



# Modelling the population trajectory of West Australian white sharks



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## ABSTRACT

White sharks (*Carcharodon carcharias*) are globally distributed, protected in several countries, including Australia, and potentially dangerous to humans. Following a recent spate of fatal white shark attacks, the Government of Western Australia introduced a range of initiatives to mitigate shark hazards. An increasing trend in shark attacks over the last 20 years has been commonly perceived to be the result of an increase in population abundance since the species' protection in Australian waters in 1997. We modelled potential population productivity and trajectories using different scenarios of life-history strategies, unexploited population sizes, reconstructed fishery catches and post-capture mortality. Under zero fishing mortality, the potential annual increase in population abundance varied from 2 to 6% per year, depending upon the assumed life history strategy. Depending upon model inputs there was a wide range of potential declines in abundance since 1938/39 and significant differences in the potential population trajectories since protection. However, no scenario ( $n = 120$ ) resulted in a total population increase of >31% since protection, with most scenarios showing population increase of 10% or less. We present a method for exploring the effects of alternative hypotheses about key population parameters when data are scarce and when scientific advice is required for guiding decision making and informing public debate.

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## 1. Introduction

Determining productivity and reconstructing population trajectories of protected shark species is challenging as the data necessary for quantitative assessments are generally uncertain and incomplete (e.g. McPherson and Myers, 2009). This information is not only required for achieving natural resource management and conservation objectives but is also needed for informing other government policy and social debate.

The white shark (*Carcharodon carcharias*) is protected in several countries and internationally but is also potentially dangerous to humans. Shark attacks are the main focus of media coverage about sharks in countries like Australia and the US (Muter et al., 2013). Hence, despite their rarity, when shark attacks occur, the disproportionately high level of media exposure and community concern can have flow-on economic effects for tourism and other marine-related industries and can trigger considerable social, as well as political debate and government policy responses (Neff, 2012; Neff and Yang, 2013). For example, following five fatal shark attacks between September 2011 and July 2012 in Western Australia (WA),

the State Government invested more than AU\$ 33 million in a broad range of shark hazard mitigation strategies.

Many theories have been proposed to explain the spate of fatalities in WA. One of the most popular claims is that the recent increase in shark attacks is a direct result of an increase in the abundance of white sharks following the species' legislated protection since 1997 (Sprivulis, 2014; Pawle, 2015). Testing whether white shark abundance has increased requires a thorough understanding of the population's biological productivity and history of fishing mortality. However, understanding how public safety outcomes may have been affected by the legislated protection of white sharks is currently hampered by a poor understanding of the species' population status. Hence, to provide scientific advice and inform public debate our aim is to model the population trajectory of Western Australian white sharks.

Under the provisions of the *Commonwealth's Environment Protection and Biodiversity Conservation Act 1999* white sharks are subject to a Recovery Plan that specifies various actions designed to ensure the species' long-term viability in Australian waters (DEWHA, 2013). Initially, the listing of white sharks assumed a single Australia-wide population. Recent genetic and electronic-tagging findings, however, indicate population subdivision east and west of Bass Strait (Blower et al., 2012; Bruce and Bradford, 2012, Appendix A Fig. A1). The review of the recovery plan (DEWHA,

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2013) subsequently included this new evidence and identified that estimates of size and trend for both populations were required to assess the efficacy of conservation actions. For the white shark population west of Bass Strait (herein referred to as the 'southwestern population'), the information required for estimating population sizes and trends (including time-series of fishing exploitation rates and relative abundance) is not available. In the absence of this information, demographic models can be used to determine the productivity and susceptibility of shark species to additional sources of mortality, such as fishing (Simpfendorfer, 2005; McAuley et al., 2007). Previous demographic analyses for white shark populations elsewhere (Smith et al., 1998; Mollet and Cailliet, 2002; Au et al., 2008; Ward-Paige et al., 2012) used limited deterministic approaches that ignored uncertainty in life history parameters, which for white sharks is substantial. Also, these studies either did not consider the anthropogenic impacts of fishing (Mollet and Cailliet, 2002) or ignored age-specific rates of reproduction and mortality (Smith et al., 1998; Au et al., 2008; Ward-Paige et al., 2012). In the present study, we combined life-history parameters currently available for white sharks (including specified levels of uncertainties), reconstructed estimates of annual commercial and recreational catches and assumptions on unexploited population sizes and post-capture mortality (PCM), to generate a range of potential population trajectory scenarios. Finally, we ran additional sensitivity tests to inform where future studies should best be directed.

## 2. Methods

### 2.1. Demographic analysis

We used a probabilistic age-structured matrix model (Caswell, 2001) to estimate key population productivity parameters (finite rate of population increase,  $\lambda$ , and population doubling time,  $T_D$ ) while accounting for uncertainty in published life history parameters. We defined possible distributions for the biological parameters (10,000 Monte Carlo simulations) to draw samples from and construct possible distributions of population productivity characteristics and their corresponding medians and confidence intervals (2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles).

We obtained life history parameter values from the most current published estimates. We considered two life history scenarios (low and high productivity, Appendix A Table A1). The first scenario (LH1) is based on published life history information and the assumptions made in previous demographic analyses (Smith et al., 1998; Mollet and Cailliet, 2002; Au et al., 2008; Ward-Paige et al., 2012). The second scenario (LH2) is based on emerging life history information.

#### 2.1.1. Longevity

Longevity estimates used in previous demographic analyses ranged from 36 (Smith et al., 1998) to 60 (Mollet and Cailliet, 2002) years based on growth studies of white sharks from the Indian and Pacific Oceans. Until recently, the maximum number of vertebral growth bands observed was 23 (Francis, 1996) so Smith et al. (1998) and Mollet and Cailliet (2002) used theoretical estimates of longevity derived from available age and growth information. Hence, for LH1 longevity had a triangular distribution (Cortés, 2002) with a mode of 40 and lower and upper bounds of 40 and 60 years, respectively (Appendix A Fig. A2). Natanson and Skomal (2015) recently showed that counts of vertebral growth bands likely underestimate the age of older individuals in the western North Atlantic Ocean. Based on more recent attempts to validate age via bomb radio-carbon signatures, the maximum age of white sharks would be considerably higher (Andrews and Kerr, 2015; Natanson

and Skomal, 2015; Christiansen et al., 2016) with estimates of up to 73 years (Hamady et al., 2014). These longevity estimates are higher than those from previous studies, and longevity could possibly be even higher as the Hamady et al. (2014) estimates were based on a sample of four females and four males that were all smaller than the maximum reported sizes of this species. These authors suggested a lifespan of at least 70 years because in exploited populations, longevity is generally higher than the observed maximum age. Whether white sharks live significantly longer in the north-west Atlantic than elsewhere or whether longevity has been underestimated in previous studies cannot currently be resolved. To account for this, in LH2, uncertainty around longevity was broadened by using a mode of 70 and lower and upper bounds of 40 and 91 years [+30% maximum age observed, as per Cortés (2002); Appendix A Fig. A2].

#### 2.1.2. Female age at maturity

Female age at maturity is also uncertain. Based on published length at age estimates, Bruce (2008) reported a female age-at-maturity range between 12 and 17 years, while Smith et al. (1998) used a range between nine and ten and Mollet and Cailliet (2002) set maturity at 15 years. Hence, for LH1 age at maturity had a triangular distribution with a mode of 13 and lower and upper bounds of nine and 17 years, respectively (Appendix A Fig. A2). Age-at-maturity values used in previous white shark demographic analyses are approximately 25% longevity, which is very low for a large predator. In contrast, age-at-maturity for other mackerel sharks (bigeye thresher, *Alopias superciliosus*, pelagic thresher, *A. pelagicus*, common thresher, *A. vulpinus*, and salmon, *Lamna ditropis*, sharks, porbeagle, *L. nasus*, and shortfin mako, *Isurus oxyrinchus*) ranges between 25 and 64% longevity (Cailliet and Goldman, 2004; Natanson et al., 2006; Goldman and Musick, 2008). Also a recent bomb radio-carbon study indicates that white sharks likely mature later than previously estimated (Natanson and Skomal, 2015). Hence, for LH2 we set age-at-maturity at 38% longevity—the mean across mackerel sharks and a value more consistent with validated estimates for other low productivity sharks (McAuley et al., 2007)—and sampled from a triangular distribution with a mode of 25 and lower and upper bounds of 15 and 35 years, respectively (Appendix A Fig. A2). We set the age at first reproduction to one year after the age at maturity for both life history scenarios.

#### 2.1.3. von Bertalanffy growth

We used the von Bertalanffy growth function (VBGF) to transform the relationships at total length (TL) to relationships at age. There is considerable variability in published growth estimates of white sharks. For example, Tanaka et al. (2011) reported a  $k$  value of  $0.159 \text{ y}^{-1}$  for female sharks from Japan whereas Cailliet et al. (1985) and Wintner and Cliff (1999) reported  $k$  values of  $0.058 \text{ y}^{-1}$  and  $0.065 \text{ y}^{-1}$  (sexes combined) for individuals collected in California and South Africa, respectively. Hence, we only used the growth findings of O'Connor (2011) for southern Australia. We used a two parameter version of the VBGF (2VBGF) as this provided the best fit (O'Connor, 2011). Growth parameters are co-dependent so we used a multivariate normal distribution (obtained using the R package mvtnorm) with means of 7.19 m ( $L_\infty$ ),  $0.056 \text{ y}^{-1}$  ( $k$ ) and 1.40 m ( $L_0$ ) to draw samples of  $L_\infty$  and  $k$  (Appendix A Fig. A2). We constrained parameter samples to feasible values (i.e.  $k > 0$  and  $L_\infty < 7.5 \text{ m}$ ). As O'Connor (2011) did not report the variance-covariance matrix (VCM) for the estimated parameters, which is needed for drawing multivariate samples, we calculated the VCM by re-fitting the 2VBGF to the data used by O'Connor (2011). The same samples of growth parameter values were used for both life history scenarios.

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