal is to assess relative rates of long-term trends. Because we applied relative population 'sizes' as indicators of biomass for the 2 modelled species rather than starting points to estimate extinction risk (not our aim), demographic stochasticity is not an issue because it generally only exacerbates extinction risk at extremely low population sizes (10s to 100s of individuals) (Traill et al.

2010b). A reduction in N_0 in VORTEX is a necessity imposed by the heavy computational cost of individual-based models (see Bradshaw et al. 2012, Prowse et al. 2013 for previous examples employing this approach). As a standard procedure, we assumed a stable age distribution for N_0 (Caswell 2001) in all model runs to provide a constant initial state from which harvest scenario outcomes could be compared.

The stochastic environment draws input parameter values from the user-set errors (standard errors of vital rates from Table 1) iterated 1000 times for each level of proportional annual harvest (0, 0.002, 0.005, 0.010, 0.020, 0.050, 0.100, 0.125, 0.150, 0.200, 0.300N_t) to provide a 95% confidence interval of average instantaneous population growth rate over the 20 yr projection ($\bar{r} = \log_e (N_{20}/N_0)/20$). Here we calculated the 2.5 and 97.5 percentiles of the 1000 $\bar{r}$ to give the upper and lower confidence bounds. Given the input demographic parameters we estimated were corrected for natural mortality, we assessed whether the fishery resulted in long-term population declines as the mean H intersecting $\bar{r} = 0$ (i.e. no average change in population trajectory). For modern harvest rates, we used the corrected f from the Brownie models based on the same logic for correcting overall mortality rates. In the case of *Carcharinus tilstoni*, $f(.) = 0.0227$ (SE = 0.0053); thus, 0.02 (rounding to 2 decimal places) represents 3.7% of 0.53 total mortality, or 0.012 (i.e. the estimated current proportional H). Subtracting this value from total estimated corrected mortality gives 0.31 (SE = 0.10) as the mortality rate applied to all age classes. For *C. sorrah*, $f(.) = 0.0083$ (SE = 0.0028); thus, the estimated current proportional H is 0.005, which modifies estimated natural mortality rate across all age classes to 0.27 (SE = 0.14).

Finally, we recently determined that sharks harvested in the current Northern Territory industry had substantial (~20%) errors in species identification (Tillett et al. 2012). For *Carcharinus tilstoni* in particular, up to 20% of harvested individuals were in fact *C. limbatus* (the common black-tip shark). *Carcharinus limbatus* is a larger and slower-breeding species compared to *C. tilstoni*, such that if fisheries catches are composed of both species, the calculation of long-term harvest limits based solely on the demographics of *C. tilstoni* could potentially compromise sustainability. Thus, we constructed a third model for *C. limbatus* based on the life-history parameters of *C. tilstoni*, but altering longevity to 20 yr, age at primiparity to 6 yr for females and 4 yr for males (Burgess & Branstetter 2005), litter size to 1–11 pups ($\bar{x} = 5.0$, SD = 1.0), and pupping to every 2 yr. Given we did not have estimates of natural mortality for *C. limbatus*,

we set age-constant mortality rates (M) based on a density-independent maximum rate of population increase (r_{max}) of 0.054 (Smith et al. 1998); to achieve this r_{max}, $M = 0.157$ (i.e. initial mortalities at $F = 0$).

RESULTS

Capture and recapture summary

Capture details and data are reported in Field et al. (2012), but we summarise those results briefly here. *Carcharinus tilstoni* and *C. sorrah* accounted for ~75% of the total catch of 2465 sharks from 25 species in the west coast of the Northern Territory and the western Gulf of Carpentaria combined. Mean (±SD) fork length of captured individuals was 782 ± 176 and 752 ± 97 mm for *C. tilstoni* and *C. sorrah*, respectively. Fishers recaptured 45 of 1141 (3.94%) tagged *C. tilstoni/limbatus* and 12 of 850 (1.41%) tagged *C. sorrah* during normal fishing operations. All recaptured sharks were harvested and processed normally.

Brownie mark-recapture survival and recovery rates

For both species, the highest probability was assigned to the time-invariant (.) survival and recovery model based on quasi-likelihood-corrected model probabilities using an over-dispersion estimate ($\hat{c}$) of 1.72 for *C. tilstoni* (*C. sorrah* was not over-dispersed, and so no correction to the AIC_c was necessary) (Table 2), giving $S(.) = 0.4685$ (SE = 0.0966) and $f(.) = 0.0226$ (SE = 0.0053) for *C. tilstoni*, and $S(.) = 0.5127$ (SE = 0.1365) and $f(.) = 0.0083$ (SE = 0.0028) for *C. sorrah*. While there was some support for time-variant f for *C. tilstoni* and time-variant S for *C. sorrah* (Table 2), the time-variant estimates fell within the uncertainty bounds of the time-invariant estimates. Coding time-varying S in VORTEX is also non-trivial, so we elected to employ the more parsimonious time-invariant estimates in the population models.

Life history tables

Estimated S_x from quadratic-smoothed (Table 3) F_x distributions (see Fig. A1 in Appendix 1) indicated that survival decreased with age and varied between species. S in the first 3 yr of life was higher for *Car-*

Table 2. *Carcharinus tilstoni* and *C. sorrah*. Brownie mark-recapture model probabilities estimated using Akaike's information criterion corrected for finite samples (AIC_c) and the quasi-likelihood adjustment ($QAIC_c$). Models include time-invariant (.) and -variant (t) survival (S) and recapture rate (f). Number of estimated parameters (k), change in $QAIC_c/AIC_c$ (*C. tilstoni*/*C. sorrah*, respectively) relative to the top-ranked model ($\Delta QAIC_c/\Delta AIC_c$) and the $QAIC_c/AIC_c$ model weights (probabilities) ($wQAIC_c/wAIC_c$)

Model	k	$\Delta QAIC_c/\Delta AIC_c$	$wQAIC_c/wAIC_c$
C. tilstoni			
$S(.)\ f(.)$	2	0	0.5598
$S(.)\ f(t)$	7	0.9872	0.3417
$S(t)\ f(.)$	6	4.4791	0.0596
$S(t)\ f(t)$	11	5.3329	0.0389
C. sorrah			
$S(.)\ f(.)$	2	0	0.6792
$S(t)\ f(.)$	6	1.9367	0.2579
$S(.)\ f(t)$	7	5.3018	0.0479
$S(t)\ f(t)$	10	7.6302	0.0150

Table 3. *Carcharinus tilstoni* and *C. sorrah*. Model weights for the linear and quadratic equations to determine the most appropriate smoothing algorithm for estimating survival from age-at-length data for black-tip and spot-tail sharks in northern Australia. Number of estimated parameters (k), maximum log-likelihood (LL), Akaike's information criterion corrected for small sample sizes (AIC_c), the AIC_c difference between the current and top-ranked model (ΔAIC_c), and model probability (AIC_c weights: $wAIC_c$)

Model	k	LL	AIC_c	ΔAIC_c	$wAIC_c$
C. tilstoni					
Linear	3	−11.810	33.048	1.976	0.2712
Quadratic	4	−8.203	31.072	0	0.7287
C. sorrah					
Linear	3	−5.471	20.370	2.162	0.2533
Quadratic	4	−1.771	18.209	0	0.7467

charinus tilstoni than *C. sorrah*, but for older sharks (>5 yr), S_x was higher for *C. sorrah* than for *C. tilstoni* (Fig. 1). Mean S across ages was similar for both species (~0.43), as was the age frequency-weighted mean (~0.33).

Harvest projection models

$\bar{r}$ declined non-linearly with the modelled increase in H (Fig. 2). According to the mortality estimates derived from the life-history table data, historical exploitation rates produced long-term rates of popula-
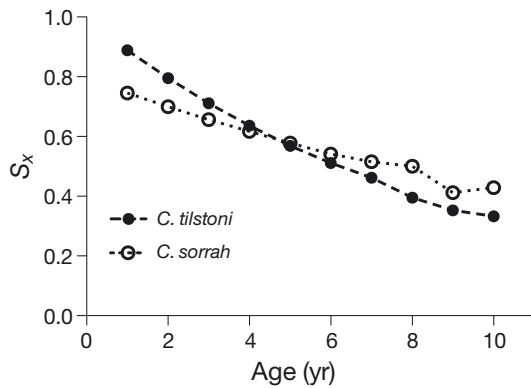
Fig. 1. *Carcharinus tilstoni* and *C. sorrah*. Age-specific survival estimates (S_x) from life tables for *C. tilstoni* and *C. sorrah*

tion decline, although the range of *H* derived from this approach was highly variable for *Carcharinus sorrah* in particular. Nonetheless, mean inferred historical *H* for all species we modelled was beyond any conservative estimate of long-term population stability (Fig. 2). In contrast, current fisheries-induced mortality derived from the Brownie mark-recapture models suggests that modern harvest results in a population that is approximately stable (i.e. 95% confidence interval of $\bar{r}$ encompasses 0) for *C. tilstoni* and *C. limbatus*, but probably well below a maximum sustainable yield scenario for *C. sorrah* (i.e. lower 95% confidence bound of $\bar{r} > 0$), even after accounting for uncertainty in predicted $\bar{r}$ (Fig. 2).

DISCUSSION

Using multiple datasets from 2 distinct phases of exploitation, our approach is the first to apply an individual-based modelling framework to estimate harvest limits for a commercial fishery. While the application of demographic models is a common practice in fisheries science, combining capture-mark-recapture methods with population viability analysis provides novel insights into fishery management. This is especially pertinent to shark populations given the relative tractability of marking and recovering individuals and the susceptibility of shark populations to overfishing (Field et al. 2009b). The ability to separate fishing-induced mortality from natural mortality by recovering individually identified fish—the 2 parameters most often confounded using traditional fisheries approaches—is a particularly effective means to test hypotheses regarding the long-term effects of harvest rates and for setting

harvest controls such as total allowable catches or effort. Additionally, incorporating theoretically supported, generationally scaled catastrophic mortality events increases the accuracy of long-term quotas set to avoid population declines estimated from relatively short-interval time series of catch data.

Shark populations have relatively low capacity to rebound following exploitation compared to teleosts (Smith et al. 1998, Field et al. 2009b), which predisposes them to overharvesting (Field et al. 2009b). Increasing focus on this inherent susceptibility has
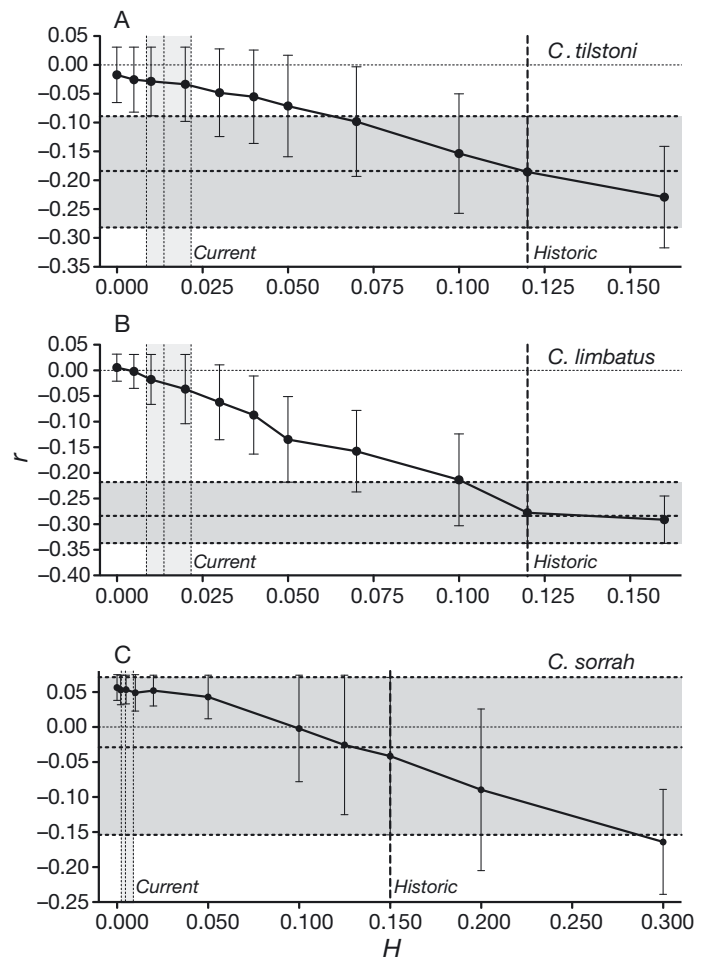

Fig. 2. *Carcharinus tilstoni, C. limbatus* and *C. sorrah*. Mean (with 95% CI) population trends (mean 20 yr rate of population change, *r*) for (A) *C. tilstoni*, (B) *C. limbatus* and (C) *C. sorrah* under incrementing proportional harvest rates (*H*). CI for *r* based on 1000 iterations of VORTEX individual-based models for each species. Shaded vertical region: range of current harvest rates estimated from Brownie mark-recapture models; shaded horizontal region: range of *r* estimated from VORTEX models parameterised with historical mortality rates estimated from life-history tables. Dashed lines: population stability (horizontal; *r* = 0) and at the 95% confidence bounds of the average historical *H* (vertical)

placed emphasis on collecting demographic information to parameterise population projection models (Cortés 2007). Modelling approaches range from empirically derived, age-based demographic models, to recruitment models used to estimate survival and productivity, or to characterise vulnerability to exploitation (e.g. Punt & Walker 1998, Smith et al. 1998, McAuley et al. 2007). While other cohort-based demographic models have been used widely in fisheries research (e.g. McAuley et al. 2007), our use of 2 independent datasets to estimate realistic survival probabilities emerging from 2 periods of different exploitation pressure, and then examining these differences within the context of a detailed population projection model, provides an extra dimension to the fishery that would not be otherwise apparent. For this reason, we were able to conclude with some confidence that the current fishery for *Carcharinus tilstoni* and *C. sorrah* results in long-term average rates of population change near zero, and that historical harvests were likely unsustainable: a conclusion supported by previous work (Stevens & Davenport 1991, Field et al. 2012).

In the present-day offshore net and line fishery in the Northern Territory, we found that for *Carcharinus sorrah*, there appears to be some opportunity for limited growth in the catch of this species; however for *C. tilstoni*, harvest rates are at or near maximum and probably should not be increased. This is a result of the latter species' life-history traits typical of less-productive species, such as later primiparity and lower fertility. However, these conclusions should be treated with some caution because we were unable to estimate age- or size-specific mortalities or fishery selectivities. That the mark-recapture dataset we collected was not sufficiently large to provide estimates of age-specific mortality and reproductive rates highlights the importance of long-term demographic studies for quantifying population growth rates (Grear & Elderd 2008). Collecting such information is not trivial; it requires many years of dedication, so reliance on alternative methods can assist managers. A powerful alternative for summarising and estimating vital rates is to collect a representative crosssection of animal sizes, illustrated in our study with the datasets from the historical (1980s) shark fishery (Stevens & Davenport 1991, Field et al. 2012). These data show quantitatively that harvest by this fishery was well above replacement rates, causing a rapid decrease in shark populations in northern Australia (Stevens & Davenport 1991).

The Taiwanese distant-water gillnet fleet targeted sharks in northern Australia and Indonesia from 1974 to 1986, fishing throughout Australian waters beyond 22 km from the coast and licenced to take 7000 t yr^{-1} (of all species retained) (Stevens & Davenport 1991). When concerns over cetacean bycatch led to a large reduction in the length of the net that was permitted to be set by any vessel, operations became 'uneconomic' and ceased in late 1986. This was probably an apparent, but not quantified, indication that populations had been over-harvested to such an extent that insufficient sharks remained in the fishery for it to remain economically viable (Stevens & Davenport 1991). Signs included a decrease in the proportion of mature *Carcharinus tilstoni* caught from 1981 to 1986, although no such trend was observed for *C. sorrah*, and a decrease in the median size of both *C. tilstoni* and female *C. sorrah* (Stevens & Davenport 1991). Using the vital rate information provided by our life-table analysis for this period and subsequently projected in VORTEX, we showed that mean population growth rates were negative during the time of the Taiwanese fishery's operations. Our models instead show that harvest rates not resulting in long-term average population decrease are substantially lower. We reiterate however that on-going collection of biological data within cohorts, and analysis of spatial and temporal variation in those attributes, is desirable because reducing the parameter variance will provide more certain long-term harvest targets.

Although our models suggest that the northern Australia shark fishery under current harvest management limits and for focal species does not result in population declines over a 20 yr projection interval, the recent identification of *Carcharinus limbatus* within the catch (part of the black-tip shark complex) adds a layer of complexity to its management. Given that the degree of spatial and temporal overlap and hybridisation of *C. tilstoni* and *C. limbatus* remains unclear (Ovenden et al. 2010, Morgan et al. 2011, Tillett et al. 2012), and that these 2 species demonstrate differential susceptibility to harvest, managers must attempt to estimate their relative contributions in catches. Our models indicate that the more *C. limbatus* is represented in catches, the lower the harvest rate the combined population can tolerate. Thus, there is a clear need to monitor the relative proportions of the 2 species within the 'black-tip' shark catch, and to manage harvest rates accordingly. This could be done efficiently and cost-effectively by periodic random tissue sampling of 'black-tip' sharks from catches followed by subsequent DNA analysis

(Tillett et al. 2012) to determine the variability in species composition within the complex.

One other potential complication is the role of illegal, unreported and unregulated (IUU) fishing in the management of shark fisheries in northern Australia. Previously, we reported the advance of illegal fisheries into Australia's northern Exclusive Economic Zone (Field et al. 2009a). The repercussions for fisheries management of this recent infiltration are still unclear, although preliminary data at highly fished reefs already indicate a reduction in shark diversity and biomass (Field et al. 2009a). Despite IUU fishing in the region, it is unlikely that our parameter estimates would have been greatly biased (e.g. from tagged sharks being removed by IUU fishers and not reported) because of the restricted, near-shore distribution of the fishery and the target species' limited dispersal rates (Stevens et al. 2000). However, with the likelihood of increasing IUU fishing pressure in the region, managers must be aware that harvest targets estimated from legally reported takes might still be too high.

We demonstrated recently that the composition of the fishery has changed since the intensive harvesting in the 1970s and 1980s, with larger specimens now being encountered more often (Field et al. 2012). This increase further suggests that the shark populations have recovered at least partially since the previous over-harvesting period. Although focal species of the current fishery are also the most productive, the other, larger species caught as by-catch need consideration. The greatest limitation for the sustainable management of this mixed fishery, and most others, is the lack of information about the catch and biological traits of all species caught. This information combined with risk analyses for rarer species should be key elements of future research.

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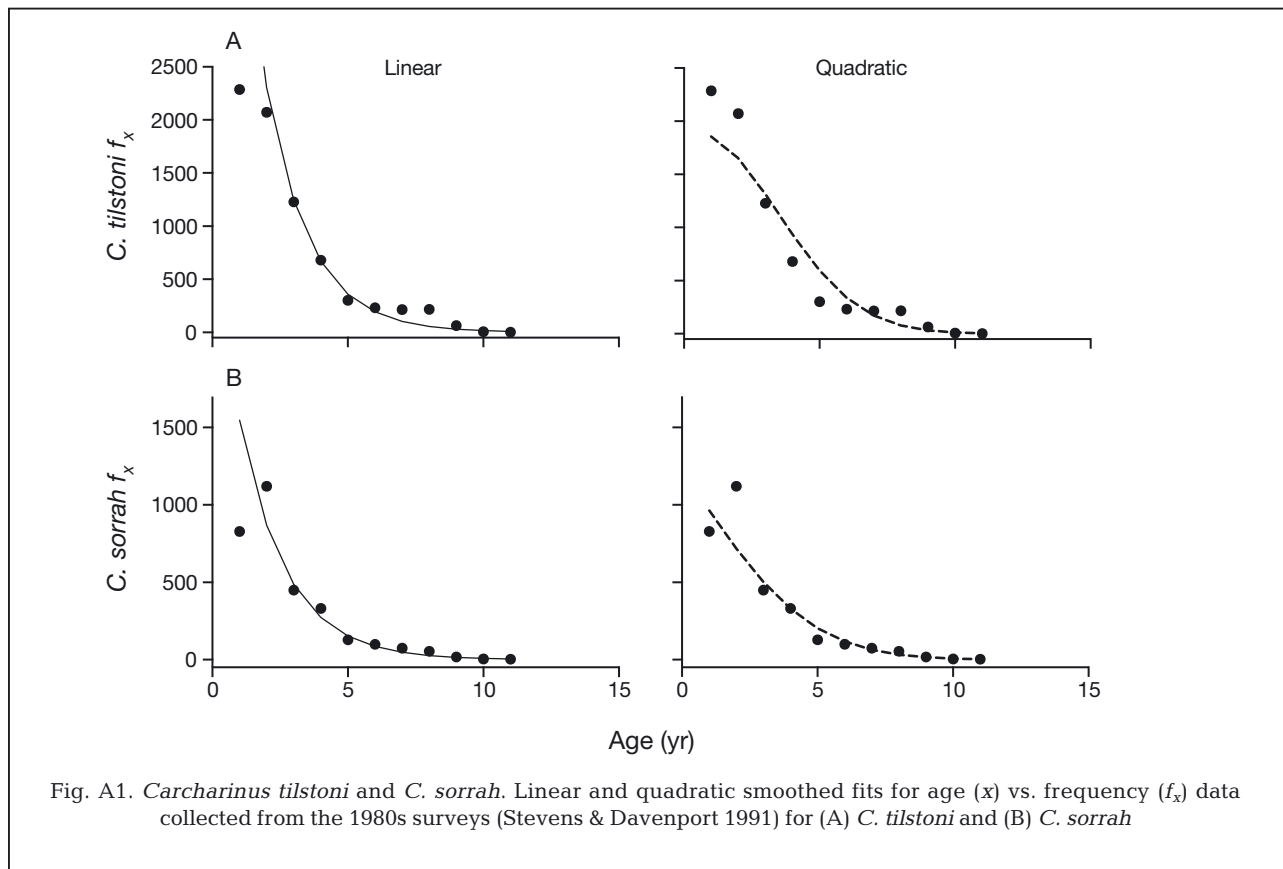
Appendix 1.

Fig. A1. *Carcharinus tilstoni* and *C. sorrah*. Linear and quadratic smoothed fits for age (*x*) vs. frequency (*f_x*) data collected from the 1980s surveys (Stevens & Davenport 1991) for (A) *C. tilstoni* and (B) *C. sorrah*