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ARTICLE

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 (standard error (SE) = 0.08) for newly recruiting subadults 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 subadult 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.

Résumé : Pour les espèces qui existent en faible abondance ou dont l'étude présente par ailleurs un défi, il est difficile d'estimer des indices vitaux comme la survie et la fécondité et il est couramment présumé que les taux de survie ne varient pas selon le sexe et le groupe d'âge. Des évaluations de populations reposant sur des indices vitaux trop simplistes peuvent mener à des conclusions erronées. Nous avons estimé les taux de survie annuels apparents en fonction du sexe et de la longueur pour de grands requins blancs (*Carcharodon carcharias*). Nous avons relevé des preuves de variation du taux de survie annuel apparent au fil de l'ontogénie dans un système caractérisé par des regroupements concurrents d'individus en quête de nourriture, ce taux allant de 0,63 (l'écart-type (ÉT) = 0,08) pour les individus subadultes récemment recrutés à 0,95 (ÉT = 0,02) pour les requins les plus grands. Nos résultats révèlent une difficulté potentielle en ce qui concerne le recrutement ontogénique chez un prédateur marin de niveau trophique supérieur très mobile et longévif, puisque les taux de survie de grands requins blancs subadultes pourraient être plus faibles que présumés auparavant. Une autre explication est que les individus plus jeunes ou moins concurrentiels pourraient être forcés d'émigrer des meilleurs sites d'approvisionnement de manière permanente. L'étude présente une nouvelle méthodologie pour estimer la survie apparente en fonction de différentes variables reliées, par une approche de capture–recapture, y compris pour les cas où l'affectation du sexe est incertaine. [Traduit par la Rédaction]

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, we need the survival schedule (survival rate as a function of age of the animal) and information on age-specific fecundity. 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).

Owing to the challenges of evaluating status of populations with sparse or nonexistent 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; Mills 2012; Caswell 2014). 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 pres-

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ent substantial 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 2018). Additionally, even when maximum life-span is known, it has been shown to be a poor statistic to estimate annual survival (Krementz et al. 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- or stage-specific population parameters, a single survival value across all ages has been inferred from maximum life-span 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, California, to colder more productive waters in central California (Weng et al. 2007*b*). 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, 2010; Mucientes et al. 2009). 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% confidence interval (CI) = 0.40–0.72) than males (0.015, 95% CI = 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 subadult 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 (standard error (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- and 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 exists 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 are 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 9-year data set 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 subadult 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 TL 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 subadult and adult white shark aggregations along the central California, USA, coast (Año Nuevo, Southeast Farallon Island, and Tomales Point; Fig. 1) during periods of peak residency (August–February) from 2006 to 2014. Owing 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 con-

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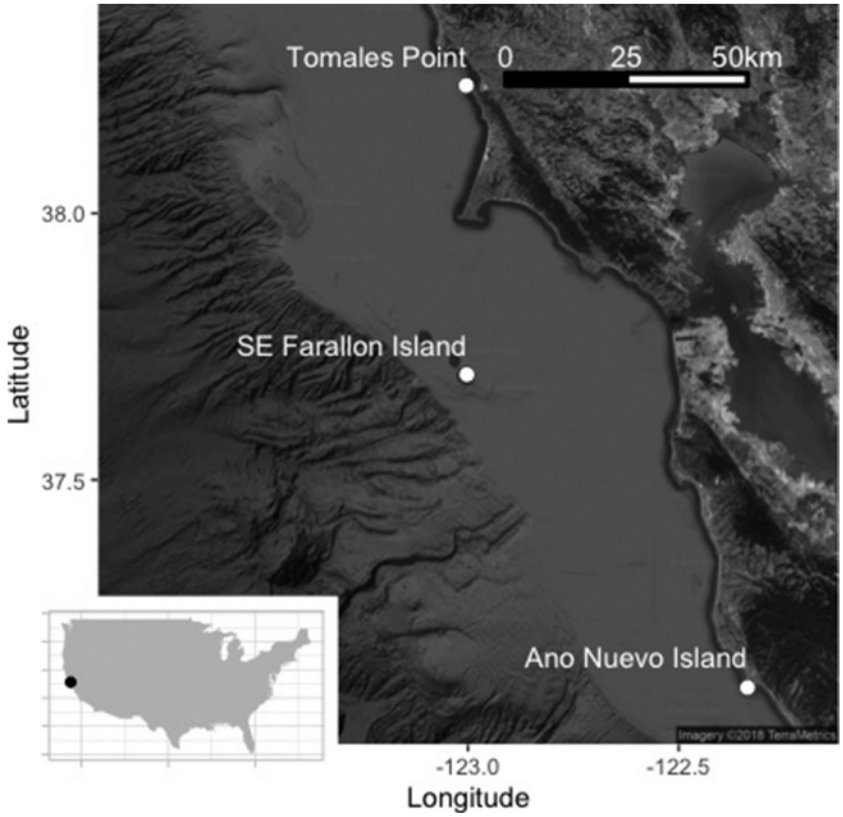
Fig. 1. The three white shark aggregation sites off California, USA, sampled in this study.



firmed when a shark was sighted and identified by its fin characteristics. Thus, we used models that allowed for unknown-sex individuals. For TL, 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 resightings of live animals with imperfect detection, are analyzed with the Cormack–Jolly–Seber (Cormack 1964; Jolly 1965; Seber 1965; Williams et al. 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 follows:

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

p_i^s = 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_i^s = 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.

To be efficient in model testing, we used the most appropriate model suite determined by Kanive et al. (2015), with the addition of a test of whether TL and survival rate were related over the 9-year data set. 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, 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 (refer to online Supplementary material, Table S1[1]). We used Akaike's information criterion adjusted for sample size (AIC_c) to evaluate the support

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0142.

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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 χ^2 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 data set, 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 with those obtained from the full data set. For our 9 years of data, the full data set yielded estimates of survival for 8 years, whereas the left-truncated subset of data yielded estimates for 7 years. For those 7 years the two data sets 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 3194 h 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 h; Ano Nuevo Island, 70 days, 321 h; Tomales Point, 495 days, 2221 h). A total of 291 individuals were identified by natural dorsal fin marks that we identified from 1187 high-quality photos of fins obtained over the 9-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 to 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 AIC_c.

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 data set 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[1]).

Of the 13 models considered (Table S1[1]), two received support from the data ($\Delta AIC_c \leq 1.12$); all others had $\Delta AIC_c > 3.24$ (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 TL 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 TLs; $\hat{\varphi}$ increased from 0.63 (95% CI = 0.47–0.77) for a 240 cm shark to 0.95 (95% CI = 0.90–0.97) for a 550 cm shark. In the second-best model, $\hat{\varphi}$ was related to both sex and body length (additive effects); point estimates from the model indicate that $\hat{\varphi}$ is higher for females than for 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, $\hat{\varphi}$ for a shark of average length (398 cm) was estimated as 0.91 (95% CI = 0.73–0.97) for a female and 0.84 (95% CI = 0.79–0.88) for a male (Fig. S1[1]). 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.

Table 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).

Model	K	AIC_c	ΔAIC_c	w_i
$\varphi(TL) \times p(sex) \times \pi(.) \times \delta(sex + t)$	15	1818.42	0.00	0.56
$\varphi(sex + TL) \times p(sex) \times \pi(.) \times \delta(sex + t)$	16	1819.54	1.12	0.32
$\varphi(sex \times TL) \times p(sex) \times \pi(.) \times \delta(sex + t)$	17	1821.66	3.24	0.10
$\varphi(TL) \times p(sex + t) \times \pi(.) \times \delta(sex + t)$	23	1826.82	8.40	0.01
$\varphi(sex + TL) \times p(sex) \times \pi(.) \times \delta(sex + t)$	24	1827.57	9.15	0.01

Note: K is the number of parameters; w_i is the relative weight of evidence for each model.

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 (hereinafter called survival) rates were positively associated with increasing TL but did not substantially differ between sexes for subadult 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 assumed that longevity is only 15 years, which recent studies have suggested may be longer (Hamady et al. 2014; Andrews and Kerr 2015; 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 (2002) study. The results from this study in combination with recent work showing annual survival of 0.63 in the first

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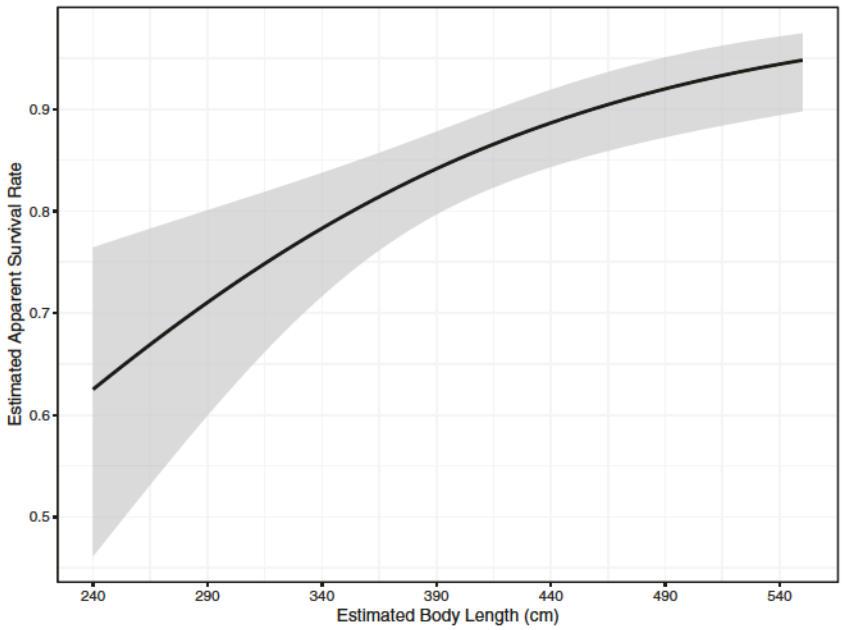
Fig. 2. Estimated survival curve as a function of total body length. The black line represents the annual apparent survival point estimate for a given length. The grey area represents the 95% confidence intervals.



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* — Van 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 9 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). Moreover, 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 composed 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 substantial evidence of transience in any year of the study. Therefore, transience likely does not cause major bias in previous abundance estimates (Chapple et al. 2011) or in the vital rates estimated here.

Potential causes of mortality

All of our study sites have high abundance of pinnipeds, the dominant prey source for subadult 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, 2012; Carlisle 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.

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Fig. 3. 275 cm female (top panel) and 305 cm male (bottom panel) white sharks with wounds inflicted by a conspecific. [Colour online.]



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 (Tricas and McCosker 1984). This strategy mitigates direct contact with the prey, avoiding potential injury from defenses of the prey. Subadult sharks in the smaller length classes incur substantial wounds and scarring inflicted by animals with claws and teeth consistent with the harbor seal (*Phoca vitulina*) and California sea lion (*Zalophus californianus*) (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 bigeye 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.

Fig. 4. 275 cm female with wounds on head inflicted by pinniped. [Colour online.]



In conclusion, using a new technique with broad applicability to mark–recapture systems, we have provided the first length-based survival rate estimates for subadult and adult white sharks based on empirical evidence. We have shown strong evidence for disparate survival rates between subadult and adult white sharks, indicating a potentially much lower rate of survival for newly recruited subadult 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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