

ESTIMATING APPARENT SURVIVAL OF SUB-ADULT AND ADULT WHITE
SHARKS (*CARCHARODON CARCHARIAS*) IN CENTRAL CALIFORNIA
USING MARK-RECAPTURE METHODS

by

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TABLE OF CONTENTS

1. ESTIMATING ANNUAL APPARENT SURVIVAL OF 1
SUB-ADULT AND ADULT WHITE SHARKS (*CARCHARODON*
CARCHARIAS) IN CENTRAL CALIFORNIA

 Introduction..... 1
 Materials and Methods..... 4
 Study Area and Data Collection 4
 Data Analysis 6
 Results..... 10
 Discussion 12

REFERENCES CITED..... 17

LIST OF TABLES

Table	Page
1. Model Selection Results	13

LIST OF FIGURES

Figure	Page
1. Sex Assignment $\delta(\text{sex}+t)$	12

ABSTRACT

Over-exploitation of sharks is a global conservation concern as losses of large apex predators will likely lead to negative consequences in marine ecosystems. The Northeastern Pacific white shark population is genetically distinct and geographically isolated from other known white shark populations in South Africa, Australia/New Zealand, and the Northwest Pacific. The Northeastern Pacific population/clade is comprised of two groups, Guadalupe Island, Mexico, and Central California, USA, that predictably aggregate at their respective coasts during late summer to early winter months. Recently, a three-year study using patterns on the trailing edge of dorsal fins to identify unique white sharks estimated an abundance of 219 (95% credible interval of 130 to 275) sub-adult and adult white sharks off Central California, assuming a closed population. However, there are no estimates for any of the population's vital rates (e.g. survival, recruitment rates). We use six years of mark-recapture data to estimate apparent survival and test for differences in survival between sexes for sub-adult and adult white sharks in central California. We collected 668 photographs that allowed us to identify 199 individual sharks over six years of sampling at three locations off Central California. Using a method developed by Nichols *et al.* (2004) that accounts for imperfect detection and imperfect sex assignment, we estimated that annual apparent survival was 0.90 (95% CI = 0.81 – 0.98) for males and females and throughout our study period. At this time, it is difficult to determine how this vital rate will affect population trend. Future research is needed to determine if this annual survival estimate is high enough for adult white sharks to produce enough offspring that will eventually recruit to the sub-adult demographic to balance annual mortality.

ESTIMATING APPARENT SURVIVAL OF SUB-ADULT AND ADULT WHITE SHARKS (*CARCHARODON CARCHARIAS*) IN CENTRAL CALIFORNIA USING MARK-RECAPTURE METHODS

Introduction

Worldwide, sharks are heavily over-fished, and many populations are now considered to be at risk. A recent study has estimated that over 100 million sharks are killed annually to support the demand for their fins (Worm *et al.* 2013). Losses of large apex consumers will likely lead to indirect, negative consequences in marine ecosystems (Myers *et al.* 2007; Estes *et al.* 2011). Like many top predators, the white shark (*Carcharodon carcharias*) likely plays an important role in helping to sustain the health of marine systems. Currently, very little is known about the vital rates or population dynamics of this species due to a lack of data. Available knowledge suggests that white sharks are long-lived, late to mature, and produce few young (Cailliet *et al.* 1985; Francis 1996), which are characteristics of populations that are vulnerable to overexploitation (Sæther & Bakke 2000). White sharks are internationally protected under the Convention on International Trade in Endangered Species (CITES) and listed as vulnerable under the World Conservation Union Red List (IUCN, Category VU A1cd+2cd) (Dulvy *et al.* 2008).

Recent genetic studies have shown that the Northeastern Pacific white shark population is genetically distinct from other known white shark clades in South Africa, Australia-New Zealand (Pardini *et al.* 2000; Jorgensen *et al.* 2010), and the Northwest

Pacific (Tanaka *et al.* 2011). Contemporary studies using electronic tags have shown that Northeastern Pacific sub-adult and adult (> 2.4 m) white sharks aggregate annually at two main sites, Central California, USA (CC) (Klimley 1985; Klimley & Anderson 1996) and Guadalupe Island, Mexico (GI) (Domeier & Nasby-Lucas 2008). Data from pop-up archival tags (PAT) have indicated that both groups typically make similar and predictable offshore annual migrations to a shared geographically defined area known as the ‘White Shark Café’ that is located roughly 1200 miles west of the Baja Peninsula, although some sharks travel as far as Hawaii (Boustany *et al.* 2002; Weng *et al.* 2007; Domeier & Nasby-Lucas 2008; Jorgensen *et al.* 2010). Though CC and GI white sharks spatially overlap while offshore, almost all sharks return back to their respective coastal aggregation site during late summer or early fall. To date, there are few data indicating that sharks visit both sites (Jorgensen *et al.* 2012b).

These predictable annual migrations of white sharks support the use of a mark-recapture framework for estimation of population parameters at coastal sites (Chapple *et al.* 2011). The pattern on the trailing edge of the first dorsal fin has been shown to be stable over many years and can be used as a means of identifying individuals, i.e., serves as a natural ‘mark’ (Anderson *et al.* 2011). Recently, Chapple *et al.* (2011) used a three-year dataset of dorsal-fin resighting data in a closed-population mark-recapture model to estimate abundance of 219 (95% credible interval of 130 to 275) sub-adult and adult white sharks off CC. Because this is the first and only estimate of white sharks numbers in CC, the population trend is unknown. Given the relatively low population size estimated by Chapple *et al.* (2011) and the genetic distinctness of CC sharks,

Northeastern Pacific white sharks are candidates to be listed as an endangered species in California and in U.S. federal waters. Given that white sharks have a slow life history and survival of mature sharks is expected to be important to population persistence (Sæther & Bakke 2000), estimates of annual survival rates for sub-adult and adult Northeastern Pacific white sharks are important for informing effective management policy. Annual survival rates estimate the proportion of the population that will survive, on average, from one year to the next. The complement of survival (i.e., $1 - \text{survival}$) provides an estimate of mortality, or what proportion of the population is lost on average over the course of a year. By developing estimates of annual survival rate for adult white sharks, we will be better positioned to consider how high recruitment likely needs to be for the population to be viable.

It is difficult to estimate vital rates for highly migratory fish that are rarely observed and have few fisheries data. Previously, Smith *et al.* (1998) used a best guess for maximum age to derive natural mortality using Hoenig's (1983) formula to assess fishing pressure on intrinsic growth rates. Cortés (2002) estimated annual survival rates using six life-history methods to assess which demographic trait that population growth (λ) would be most sensitive to. It should be noted that these natural mortality estimates and annual survival rates were based on life-history parameters (i.e., maximum age, age at maturity, and fecundity) that remain unknown or that were estimated with very few data.

When estimating annual survival rate for adults in this population, it is important to consider sex-based differences in annual movement patterns (Domeier & Nasby-Lucas

2008; Jorgensen *et al.* 2010) and in spatial use of the Northeastern Pacific (Domeier, Nasby-Lucas & Palacios 2012; Jorgensen *et al.* 2012a). Males show a very consistent ‘to and fro’ annual migration from coastal aggregation sites at CC. In contrast, females spend more time offshore and have a more expansive range, which includes more southerly locations than those used by males. Further, Klimley (1985) reported that historical catch records from south of Point Conception, CA included mostly adult females, young of the year, and juvenile white sharks. Thus, adult females might be exposed to greater diversity of potential natural and anthropogenic mortality sources. Since 2006, we have identified 199 individual sharks based on their dorsal fins and estimated a sex ratio of 3 males per female based on 172 sharks whose sex was determined. This skewed sex ratio is in keeping with the possibility of lower survival in females but could also be due to sampling artifacts, e.g., females might be less detectable with the methods used to observe sharks (see methods).

In this paper, we use capture-recapture models to estimate annual survival rates for white sharks while accounting for imperfect detection and imperfect sex assignment. We evaluate possible differences in survival rates that might occur between males and females and among years for sub-adult and adult white sharks in the CC population.

Materials and Methods

Study Area and Data Collection

In this study, we focused our sampling effort at known sub-adult and adult white shark aggregations along the CC coast during periods of peak residency from 2006-2011.

Several independent lines of evidence indicate that white sharks are available to be sampled off CC from late summer to winter (August-February) (Klimley 1985; Long *et al.* 1996; McCosker & Lea 2006). White sharks were sampled from three sites off CC: Año Nuevo Island, Southeast Farallon Island, and Tomales Point.

White sharks were observed during natural predation events or were attracted to 4.6-5.9m research vessels using a floating, seal-shaped decoy ~ 1m in length in tandem with a small (2-5 kg) piece of salvaged marine mammal blubber (*Physeter macrocephalus*, *Megaptera novaeangliae*, *Balaenoptera physalus*, *Mirounga angustirostris*, *Phoca vitulina*, or *Zalophus californianus*) tethered to the vessel. The decoy was floated ~10m off the stern of the vessel attached via 36 kg test monofilament to a fishing pole. The decoy served as a visual attractant for the shark to inspect, and the blubber created a localized scent around the research vessel to offset any natural inhibition the shark might have to coming close to the vessel.

White shark dorsal fins are unique to individuals, and the unique features have been shown to last >20 years (Anderson *et al.* 2011). Therefore, in this study, we used the dorsal fin as a 'mark'. High-resolution photographs were taken of the dorsal fin above the surface of the water. If a shark did not surface but could be seen in the water near the vessel, we used an underwater HD video camera to try to collect high-definition still images of the dorsal fin. We attempted to determine sex, using the underwater video camera to determine the presence (male) or absence (female) of claspers located posterior to the pelvic fins. These methods favored sex assignment of males because it was easier to confirm the presence of claspers than to confirm their absence. Any uncertainty in sex

assignment resulted in an individual's sex being unknown until it was determined in a subsequent encounter with the individual. For some sharks, especially those encountered in multiple years, sex was eventually determined. For others, sex was never determined.

Over the course of the study, the set of dorsal fin photos obtained that met the standard described by Chapple *et al.* (2011) were used to develop mark-recapture encounter histories for individuals. Each time we obtained a new fin photo, researchers experienced with matching fin photos checked to see if it matched a previously catalogued fin photo. If there was no match, the fin photo was catalogued as representing a new individual. An individual was considered 'marked' in the field season when it was first identified, and 'recaptured' in each subsequent field season when its dorsal fin was successfully photographed. Our sampling occasions were thus defined as the annual field seasons, which ran from August of year t to February of year $t+1$, and each was referenced by year t (e.g., 2006 season was Aug 2006 - Feb 2007).

Data Analysis

The encounter history for each shark provided information on whether the individual was observed or not on each occasion. In the encounter histories, we also recorded information on what was known about the sex of the individual on each sampling occasion (0 = not seen on given occasion, U = shark seen on given occasion but sex was unknown based on this and all previous sightings, M or F = shark seen on given occasion and sex was unambiguously assigned on this and/or a previous occasion).

To estimate annual survival rate from the mark-recapture data we collected, we needed to adjust for imperfect detection of sharks (Williams, Nichols & Conroy 2002).

This was necessary because after a shark was first encountered a subsequent 0 could occur in the encounter history because the shark either (1) was alive but went undetected by us or (2) died or permanently emigrated from the study area. Typically, mark-recapture data such as these based on resightings of live animals with imperfect detection are analyzed with the Cormack-Jolly-Seber (CJS) (Cormack 1964; Jolly 1965; Seber 1965) approach (Williams, Nichols & Conroy 2002) using Program MARK (White & Burnham 1999). The approach uses encounter histories that indicate whether each animal was detected or not on each occasion. An example history of 011101 would indicate that a shark was seen on occasions 2, 3, 4, and 6 but not on 1 or 5. With this approach an individual's sex would be an individual covariate that could be related to either of the parameters estimated by the CJS model: apparent survival rate (ϕ , the probability of remaining alive from one year to the next and not permanently emigrating) and/or capture probability (p , the probability of resighting a shark already identified in a previous year of the study). This approach has been used successfully in numerous studies (e.g., Lebreton *et al.* 1992). However, when encounter histories include animals of unknown sex, sex-specific estimates can be biased high for known sexes and biased low for animals of unknown sex (Nichols *et al.* 2004). To avoid such biases, we employed a method developed by Nichols *et al.* (2004) designed to estimate ϕ from encounter histories where sex is known for some but not all individuals and sex-specific estimates of ϕ are of interest. Encounter histories used with this approach provide information on when animals were observed or not and what was known about their sex on each of the occasions when they were observed. As an example, the history 0UMM0M provides

information for a shark that was first observed on occasion 2 when insufficient evidence was obtained to verify sex. It was observed again on occasion 3 and determined to be male. Consequently on occasions 4 and 6 when the animal was observed again, sex was automatically assigned regardless of whether claspers were observed on those occasions because sex is a permanent attribute that does not change among occasions.

Model parameters estimated by this approach involve survival and detection as well as additional parameters related to sex ratio and sex assignment. The parameters are defined as:

φ^s_i = probability of apparent survival from occasion i to $i + 1$ for sharks of sex s , where $s \in \{M, F\}$,

p^s_i = probability of capture in period i for sharks of sex s , where $s \in \{M, F\}$,

δ^s_i = probability that sex is determined in period i for a shark of sex s that is captured in period i , where $s \in \{M, F\}$,

π_i = probability that a shark first released in period i is a male.

Because no published studies exist on annual survival rates for the CC population of white sharks, we used an exploratory approach to develop a list of candidate models. For φ and p , we considered models that either held the parameter constant (.) or let it vary by year (t), sex (s), or both (additive [t + s] or interactive [t × s]). We fit models that either let π vary among years (t) or held it constant (.). For δ , we fit models for which the parameter varied by sex (s), time (t), or both (t + s or t × s). We evaluated all-possible combinations of the models for each of the 4 parameters, which resulted in 150 candidate models. Analyses were conducted using the software program LOLASURVIV developed

by Jim Hines (Nichols *et al.* 2004). We used the corrected Akaike's Information Criterion (AICc), for our relatively small effective sample size to evaluate the support from the data for each of the models (Burnham & Anderson 2002). When evaluating model-selection results, we reviewed estimates to identify competing models containing uninformative parameters (Arnold 2010). A Model $\sim 2 \Delta\text{AICc}$ units away from the top model that have one more parameter and essentially the same values of the maximum log-likelihood indicate that the extra parameter is uninformative to an otherwise good model (Burnham & Anderson 2002).

Model Assumptions

For CJS models:

1. Every marked animal present in the population at sampling period i has the same probability p_i of being recaptured.
2. Every marked animal present in the population immediately following i has the same probability of survival (ϕ_i) until $i + 1$.
3. Marks are neither lost or overlooked, and are recorded correctly.
4. Sampling periods are instantaneous (in reality they are very short periods).
5. All emigration from the sampled area is permanent.
6. The fate of each animal with respect to capture and survival probability is independent of the fate of any other animal.

In addition to assumptions above, Method B in Program LOLASURVIV assumes:

7. There is a probability > 0 but < 1 that sex can be unambiguously assigned to a shark via morphology (presence/absence of claspers).

8. All males have homogenous probability of capture. All females have homogenous probability of capture.
9. There is no error in sex assignment.

Our dataset was too sparse to test for goodness-of-fit within LOLASURVIV to test assumptions 1 and 2. Therefore, we evaluated goodness-of-fit using the median \hat{c} approach in Program MARK (White & Burnham 1999) for 3 different versions of our dataset. In the first 2 versions, unknowns were considered to be 1) all females (φ and p were sex specific in the model evaluated) or 2) all males (φ and p were sex specific in the model evaluated). In the 3rd version of the dataset, unknowns, males, and females were pooled and φ and p were held constant for all individuals in the model evaluated.

Though Chapple et al. (2011) did not find evidence of temporary emigration using electronic tags during their shorter study period, our longer time series showed evidence that some adult females temporarily emigrated from the study area, whereas males demonstrated strong annual site fidelity. When temporary emigration (TE) is non-random (Markovian) with respect to an animal's current emigration status, animals have a different probability of being a temporary emigrant in year $t+1$ depending on whether they are a temporary emigrant in year t or not, and CJS estimates of φ can be biased (Kendall, Nichols & Hines 1997). However, if TE is completely random with respect to an animal's current emigration status, φ remains unbiased (Schaub *et al.* 2004; Rotella 2009). To test for evidence of whether TE for adult females in our data might have been random or Markovian (Schaub *et al.* 2004), we used Test 2.CT in Program U-CARE

(Choquet *et al.* 2009) and ran two tests based on data for: 1) all known adult (>4.5m) females and 2) all known females (>2.4m).

Results

From 2006-2011, we spent a total of 1,897 hours over 404 days at three CC locations collecting a total of 668 high-quality fin ID's that allowed us to identify 199 different individual white sharks. The ratio of known males to females was heavily skewed (3.0:1 respectively), and 13.6% of the individuals were of unknown sex (129 M; 43 F; 27 U). Total length averaged 4.1 m (SD = 0.7 m, range = 2.4 to 5.5 m) for the 187 sharks whose length could be estimated.

Using the median \hat{c} approach, a program in Program MARK, the three models we ran produced estimates of median $\hat{c} < 1.19$. Based on this, we were not concerned about overdispersion in our data, and used AICc to evaluate the support from the data for the competing models considered. We found no evidence to suggest that TE by females was Markovian. In our test for randomness (Test2.CT in U-CARE), we found insufficient evidence in our dataset to reject the null hypothesis that TE in females was random, (two-sided p-values >0.48). Based on this, we concluded that modeling in LOLASURVIV was appropriate.

In the best-supported model, ϕ was the same for male and female sharks and constant across all years, p differed by sex but not by year, π was held constant, and δ differed by sex and by year (additive form, sex+t). Among those models containing no uninformative parameters, no other model was well supported by the data (Δ AICc values

>4.47 for all other models). In the top model, ϕ for males and females was estimated as 0.90 (95% CI = 0.81 – 0.98). The best-supported model estimated p as 0.41 (95% CI = 0.30 – 0.52) for males and 0.19 (95% CI = 0.06 – 0.33) for females. Estimates of δ were higher for males than females and tended to increase as the study progressed, especially for females (Fig. 1).

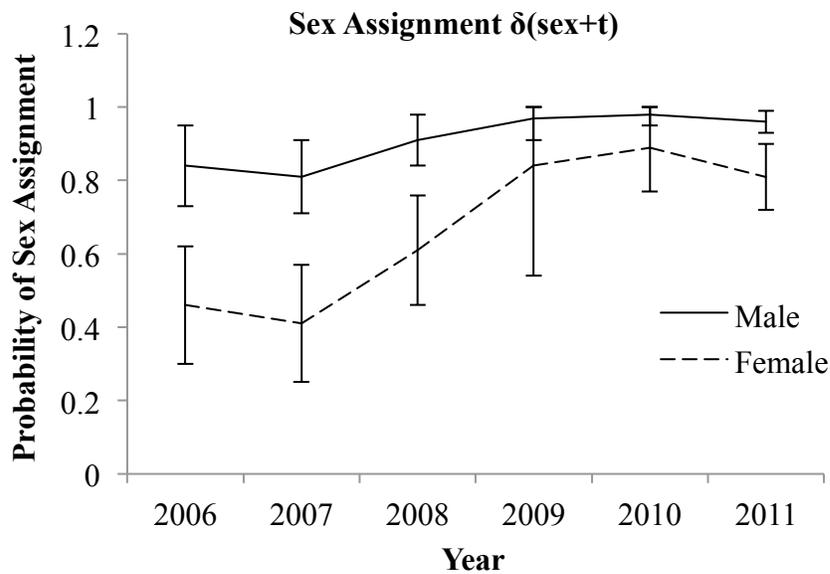


Figure 1. This graph represents sex-based probabilities (with their associated SE) of unambiguously assigning sex to an unsexed shark for a given sampling occasion (year).

The sex ratio of the sample of sharks for which we obtained fin-ID photos, was skewed in favor of males with π estimated as 0.68 (95% CI = 0.57 – 0.78), which is lower than the naïve sex ratio estimate of 0.75 (129 males of 172 sharks with sex assigned) obtained from the raw data that ignores the possibility that females might be harder to assign sex to and be more likely to be of unknown sex.

Models in which φ differed for males and females were not well supported. In the best-supported version of such models, the coefficient that distinguished between φ for males and females was deemed a redundant parameter (Table 1): the sex-specific survival rates were very similar to each other and the respective confidence intervals overlapped one another to a high degree. This model estimated φ as 0.93 (SE = 0.21, 95% CI: 0.53 – 1.00) for females and 0.89 (SE = 0.05, 95% CI: 0.79 – 0.98) for males. Time variant models for φ were also poorly supported ($\Delta\text{AICc} > 7.12$): in the best-supported version, estimates of φ ranged from 0.82 (SE = 0.13) to 1.0 (SE = 0.22).

Table 1. Model selection results for models representing hypotheses about sex-based differences in survival. Selection is based on lowest ΔAICc scores. Only the top 3 models whose $\Delta\text{AICc} < 5.00$ are presented. K represents the number of parameters. w_i represents the relative weight of evidence for each model.

Model	K	AICc	ΔAICc	w_i
$\varphi(.) p(\text{sex}) \pi(.) \delta(\text{sex}+t)$	11	401.70	0.00	0.90
$\varphi(\text{sex}) p(\text{sex}) \pi(.) \delta(\text{sex}+t)^*$	12	403.71	2.01	-
$\varphi(.) p(\text{sex}+t) \pi(.) \delta(\text{sex}+t)$	15	406.17	4.47	0.10

* Redundant model as defined by Burnham & Anderson (2002)

Discussion

White sharks take a long time (at least 10 years) to reach sexual maturity, and females produce few young (7-12 pups) after a long gestation (at least a year) (Francis 1996; Pratt 1996). Therefore, survival rates for sexually mature white sharks need to be high if the population is to persist. Based on data collected from 2006-2011 from 199 different sub-adult and adult male and female white sharks, we estimated that annual apparent survival (φ) was 0.90 (95% CI: 0.81 – 0.98) for males and females during the

study period. This estimate is close to, but higher than, the value of 0.87 reported by Smith *et al.* (1998) and in the upper range of 0.81 to 0.92 used by Cortés (2002). Given our estimate, annual recruitment of new individuals into the sub-adult class of white sharks would need to exceed ≥ 0.10 (95% CI: 0.02 – 0.19) to account for annual mortality. However, at present, details of the recruitment process and recruitment rates for white sharks are unknown.

We can speculate as to possible causes of mortality for sub-adult and adult white sharks. However, documenting actual mortality and its causes of death is extremely difficult because specimens are seldom obtained as white sharks are negatively buoyant and sink when they die. Mortality could come from intraspecific aggression, wounds inflicted by marine mammal prey, attacks by Orcas (*Orcinus orca*), or from human-induced mortality. We have observed grievous wounds (especially in the gill region) on both sexes of white sharks, and based on their appearance, the wounds were apparently inflicted by other white sharks. It is reasonable to infer that some sharks are not able to survive severe intraspecific interactions, but the nature and importance of such interactions are poorly understood. When white sharks reach ~ 2.4m an ontogenetic shift in diet from fishes, rays, and squids to pinnipeds takes place to supply the physiological demands of large endotherms (Carlisle *et al.* 2012). Morphological changes in dentition (broad and deeply serrated teeth for shearing) occur that make the teeth effective in tearing large portions of flesh and fat from marine mammal prey as well as whale carcasses (Long & Jones 1996). However, the marine mammals that constitute their primary prey (*Mirounga angustirostris*, *Zalophus californianus*, *Phoca vitulina*) are

capable of defending themselves with their claws and teeth. We have seen numerous wounds inflicted by these prey on the heads of white sharks. It is possible these interactions could result in the loss of an eye that we speculate could lead to eventual death, as white sharks rely on their vision to ambush their prey. Orcas have been observed preying on white sharks (Pyle *et al.* 1999), but this type of interspecific interaction is very poorly understood. Thus, it is unclear as to what extent orca predation can have on a white shark population. Sharks in the CC population cannot be legally harvested, and poaching of sub-adult and adult white sharks is considered to be rare. However, it is impossible for authorities to rigorously enforce regulations over the entire range of white sharks, and mortality due to illegal harvest is possible.

The estimated sex ratio of our sample population is 2.1 males per females after sharks of unknown sex were probabilistically assigned to sex. This is somewhat more even than the observed sex ratio of 3 known males for each known female in our raw dataset. We do not know why the sex ratio is skewed but can speculate on possible reasons. One possible explanation is that on an annual basis, we detect a lower proportion of the females in the CC population (compared to males) because females, perhaps as part of their reproductive strategy, are more likely on an annual basis to be temporary emigrants, i.e., stay outside of our study area during some field seasons. Another possibility is that the skewed sex ratio is an artifact of our sampling methods. The locations and the time of year we sample could be favoring higher detection for males. A large portion of the females in this population could also be aggregating at locations unknown to us, making them impossible to observe at our sample area. Females could

also be spending less time, on any given occasion, in our sample area making it more difficult to observe them. There is also the possibility that there are less sub-adult and adult females in this population and a sex-based mortality occurs at an earlier life stage. We have identified and unambiguously assigned sex to only 43 females in six years. Twenty-four of these females are estimated to be sexually mature ($>4.5\text{m}$). Given this low number and the high reproductive value they have in the CC population, it will be important to further study how well the number detected represents the actual number in the population and, if the true abundance is low, to consider why the number is so low and how to best manage the population in light of such low numbers.

Survival estimates for sub-adult and adult white sharks at Guadalupe Island, Mexico, based on CJS models, also found no evidence for a difference in survival between sexes, but estimated ϕ did vary among years (Sosa-Nishizaki *et al.* 2012). Their estimate was based on mark-recapture data from 113 individuals (67 males, 56 females) over a nine-year study period. During this time, ϕ ranged from 0.80 to 0.99 (mean = 0.94), which is similar to our estimate of 0.90 for the CC population. Identified white sharks in the Mexico population also had a skewed sex ratio (1.5 males per female) (Nasby-Lucas & Domeier 2012). It should be noted that in the sample population of the Mexico study, a different type of natural marks was used to identify individuals (Domeier & Nasby-Lucas 2007). They used natural pigment patterns on 6 regions of the body (3 on each side of the body) as marks that could be used in combination to identify individuals. Sharks that have <6 regions photographically recorded were considered ‘orphans’ and not used for analyzing survival unless observations were obtained for all 6 regions at some

later date (Nasby-Lucas & Domeier 2012). It is unknown to what extent, if any, this method of censoring versus including records of encounters might have biased survival estimates, but it seems likely that the censoring of those animals that were seen fewer times could have biased survival estimates high if the reason for fewer sightings was related to death of animals.

Despite equivalent estimates of ϕ , males and females had a significant difference in estimated capture probabilities (p). In our study, p was lower for males (0.41, 95% CI = 0.30 – 0.52), than for females (0.19, 95% CI = 0.06 – 0.33). Temporary emigration by females is likely responsible for some of the difference given that capture probability is zero for females in years when they do not visit the study area during our sampling season. It is also possible that females might behave differently than males and simply be harder to detect with our methods. The extent to which these factors cause the discrepancy is unknown at this time.

In conclusion, it is clear that further research is needed to investigate the implications of a survival rate of 0.90 for a relatively small population of sub-adult and adults for the dynamics and likely future status of the CC white shark population. In particular, research is needed to evaluate whether recruitment in the population is adequate to replace sub-adult and adult white sharks that are lost to mortality and/or permanent emigration in this population. Currently, there is no information on vital rates for white sharks <2.4m. However, young of the year and juveniles are incidentally caught south of Point Conception, CA by gill net fisheries (Lowe *et al.* 2012) and recreational anglers. Since nothing is known about vital rates for this demographic, it is currently

difficult to assess the impact these fisheries have on sub-adult recruitment. Information on the recruitment process and vital rates for juveniles are lacking but required if we are to be able to discern whether recruitment is adequate to offset mortality for CC white sharks. Further refinements of estimates for adult survival would also be valuable. If data can be accumulated for more sharks in more years, it might be possible to consider sources of variation in survival among individuals (e.g., due to size, a factor that could not be investigated here due to lack of data but that might influence survival) and years (e.g., environmental conditions might cause survival to vary at detectable levels if data are collected over important gradients of key conditions). The use of natural marks and improved methods for data collection used here along with other improved electronic technologies for monitoring animals in marine environments (Block *et al.* 2011) should allow for important advances in the understanding of the population dynamics of this species.

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