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A first estimate of white shark, *Carcharodon* carcharias, abundance off Central California

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The decline of sharks in the global oceans underscores the need for careful assessment and monitoring of remaining populations. The northeastern Pacific is the home range for a genetically distinct clade of white sharks (Carcharodon carcharias). Little is known about the conservation status of this demographically isolated population, concentrated seasonally at two discrete aggregation sites: Central California (CCA) and Guadalupe Island, Mexico. We used photo-identification of dorsal fins in a sequential Bayesian mark-recapture algorithm to estimate white shark abundance off CCA. We collected 321 photographs identifying 130 unique individuals, and estimated the abundance off CCA to be 219 mature and sub-adult individuals ((130, 275) 95% credible intervals), substantially smaller than populations of other large marine predators. Our methods can be readily expanded to estimate shark population abundance at other locations, and over time, to monitor the status, population trends and protection needs of these globally distributed predators.

Keywords: white shark; Bayesian; mark-recapture; photo-identification; population estimate

1. INTRODUCTION

The susceptibility of shark populations to decline across ocean basins and their role as top predators in ecosystems [1] have resulted in considerable concern about the conservation status of many populations. White sharks (*Carcharodon carcharias*) are circumglobally distributed apex predators with at least three genetically distinct populations, including one in the northeastern Pacific (NEP) [2]. They are highly susceptible to overexploitation [3] and are currently listed on the IUCN Red List (Category VU A1cd + 2cd) [4]. There has been no rigorous attempt to

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estimate white shark population abundance in the Pacific and attempts to quantify their abundance at other locations suffer from low capture rates or abbreviated observation time [5,6].

Electronic tagging and genetic studies have rapidly advanced our knowledge of migration and the population structure of white sharks by characterizing movements and residency patterns of mature and subadult individuals [2,7-9]. These studies indicate that white sharks in the NEP display philopatric behaviours that result in a genetically discernible, separate population [2]. These sharks migrate seasonally between discrete coastal areas in North American shelf waters (figure 1a), primarily involving sites off Central California (CCA) (figure 1b) and Guadalupe Island, Mexico (figure 1c), and two locations in the central Pacific: (i) the slope and offshore waters around Hawaii and (ii) the eastern Pacific offshore waters, an area called the White Shark 'Café' [2,7-9]. Tagging data have shown that white sharks inhabit the CCA from August to January and that the CCA and Guadalupe groups primarily remain separate [2,9].

Demonstrated site fidelity to specific coastal aggregation sites [10] indicates that mark-recapture methods are appropriate for quantifying population abundance. While tagging individuals can provide a means of censusing the population, this is expensive and takes considerable effort over many years. However, in white sharks, the trailing edge of the dorsal fin is analogous to a fingerprint, hence provides a unique identifying trait of individual sharks over long time periods (greater than 22 years) [10]. Similar identification techniques have been described to identify nurse sharks, Ginglymostoma cirratum [11], and marine mammals [12]. The goal of this study was to estimate the abundance of mature and sub-adult white sharks at seasonal aggregation sites in CCA, to serve as a baseline for future assessment and monitoring of this population.

2. MATERIAL AND METHODS

This study was conducted from September–January in 2006, 2007 and 2008 at two known aggregation sites in CCA: Tomales Point and the Farallon Islands. Sharks were attracted to research vessels using a seal-shaped decoy and a small piece of bait. Digital images of individual dorsal fins were taken from either above or below water, depending on water clarity (see the electronic supplementary material for more detailed sampling methods). Images of sufficient quality were compared by eye to determine new marks and recaptures between samplings events (see the electronic supplementary material for photograph processing details).

Mark-recapture data were analysed in a sequential Bayesian algorithm designed for populations with low recapture rates, based on a hypergeometric distribution to represent sampling without replacement (see the electronic supplementary material for model discussion). Tests for the assumption of a closed population were conducted using the program CloseTest following Stanley & Burnham [13] and Otis *et al.* [14]. We compared the results of this method with seven other methods for estimation of abundance from mark-recapture data (see the electronic supplementary material for discussion of models).

3. RESULTS

Sharks ranged in estimated size from 260 to 530 cm total length, with a mean of 437 cm and s.d. of 52 cm. The sex ratio (69 males; 19 females; 42 unknown) was probably skewed towards males because it is easier to confirm the presence of claspers than to



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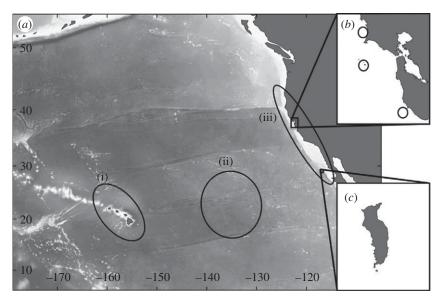


Figure 1. (a) The known focal use areas in the NEP. Coastlines and landmasses are designated by dark grey (i) slope and offshore waters around Hawaii, (ii) the White Shark 'Café', and (iii) North American shelf waters, comprised of (b) aggregation sites in CCA (open circles from north to south: Tomales Point, Farallon Islands, Año Nuevo Island) and (c) Guadalupe Island, Mexico.

confirm the absence, leading to high numbers of unknown sex.

In test trials, experts correctly matched fin photographs with 98 per cent success; there were no false positives and only one false negative. Attempts to use available software (e.g. DARWIN, FINSCAN) designed to identify marine mammal dorsal fins resulted in unacceptable levels of error (T. K. Chapple 2009, unpublished data) and were therefore not used. We catalogued a total of 321 photographs with sufficient quality and determined 130 unique individuals matched by eye (41 unique in 2006; 42 new unique and 12 recaptures in 2007; 47 new unique and 26 recaptures in 2008). Data from tagging experiments indicated animals were not likely to have left the population and returned [2], and the tests for closure were met following Stanley & Burnham [13] ($\chi^2 = 1.07$, p = 0.58) and Otis et al. [14] (z = -0.27, p = 0.39). Oualitative discussion of closure can be found in the electronic supplementary material.

The number of unique individuals was set as the minimum abundance value $(N_1=130)$. Following the Bayesian framework from Gazey & Staley [15], we calculated an appropriate range for the prior $(N_k=401)$ from the shape of multiple initial calculations of the posterior distribution. The mode of the posterior probability was N=219 ((130, 275) 95% credible intervals). Comparison of this Bayesian estimate to more traditional mark—recapture frameworks, as well as methods that account for heterogeneity in capture probabilities, showed that these methods produce similar abundance estimates (see the electronic supplementary material).

4. DISCUSSION

Our Bayesian estimate, and the similarity of estimates from seven other methods (electronic supplementary material), indicates that the coastal population in the NEP is quite low. Electronic tagging studies indicate that the coastal phase of mature and sub-adult white sharks in the NEP is comprised of sites in either CCA or Guadalupe Island, with little evidence for long-term occupation at other coastal sites [2]. Because the abundance at Guadalupe Island is probably even smaller [16], we estimate that the CCA comprises approximately half the total abundance of mature and sub-adult white sharks in the NEP.

This population is relatively small, even for apex predators. For comparison, population estimates (including all age classes) of air-breathing marine apex predators in the NEP such as the killer whale (Orcinus orca) and Southern Beaufort Sea stock of polar bears (Ursus martimus) are markedly larger (1145 and 1526, respectively) [17,18], despite occupying smaller ranges and having been reduced from historical levels by humans. Although our estimate at this time does not include juvenile and young of the year white sharks, high recapture rates of these early classes from a low incidence of fisheries interactions in the Southern California Bight [19,20] suggest that even with the addition of all age-classes, white sharks would still be at far lower abundance than other apex predators. Though historical abundances remain unknown for white sharks, recent findings illustrate the low genetic diversity in this population [2], which support our results of a low population abundance. This small estimate of abundance may therefore reflect a naturally low carrying capacity after an initial founding event from the western Pacific, or may reflect the consequences of anthropogenic pressures (e.g. human-induced prey reduction of pinnipeds [21] or fishing mortality [22]). Although it is not known how this abundance compares with historical levels, establishing a baseline at this time will allow quantitative assessment of the future effects of anthropogenic disturbances or natural population fluctuations.

The dorsal fin identification scheme we used here was an effective method to identify individual white sharks and may prove useful in estimating other shark populations globally. This method has been effective in identifying individuals, because it requires

less data and allows more flexibility (a single photo, from either side) as compared with other methods (e.g. pigmentation patterns). In addition, the estimation framework we developed can be readily expanded to include sharks from global databases, and over extended time series, to monitor the status, population trends and protection needs of white sharks globally. In the future, combining photographic identification with acoustic tagging of individuals that report to a network of receivers could provide a near-real time methodology for monitoring the sharks in the CCA.

This study establishes, to our knowledge, the first quantitative measure of white shark population abundance in the CCA and demonstrates that white sharks, among the largest predators in the oceans, exist in relatively low numbers in the NEP. These results emphasize the critical need to protect and monitor white sharks; especially given genetic data indicating discrete population structure [2] and the importance of sharks for the health of marine systems [1].

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