

VITAL RATES, ANNUAL ABUNDANCE, AND MOVEMENT OF WHITE SHARKS IN
THE NORTHEASTERN PACIFIC.

by

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of

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in

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ABSTRACT

Reliable estimates of populations' vital rates and abundance are fundamental requirements for making assessments and informed management decisions regarding any species. For large marine fish species whose movements are extensive throughout ocean basins, data for individuals are difficult to acquire. Without empirical data, large assumptions must be made about a species' vital rates (i.e. survival and fecundity) to make population assessments, which can potentially lead to erroneous results. Using mark-recapture and acoustic-telemetry data, I conducted analyses estimating vital rates, annual abundance, and coastal movement for white sharks (*Carcharodon carcharias*) off California, US. First, I used a novel approach to estimate size-specific annual apparent survival rates and to test for differences in survival between sexes after accounting for imperfect sex assignment. Our results provide little evidence for differences in sex-specific survival rates. However, I estimated the first size-specific annual apparent survival rates for sub-adult and adult white sharks. Second, I estimated annual abundance for four white shark demographic groups off the coast of California over an eight-year study period. The estimated total annual population of sub-adult and adult white sharks increased from 180 to 266 individuals during the study. Additionally, group-specific population growth rate point estimates were all > 1.00 , which indicates that all groups had positive annual positive growth during the study period, although, uncertainty around those estimates were greater for sub-adults than adults and does not rule out other possibilities for population trajectories. Finally, through collaboration between Mexico and the US, I was able to analyze a comprehensive acoustic telemetry dataset that explored connectivity between two main aggregation sites that form the northeastern Pacific population of white sharks. I found that movement between the two regions was rare and more probable to be sub-adult sharks. These analyses underscore the value of collecting and analyzing empirical data to develop reliable estimates of vital rates for a top marine predator. The work also illustrates the ongoing need to cultivate international research collaboration to include data from both the US and Mexico to make accurate population inferences for the northeastern Pacific population of white sharks.

CHAPTER ONE

INTRODUCTION TO DISSERTATION

Shark populations are highly susceptible to overfishing or exploitation due to life history patterns characterized by slow growth, late sexual maturity, long gestation periods, low fecundity, and long lives (Cortés 2000). Shark populations have experienced severe declines in many of the world's oceans (Worm et al. 2006; Baum and Worm 2009; Myers et al. 2007) leading to negative impacts on ecosystems (Ferretti et al. 2010; Stevens et al. 2000). However, the capacity to acquire the information needed to make informed management decisions on species that are inherently difficult to observe remains a fundamental challenge for cryptic or elusive species. For marine top predators that exist in low abundance, have a expansive home ranges, and lack traditional fisheries catch data, it can be difficult to obtain adequate data needed to assess the status for these populations.

Advancements in tagging technologies have allowed researchers to identify predictable temporal aggregations enabling efficient sampling schemes (Block et al. 2011; Block et al. 1998). By combining empirical data collected using advanced tagging technologies and analyses recently developed for data on marked individuals, long-term mark-recapture studies can provide estimates of critical population parameters that are needed for determining population status (Williams, Nichols, and Conroy 2002).

White sharks (*Carcharodon carcharias*) are listed as 'Vulnerable' under the International Union for Conservation of Nature (IUCN 2019) as limited data provide

some evidence of a decreasing global population of adults, albeit with great uncertainty (Rigby et al. 2019). The population of white sharks in California is genetically distinct (Jorgensen et al. 2010) from other populations around world such as those in South Africa, Australia-New Zealand, western Atlantic, Japan, Mediterranean Sea (Pardini et al. 2000; Tanaka et al. 2011; Blower et al. 2012; O’Leary et al. 2015; Gubili et al. 2010). White sharks in the northeast Pacific were once thought to be exclusively neritic (Klimley 1985), however tagging technologies have revealed that white sharks migrate great distances offshore (Bonfil et al. 2005). Additional tagging studies have shown that white sharks have high fidelity to coastal aggregation sites along the western coast of North America; central California, USA, and Guadalupe Island, Mexico (Weng et al. 2007; Jorgensen et al. 2010; Domeier and Nasby-Lucas 2008). These two metapopulations are thought to comprise the entire northeastern Pacific population of sub-adult and adult white sharks. Predictable migratory patterns have been observed for both aggregation sites, where sub-adult and adult white sharks arrive to the coast around July/August where they occupy waters around pinniped rookeries until around February/March (Domeier and Nasby-Lucas 2007; Domeier and Nasby-Lucas 2008; Jorgensen et al. 2010; Hoyos-Padilla et al. 2016). After this coastal phase, sub-adult and adult white sharks from central California and Guadalupe Island return to a focal area, a sub-tropical gyre in the Pacific, located ~1500 km west of Baja, Mexico called ‘The White Shark Café’ (Jorgensen et al. 2010). This predictable coastal residency allows researchers to focus sampling efforts at white shark aggregation sites during the time of year when white sharks are present.

Population characteristics, such as vital rates and abundance for populations of animals can be estimated using mark-recapture techniques when researchers can identify individuals or ‘mark’ animals over time (Williams, Nichols, and Conroy 2002). White sharks can be identified by unique notches on the trailing edge of their first dorsal fin, and those features can last >26 years (Anderson et al. 2011). The ability to identify individuals in tandem with knowledge of coastal aggregation presence off California has led to important insights into the abundance (Chapple et al. 2011) and sex-specific vital rates for this population (Kanive et al. 2015).

This dissertation expands our knowledge on sex- and size-specific vital rates, abundance, and population growth rates for sub-adults and adult white sharks off in the northeastern Pacific. A previous mark-recapture study provided the first abundance estimate for sub-adult and adult white sharks in California and estimated the population size as 219 individuals (95% credible intervals, 130 to 275) based on a closed-population (no immigration, emigration, recruitment, or mortality) mark-recapture model that analyzed data from three years of sampling (Chapple et al. 2011). That study provided a baseline reference of abundance for sub-adult and adult white sharks. Additionally, Chapple et al. (2011) established that a mark-recapture dataset was a viable method of estimating population parameters for white sharks. However, the closed-population assumption used in the modeling prevented estimation of survival rates. In a subsequent study, the first empirical estimates of sex-specific apparent survival rates for white shark

were estimated using data from additional years of data establish (Kanive et al. 2015).

This dissertation seeks to further what has been learned in those earlier efforts. In particular, the work presented here focuses on three topics. First, I use a 9-year mark-recapture dataset to implement a method to estimate sex- and size-specific apparent survival rates after accounting for imperfect sex assignment (chapter 2). The estimates that result from that work are the first empirical size-specific estimates for white sharks that reflect a more biologically realistic annual survival rate disparity among wide ranging age-classes. Those estimates update and inform existing demographic-assessment models that oversimplify and underestimate mortality in smaller, sub-adult age classes. In chapter 3, I use an 8-year mark-recapture dataset to construct Jolly-Seber (Jolly 1965; Seber 1965) open-population mark-recapture models using the POPAN (Schwarz and Arnason 1996) formulation in Program MARK (White and Burnham 1999) to estimate annual abundance for four demographic groups of white sharks; sub-adult and adult males and females. From these estimates, I investigate potential changes in population growth rates for each group over the study period. Finally, in chapter 4 I use a comprehensive dataset from an international collaboration to examine sex- and maturity-specific annual movement rates between the two metapopulations, central California and Guadalupe Island, Mexico. An analysis of these movement data quantify connectivity between these two sites and underscores the need for collective collaboration with a unifying methodology of identifying (‘marking’) white sharks to create robust datasets to estimate the overall northeastern Pacific population of sub-adult and adult white sharks.

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CHAPTER TWO

SIZE-SPECIFIC APPARENT SURVIVAL RATE ESTIMATES OF WHITE SHARKS USING MARK-RECAPTURE MODELS

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Abstract

For species that exist at low abundance or are otherwise difficult to study, it is challenging to estimate vital rates such as survival and fecundity and common to assume that survival rates are constant across ages and sexes. Population assessments based on overly simplistic vital rates can lead to erroneous conclusions. We estimated sex and length-based annual apparent survival rates for white sharks (*Carcharodon carcharias*). We found evidence that annual apparent survival differed over ontogeny in a system with competitive foraging aggregations, from 0.63 (SE = 0.08) for newly recruiting sub-adults to 0.95 (SE = 0.02) for the largest sharks. Our results reveal a potential challenge to ontogenetic recruitment in a long-lived, highly mobile top marine predator, as survival rates for sub-adult white sharks may be lower than previously assumed. Alternatively, younger and competitively inferior individuals may be forced to permanently emigrate from primary foraging sites. This study provides new methodology for estimating apparent survival as a function of diverse covariates by capture-recapture study including when sex assignment is uncertain.

Keywords: sex ratio; imperfect sex assignment; mark-recapture; survival rate; white shark

Introduction

Effective assessment of population viability and temporal variability in abundance depends on accurate estimation of population vital rates (i.e. survival and reproductive rates) and variation in these vital rates by class or age. In long-lived animals, for instance, survival rates of adults and animals about to recruit to the breeding class typically exert strong influence on population status and growth due to their disproportionately high reproductive potential (Caswell 2014). To assess population persistence via life history matrix models, the survival schedule (survival rate as a function of age of the animal) and information on age-specific fecundity are needed. However, obtaining the data required to estimate these rates can be extremely difficult depending on the species, and especially so with top predators, which typically exist at low abundance and are highly mobile (e.g., in marine systems).

Due to the challenges of evaluating status of populations with sparse or non-existent data, survival rates are sometimes calculated as a single value across all classes based on life-history metrics such as longevity or life span (Hoenig 1983). However, longevity is rarely known and often derived from empirical or estimated values in other species within the taxon. Additionally, ignoring variation in age or stage specific survival rates can overestimate population growth rates, underestimate extinction risk, especially for small populations, and lead to erroneous conclusions about a species' population status (Case 2000; Caswell 2014; Mills 2012). When feasible, it is important to consider age or stage-based survival rates to more realistically represent the population characteristics of the species.

Given the paucity of empirical data for most shark species, longevity-derived constant survival estimates are common in population assessments of shark species (Smith et al. 1998; Cortés 2002; Mollet and Cailliet 2002), even though longevity remains unknown for most species. Determining longevity in turn depends on the accuracy of age/growth studies which might present significant error of longevity estimates (Cailliet et al. 1985). Age underestimation is a recurring bias in concentric vertebral growth-ring aging of sharks and rays, even in studies that included carbon date validation (Harry 2017). Additionally, even when maximum lifespan is known, it has been shown to be a poor statistic to estimate annual survival (Krementz, Sauer, and Nichols 1989).

The white shark, (*Carcharodon carcharias*), is a highly mobile top predator that has extensive oceanic ranges but predictable temporal patterns of coastal residency revealed by electronic tagging studies (Boustany et al. 2002; Bonfil et al. 2005; Weng et al. 2007; Domeier and Nasby-Lucas 2008; Jorgensen et al. 2010). Genetically distinct populations have been identified in the Northeastern Pacific (NEP), Northwestern Pacific, Australia-New Zealand, Atlantic, South Africa, and Mediterranean (Pardini et al. 2000; Jorgensen et al. 2010; Gubili et al. 2010, 2012; Tanaka et al. 2011; O’Leary et al. 2015). Individual identification using distinguishable notches on the trailing edge of dorsal fins has proven stable for time periods > 26 years (Anderson et al. 2011). These patterns have facilitated long-term mark-recapture studies to estimate region-specific population parameters such as abundance (Chapple et al. 2011; Towner et al. 2013; Andreotti et al. 2016), temporary emigration (Chapple et al. 2016) and apparent survival (Kanive et al.

2015). However, in the absence of age/stage specific population parameters, a single survival value across all ages has been inferred from maximum lifespan and applied in population assessments (Burgess et al. 2014), potentially masking important ecological and demographic effects on fitness.

In California, small immature white sharks undergo an ontogenetic transition from warmer waters south of Point Conception, CA to colder more productive waters in central California habitat (Weng et al. 2007). This transition includes a shift in diet, habitat, and dentition morphology when they reach ~ 250 cm (Tricas and McCosker 1984; Hubbell 1996). The transition is from a nursery habitat with reduced predation/competition from adults (Klimley 1985), to a habitat where competition is likely intense from established and substantially larger adult conspecifics occurring in relatively dense aggregations around pinniped rookeries in central California (Jorgensen et al. 2010). Serious and potentially fatal wounds inflicted on smaller sharks by conspecifics are regularly observed. The hunting strategy for new recruits also shifts in this stage from a relatively benign acquisition of teleosts, elasmobranchs, and cephalopods (Klimley 1994) to a potentially perilous activity of hunting highly maneuverable pinnipeds that defend themselves with teeth and claws. As they approach maturity, white sharks in the NEP make their first offshore annual migrations (Domeier 2012; Hoyos-Padilla et al. 2016) to the oligotrophic waters of the North Pacific which, given their smaller size, inexperience, and potentially smaller energetic reserves (Raye et al. 2013), might also expose them to greater mortality risk.

Sexual segregation is widespread among vertebrate taxa including sharks (Ruckstuhl and Neuhaus 2005; Wearmouth and Sims 2008; Mucientes et al. 2009; Wearmouth and Sims 2010). For white sharks, sexual segregation appears to be consistently detected at study sites worldwide (Bruce 1992; Robbins 2007; Domeier and Nasby-Lucas 2012; Kock et al. 2013; Kanive et al. 2015). In the NEP, sex-specific temporal use of aggregation sites has been observed (Anderson and Pyle 2003; Domeier and Nasby-Lucas 2012) which may be linked to female reproductive behavior and the extended (> 1 year) gestation period in white sharks (Francis 1996). Chapple et al. (2016) reported that annual temporary emigration is more prevalent for females (0.57, 95% C.I. = 0.40 – 0.72) than males (0.015, 95% C.I. = 0.00 – 0.31). This sex-specific unavailability for sampling occasions can inherently bias the observed sex ratio over a long study period and needs to be considered when conducting population dynamic studies (Bruce and Bradford 2015).

Initial empirical survival rate estimation for sub-adult and adult white shark in central California used mark-recapture techniques based on individual fin photo identification (Kanive et al. 2015). After accounting for imperfect sex assignment within the model framework using a software program LOLASURVIV (<https://www.mbr-pwrc.usgs.gov/software/lolasurviv.shtml>), a time invariant annual apparent survival rate of 0.90 (SE = 0.04) resulted and did not vary by sex (Kanive et al. 2015). In that study, the annual apparent survival rate was applied to individuals of all lengths in the sample (240 – 550 cm) and underscored the need to add methodological functionality to the LOLASURVIV software (Nichols et al. 2004) which could account for relevant survival

covariates such as length or maturity. This new capacity within LOLASURVIV addresses the need for increased ability to assess survival across age classes and enables sex-specific length/stage based apparent survival estimates for species where it is not possible to obtain sex assignment for every individual on every sampling occasion. This framework can be further applied to many species of interest where a potential length effect on survival rates exist and is particularly relevant in systems where sex assignment is challenging.

Apparent survival rate estimates cannot distinguish mortality from permanent emigration (animal is still alive but has permanently left the study area), therefore true survival rates can be higher if fidelity is low (Cormack 1964; Jolly 1965; Seber 1965). However, if fidelity is high, then apparent survival rates are comparable to true survival. Furthermore, sampled populations of animals can contain animals considered to be ‘residents’ that predictably use the study area in multiple years and ‘transients’ that can initially be detected via sampling methods when passing through the sample area but undetected in subsequent years because they are outside of the study area (Pradel et al. 1997). If not treated properly, transiency can negatively bias survival estimates (Pradel et al. 1997). Differences in apparent survival rate estimates across size classes can therefore be representative of actual underlying annual survival but might also result in whole or in part from size-based differences in permanent emigration or transience.

To better understand the survival schedule and demographic ecology of white sharks, we used a nine-year dataset in a mark-recapture framework to test for evidence of a relationship between total body length (TL) and apparent survival rate. From these data,

we could develop size-based survival rate estimates for sub-adult and adult white sharks and explore sex-specific differences in survival and capture probabilities with incomplete sex assignment of individuals within the sample population. This approach of including a total length covariate expands upon the method described by Nichols et al. (2004) and can be applied to species where differential survival rates are of interest at different life stages or ages.

Methods

Data Collection

Our sampling effort was conducted at known sub-adult and adult white shark aggregations along the central California, USA coast (Año Nuevo, Southeast Farallon Islands, and Tomales Point; Fig.1) during periods of peak residency (August-February) from 2006-2014. Due to the relatively close proximity of these aggregation sites and previous studies showing that individual sharks use multiple sites during the sampling season (Jorgensen et al. 2010), we have pooled the data collected at all sites. We used natural patterns on the dorsal fins to distinguish individuals and develop annual mark-recapture records. See Chapple et al. (2011) for description of shark-attraction and photo-identification methods. Sex was determined by confirmation of the absence (female) or presence (male) of claspers using underwater video. It was more difficult to unambiguously assign sex to females, as the confirmation of a lack of claspers was more difficult than confirmation of the presence of claspers. Consequently, sex was not always confirmed when a shark was sighted and identified by its fin characteristics. Thus, we used models that allowed for unknown-sex individuals. For total body length, we used

the mean of visually estimated lengths obtained by at least two experienced researchers as the shark swam alongside a research vessel of known length.

Data Analysis

The encounter history for each shark provided information on whether the individual was observed or not on each sampling occasion (August-February). 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 unknown based on this and all previous sightings; M or F = shark seen on given occasion and sex unambiguously assigned on this and/or a previous occasion).

Typically, mark-recapture data such as these, which are based on a time-series of re-sightings of live animals with imperfect detection, are analyzed with the Cormack-Jolly-Seber (Cormack 1964; Jolly 1965; Seber 1965; Williams, Nichols, and Conroy 2002) approach to produce estimates of apparent survival rate (ϕ) and detection rate (p). However, when encounter histories include animals of unknown sex, sex-specific estimates can be biased high for animals of known sex 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) to estimate ϕ from encounter histories where sex is known for some but not all individuals and where sex-specific estimates of ϕ are of interest. Additionally, we extended the model to allow an individual's body length to be a continuous covariate related to ϕ .

Model parameters estimated by this approach involve survival and detection as well as additional parameters related to sex ratio and sex assignment (Nichols et al. 2004).

The parameters are defined as:

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

p^s_i = probability that a previously identified shark of sex s was sighted and identified during sampling efforts in year i , where $s \in \{M, F\}$,

δ^s_i = probability that sex was determined when a shark of sex s was sighted and identified during sampling efforts in year i , where $s \in \{M, F\}$,

π_i = probability that a shark first sighted in year i was a male.

In order to be efficient in model testing, we used the most appropriate model suite determined by Kanive et al., with the addition of a test of whether total body length (TL) and survival rate were related over the nine-year dataset. For ϕ , five model structures were considered in which ϕ was held constant (.) or allowed to depend on sex (sex), length (TL), or both (models with additive [sex + TL] and interactive effects [sex * TL] of sex and length on ϕ were each evaluated). We employed competing models of p that allowed p to depend on sex (sex), length (TL), or both (models with additive [sex + TL] and interactive effects [sex * TL] of sex and length on p were each evaluated). We allowed π to be either constant (.) or time varying (t). The parameter δ was only considered to be additive (sex+t), as this model had the highest support from Kanive et al. (2015). These possible combinations led to a total of 13 models in our suite (Table S1). We used Akaike's Information Criterion adjusted for sample size (AICc) to evaluate the

support from the data for each of the competing models that we considered (Burnham and Anderson 2002).

Analyses were conducted using the software program LOLASURVIV (Nichols et al. 2004) and extended for the work presented here to include a continuous individual covariate (TL). The data were too sparse to be tested for goodness-of-fit using the Chi-square test available in LOLASURVIV. Therefore we repeated the methods used in Kanive et al. (2015) to evaluate goodness-of-fit using program MARK (White and Burnham 1999), which offers an alternative approach to what is available in LOLASURVIV. We used the median $\hat{c}$ approach that uses simulation to evaluate overdispersion, informing us of potential issues with goodness-of-fit due to lack of independence or missing covariates.

Program MARK does not accommodate uncertainty in sex assignment and the median $\hat{c}$ approach does not incorporate continuous covariates (i.e. TL), so we evaluated three different versions of sex assignment, which represent the range of possible conditions that exist with unknown sex animals and sex-specific parameters. In the first version, all unknown animals were considered to be male (φ and p were sex specific in the model evaluated). In the second version, all unknown animals were considered to be female (φ and p were sex specific in the model evaluated). Finally, the third version all animals were pooled and φ and p were held constant in the model evaluated. We assumed that if potential overdispersion exists within our data, it would be identified by one of the three approaches.

To test for transients within our dataset, we used the *ad hoc* approach described by Pradel et al. (1997). Specifically, we omitted the first marking occasion for each individual and compared estimates from this subset of data to those obtained from the full dataset. For our nine years of data, the full dataset yielded estimates of survival for eight years, whereas the left-truncated subset of data yielded estimates for seven. For those seven years the two datasets shared in common, we tested for significant differences between survival estimates using Program CONTRAST (<https://www.mbr-pwrc.usgs.gov/software/contrast.html>) (Hines and Sauer 1989).

Results

From 2006 to 2014, we spent 3,194 hours over 696 days attracting white sharks to our boats for observation at three known aggregation sites off the coast of central California (Southeast Farallon Island, 131 days, 652 hrs; Año Nuevo Island, 70 days, 321 hrs; Tomales Point, 495 days, 2,221 hrs). A total of 291 individuals were identified by natural dorsal-fin marks that we identified from 1,187 high-quality photos of fins obtained over the nine-year study period. The observed sex ratio for those sharks that we were able to unambiguously assign sex was heavily skewed towards males; 187 males: 84 females (2.23: 1). In total, 20 (6.9%) sharks remained unsexed throughout the study. The mean estimated TL was 399 cm (sd = 73.73 cm) and the estimated TL of observed sharks ranged from 240 - 550 cm.

Results from the median $\hat{c}$ procedure that tested for overdispersion in the data was low (≤ 1.12) for all three scenarios tested. Therefore, support from the data for competing models was evaluated using AICc.

There was no support for the occurrence of transient individuals in the sample. No significant difference was found in ϕ estimation when comparing the full and truncated dataset after removing all first observations (p-values ≥ 0.16) indicating a very low probability of transient behavior negatively biasing our estimates of ϕ (Table S2).

Of the 13 models considered (Table S1), two received support from the data ($\Delta\text{AICc} \leq 1.12$); all others had $\Delta\text{AICc} > 3.24$ (Table 1), although estimates of ϕ were similar to estimates in the top two models. In the top two models, identical model structures were used for estimating p , π , and δ . In the best-supported model, ϕ was positively related to body length but did not support any relationship to sex or time effects (Fig. 2). Estimates indicated strong levels of variation in ϕ across the range of observed shark body lengths: $\hat{\phi}$ increased from 0.63 (95% C.I. = 0.47 – 0.77) for a 240-cm shark to 0.95 (95% C.I. = 0.90 – 0.97) for a 550-cm shark. In the second-best model, $\hat{\phi}$ was related to both sex and body length (additive effects): point estimates from the model indicate that $\hat{\phi}$ is higher for females than males. However, the imprecision of estimates from this model, especially those for females prevent us from making strong inferences about sex-specific differences. For example, $\hat{\phi}$ for a shark of average length (398 cm) was estimated as 0.91 (95% CI = 0.73 to 0.97) for a female and 0.84 (95% CI = 0.79 to 0.88) for a male (Fig. S1). In conclusion, there is strong support in the models for

length-based apparent survival estimates in this study, but our estimates lack the precision to indicate whether there are sex-based differences.

In our top model, $\hat{p}$ was higher for males (0.45, SE=0.03) than for females (0.22, SE=0.03). The top model estimated π as being constant through the study at a value of 0.67 (SE = 0.03), which indicated that our sample of observed sharks had two males for every female after sharks of unknown sex were probabilistically assigned to sex based on the data. The model structure for δ contained additive effects of sex and year. The estimates indicate an increasing probability of unambiguous sex determination by researchers over time.

Discussion

We found strong evidence that apparent survival (hereafter called survival) rates were positively associated with increasing total body length but did not substantially differ between sexes for sub-adult and adult white sharks off California. This finding indicates that survival rates may be quite variable among size classes in the study population and that future assessments of the population's viability or abundance should include length-based survival estimates.

Our annual survival rate estimates presented herein contribute to a better understanding of what the annual survival rate is for the more vulnerable smaller size classes of the NEP population. Some studies have reported that population growth rate for white sharks is most sensitive to the survival rates of immature individuals (Cortés 2002), though most population assessments for NEP white sharks have assumed a

constant survival rate across size classes (Dewar et al. 2013; Burgess et al. 2014); potentially leading to erroneous population assessment results and conclusions. Additionally, this sensitivity analysis was based on the assumption that longevity is only 15 years, which recent studies have suggested may be longer (Hamady et al. 2014; Andrews and Kerr 2014; Natanson and Skomal 2015; Christiansen et al. 2016). Other studies have shown population growth rate for long-lived animals to be most sensitive to adult survival (Heppell et al. 2000; Sæther and Bakke 2000), so revisions of white shark longevity estimates could potentially change the conclusions of population growth rate sensitivity in the Cortés (2000) study. The results from this study in combination with recent work showing annual survival of 0.63 in the first years of life (Benson et al. 2018) can better inform future assessments of NEP white shark population abundance and persistence.

More generally, mark-recapture using natural and unique markings is used extensively to estimate important population parameters such as abundance, survival, recruitment, and population growth rates (Williams et al. 2002). Increasingly, computer-aided pattern recognition techniques applied to digital imagery have enabled researchers to apply mark-recapture techniques to a growing number of species such as polar bears (*Ursus maritimus* - Anderson et al. 2010), African penguins (*Spheniscus demersus* - Sherley et al. 2010), cheetahs (*Acinonyx jubatus* - Kelly 2001), spotted ragged toothed sharks (*Carcharias taurus* - Tienhoven et al. 2007), and marbled salamanders (*Ambystoma opacum* - Gamble et al. 2008). Many of these species exhibit size and sex-specific life history characters. Therefore, when sex and size-specific parameters are of

interest such as apparent survival and capture probability, our methods can be used to extend the work of Nichols et al. (2004) by integrating a size covariate within the model for size-based estimation of survival rates.

Sex Ratio

For many white shark populations around the world, researchers have reported male-dominant sex ratios (Chapple et al. 2011; Domeier and Nasby-Lucas 2012; Kock et al. 2013; Bruce and Bradford 2015). In this study we estimated two males for every female shark in our sample over a period of nine years after probabilistically assigning sex to individuals that remained unsexed throughout the study period. Male bias could be a result of a large portion of females remaining outside the study area for some sampling occasions (i.e., temporary emigration from the study area), females responding differently to our sampling methods, or an elevated mortality rate for females at an early life stage (Kanive et al. 2015). It has recently been shown that female white sharks temporarily emigrate such that they are half as likely to be present in the study area as are males, which predictably come back annually (Chapple et al. 2016). The net result of these sex-specific differences in temporary emigration and study-area attendance rates is that a given individual female is available for observation in fewer field seasons than is an individual male. This might skew the sex ratio in our observed sample of individuals in favor of males relative to the true sex ratio in the broader population that includes animals that have temporarily emigrated away from the study area for a sampling occasion. Although we observed twice as many males as females, the average capture probability estimate for females was half that of males. If the disparity in capture rates for

males and females is largely due to sex differences in temporary emigration rates, it is possible that the overall population that we sampled from has a sex ratio closer to parity. Although it is not possible at this time to know the underlying sex ratio of the broader population, future research should investigate this possibility with longer-term sampling and possible use of methods such as robust design (Williams et al. 2002). Further, until further results are available on sex ratio in the population, population modeling efforts should consider the possibility that the sex ratio might be somewhere in the range of 2:1 to 1:1.

Transients

Previous speculation suggested that white sharks in Central California are potentially comprised of a high percentage of transient individuals (up to 90%), which, if true would introduce bias in mark-recapture population assessments (Burgess et al. 2014). In this study using empirical data, we did not find significant evidence of transience in any year of the study. Therefore, transience likely does not cause significant bias in previous abundance estimates (Chapple et al. 2011) or the vital rates estimated here.

Potential Causes of Mortality

All of our study sites have high abundance of pinnipeds, the dominant prey source for sub-adult and adult white sharks (Tricas and McCosker 1984; Brown et al. 2010), and primarily serve as feeding grounds for white sharks during the late summer to early winter months (Jorgensen et al. 2010; Carlisle et al. 2012; Jorgensen et al. 2012). The smallest white shark in our sample was 240 cm, much smaller in length and girth than the

adults, which reach upwards of 550 cm. Established adults may compete with smaller conspecifics at preferred hunting grounds. White sharks in the smaller size range are frequently observed with fresh bite wounds inflicted from larger conspecifics suggesting possible competitive aggression (Fig. 3). Such intraspecific competition could lead to reduced survival or higher permanent emigration in smaller sharks but is still not well understood.

Adult white shark predations on pinnipeds have been described and documented to be of a single ambush strike, followed by the shark leaving the prey to exsanguinate, then returning to consume the prey (Tricas and McCosker 1984; Klimley 1994). This behavior is referred to as the ‘bite and spit’ strategy (McCosker 1984). This strategy mitigates direct contact with the prey, avoiding potential injury from defenses of the prey. Sub-adult sharks in the smaller length classes incur substantial wounds and scarring inflicted by animals with claws and teeth consistent with the harbor seal and California sea lion (Fig.4). We hypothesize that inexperience and smaller size could result in higher rates of injury and potential mortality during prey handling. For example, the crippling loss of an eye could hinder the ability for a white shark to successfully identify and ambush prey leading to a disproportionately lower survival than their more experienced and larger conspecifics.

Another cause of mortality for white sharks in the size classes depicted in this study is predation by killer whales (*Orcinus orca*). The predation on white sharks by killer whales is known to occur in California and South Africa where observations have been published. In 1997, an orca killed an adult white shark and fed on its’ liver at the

Southeast Farallon Island (Pyle et al. 1999). Similarly, in 2002 a male killer whale from a group of three attacked and killed a 4 m white shark (Best et al. 2010).

High seas fishing vessels that use long-line gear capable of hooking and holding a white shark on the line could also be a potential source of mortality. During the time of the year (late winter to late summer) when white sharks are pelagic (Jorgensen et al. 2010), they spatially overlap with fishing effort for big-eye tuna (*Thunnus obesus*). Long-line gear hooking species that white sharks consume could potentially result in a white shark becoming hooked as the shark eats the prey now serving as bait. As the high seas are often unregulated and fisheries observer data are sparse, it is not known as to the extent this fishery could impose mortality on the white shark population. Increased use of vessel positioning systems and mortality indicating electronic tags will improve our understanding of the overlap between white shark habitat and commercial fisheries.

In conclusion, using a new technique with broad applicability to mark-recapture systems, we have provided the first length-based survival rate estimates for sub-adult and adult white sharks based on empirical evidence. We have shown strong evidence for disparate survival rates between sub-adult and adult white sharks indicating a potentially much lower rate of survival for newly recruited sub-adult sharks to adult feeding aggregations in northern California. Additionally, we found no evidence for significant transience within the sample population. Taken together, these results better inform important population characteristics of a large top predator in the California Current.

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Model	K	AICc	Δ AICc	w_i
$\phi(\text{TL}) p(\text{sex}) \pi(.) \delta(\text{sex}+t)$	15	1818.42	0.00	0.56
$\phi(\text{sex}+\text{TL}) p(\text{sex}) \pi(.) \delta(\text{sex}+t)$	16	1819.54	1.12	0.32
$\phi(\text{sex}*\text{TL}) p(\text{sex}) \pi(.) \delta(\text{sex}+t)$	17	1821.66	3.24	0.10
$\phi(\text{TL}) p(\text{sex}+t) \pi(.) \delta(\text{sex}+t)$	23	1826.82	8.40	0.01
$\phi(\text{sex}+\text{TL}) p(\text{sex}) \pi(.) \delta(\text{sex}+t)$	24	1827.57	9.15	0.01

Table 2-1. Results for models representing hypotheses about the effect of total length (TL), sex, and time (t) on apparent survival (ϕ), probability that previously identified shark of sex s was sighted and identified (p), probability that sex was determined when a shark of sex s was sighted and identified in year i (δ), and probability that a shark first sighted in period i was a male (π). K is the number of parameters. w_i is the relative weight of evidence for each model.

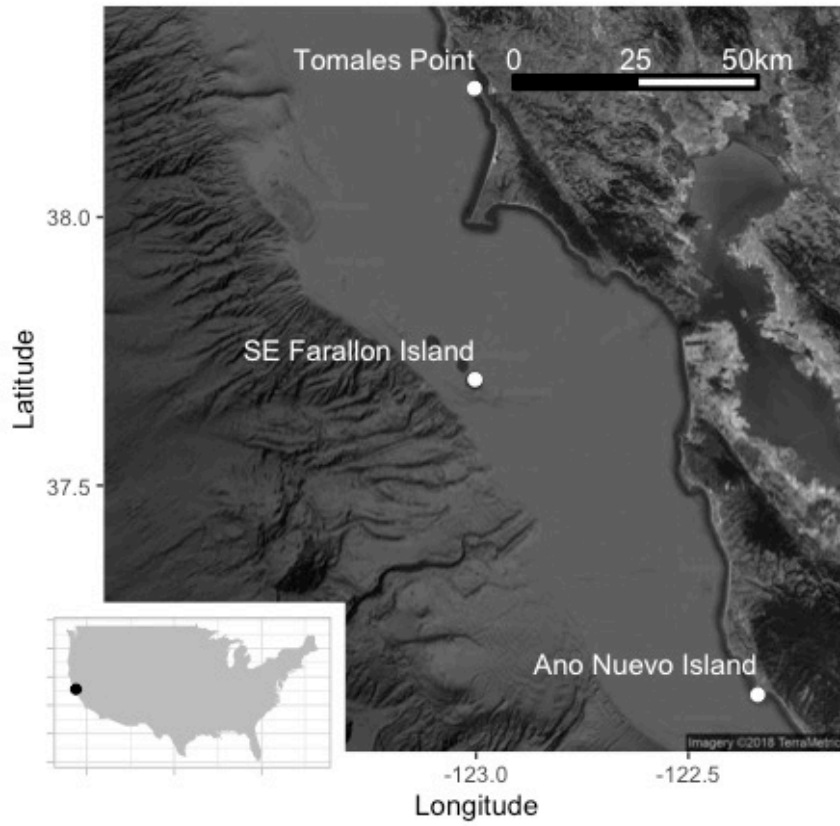


Figure 2-1. The three white shark aggregation sites off California, USA sampled in this study.

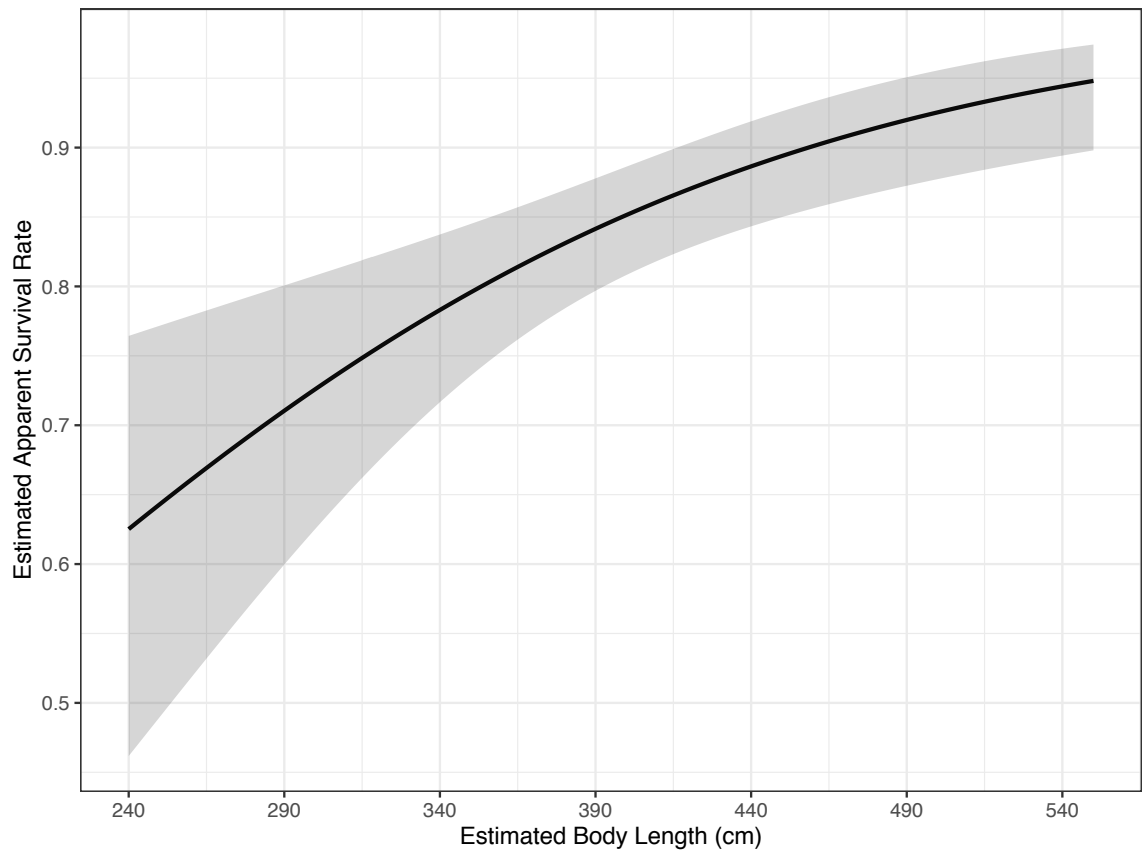


Figure 2-2. Estimated survival curve as a function of total body length. The black line represents the annual apparent survival point estimate for a given length. The grey area represents the 95% confidence intervals.



Figure 2-3. 275 cm female and 305 cm male white sharks with wounds inflicted by a conspecific.



Figure 2-4. 275 cm female with wounds on head inflicted by pinniped

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CHAPTER THREE

ESTIMATION OF REGIONAL ANNUAL ABUNDANCE AND EVIDENCE FOR
INCREASING NUMBERS OF WHITE SHARKS OFF CALIFORNIA

Contribution of Authors and Co-Authors

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Manuscript in Chapter 3

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Abstract

1. Determining population trends is critical for evaluating management actions and prioritizing species protections. However, for many marine species, the trajectory of population abundance remains unknown.

2. In this study, we used empirical data to produce an estimate of the population trend for protected sub-adult and adult white sharks in central California. We analyzed photographic images of the unique dorsal fin morphology of white sharks to build a long-term mark-recapture data set in a modified Jolly-Seber model (POPAN formulation) to estimate the super-population for four demographic groups of this marine top predator. This approach allowed us to derive annual abundance estimates and then investigate population growth rates using parametric bootstrapping methods for sub-adult and adult males and females over 8 years.

3. For all demographic groups combined we found equivocal evidence for a positive regional population growth ($\lambda = 1.07$ (95% CI = 0.91 to 1.23)). However, sex- and size-specific population growth rate estimates provided stronger evidence of population increases for reproductive mature males ($\lambda = 1.06$ (95% CI = 0.99 to 1.13) and females ($\lambda = 1.06$ (95% CI = 0.95 to 1.17)). For sub-adult male and female white sharks, point estimates of λ were positive but lack of precision prevents strong inference ($\lambda = 1.07$ (95% CI = 0.85 to 1.29) and $\lambda = 1.08$ (95% CI = 0.88 to 1.28)), respectively.

5. *Policy implications.* Though we cannot extrapolate to the entire northeast Pacific population, our findings of a modest increase in reproductive-aged white sharks in central California may be a result of regional fluxes in density or attributed to protection and

subsequent increase in abundance of pinnipeds as well as reduced gill-net fisheries mortality of juveniles. Our analyses suggest that current California marine management policy protecting white sharks, their prey, and habitat may be favoring positive population growth in central California.

Key Words: abundance, population trend, mark-recapture, white shark, California, POPAN, population dynamics

Introduction

Determining whether the number of individuals in a population is increasing, decreasing or stable over time is a central goal for assessing the status of wildlife populations (Williams, Nichols, & Conroy, 2002). However, population trends remain challenging to estimate because long-term monitoring is required, especially for long-lived species. In marine systems, assessing non-target species remains particularly difficult (Hilborn and Waters 1992; Pope et al., 2000) and even more so for large, highly mobile species with extensive home ranges and relatively low abundance. As a result, ~20% of marine vertebrates globally remain in the ‘Data Deficient’ assessment category under the International Union for Conservation of Nature (IUCN 2019).

While catch data is traditionally used in marine fisheries to assess populations, the proliferation of high-quality and low-cost photographic and video technologies, along with pattern recognition techniques, has increased opportunities to assess more cryptic

species through photo identification mark recapture (Drechsler, Helling, & Steinfartz, 2015). Simultaneously, the increasing accessibility of genetic (Miller, Joyce, & Waits, 2005) and electronic biologging data (Dudgeon, Pollock, Braccini, Semmens, & Barnett, 2015) is helping define the relevant geographic scope of populations targeted for assessment using image-based mark recapture.

Elasmobranchs are a taxa of conservation concern due to intrinsically low reproductive rates and vulnerability to direct and indirect fishing mortality, which has decimated many populations (Myers, Baum, Shepherd, Powers, & Peterson, 2007; Worm et al., 2013) and numerous species lack robust population assessments due to insufficient data (Dulvy et al., 2008; Queiroz et al., 2019). However, many shark and ray species possess morphological (Holmberg, Norman, & Arzoumanian, 2009; Tienhoven, Hartog, Reijns, & Peddemors, 2007), behavioral (Barnett, Abrantes, Stevens, & Semmens, 2011; Kneebone, Chisholm, & Skomal, 2012) and life history traits (Cortés, 2000) that are particularly suited for assessment using photo identification mark-recapture.

White sharks (*Carcharodon carcharias*) are a circumglobally distributed marine top predator currently listed as Vulnerable on the IUCN Red List of Threatened Species (IUCN 2019). Electronic tagging studies indicate migratory behavior on the scale of ocean basins but high site fidelity where individuals aggregate repeatedly in predictable coastal locations (Bruce, Stevens, & Malcolm, 2006; Domeier & Nasby-Lucas, 2008; Jorgensen et al., 2010; Skomal, Braun, Chisholm, & Thorrold, 2017; Weng et al., 2007). Genetic evidence suggests natal philopatry (Jorgensen et al., 2010) resulting in discrete population structure, with clearly defined population segments such as South Africa

(Pardini, Jones, Scholl, & Noble, 2000), Australia-New Zealand (Blower, Pandolfi, Bruce, Gomez-Cabrera, & Ovenden, 2012), northeast Pacific (Jorgensen et al., 2010) northwest Pacific (Tanaka, Kitamura, Mochizuki, & Kofuji, 2011), Mediterranean (Gubili et al., 2010) and northwest Atlantic (O’Leary et al., 2015).

The northeast Pacific population of sub-adult and adult individuals (hereafter called white sharks) primarily ranges from aggregations in Guadalupe Island, Mexico (Domeier & Nasby-Lucas, 2008) and central California, USA out to the north Pacific subtropical gyre (‘White Shark Café’) (Jorgensen et al., 2010; Weng et al., 2007). Additional aggregation areas may exist but to date none have been described in the north Pacific. In central California, a predictable migratory pattern reflects high fidelity for both sexes to the region and white shark individuals can be identified by a unique pattern of notches on the trailing edge of the dorsal fin that does not change significantly through time (Anderson et al., 2011). These attributes have led to multiple mark-recapture studies to estimate essential population parameters (Chapple et al., 2011, 2016; Kanive et al., 2015, 2019).

White shark populations have a low resilience to mortality (Chapple & Botsford, 2013) and have been protected since 1994 in California waters (Heneman & Glazer, 1996). Measures to protect sharks such as the banning of gillnets within five kilometers of the California coast may be reducing incidental mortality of juvenile white sharks in fishing gear (Benson et al., 2018; Lowe et al., 2012). Additionally, pinniped population increases (Boeuf & Laws, 1994; Laake, Lowry, DeLong, Melin, & Carretta, 2018)

following the Marine Mammal Protection Act (1972) are factors that could potentially influence white shark population growth.

An initial photo ID based estimate of abundance for white sharks off central California suggested 219 individuals (95% credible intervals, 130-275) (Chapple et al., 2011). This study provided a proof of concept for photographic mark-recapture as a viable assessment tool for white sharks, however no baseline value pre-dated this estimate so no temporal trend could be inferred.

In this study we estimate the abundance and population growth rates of a regional sub-population of white sharks in central California (hereafter simplified as ‘population’) using 8 years of data from all three known aggregation sites. We tested competing models within a Jolly-Seber mark-recapture framework, based on size and sex-specific demographic assumptions derived from previous work (Chapple et al., 2016; Kanive et al., 2015, 2019) to estimate annual abundance and determine whether there have been changes in the population size over time. This was conducted for the overall population, and among demographic groups (based on sex and maturity) within the sampled population.

2 MATERIALS AND METHODS

2.1 Data Collection

From 2011 to 2018, we sampled at known white shark aggregation sites (Southeast Farallon Island, Año Nuevo Island, and Tomales Point) along the central coast of California, USA (Figure 1) during periods of peak coastal residency (September – February; Klimley 1985; Jorgensen et al. 2010). We pooled data from the three sites given their proximity (< 150 km; total study area = ~ 1500 km²) and the species' mobility.

White sharks were attracted to a research boat using a seal decoy and a localized scent of marine mammal (Kanive et al., 2015). Individual sharks were identified from photographs and video images of the unique patterns on the trailing edge of their dorsal fin. To estimate abundance, we used seasonal sighting records of all sampled individuals to generate mark-recapture encounter histories.

We determined sex by unambiguous confirmation of presence (male) or absence (female) of claspers using underwater video. In this study, however, because sex assignment was imperfect, some sharks remained unsexed throughout the study and were thus classified as “unknown sex”. To account for this uncertainty, we used the program LOLASURVIV (Nichols, Kendall, Hines, & Spendelow, 2004) to estimate the sex ratio of the sample population. Unsexed individual sharks were then randomly assigned to sex

based on the estimate of the sex ratio from the LOLASURVIV analysis. Data used to estimate sex ratio extended from 2006 to 2018.

Total body length was estimated as the shark swam near a vessel of known size and maturity was assigned based on published values (males ≥ 380 cm and females ≥ 440 cm based on Pratt (1996) and Francis (1996), respectively). These length-based classifications resulted in four groups: adult males and females, sub-adult males and females.

2.2 Jolly-Seber Abundance Estimation

To estimate annual abundance of the sub-adult and adult males and females, we constructed Jolly-Seber (Jolly 1965; Seber 1965) open mark-recapture models using the POPAN (Schwarz & Arnason, 1996) formulation in Program MARK (White & Burnham, 1999). We implemented MARK using the RMark package (Laake, 2013) in the R software environment (R Core Team 2018). The POPAN parameterization includes:

ϕ_i = probability of apparent survival from year i to $i + 1$,

p_i = probability of capture (observation) on occasion i ,

N_{super} = super-population consisting of all sharks that were alive and available for detection at some point during the sampling periods of the study,

β_i = probability that a shark from the super-population, N_{super} , would enter the population between occasion i and $i + 1$.

Jolly-Seber models use information from the number of unmarked individuals observed on each sampling occasion and assume that unmarked animals have the same capture probabilities as marked animals, which allows for the estimation of abundance (Schwarz & Arnason, 1996). We analyzed data from 2011 through 2018 when sharks at all three sampling sites were consistently sampled. Assumptions for this model include: (1) sharks retain their fin pattern throughout the study and are recorded and matched properly, (2) sampling is instantaneous (or realistically conducted over a short time), (3) survival probabilities are the same for marked and unmarked sharks between each sampling occasion (homogeneous survival), (4) catchability is the same for marked and unmarked sharks (homogeneous catchability) and (5) the study area remains constant throughout the study period.

Multiple combinations of model structures for ϕ , p , and β were tested, and the super-population size (N_{super}) was estimated for each group in each model. Following evidence that ϕ increases with total length (Kanive et al, 2019), we allowed ϕ to vary by maturity (mat) where adult males and females were pooled, and sub-adult males and females were pooled or allowed to vary by maturity and time via an interaction ($mat*t$). For capture probability, p , we assessed the effects of sex, effort, time (t), group (g), as well as the following combinations: $sex*effort$, $sex*t$, $g*t$. We also defined group effects where p for sub-adult males and females was constrained to be the same but p for adults was allowed to vary by sex and year via an interaction [$((subs(.))ads(sex))*t$] or held constant across years [$(subs(.))ads(sex)$]. An alternative model structure for p was also considered where p for sub-adult males and females was allowed to vary by sex and rate

for adult males and females was constrained to be the same but either (a) allowed to interact with year [$((\text{subs}(\text{sex})\text{ads}(.)) * t)$] or (b) was held constant across years [$(\text{subs}(\text{sex})\text{ads}(.))$]. For models where p , β , and ϕ were all allowed to vary over time, not all parameters in the model were estimable (Schwarz & Arnason, 1996). Therefore, for models where p and β were both time variant, the first and second capture probabilities were constrained to be equal for sharks of each sex ($p_1 = p_2$) and other capture probabilities were allowed to vary. To eliminate inestimable parameters in models where p and ϕ were both time variant, the last two capture probabilities were constrained to be equal for sharks of each sex (in this case $p_7 = p_8$) and other capture probabilities to be time-variant. Probability of entry, β , was allowed to differ by group and was either held constant over time (g), allowed to vary independently over time in each group ($g * t$), or to vary by maturity class while either being held constant over time (mat) or allowed to vary independently over time in each maturity class ($mat * t$). Finally, N_{super} was estimated for each group (g) for every model. The models were fitted using the logit-link function for ϕ and p , the log-link function for N_{super} , and the multinomial-link for β to constrain the set of parameters to have a sum that was ≤ 1.00 (Schwarz & Arnason, 1996; Williams et al., 2002). We considered models that contained all-possible combinations of parameterizations for each of the parameters, which yielded 88 different competing models (see supplement). Model selection was based on Akaike's Information Criterion for small sample sizes (AICc) (Burnham & Anderson, 2002). Given issues of model selection uncertainty, we also used model averaging to obtain estimates for parameters of interest (Burnham & Anderson, 2002).

We derived the number of new animals (B_i) that joined the super-population during each year and the size of the annual population sizes (N_i) using standard methods for POPAN results (Schwarz & Arnason, 1996). To estimate total abundance for each year, we summed the group abundances for and quantified uncertainty using the delta method (Powell, 2007).

2.3 Population Growth Rate Calculation

To obtain estimates of population growth rates (λ), we used parametric bootstrapping on results from the top model for each of the four groups of White sharks. Specifically, we generated 5,000 random samples of annual abundance (N_i) for each group, for each year. Population growth rates (λ) were then calculated using the 5,000 randomly generated estimates of annual abundance for each group from the top model. Specifically, from 2011-2018, we estimated λ by dividing subsequent abundance estimates (i.e. N_{2012}/N_{2011} , N_{2013}/N_{2012} , ..., N_{2018}/N_{2017}) yielding seven inter-annual estimated λ s' representing the growth rate from one time step (year) to the next. For each of the 5,000 sets of 7 estimated inter-annual λ s', we estimated a geometric mean λ that accounts for temporal variation in rates of annual population growth (Cooch & White, 2019; Lewontin & Cohen, 1969). Geometric means yielded approximately normal distributions and allowed us to calculate 95% confidence intervals for each group's estimated geometric mean.

3 RESULTS

3.1 Data Summary

During the sampling seasons from 2011 to 2018, we logged 2,587 hours attracting white sharks to research vessels at Southeast Farallon Island (478 hrs), Año Nuevo Island (755 hrs) and Tomales Point (1,354 hrs). A total of 419 individual White sharks (241 male; 147 female; 31 unknown) ranging from 200 to 550 cm total length (mean = 390 cm, SE = 3.71) were identified. Unique fin identifications were logged from 1,533 images. The observed sex ratio of the sample population was 1.6 males per female. The number of unique and resights per unit effort is summarized in Table 1.

Estimates from the LOLASURVIV model (see supplement) for animals that could not be sexed indicated that the sample populations' sex ratio was 1.50 (SE = 0.02) males per female. Therefore, for this sample population to equate to 1.50, we randomly assigned 10 of 31 unsexed sharks to male and the remainder as female for a total of 251 males (144 adults, 107 sub-adults) and 168 females (71 adults, 97 sub-adults) (Figure 2).

3.2 Model Results

Our best-supported model among a suite of 88 models had an AICc score with a difference of 2.63 units from the next best model and had 54% of the AICc weight. The

second and third best-supported models each had 14% of the AICc weight (Table 2). Given the resulting model-selection uncertainty, we report the parameter estimates from the top model alongside model-averaged results obtained from all models that received any model weight (Table 2) (Burnham & Anderson, 2002). In the best-supported model, ϕ differed by maturity class but not by year and was estimated as 0.70 (SE = 0.03) for sub-adults and 0.85 (SE = 0.02) for adults. In the best-supported model, p was allowed to vary by sex in the mature class, but held constant by sex for sub-adults, and allowed to vary by year [((subs(.).ads(sex)) * time)]. Time-varying estimates of p varied from 0.21 (SE = 0.08) to 0.66 (SE = 0.08) for sub-adult sharks (both sexes), from 0.25 (SE = 0.05) to 0.87 (SE = 0.13) for adult males, and 0.17 (SE = 0.06) to 0.44 (SE = 0.12) for adult females. Estimated annual probability of entry into the population, β_i was best estimated as being different by maturity class but constant over time was 0.09 (SE = 0.01) for adults and 0.10 (SE = 0.01) for sub-adults. The probability of being present at the start of the study, β_0 (i.e., $1 - (\beta_1 + \dots + \beta_7)$), was 0.34 (SE = 0.06) for adults and 0.28 (SE = 0.08) for sub-adults. The super-population (N_{super}) for each group based on results from the best-supported model was 161.15 (SE = 13.56) for sub-adult males, 146.04 (SE = 12.57) for sub-adult females, 177.57 (SE = 7.99) for adult males, and 114.01 (SE = 12.50) for adult females (model-averaged parameter estimates can be found in the supplementary material).

3.3 Annual Abundance Estimates

Derived annual abundance point estimates from our top model increased from 2011 to 2018 for each group. Point estimates increased from 45.35 (SE = 15.27) to 54.58 (SE = 7.11) for sub-adult males, 41.10 (SE = 13.86) to 49.46 (SE = 6.50) for sub-adult females, 59.64 (SE = 9.85) to 95.93 (SE = 10.52) for adult males, and 38.29 (SE = 7.75) to 61.59 (SE = 8.69) for adult females (Figure 3) over the study period. Model-averaged seasonal point estimates of abundance also increased from 2011 to 2018 in each group. Model-averaged point estimates increased from 40.96 (SE = 20.62) to 56.63 (SE = 9.47) for sub-adult males, 36.73 (SE = 15.92) to 56.12 (SE = 13.08) for sub-adult females, 61.38 (SE = 12.08) to 94.39 (SE = 10.89) for adult males, and 41.18 (SE = 12.00) to 58.91 (SE = 9.20) for adult females (Figure 3).

Seasonal total abundance estimates summed over all groups of sub-adult and adult male and female white sharks in our study area provided some evidence that overall abundance increased over the study (Figure 3). Estimates from the top model increased from 184.38 (SE = 33.42) in 2011 to 261.56 (SE = 21.42) in 2018. Similarly, model-averaged values increased from 180.25 (SE = 38.29) in 2011 to 266.05 (SE = 24.35) in 2018.

3.4 Estimates of Population Growth Rate ($\hat{\lambda}$)

Top model and model averaged estimates of overall geometric mean $\hat{\lambda}$ were 1.05 (95% C.I. = 0.91 – 1.16) and 1.07 (95% C.I. = 0.91 – 1.23) respectively. Of the 5,000 bootstrap estimates generated for $\hat{\lambda}$ for the overall shark population, 83.4% of values from the best-

supported and 83.5% of values from model averaging were >1.00 . The bootstrap results provide evidence that the population's stochastic growth rate, as measured by geometric mean $\hat{\lambda}$ was adequate for population growth over the study period. However, the uncertainty associated with the estimates does not rule out other possibilities.

Group-specific estimates of geometric mean $\hat{\lambda}$ from the top model provide strong evidence that adult males and females had a stochastic growth rate >1.00 (98.8% of estimates of bootstrapped values were >1.00 for each sex) indicating an increase in abundance over the study period. In contrast, results for sub-adults were more equivocal (68.5% and 68.6% of values for sub-adult males and females, respectively, were >1.00) (Figure 4). Annual geometric mean estimates for each group from top model were calculated as 1.07 (95% C.I. = 1.01 to 1.13) for adult males, 1.07 (95% C.I. = 1.00 to 1.15) for adult females, 1.04 (95% C.I. = 0.90 to 1.17) for sub-adult males, and 1.04 (95% C.I. = 0.90 to 1.17) for sub-adult females.

Model-averaged results were similar to those from the top model but slightly more uncertain (96.1% and 87.0% of estimates of bootstrapped values were >1.00 for adult males and females, respectively). For sub-adults, results from model-averaging provided slightly more evidence than results from the top model that the stochastic growth rate was >1.00 ; however, results from both had notable levels of uncertainty (71.4% and 78.3% of estimates of bootstrapped values were >1.00 for sub-adult males and females, respectively). Annual geometric mean estimates based on results from model averaging were 1.06 (95% C.I. = 0.99 to 1.13) for adult males, 1.06 (95% C.I. = 0.95 to 1.17) for adult females, 1.07 (95% C.I. = 0.85 to 1.29) for sub-adult males, and

1.08 (95% C.I. = 0.88 to 1.28) for sub-adult females. Consequently, we found relatively strong evidence for positive population growth in adult males and females during the 8-year study period and more equivocal evidence for positive population growth among sub-adult males and females, although a stable population growth rate can be conservatively inferred for all groups.

4 DISCUSSION

Using visual mark-recapture techniques based on dorsal fin morphology, we estimated the regional abundance over eight years for sub-adult and adult white sharks that seasonally aggregate off central California. Importantly, our results are indicative of a relatively small group of white sharks (< 300 individuals) that appears stable or slightly increasing. However, our analysis of separate demographic classes suggests a modest increase in the abundance of adults (male and female) yet an equivocal estimate for the growth rate for sub-adults (also both male and females). The result suggests the sub-adult demographic is either stable or slightly increasing. These findings represent the first empirical estimate of population trend of white sharks in central California.

The abundance estimates and inferences of this study are specific to the region of central California encompassing the three primary aggregation sites sampled. However, electronic tagging data have shown sharks tagged within our study area to move to, and return from, coastal areas both to the north and south of the study area from Mexico to Washington state (Block et al., 2011; Jorgensen et al., 2010). Additionally, opportunistic

dorsal fin photographs of white sharks taken outside the study area including Hawaii, Mexico and throughout California, have been matched to white sharks identified in central California. The hypothesis that the central California white shark population may comprise a substantial proportion of ‘transient’ individuals (Burgess et al. 2014) has been robustly ruled out (Kanive et al., 2019) based on empirical data testing (Pradel, Hines, Lebreton, & Nichols, 1997). Whether this regional increase of reproductive-age white sharks in central California is representative of an overall increase in the total northeastern Pacific white shark population (Jorgensen et al., 2010) or a result of regional fluxes in density remains to be determined. A trend estimate for the entire northeastern Pacific will require integration of data among their known aggregation areas along the west coast of North America.

Although, it is uncertain what is driving this modest increase, two key protections likely contributed to the success of white sharks in central California. First, white sharks were first protected in California waters in 1994 and federally in 2004 (CITES, appendix ii), and bans on coastal gillnetting in 1990 (California Proposition 132) likely greatly reduced early incidental mortality of juveniles. Secondly, pinnipeds, their main prey were protected under the Marine Mammal Protection Act and have greatly increased in abundance since (Boeuf & Laws, 1994; Laake et al., 2018; Lowry, 2014). These protections likely set the stage for the apparent trends in this important marine predator.

Our findings provide evidence that mature individuals are increasing in this region, and that sub-adults are at least stable. Ancillary information from increased sightings of age-0 and juvenile sharks (Lowe et al., 2012) and an increase in sea otter

mortality due to white shark bites (Tinker, Hatfield, Harris, & Ames, 2016) provide support to our findings although it remains unclear what demographic is responsible for the increased mortality. An increase in incidental fisheries landings of juvenile white sharks between the mid 1990s' and 2008, following the 1994 California near shore gill net ban has frequently been cited as evidence of population increase (Lowe et al., 2012). However, this potential abundance index, which depends on consistent reporting by fishers, decreased to zero for many years following the 2012 petitions for this segment of the white shark population listing under the Endangered Species Act. Public reports of juvenile white shark sightings in California have also increased substantially in recent years, but the number of sightings has been highly variable in magnitude and location year-to-year, and may also be linked climatic variation in optimal temperature habitat across their latitudinal range (White et al., 2019). These observations suggest a possible increase in the abundance of white sharks in the juvenile size class (< 240 cm), smaller than the sizes sampled in this study. However, influences of distributional changes, climate variation, effort consistency, and fisheries reporting accuracy are confounding factors that need to be resolved before firm conclusions can be made.

Among adults and sub-adults, length-based apparent survival rate estimates show that adults have a substantially higher probability of surviving and reusing sites in the study area (Kanive et al., 2019). The 'apparent' term means that mortality is confounded with potential permanent emigration, where the animal is alive and leaves the study area for the remainder of the study period. As sub-adults recruit to prime foraging ground occupied by adults, intraspecific competition could force out smaller, less competitive

individuals (Kanive et al., 2019). It is therefore possible sub-adult sharks are actually alive but dispersed outside of the prime hunting grounds of our study area. Future research should examine the coastal movement of sub-adult white sharks tagged at the three aggregation sites described in this study to determine if they remain alive and outside of the study area. Resolution of the movement of smaller and less competitive sub-adults could reveal whether density-dependent recruitment is a factor at prime adult aggregation sites (Kanive et al., 2019).

This is the first empirical assessment of regional population trend for white sharks in the northeastern Pacific. A similar regional increase in white shark numbers in the US Economic Exclusive Zone of the northwest Atlantic showed a recovery towards early historical numbers (Curtis et al., 2014). While there are no historic baselines of white shark abundance in the northeast Pacific, the results of this study suggest recent favorable management in California (including marine mammal protection, and white shark bycatch mitigation) are providing a pathway for the positive population growth for this important marine top predator.

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Year	2011	2012	2013	2014	2015	2016	2017	2018
# Unique Sharks	85	82	88	77	117	87	148	92
# New Sharks	85	56	43	36	49	34	74	42
# Sharks Resighted	NA	26	45	41	68	53	74	50
Resight %	NA	0.32	0.51	0.53	0.58	0.61	0.50	0.54
Effort (hrs)	408	469	361	225	352	218	329	223
Individual Sharks/hr	0.21	0.17	0.24	0.34	0.33	0.40	0.45	0.41

Table 3-1. Summary of sharks identified in our central California study area over the study period.

Model	K	AICc	ΔAICc	w_i
$\varphi(\text{mat}) p[((\text{subs}(\cdot)\text{ads}(\text{sex}))^*t] \beta(\text{mat}) N(\text{g}))$	32	1703.25	0.00	0.53
$\varphi(\text{mat}) p[((\text{subs}(\cdot)\text{ads}(\text{sex}))^*t] \beta(\text{g}) N(\text{g}))$	34	1705.88	2.63	0.14
$\varphi(\text{mat}) p(\text{sex}^*t) \beta(\text{mat}) N(\text{g})$	24	1705.98	2.73	0.14
$\varphi(\text{mat}) p(\text{g}^*t) \beta(\text{mat}) N(\text{g})$	40	1707.69	4.44	0.06
$\varphi(\text{mat}) p(\text{sex}^*t.\text{pool}) \beta(\text{mat}^*t) N(\text{g})$	34	1708.17	4.92	0.05
$\varphi(\text{mat}) p(\text{sex}^*t) \beta(\text{g}) N(\text{g})$	26	1708.29	5.04	0.04
$\varphi(\text{mat}) p((((\text{subs}(\cdot)\text{ads}(\text{sex}))^*t] \beta(\text{mat}^*t) N(\text{g}))$	41	1708.68	5.43	0.04

Table 2. Models with Akaike weights > 0.01 where K is the number of parameters estimated in the model, AICc is the Akaike Information Criterion score corrected for small sample size, ΔAICc is the difference in the AICc values from the top model, and w_i are the calculated Akaike weights.

Group	Top Model λ (95% C.I.)	Model Avg. λ (95% C.I.)
All	1.05 (0.94 – 1.16)	1.07 (0.91 – 1.23)
Adult Males	1.07 (1.01 – 1.13)	1.06 (0.99 – 1.13)
Adult Females	1.07 (1.00 – 1.17)	1.06 (0.95 – 1.17)
Sub-Adult Males	1.04 (0.90 – 1.17)	1.07 (0.85 – 1.29)
Sub-Adult Females	1.04 (0.90 – 1.17)	1.08 (0.88 – 1.28)

Table 3. Estimated seasonal geometric mean of λ with associated 95% confidence intervals for each group of white shark as well as the overall estimate.

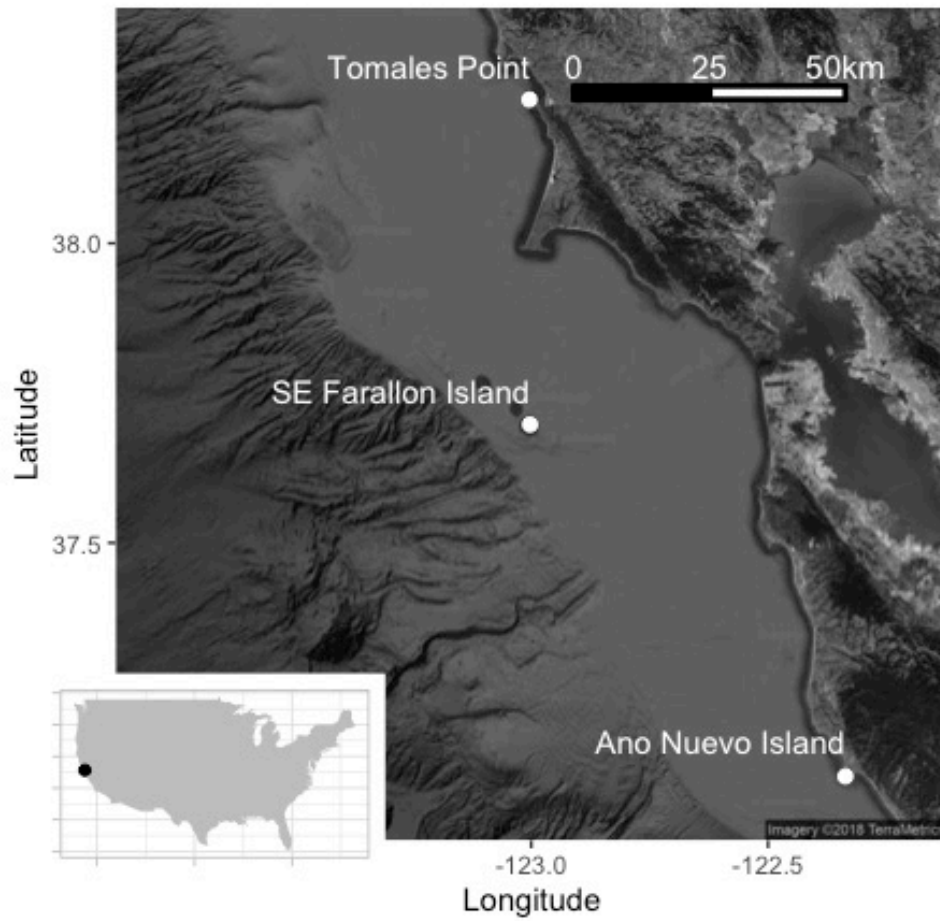


Figure 1. Map of the United States of America with the locations of the 3 sampling sites off central California.

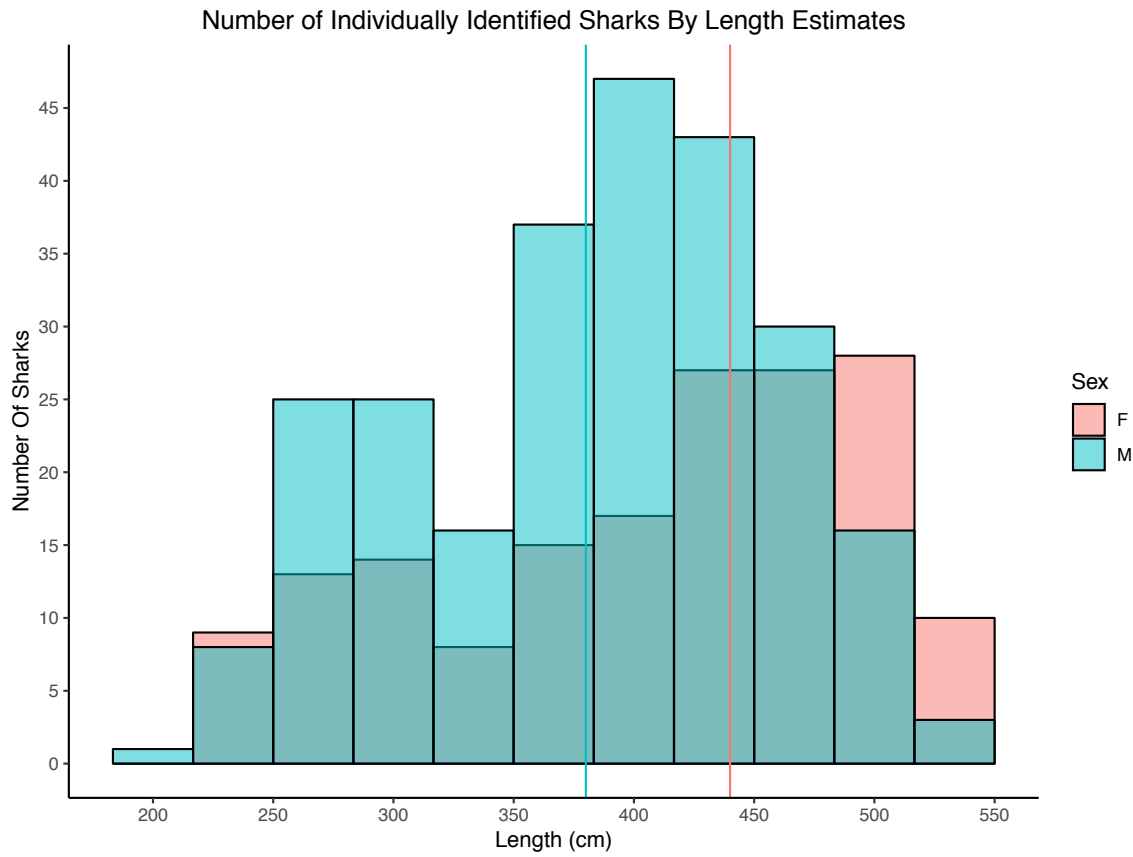


Figure 2. Histogram detailing the number of individually identified white sharks with associated total length estimation and sex over the course of the 8-year study period. The vertical lines represent the estimated length at which males (in blue) and females (in red) transition from sub-adult to adult.

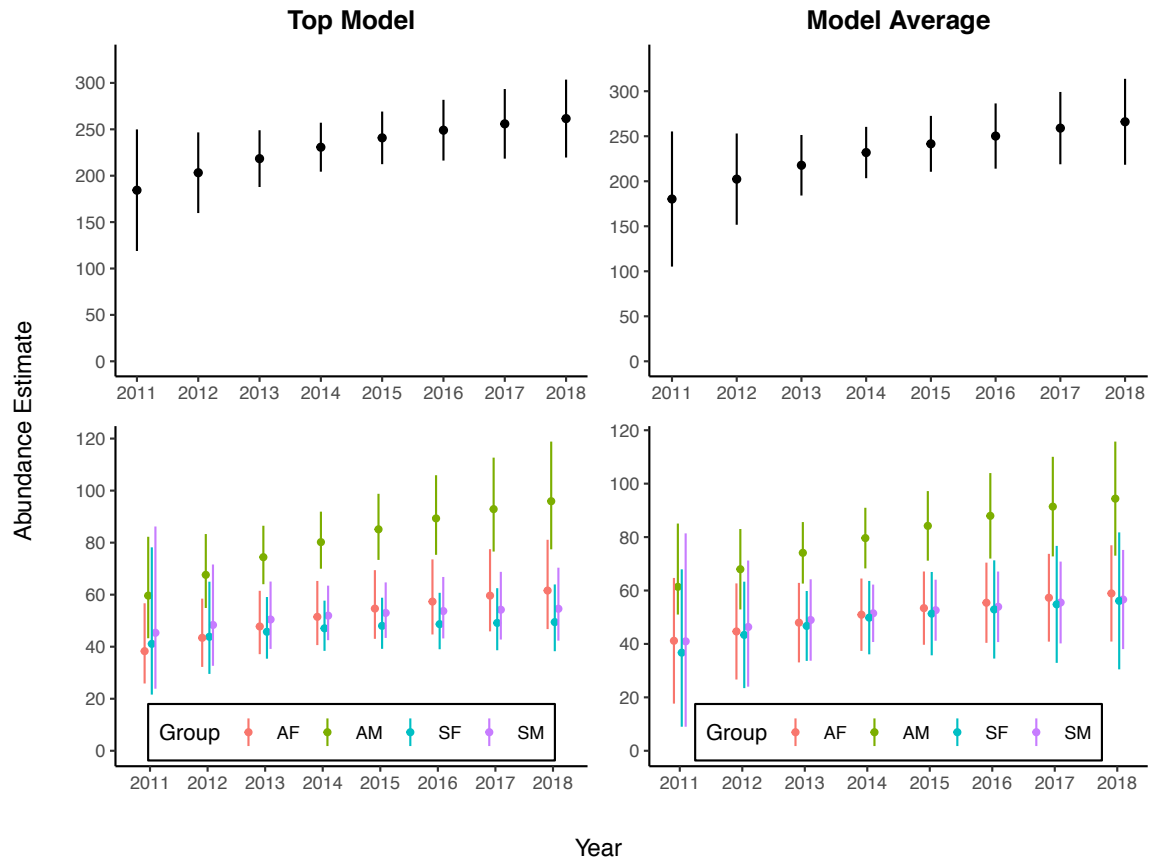


Figure 3. Annual abundance estimates of white shark (*Carcharodon carcharias*) off central California with 95% confidence intervals for all demographic groups combined (black), and each separate group (colored) for the top model, and the model average POPAN results.

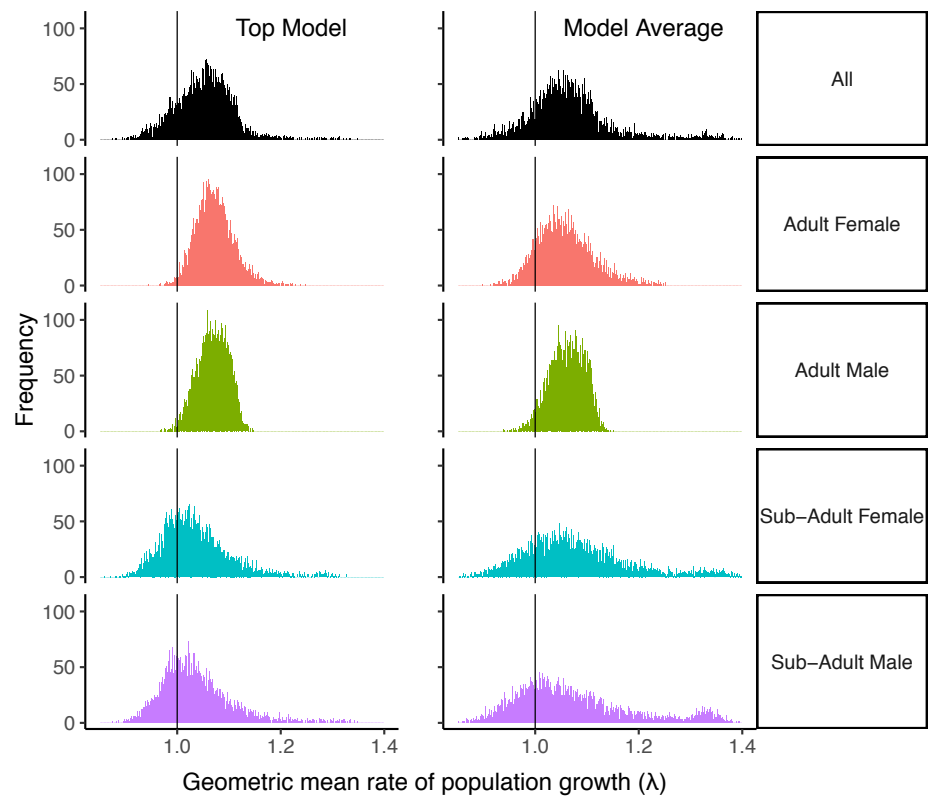


Figure 4. Frequency distributions of geometric mean rate of population growth values calculated from bootstrap sampling for each group (colored) of white shark as well as the overall population (black).

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CHAPTER FOUR

CONNECTIVITY BETWEEN THE CENTRAL CALIFORNIA AND GUADALUPE ISLAND WHITE SHARK POPULATIONS

Contribution of Authors and Co-Authors

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Abstract

Populations of animals whose ranges overlap international boundaries are potentially subject to disparate management practices or protection status. In this study, through a collaborative effort we have conducted a comprehensive analysis of sub-adult and adult white sharks' connectivity between two main aggregation regions; one off central California, USA (CC) and one off Guadalupe Island, Mexico (GI). From 2008 to 2019, we tagged 210 sub-adult and adult white sharks in CC and 116 in GI. Of the 326 white sharks tagged with acoustic transmitters, 30 (9.20%) were detected at both regions at some point during the study period. We used logistic regression with a binomial distribution to estimate the effect of sex, maturity, and tag location to the response variable, the probability of moving to the other region. Additionally, we tested for random effects individuals and sampling seasons could have on movement. Overall, we found evidence for a low probability of moving between sites (0.015, 95% credible interval = 0.002, 0.061) for the sharks in our sample. Among the sex and size classes that used both regions, sub-adult sharks were more likely than adults to move to the other region. We provide the first evidence of adult white sharks using both coastal regions, an important consideration for the overall northeastern Pacific population. There was little evidence that sex and year were important factors influencing movement. Although rare, the connectivity and potential genetic exchange between these two main aggregations suggests that these two aggregations form one continuous population of white sharks in the northeastern Pacific.

Introduction

Resource use and management decisions are derived from an understanding of population structure and life-history parameters. Demarcating populations of marine animals on ocean-basin scales can be difficult due to large home ranges and inability to observe animals in the ocean habitat. However, advances in tagging technologies have increased our capacity to observe movements and ocean-scale migratory paths for multiple species across taxa (Block et al., 2011; Block, Dewar, Farwell, & Prince, 1998). These technologies have provided bounds on many highly mobile species, indicating predictable species-specific migratory pathways and high-use areas where focused sampling efforts can provide important population characteristic data.

The white shark (*Carcharodon carcharias*) is a top marine predator with a circumglobal distribution. Tagging studies in tandem with genetic techniques provide evidence that suggests that natal philopatry is strong (Jorgensen et al., 2010), which results in discrete population structure with clearly defined population segments that have been identified in South Africa (Pardini, Jones, Scholl, & Noble, 2000), Australia-New Zealand (Blower, Pandolfi, Bruce, GomezCabrera, & Ovenden, 2012), the northeast (Jorgensen et al., 2010) and northwest Pacific Ocean (Tanaka, Kitamura, Mochizuki, & Kofuji, 2011), the Mediterranean Sea (Gubili et al., 2010), and the northwest Atlantic Ocean (O'Leary et al., 2015).

Off the western U.S. coast, white sharks in the northeastern Pacific are thought to give birth in the Southern California Bight (area between Point Conception and San Diego). This assumption is based on incidental catches of neonate and age-0 white sharks

(120 -150 cm) in near-shore waters (<3 nm from shore, <50 m depth) from gill-net fisheries that target other fishes such as California halibut (*Paralichthys californicus*), white seabass (*Atractoscion nobilis*), and Pacific angel shark (*Squatina californica*) (Lowe et al., 2012; Lyons et al., 2013). To the south in Baja, Mexico, another nursery ground has been described in Bahia Sebastian Vizcaino (Oñate-González et al., 2017). It is thought that white sharks spend ~3 years in these nursery grounds feeding upon cephalopods, teleosts, elasmobranchs until they reach lengths ~ 200-250 cm. As they gain mass and can withstand colder water temperatures, white sharks recruit to areas in central California (CC) to the north of Point Conception, CA and ~250 km offshore to Guadalupe Island (GI) that have large aggregations of pinnipeds (Weng et al., 2007). The two main sub-adult and adult white shark aggregations are separated by 1,000 km. Data for this recruitment phase to predominately adult hunting grounds is relatively sparse, however new recruits potentially experience higher mortality during this transition (Kanive et al., 2019). It is also unclear if recruitment to the CC or GI aggregations is based on the nursery the sharks were born at or if there is a mixture of animals that eventually choose a site that they then have high fidelity to.

Multiple tagging studies (Boustany et al., 2002; Domeier & Nasby-Lucas, 2012; Domeier & Nasby-Lucas, 2008; Jorgensen et al., 2010; Weng et al., 2007) have provided evidence that sub-adult and adult white sharks undertake predictable seasonal migrations in the northeastern Pacific between three main focal areas: (i) North American shelf waters, (ii) the slope and offshore waters of the Hawaiian archipelago, and (iii) the offshore White Shark Café, located ~ 1500km between Baja, Mexico and Hawaii, USA

(Domeier, 2012; Jorgensen, Chapple, Hoyos, Reeb, & Block, 2012; Weng et al., 2007).

While sharks from both regions overlap while offshore in the White Shark Café and Hawaii, tagged white sharks have been shown to consistently return to their respective tagging region in CC or GI (Domeier & Nasby-Lucas, 2008; Jorgensen et al., 2010).

Adults from both locations predictably travel offshore and have similar timing for when they depart and when they return to coastal areas (Domeier & Nasby-Lucas, 2008; Jorgensen et al., 2010). However, sub-adults in GI mostly remain coastal (Hoyos-Padilla, Klimley, Galván-Magaña, & Antoniou, 2016), and sub-adults that do travel offshore do not appear to have off-shore movements that are synchronized with adult seasonal patterns (Domeier, 2012). In CC, the onset of seasonal migration with maturity migratory remains largely unknown due to a scarcity of research on this specific transition stage.

Though telemetry allows us to track shark movement patterns while offshore, research efforts to evaluate regional population parameters have been conducted while sharks are coastal (Chapple et al., 2011, 2016; Kanive et al., 2015, 2019). Estimating abundance for the combined northeastern Pacific region could potentially lead to inflated estimates if animals use both regions and were counted twice. Therefore, it is important to accurately define annual rates of overlap between regions. Prior to this study, five sub-adult sharks tagged with acoustic tags had been detected in CC and GI (Jorgensen et al. 2012; Hoyos-Padilla, 2016) but a comprehensive analysis has been lacking between regions to quantify connectivity. Additionally, it has been unclear if these occasional movement events are common occurrences or if underlying factors could be driving these movements.

Quantifying the movement of this protected species between regions that straddle international boundaries needs to be considered when assessing about the overall northeastern Pacific population and the connectivity of these seemingly discrete groups (Jorgensen et al. 2010; Domeier et al. 2008). In this study, we conducted a comprehensive analysis of data collected over 12 years from two populations overlap waters managed by US and Mexico. Through collaboration between two research groups using parallel tagging methods and technology, we quantified movement between these two important aggregations in USA and Mexico and explored demographic-specific movement rates for sub-adult and adult white sharks.

Methods

From 2006 to 2018, we tagged sharks at known sub-adult and adult aggregation region in California, USA (Southeast Farallon Island, Año Nuevo Island, and Tomales Point) and Guadalupe Island, Mexico (Figure 1) during periods (September – February) of peak coastal residency (Klimley 1985; Jorgensen et al. 2010). White sharks were attracted to a research boat using a seal decoy, and motivated to circle the boat with a small (<2kg) piece of salvage marine mammal blubber tethered against the boat at the water line (Kanive et al., 2015). Individual sharks were identified from photo and video images of the natural and unique patterns on the trailing edge of their dorsal fin as fin morphological patterns have been validated for stability over periods exceeding 25 years (Anderson et al. 2011). Total lengths of the sharks were estimated from one to three experienced researchers using the known length of the research vessel as a reference as

the shark swims close to the vessel. If there was a disparity of an estimate of the total length among the researchers, the mean was used as the estimate.

Free-swimming sharks were tagged with individually coded acoustic transmitter tags (V16-4H; Vemco, Halifax, Nova Scotia) using a 59-mm titanium dart with an 18-20 cm 136-kg test monofilament leader protected by hollow braided Dacron and shrink-wrap (Jorgensen et al. 2010). The darts were inserted into the dorsal musculature using a tagging pole (Boustany et al. 2002; Weng et al. 2007a) as the shark swam by the research vessel.

Acoustic receivers (Vemco; VR-2, VR-3, VR-4) were placed at known white shark aggregation sites in California and Guadalupe Island. Receivers archived the acoustic detections of each white shark with an individual acoustic code as they swam within ~500 m of the receiver. The data from the receivers were downloaded (VR-3) via underwater modem or physically retrieved (VR-2). VR-4 receivers transmitted data in near-real time via satellite.

GLMM Analysis

We modeled the probability of transitioning from one region (GI or CC) site to the other using logistic regression using a binomial distribution for the response variable with a logit-link between the response variable and covariates of interest. We used a Bayesian approach to implement one overall, general model that included five factors that we predicted might be associated with variation in an individual's probability of movement. Those included sex, maturity class, and the aggregation site at which it was observed at the start of the binomial trial. Because some individuals provided data for

multiple binomial trials and because multiple individuals were studied in each year, we also included random effect of individual and year in our models. As the annual migratory pattern consists of an offshore phase followed by a coastal phase, our model defines a ‘movement’ as either (i) a shark migrates offshore from one region and returns to the coast at the other region or (ii) a shark returned to where it departed at previous time step, then moved to other region within the season. Individual sharks were coded as ‘1’ if the shark moved or ‘0’ if the shark did not move between sites in a given season. Therefore, the probability of ‘moving’ to the other site at least one time in a season can be defined as:

$$\text{logit}(\text{moved}) = \alpha + \beta_s \times \text{sex} + \beta_m \times \text{maturity} + \beta_l \times \text{location} + \hat{s}_{\text{ind}}^2 \times \text{individual} + \hat{s}_{\text{year}}^2 \times \text{year}$$

We implemented the model in the R software (R Core Team 2019) environment using the ‘rstanarm’ (Goodrich et al. 2020) and ‘shinystan’ (Gabry 2018) packages (Geweke 1991). We ran 4 chains using diffuse priors and ran each chain for 1,000 iterations after a burn-in of 1,000 iterations was completed and discarded (Gelman et al. 1996). We used the standard priors set by ‘rstanarm’ and used normal distributions for the priors for random effects of individual and year (random effects were $\sim N[0, \hat{s}_{\text{individual}}^2]$ and $\sim N[0, \hat{s}_{\text{year}}^2]$). We ran an additional 1,000 iterations per chain, resulting in 4,000 total samples from the posterior distribution. Model convergence was assessed by inspecting the trace plots and Geweke diagnostics (Geweke 1991) and evaluating whether the Gelman-Rubin statistic, $\hat{R}$, was <1.1 for each monitored parameter (Gelman and Rubin

1992). We evaluated how well predicted values from the fitted model corresponded with actual observations using posterior predictive checks (Gelman et al. 2000). Specifically, we evaluated how well distributions of predicted values corresponded to the mean, standard deviation, density, and 2.5% and 97.5% quantiles of the observed data. We also examined the distribution of discrepancies between predicted and observed values to evaluate whether there was evidence that some observations were not predicted well by the model.

Results

Off central California, from 2008 to 2018, a total of 249 tags were deployed onto 210 individual (39 sharks were tagged twice during study) white sharks (Figure 1) that varied in estimated total length from 240cm to 550cm in total length (mean = 401.75 cm; SD = 75.14) (Figure 2). Of the sharks tagged, 81 were adult males, 46 were sub-adult males, 43 were adult females, and 40 were sub-adult females.

At Guadalupe Island, 122 acoustic tags were deployed onto 116 sharks (Figure 1) that ranged in estimated total length from 200cm to 570cm in total length (mean = 374.27cm; SD = 80.44). Of those sharks tagged, there were 26 adult males, 33 sub-adult males, 18 adult females, and 39 sub-adult males.

Mean length of time that acoustic tags remained attached to a white shark and had a functional battery that transmitted a signal was 572 days (SD = 508; range = 6 to 2983 days). Over the course of the study, we recorded a total of 2,871,286 detections from receivers placed at both locations in CC and GI. In CC, there were a total of 630,230

detections from receivers (VR-2, VR-3, and VR-4) and 2,241,056 detections from receivers in GI (VR-2) (Figure 2). A summary of the number of sharks with functioning acoustic tags for each year of the study can be found in Table 1.

Of the 326 total sharks tagged in the study, 210 (64.42%) were tagged in CC while the other 116 (35.58%) were tagged off GI. Of the 326, 30 (9.20%) were detected in both locations, and 296 (90.80%) were detected only at the aggregation sites (CC or GI) where the tag was originally applied. Of the 30 sharks detected at both locations, 20 (66.67%) were tagged in CC and included four adult males, seven sub-adult males, two adult females, and seven sub-adult females. The 10 (33.33%) sharks tagged in GI that were detected at both locations included zero adult males, six sub-adult males, one adult female, and three sub-adult females. It is interesting to note the proportion of sharks tagged at each region is similar to the proportion of sharks that have moved from each region.

Of the 30 sharks that moved, 20 made one move to the other region and apparently remained in the other region for the remainder of tag function. There were eight sharks that made two movements meaning they moved to the other region and then returned to the original tag location. There was one shark that made three movements and one shark that made four movements.

There were three sharks that made more than one transition within a season (shark # 300, 350-cm male; shark # 114, 450-cm female; shark # 89, 300-cm female). The straight-line distance from the southernmost location in CC to GI is ~ 950 km. The mean length of time of within season movement between CA and GI ranged from 8 to 91 days

(mean = 32.56 days; SD = 24.81). Therefore, the fastest minimum rate of travel was 133 km/day at 4.7 km/hr.

Model Results

The model converged successfully, and the posterior distribution for model coefficients generated predicted values that corresponded well with features of the observed data. The model results indicated that the probability of moving in between CC and GI (regardless of direction) was quite rare ($\alpha = -4.16$; SE = 0.86; 90% credible intervals [CI] = -6.11 to -2.72). The model indicated that males and females were quite similar with respect to movement probability ($\beta_s = 0.15$; SE = 0.63; 90% CI = -1.15 to 1.37). Adults were less likely to move than sub-adults ($\beta_m = -2.10$; SE = 0.71; 90% CI = -3.63 to -0.79), and sharks were similar in movement probability given their starting location ($\beta_l = 0.55$; SE = 0.51; CI = -1.54 to 0.47). The estimated variance term for the random effect for individual sharks was larger ($\hat{s}^2_{\text{ind}} = 7.65$; 90% credible intervals = 2.68 to 16.67) (Figure 3) than the random effect for years ($\hat{s}^2_{\text{year}} = 0.12$; CI = 0.00 to 0.64) (Figure 4). The mean annual probability for each demographic at each study site (CC or GI) can be found in Table 2. As only 30 of the 326 sharks in this study moved to the other region, accordingly, the individual random effect-outcomes predicted for all but the 30 sharks were small and below 0, whereas the remaining 30 tended to be small and positive with only a very few sharks predicted to have positive random effects that notably increased their probability of movement. Predicted probabilities of moving between CC and GI for each of the 30 individuals that moved averaged 0.39 (SE = 0.22)

(Figure 3), whereas movement probabilities for the other individuals averaged <0.02 (SE = 0.05).

Discussion

The purpose of this study was to better understand the connectivity between the two main aggregations that comprise the northeastern Pacific population of sub-adult and adult white sharks. Our results indicate that the majority of sharks have high annual fidelity to their respective site, consequently only a small proportion of sharks use both aggregation sites. However, depending on whether white sharks mate while coastal as opposed to offshore, a small amount of coastal connectivity for adult size classes can have consequences for genetic structure of the population.

Of the sharks that have been detected at both aggregation sites, sub-adult sharks were more likely than adults to be using or exploiting both aggregation sites. These results are consistent with previous studies that have found sub-adult sharks to be present at some time at both major aggregations (Jorgensen et al. 2012; Hoyos-Padilla et al. 2016). Sub-adult connectivity has also been hypothesized to be the source of mixing between the two aggregations (Domeier 2012). However, in this study, we also detected seven adult white sharks (four male, three female) at both locations, a first for this population that is not consistent with the hypothesis that only sub-adults move between sites (Domeier 2012). The mechanisms driving a small number of individual sharks to use or exploit both areas as opposed to the majority of the population that is faithful to

one site remains unknown. It could be associated with density of white sharks at aggregation areas, potentially leading to increased intraspecific competition.

Sub-adult white sharks are a demographic of which relatively little is known. However, sub-adult white sharks undergo an ontogenetic shift in diet and habitat (Tricas and Mccosker 1984) and transition to aggregations where adult white sharks are well established and have been successfully exploiting those areas for food resources (Weng et al. 2007b). There is likely intense intraspecific competition for newly recruiting sub-adult sharks prospecting for new resources around pinniped prey concentrations to fulfill their increased physiological demand in colder waters. It has been shown that the smaller size classes in CC have substantially lower apparent survival rates than larger conspecifics (Kanive et al. 2019). However, because mortality is confounded with permanent emigration in apparent survival, this could mean that smaller sub-adults may fail to recruit at adult aggregating sites resulting in either mortality or emigration to secondary locations. Grievous wound have been observed on multiple sub-adult sharks that appear to have been inflicted by a larger white shark (Kanive et al. 2019). Increased exploration for sub-adults could be motivated by such intense competition at established, predominately adult hunting grounds.

This study provides critical information for a future estimation and assessment of the overall abundance of the northeastern Pacific that includes both groups, CC and GI, which to date have largely been considered separately. As described in this paper, there is connectivity between the two main aggregation of both sub-adults and adults that must be considered when incorporating data from both locations to estimate overall population

characteristics, as simply summing independent estimates could include ‘double-counted’ individuals. Furthermore, a joint method of ‘marking’ or identifying individuals, such as using the long-lasting (>26 years) natural and unique patterns on dorsal fins (Anderson et al. 2011) is needed to incorporate data into a mark-recapture framework, an established method to identify population vital rates (Kanive et al. 2015, 2019; Chapple et al. 2016) and abundance estimates (Chapple et al. 2011; Towner et al. 2013; Chapter 3). Lastly, continued and expanded mutually beneficial collaborative efforts and shared information are needed to enable researchers to estimate robust population parameters that can be used for international management.

Year	2008	2009	2010	2011	2012	2013
Non-movers	55	72	72	92	92	71
Movers	1	4	3	3	4	3
Total Tags	56	76	75	95	96	74
% Move	0.018	0.053	0.04	0.032	0.042	0.041

Year	2014	2015	2016	2017	2018	2019
Non-movers	70	53	35	74	55	28
Movers	3	1	1	6	8	3
Total Tags	73	54	36	80	63	31
% Move	0.041	0.019	0.028	0.075	0.127	0.097

Table 1. Summary of white shark's movements throughout the 2008-2019 study period. Non-movers are the number of sharks that stayed in their respective tagging location. Movers are the number of sharks detected at the alternate tagging location. Total tags are the number of active tags detected on receivers each year of the study.

Group by Location	No. Annual Transitions	#No. Moved	Obs. Prop. Moved	Pred. Mean Prob. of Moving	Pred. Mean SE	90% Credible Intervals	
GI SAF	71	5	0.070	0.087	0.113	0.000	0.467
GI SAM	59	10	0.169	0.154	0.128	0.000	0.778
GI AF	42	2	0.048	0.028	0.052	0.000	0.014
GI AM	47	1	0.021	0.030	0.055	0.000	0.013
CC SAF	101	8	0.079	0.073	0.091	0.000	0.390
CC SAM	131	11	0.084	0.084	0.086	0.000	0.487
CC AF	97	2	0.021	0.024	0.046	0.000	0.014
CC AM	262	4	0.015	0.017	0.036	0.000	0.007

Table 2. Results from the GLMM analysis that summarize movement probabilities for each demographic at central California, USA (CC) and Guadalupe Island (GI), Mexico. Age and sex-class codes are as follows; SAF = sub-adult female, SAM = sub-adult male, AF = adult female, AM = adult male.

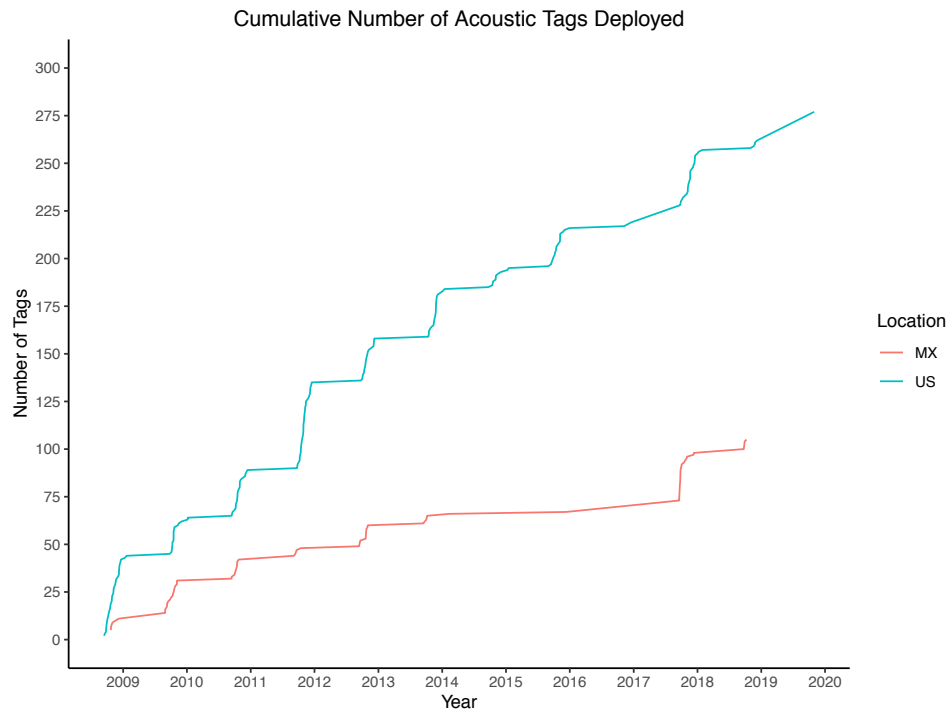


Figure 1. Cumulative number of acoustic tags deployed on white sharks for both locations (Mexico in red, California in blue) for the 2008 to 2018 sampling seasons.

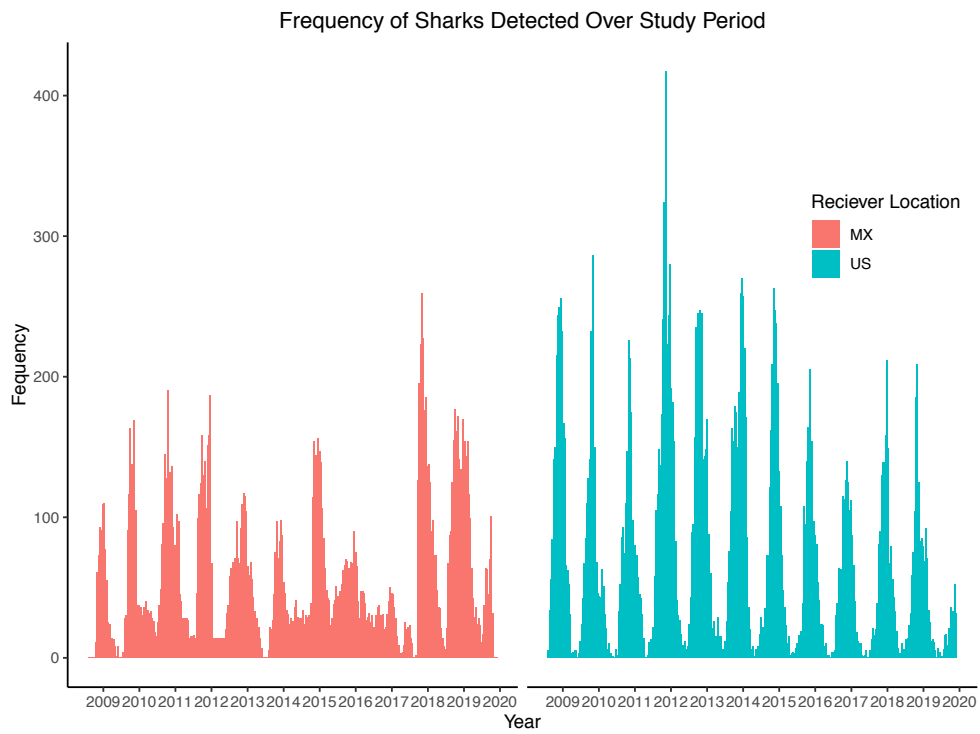


Figure 2. Frequency distributions of acoustic detections for individual white sharks at each study region over the study period. Number of detections are binned in 14 day intervals.

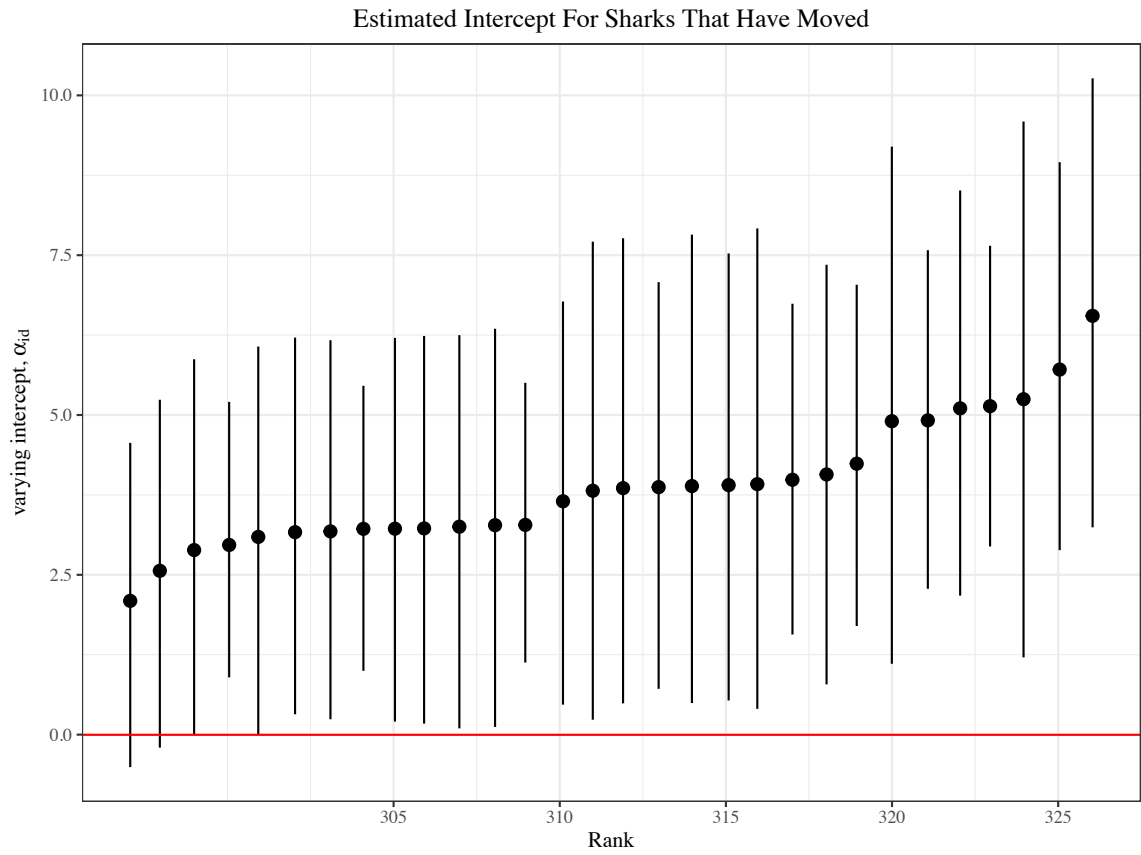


Figure 3. The estimated intercept with 90% credible intervals for each of the 30 individuals that were detected at both study sites. The horizontal red line is the mean probability of moving for this group of 30 sharks.

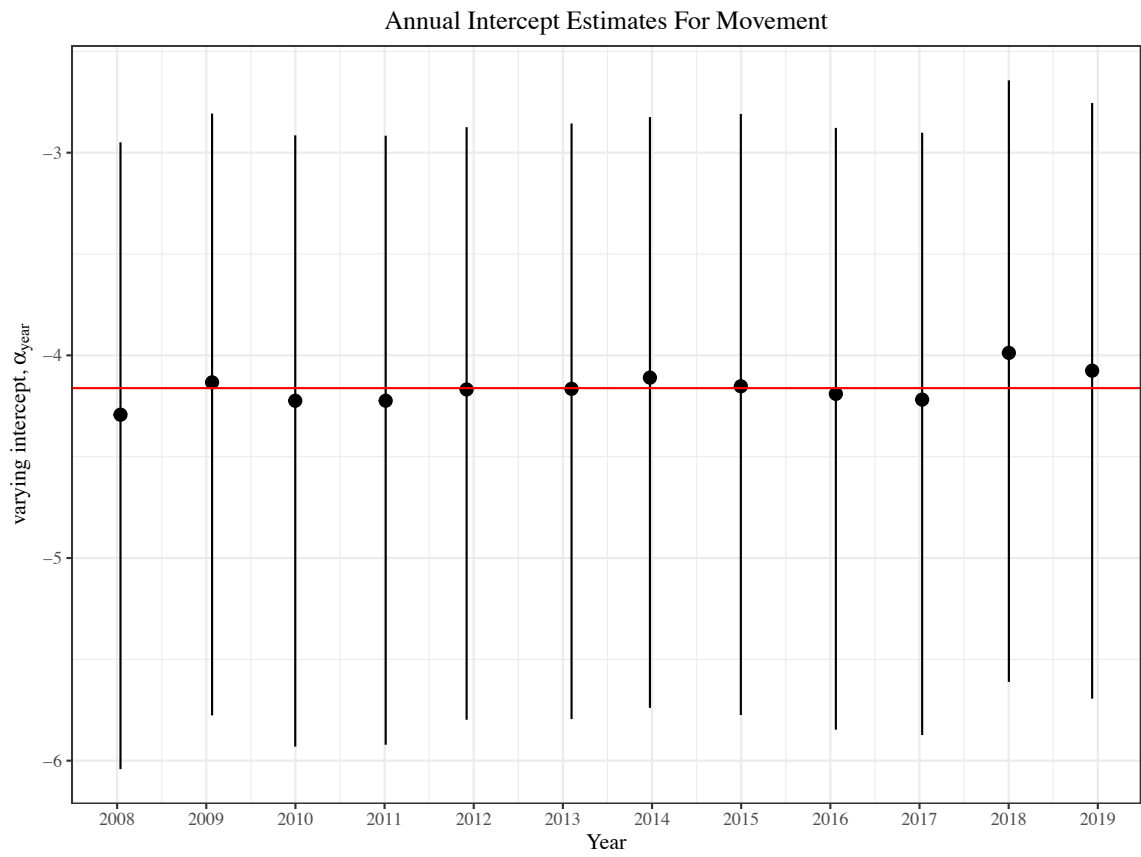


Figure 4. The annual log-odds of movement with 90% credible intervals for sharks tagged from 2008 to 2019.

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CHAPTER FIVE

CONCLUSION OF THE DISSERTATION

This dissertation focused on multiple aspects of population dynamics for white sharks off California, USA. White sharks have recently become one of the most studied elasmobranchs in the world with advances in tagging technology, analytics, and genetic technics (Huveneers et al. 2018). However, assessments of size and status of white shark populations remain the highest priority among white shark experts (Huveneers et al. 2018). In this dissertation, I analyzed long-term mark-recapture and acoustic telemetry data to assess the California population of sub-adult and adult white sharks and its connectivity with a Mexican population around Guadalupe Island.

First, I used empirical data and a mark-recapture model to produce the first set of estimates of size-specific apparent survival rates for sub-adult and adult males and females in California (chapter 2). Model results in chapter 2 provide evidence that annual apparent survival rates for smaller sub-adults are lower than rates for adults. These results indicate that smaller age-classes are potentially experiencing high mortality adapting to new prime foraging grounds where adult white sharks are established, and intraspecific competition is likely high and leading to mortality. Alternatively, as mortality is confounded with permanent emigration in the apparent survival estimates presented in this dissertation, it is possible that some or perhaps even all of the disparity between rates for smaller sub-adults and adults could be the results of sub-adults responding to intraspecific competition emigrating away from our sampled area after their last sighting for the remainder of the study (i.e. permanently emigrating from the site with respect to

the work presented here). Sub-adults may be driven through density-dependent competition to sub-prime foraging habitat outside the study area. Future tagging studies that provide information on fine-scale coastal movement could help decouple these possibilities. Further, future technology advances might provide telemetry devices that would allow researchers to determine a shark's live-dead status anywhere that it goes, e.g., satellite transmitters with long life. If so, true survival rates could be compared to apparent rates to determine the nature of emigration by sub-adults and its potential impacts on estimates of apparent survival.

White sharks have been protected in California since 1994 (Heneman and Glazer 1996) and their preferred prey, pinnipeds, have been protected since 1972 (Marine Mammal Protection Act). Additionally, bans on gill-net fisheries (out to 5 km) to mitigate sea otter mortality have also decreased bycatch (leading to decreased mortalities) of juvenile white sharks (Lyons et al. 2013). These direct and indirect management measures are potentially leading to increases in the numbers of white sharks in California. There is ancillary evidence of white shark numbers increasing from increased mortality in sea otters due to white shark bites (Tinker et al. 2016) and increased sightings and incidental captures of juvenile size classes in the Southern California Bight (Lyons et al. 2013; Lowe et al. 2012). White sharks were thus deemed to be 'likely increasing' in a 2013 NOAA white shark status review (Dewar et al. 2013). However, population growth rates of white sharks had not previously been estimated. In this dissertation, I provide estimates of the annual abundance of sub-adult and adult males and females and investigate population growth rates for each demographic group (chapter 3). Overall, the

population of sub-adult and adult white sharks in central California is estimated to be small (< 300 individuals total), but I also found evidence that the adult demographic was increasing in size over the 8-year study period (chapter 3). However, investigating the annual abundance for each group reveals strong evidence of a modest annual increase in numbers of adult males and females. The results were more equivocal for the sub-adults, a group for which I report point estimates of positive annual population growth rate that are accompanied by measures of uncertainty that do not rule out alternative trajectories. The evidence provided suggests that management policies to protect white sharks and their prey have likely enabled the white shark population to modestly increase over the study period 2011 to 2018.

White sharks that aggregate off of northern California, USA and off of Guadalupe Island, Mexico comprise the northeastern Pacific white shark population. However, little evidence of connectivity between the sites has been obtained in over a decade of research involving marked individuals at the two locations (Jorgensen et al. 2012; Hoyos-Padilla et al. 2016). In chapter 4 of this dissertation, I quantified rates of movement between the two metapopulations using a comprehensive acoustic telemetry dataset from an international collaborative effort between USA and Mexico. The results of the analysis reveal that annual movements between the two sites are rare when compared to the majority of sharks observed to have high fidelity to their respective coastal aggregations. However, of the sharks that were shown to use both locations, the sub-adults were more likely than adults to move. It is important to note that this study showed empirical evidence that adult sharks did move between these two locations, a behavior previously

unobserved. This analysis underscores the need to have a common methodology of identifying individual white sharks in both metapopulations to conduct a comprehensive population assessment of the total northeastern Pacific population of white sharks.

Vital rates and population assessments are an essential component of determining whether management practices are effective and using empirical data as the basis for those vital rates (1) removes a number of simplifying assumptions and (2) reduces some of the uncertainty associated with previously available estimates of key white shark parameters presented here. Although this dissertation moves our understanding of the northeastern Pacific white shark population forward, more research is needed to better understand when sub-adults transition into the population, how transition rates vary with age and year, and how their resource use compares to that of adults. Additionally, the two northeastern Pacific aggregation sites are not completely distinct, requiring further collaboration to develop shared identification practices to build more-complete information for the northeastern Pacific population that incorporates spatial connections between the two population units and that can better inform international management of this species. Overall, this dissertation provides an important population assessment of a marine top predator in the northeastern Pacific and provides a framework for future work that involves international collaboration and unified management goals.

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