

**Problems with Photo Identification as a
Method of Estimating Abundance of White
Sharks, *Carcharodon carcharias*
*An Example from Guadalupe Island, Mexico***

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ABSTRACT

White Shark aggregation sites offer some of the best opportunities to gather data on species biology and ecology. Mark-recapture methods are useful for estimating abundance, as long as their underlying assumptions are met. In this chapter, we employed the encounter histories of 113 (67 males and 46 females) photo-identified White Sharks as the base information for a mark-recapture analysis for the Guadalupe Island aggregation site. We estimated apparent survival, recapture probabilities, permanent entry into the population, and the superpopulation size by using the Cormack-Jolly-Seber (CJS) model and a generalization of the Jolly-Seber (JS) model for the open-population

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mark-recapture experiments. We fitted several model structures for each of the CJS and JS types and selected the best-fit model structure using the corrected Akaike's Information Criterion. Our results indicated that although apparent survival and permanent entry into the population varied with time, the recapture probability varied with sex ($p_{\text{female}} = 0.51 \pm 0.044$; $p_{\text{male}} = 0.79 \pm 0.029$). The superpopulation size by sex were 51 females (SE = 2.7) and 69 males (SE = 1.6). However, the assumption of equal recapture probability was violated by our encounter histories of males, producing an underestimation of the population size by the model. We discuss all the possible explanations for the violation of the assumption, based on this and another recent study. We recommend the use of this type of analysis as an index of abundance only, which can provide a long-term population trend but not an absolute abundance until methods can be improved.

INTRODUCTION

Elasmobranch aggregation sites offer some of the best opportunities to gather data on species whose population sizes or distributions are otherwise unclear or unknown (Marshall et al., 2011). For the White Shark (*Carcharodon carcharias*), such aggregations have been identified off of Central California (CC), California (Klimley et al., 1992; Klimley and Anderson, 1996); the southern coast of South Africa (Cliff et al., 1996; Ferreira and Ferreira, 1996); Spencer Gulf, South Australia (Strong et al., 1992, 1996); and Guadalupe Island (GI), Mexico (Domeier and Nasby-Lucas, 2007; Chapter 25, this book).

Satellite tagging studies in the northeastern Pacific have shown annual offshore migrations of subadult and adult White Sharks tagged at the aggregation sites in CC and GI (Boustany et al., 2002; Weng et al., 2007; Domeier and Nasby-Lucas, 2008; Jorgensen et al., 2010). The return of tagged White Sharks to their original tagging location, after an offshore migration that lasted many months, documented seasonal philopatry in White Sharks (Weng et al., 2007; Jorgensen et al., 2010; Chapters 11 and 16, this book). This site fidelity has allowed for long-term monitoring of individual White Shark visitation patterns, via photo identification (photo-ID) methods, at both the CC (Anderson and Goldman, 1996; Anderson et al., 1996, 2011) and GI (Domeier and Nasby-Lucas, 2007; Chapter 25, this book) aggregation sites.

Photo ID, which uses natural marks to recognize and catalogue individuals, has been widely applied as a population biology tool, particularly for the study of cetaceans (Stevick et al., 2001). Photo-ID studies of elasmobranchs are relatively recent (Marshall et al., 2011) and have examined a suite of species using natural pigment patterns, dorsal fin shape, and scars as natural tags (e.g., Anderson and Goldman, 1996; Sims et al., 2000; Castro and Rosa, 2005; Porcher, 2005; Domeier and Nasby-Lucas, 2007; Dudgeon et al., 2008; Holmberg et al., 2009; Anderson et al., 2011; Marshall et al., 2011; Chapter 25, this book). Photo-ID methods have allowed the description of individual growth rates, reproductive cycles, sex difference in aggregations, demography analysis, and estimations of population structure and size.

The ability to assess the number of individuals in a given population is one of the most important process to effectively managing marine fish species, and mark-recapture techniques are an established means of conducting such studies (Castro and Rosa, 2005). After reviewing several approaches for conducting estimates of White Shark populations, Cailliet (1996) suggested that mark-recapture methods may be the most viable. Conventional tags were used to estimate the White Shark populations off the coast of South Africa (Cliff et al., 1996) and off Spencer Gulf, South Australia (Strong et al., 1996). More recently a photo-ID study used unique marks on the trailing edge of the dorsal fin to estimate the population of White Sharks off CC (Chapple et al., 2011).

Mark-recapture methods are powerful for estimating abundance, as long as their underlying assumptions are met (Letting and Armstrong, 2003). These methods consider different assumptions depending on whether the population is closed or open. Open populations are those subject to births,

death, immigration, and emigration during the time of the study and require four main assumptions to be met: individuals do not lose their mark and are not overlooked; the duration of each capture occasion is instantaneous in relation to the interval between occasions; all animals have the same survival probability; and all animals (tagged or not) have the same capture probability (Krebs, 1990). The heterogeneity of survival and capture probabilities is likely to exist, in some point, in all mark-recapture studies (Pollock et al., 1990). However, if assumptions are violated in some degree, you might still use the mark-recapture methods and recognize that the resulting estimates are biased, but you should be careful in using them only as indices of population size (Krebs, 1990).

In this chapter, we employed encounter histories of photo-identified White Sharks as mark-recapture information (Chapter 25, this book) to estimate their apparent survival and resighting (hereafter termed recapture for the purpose of this study) probabilities as well as annual and superpopulation sizes at GI. We applied the Cormack-Jolly-Seber (CJS) model and a generalization of the Jolly-Seber (JS) model for the open-population mark-recapture experiments (Schwarz and Arnason, 1996). Our results are discussed based on the methodology assumptions. In terms of biodiversity, GI is one of the most important Mexican islands in the Pacific Ocean, earning Biosphere Reserve status in 2003 (Ezcurra et al., 2005). White Sharks are protected under Mexican law (Chapter 15, this book), and the conservation of this species is one of the main objectives of the Biosphere Reserve management plan (Nadia Olivares, personal communication).

MATERIALS AND METHODS

The encounter histories for the 113 White Sharks described by Nasby-Lucas and Domeier (Chapter 25, this book) were analyzed by a mark-recapture approach to obtain population estimates of the White Sharks that aggregate at GI. Using pigment patterns and external reproduction organs to identify individual sharks, they photographically identified 67 males (59%) and 46 females (41%) between 2001 and 2009. Each White Shark was considered “tagged” at the time of first identification, and subsequent resightings were considered “recaptures.” Because of the low number of tagged sharks during 2001, sharks of years 2001 and 2002 were pooled for all analyses (see Table 25.1 of Chapter 25, this book for encounter histories).

Closed-Population Test

The assumptions for a closed population (i.e., emigration, immigration, mortality, or recruitment do not occur during the study period) were tested using the Stanley and Burnham (1999) and Otis et al. (1978) developments implemented in the CloseTest program (Stanley and Richards, 2005). Test results indicated that closed-population assumptions were violated by the encounter histories of the White Sharks that aggregate in Isla Guadalupe ($\chi^2 = 145.98$, $p < 0.0001$; z value = -8.21 , $p < 0.0001$), so open-population models were implemented.

Open-Population Models

CJS models were used to estimate apparent survival (ϕ) between annual shark-sighting seasons, and recapture probabilities (p) for each shark during a sighting season. The JS model provided estimates by sex for apparent survival (ϕ), initial capture (tag), and recapture probability (p), permanent entry into the population (β) and initial population size (N). Therefore, allowing us to estimate annual population size and superpopulation size, defined as the number of individuals visiting the study area each sighting season and the total number of individuals visiting the study area over the duration of the study, respectively (Marshall et al., 2011). Data analysis and model selection were carried out using the CJS and POPAN (for JS) routines in program MARK version 6.1 (White and

Burnham, 1999). To select the best-fit model, the corrected Akaike's Information Criterion (AICc; a second order AIC necessary for small samples) was used (Burnham and Anderson, 2002).

Test of Assumptions

The use of open-population models to estimate demographic parameters is based principally on the following main assumptions (Krebs, 1990):

1. Individuals do not lose their marks, and marks are not overlooked at capture.
2. Sampling time is negligible (instantaneous sampling) in relation to intervals between samples.
3. Every individual has the same probability (p_t) of being caught in the t th sample, regardless of whether it is marked or unmarked (JS model).
4. Every marked individual has the same probability of surviving (ϕ_t) from the t th to the $(t + 1)$ th sample.

For the CJS model, the third assumption refers to only marked individuals (Marshall et al., 2011). The achievement of the first and second assumption is discussed in the Discussion section. To test the third and fourth assumption for the CJS model, Tests 2 and 3 were applied to the encounter histories, using the program RELEASE, implemented through MARK (White and Burnham, 1999). Additionally, to assess overdispersion (lack of independence among individuals) in the data for the CJS model, the variance inflation factor c -hat was calculated by dividing the combined Test 2 and Test 3 χ^2 statistic by the degrees of freedom (df). When c -hat $>$ 1.0, there is indication of overdispersion, and CJS and JS models have to be adjusted using this estimated value (Burnham et al., 1987).

RESULTS

Test of Assumptions

Application of Test 2 to the overall encounter histories showed a nonsignificant heterogeneity in capture probabilities ($\chi^2 = 17.61$, $p = 0.062$) considering $\alpha = 0.05$. When analyzing by sex, the female group gave nonsignificant heterogeneity ($\chi^2 = 3.59$, $p = 0.601$), and the males showed significant heterogeneity ($\chi^2 = 14.02$, $p = 0.0155$); however, the test also indicated that the data were insufficient, so open models can be applied, but this result must be considered during the data interpretation. Test 3, in its two components (Test 3 Sm and Test 3 Sr), showed nonsignificant heterogeneity in survival probabilities in the overall data and by sex, yielding p values $>$ 0.22. These results support the underlying assumption for the open model. The combined goodness-of-fit testing (Test 2 + Test 3) for the full-time dependent CJS model showed a good fit to the data ($\chi^2 = 28.13$, $df = 30$, $p = 0.564$) indicating no overdispersion (c -hat = 0.938), so no further adjustment to the CJS and JS models were need.

CJS Models

CJS models were constructed considering the apparent survival (ϕ) and the recapture (p) probabilities as constant (\cdot) or varied with sampling interval (t) or by sex (sex) or their combination ($t*sex$). From 16 possible model variants, seven were selected based on their AICc weight and model likelihood values (Table 26.1). Burnham and Anderson (2002) state that values of $\Delta AICc <$ 2 indicate approximately equal support of candidate models and parameters of the models should be averaged. The difference between our model with the minimum AICc and the following one was 6.04 (Table 26.1), so there was no need for averaging. We found the best-fit model of $\phi(t) p(sex)$ with an AICc weight of 0.915 compared with other model variants. These results indicate that apparent survival varied between years independent of the sex and without a clear tendency through time ($\phi_1 = 0.97$

Table 26.1 Model Selection for the Cormack-Jolly-Seber Models of Survival and Capture Probability

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Number of Parameters
$\varphi(t) p(\text{sex})$	643.17	0	0.915	1	8
$\varphi(.) p(\text{sex})$	649.21	6.04	0.045	0.049	$3\varphi(t^*\text{sex})$
	650.82	7.65	0.020	0.022	12
$\varphi(\text{sex}) p(\text{sex})$	651.25	8.08	0.016	0.018	4
$\varphi(t) p(t^*\text{sex})$	654.82	11.64	0.003	0.003	19
$\varphi(.) p(t^*\text{sex})$	657.11	13.94	0.001	0.001	15
$\varphi(\text{sex}) p(t^*\text{sex})$	659.06	15.89	0.000	0.000	16

The table shows model selection for the CJS models of survival (φ), capture probability (p), considered as constant ($.$) or varied with time (t) or with sex (sex) or a combination. AICc, corrected Akaike information criterion; ΔAICc , difference in the AICc of a model from the minimum AICc model; AICc weight, Akaike weight.

± 0.028 SE, $\varphi_2 = 0.98 \pm 0.300$, $\varphi_3 = 0.99 \pm 0.000$, $\varphi_4 = 0.80 \pm 0.052$, $\varphi_5 = 0.97 \pm 0.042$, $\varphi_6 = 0.88 \pm 0.056$, and $\varphi_7 = 0.98 \pm 0.082$). Recapture probabilities varied depending on sex, where females recapture probability ($p_{\text{female}} = 0.51 \pm 0.044$) was smaller than males ($p_{\text{male}} = 0.79 \pm 0.029$). The second most parsimonious model $\varphi(.) p(\text{sex})$, with only 0.04 of AICc weight (Table 26.1), supported a constant survival over time ($\varphi = 0.93 \pm 0.014$ SE) with recapture probabilities that varied depending on sex ($p_{\text{female}} = 0.50 \pm 0.044$; $p_{\text{male}} = 0.79 \pm 0.029$) and were equal with the most parsimonious model considering the SE overlaps.

JS Models

In total, seven JS models were constructed considering apparent survival (φ) and recapture (p) probabilities and the permanent entry into the population (β) as varied with sampling interval (t) or by sex (sex) or their combination ($t^*\text{sex}$). The models were fitted using the logit link function for φ and p , the log link function for N , and the multinomial logit link function for β to constrain the set of parameters to $\beta < 1$ (White and Burnham, 1999). The best-fit model was $\varphi(t) p(\text{sex}) \beta(t)N$ with an AICc weight of 0.932 compared to other model variants (Table 26.2). Estimations of the apparent survival and recapture probabilities from this model were similar to those of the CJS model considering overlapping SE margins (Table 26.3). There were pulses of permanent entry into the populations (β , recruitment + immigration) (Table 26.3), likely an artifact of sampling effort. The examination of the parameter estimates from the first, less parsimonious model $\varphi(t) p(\text{sex}) \beta(t^*\text{sex})N$ with a AICc weight = 0.029 (Table 26.2) allowed an understanding of the variations of β deeper, as values varied with time and sex in the model. The tendency of the estimated values showed an every-other-year cycle and was mainly related with the permanent entry of females ($\beta_{2005-2006 \text{ female}} = 0.49 \times 10^{-7} \pm 0.000$ contrasted with $\beta_{2006-2007 \text{ female}} = 0.10 \pm 0.052$).

White Shark Population Estimates

White Shark annual population estimates by sex using the best-fitted model showed a general increasing tendency with values varying between 21 and 36 females and 28 to 49 males, with a decline in 2006, associated with the decline of β between 2005 and 2006 (Table 26.4). The numbers of White Sharks visiting the study area over the duration of the study (superpopulation) (Schwarz and Arnason, 1996) by sex were 51 females (SE = 2.7) and 69 males (SE = 1.6) (Table 26.4).

Table 26.2 Model Selection for the Jolly-Seber Models of Survival, Capture Probability, and Permanent Entry into the Population

Model	AICc	Δ AICc	AICc Weights	Model Likelihood	Number of Parameters
$\phi(t) p(\text{sex}) \beta(t)$	720.00	0	0.932	1	17
$\phi(t) p(\text{sex}) \beta(t^*\text{sex})$	726.97	6.97	0.029	0.031	22
$\phi(t^*\text{sex}) p(\text{sex}) \beta(t)$	727.49	7.49	0.022	0.024	21
$\phi(\text{sex}), p(\text{sex}) \beta(t)$	728.85	8.85	0.011	0.012	13
$\phi(t) p(t^*\text{sex}) \beta(t)$	732.18	12.17	0.002	0.002	29
$\phi(t) p(t^*\text{sex}) \beta(t^*\text{sex})$	732.80	12.80	0.002	0.002	31
$\phi(t^*\text{sex}) p(t^*\text{sex}) \beta(t)$	743.29	23.29	0.000	0.000	34

The table shows model selection for the JS models of survival (ϕ), capture probability (p), and permanent entry into the population (β) considered as varied with time (t) or with sex (sex) or a combination. AICc, corrected Akaike information criterion; Δ AICc, difference in the AICc of a model from the minimum AICc model; AICc weight, Akaike weight.

Table 26.3 Parameter Estimates from the Best-Fitted Jolly-Seber Model $\phi(t) p(\text{sex}) \beta(t)$

Parameter	Year/Sex	Estimate	SE	
ϕ	01&02-03	0.97	0.026	
	03-04	0.98	0.029	
	04-05	0.99	2.8×10^{-5}	
	05-06	0.79	0.052	
	06-07	0.97	0.042	
	07-08	0.88	0.055	
	08-09	0.98	0.082	
	p	Female	0.53	0.042
		Male	0.80	0.029
β	01&02-03	0.15	0.058	
	03-04	0.12	0.050	
	04-05	0.06	0.039	
	05-06	0.01	0.018	
	06-07	0.16	0.043	
	07-08	0.03	0.032	
	08-09	0.06	0.030	

Table 26.4 Annual Population Size Estimations and Superpopulation Size Estimates by Sex

Year	Female (SE)	Male (SE)
2001 and 2002	21 (3.2)	28 (4.2)
2003	27 (3.1)	37 (4.0)
2004	33 (2.9)	44 (3.7)
2005	36 (2.7)	48 (3.3)
2006	29 (2.8)	39 (3.5)
2007	36 (3.1)	49 (3.7)
2008	33 (3.0)	45 (3.7)
2009	36 (3.8)	49 (4.7)
Superpopulation	51 (2.7)	69 (1.6)

DISCUSSION

Using 9 yrs. of encounter histories of photographically identified White Sharks allowed us to estimate a superpopulation size of 120 subadult and adult sharks with $N = 51$ females (95% confidence interval = 47, 59), and $N = 69$ males (95% confidence interval = 67, 75) that aggregate at GI. Chapple et al. (2011) conducted a population estimate for White Sharks that aggregate off CC, and using a Bayesian closed-population model they arrived at a number of 219 (range, 130–275). Together these population estimates suggest a total of 349 subadult and adult White Sharks visiting these two aggregation sites. Because this likely constitutes the majority of White Sharks in the northeastern Pacific (within these age classes), the number is alarming low. However, before we accept this as an absolute population size, we have to evaluate how well the assumptions of the models were met.

Closed versus Open Population

A closed population is one that does not change in size during the study period; that is, the effect of births, deaths, and movements are negligible. Thus the populations are typically closed over only a short period of time. An open population is the more usual case, a population that changes in size and composition from birth, death, and movements (Krebs, 1990). Our estimate assumed an open population, while that of Chapple et al. (2011) assumed a closed population over a 3-yr. sampling period. Our long term photo-ID monitoring at Guadalupe Island (Domeier and Nasby-Lucas, 2007; Chapter 25, this book), as well as our satellite-linked radio transmitting tags, have shown individuals to disappear (Chapter 16, this book); these sharks either died or migrated elsewhere. We have also seen the sudden appearance of new sharks that are so big it is unlikely they have been present for many years and never before observed (Chapter 16, this book). Furthermore, Chapter 13, this book documented the migration of a White Shark from CC to GI; this shark did not return to CC. Clearly these populations are not closed, and our data did not pass the closed-model test, but how much of a difference will this ultimately make in the resulting population estimate?

Initial testing of our data under the assumption that the population is closed (Petersen maximum likelihood version) resulted in a population estimate of one hundred thirty-two, only 9% greater than the open model method presented here. The data from Chapple et al. (2011) passed the closed-population test, but this could be a result of their use of only 3 yrs. of data, compared with our 9 yrs. of data, or perhaps the population is so marginally open that the data can be modeled either way. Modeling an open population as closed would force the population size to be constant during the time of the study, restricting the analysis year by year without the possibility of estimating the superpopulation size.

Assumptions

The use of individual identification for tag-recapture estimates of abundance is based on four assumptions (Krebs, 1990). The first assumption is that no animal will lose its tag during the study or be overlooked during efforts to recapture tagged individuals. The violation of this assumption is likely to result in the underestimation of recapture probabilities and an inability to calculate survival/mortality and will result in an overestimation of abundance estimates (Pollock et al., 1990; Stevick et al., 2001; Marshall et al., 2011). Both photo-ID methods used on northeastern Pacific White Sharks have proven to be very effective over long time periods (Domeier and Nasby-Lucas, 2007; Anderson et al., 2011; Chapter 25, this book), validating this first assumption.

The second assumption requires instantaneous sampling that allows sufficient time between sampling intervals for mixing of the tagged and untagged sharks; this ensures the homogeneity of

recapture probability (Pollock et al., 1990; Strong et al., 1996). Photographically identified White Sharks were recaptured during the annual aggregation season at GI (August to January) with most recaptures occurring between August and November (Figure 26.1). The 8-month period between sampling was sufficient for population mixing and allowed robust survival estimates (see below). Mixing was further insured by the fact that the sharks leave the GI aggregation for an extended migration to offshore environments (Chapters 11, 12, and 16, this book) before sampling begins again upon their return. This is very similar to the situation off CC, and therefore both our study and that of Chapple et al. (2011) likely meet this assumption. This assumption is important for establishing conditions that allow for an equal probability of sighting all individuals during a sampling period (the third assumption).

The third assumption is that there is equal probability of recapture for all individuals during sampling, regardless of whether it is tagged or not. Although our entire encounter history resulted in a homogenous recapture probability, the result was very close to failing this test ($p = 0.062$). Furthermore, when the sexes were tested independently, the males failed the test of homogeneous recapture probability. To some degree, heterogeneity of capture probabilities is likely to exist in all tag-recapture studies (Pollock et al., 1990) and is generally the result of three factors (Krebs, 1990):

1. Learning by captured animals such that they avoid recapture in the future (called trap-happy or trap-shy individuals).
2. The behavior of individuals in the vicinity of the trap influences the recapture rate.
3. The position of the trap causes unequal opportunity for capture (heterogeneous sampling intensity).

Violating this assumption will result in an underestimate of the true population; because we empirically know our estimate is biased (because the modeled population is smaller than the number of known sharks; Chapter 25, this book), we must closely look at each of these causes of unequal catchability and assess whether any or all of them may be influencing our results.

Trap-happy responses are often associated with the use of baited traps (Pollock et al., 1990); although cage dive operators at GI and researchers off CC use bait to attract White Sharks within photographic range (Chapple et al., 2011; Chapter 25, this book), the fish are not actually captured, and therefore it is unlikely that this would cause individuals to avoid the vicinity of the bait in the future. Furthermore, it is not logical that cage-dive operations would produce a trap-happy response for males but not females. To the contrary, some individuals may become habituated to the bait and therefore be more likely to be attracted to the baiting site than nonhabituated individuals.

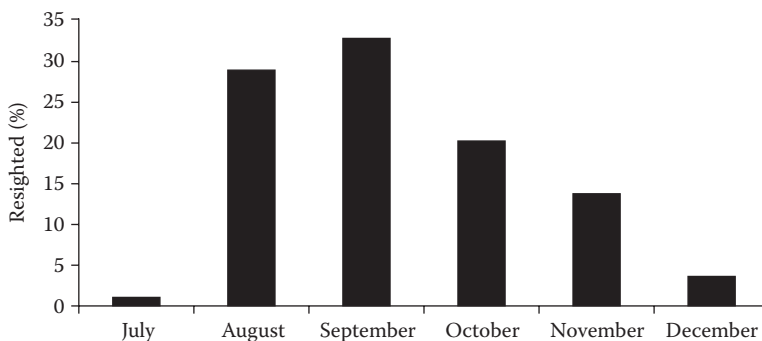


Figure 26.1 Monthly subadult and adult White Shark resighting percentage at Guadalupe Island, Mexico, during the 2001–2009 aggregation seasons.

Individual shark behavior may be influencing our results. Strong et al. (1996) suggested that social dominance influenced the probability of sighting individual White Sharks once they arrived at the bait source, based upon their observation of a size-based feeding hierarchy. They observed smaller White Sharks defer to larger conspecifics during direct interactions; however, subordinates were not completely excluded from the area. The dominance of larger animals over smaller individuals has often been observed at GI (M. Domeier, personal observation), and the male encounter history revealed a tendency for certain individuals to consistently have a higher recapture probability. Sex-specific migratory behaviors (Chapter 11, this book) also demonstrated a violation of equal recapture probability. For example, adult females have a 2-yr. migration cycle that may not bring them to the sampling sites (adult aggregation sites at GI and CC) every year (Anderson and Pyle, 2003; Domeier and Nasby-Lucas, 2007; Chapters 11, 16, and 25, this book). This would imply that up to 50% of the adult female population has a 0% chance of being resighted during every sampling period. In light of this, it is interesting that the female-recapture probability did not show recapture heterogeneity when tested, whereas the males failed the test, the opposite of what we would expect and perhaps an indication of inadequate sampling despite 9 yrs. of effort. However, this difference between the sexes could also be explained by the pattern of cage-dive operations that tend to be more intensive during the early portion of the aggregation season, when females are largely absent (Domeier and Nasby-Lucas, 2007; Chapters 16 and 25, this book). Although sampling occurs during the months females are present, the effort is less, and sampling does not occur through the end of the aggregation season.

The third potential cause of biased recapture probability involves the position of the trap or in this case the boat that is dispersing an attractant to lure White Sharks within photographic range. The boat and bait are at the surface, and sharks must be attracted close to the surface to be photographed from cages moored behind the vessel. Because White Sharks that visit the GI aggregation site tend to remain at the island for the duration of the aggregation season (Chapter 16, this book), and the cage-dive vessels operate at the same site year after year (northeastern corner of GI), this potential cause of heterogeneity of recaptures is not likely a factor at GI. For the Chapple et al. (2011) study, the position of the trap might have influenced the heterogeneity of the recapture probability. Jorgensen et al. (2010) described four sites of high White Shark density within the CC area and indicated that individual White Sharks showed some preference for one or more of these sites, and yet sampling for the CC population estimate only occurred at two of the four known sites of high White Shark abundance (Southeast Farallon Island and Tomales Point) (Chapple et al., 2011). For example, a shark with a preference for Tomales Point would not have the same probability of being reidentified at Southeast Farallon Island when compared with a shark with a known preference for Southeast Farallon Island. Furthermore, a third important CC site, Año Nuevo, was not sampled for the CC population estimate.

The fourth and final assumption used for estimating the population of White Sharks at adult aggregation sites requires equal apparent survival among tagged individuals, for the entire population as well as each sex separately. It is important to emphasize that the JS analysis cannot discriminate between survival and emigration, so the estimated apparent survival includes both permanent and temporary emigration as well as low-level mortality (Schwarz and Arnason, 1996). Our test result showed a homogeneous apparent survival between individuals, but the best-fit model indicated that permanent entry to the GI White Shark population varied over time. However, these pulses of recruitment match the pattern of newly identified individuals and are therefore explained by the variation in sampling effort between years (Chapter 25, this book). Given the different migratory patterns of males and females, we might have expected differing survival rates between the sexes. For example, females must migrate to coastal nursery areas where they may be more susceptible to incidental take by longline or gillnet gear (Chapter 16, this book), and females also spend more time in the open ocean where there are no protective measures in place that would restrict the take of White Sharks. However, the best-fit model indicated that there were no significant differences between the sexes.

Population Estimate versus Index of Abundance

The White Shark is a highly migratory, widely distributed apex predator with naturally low abundance, low natural mortality, and low reproductive potential (Bruce, 2008). These life-history traits, along with the fact that they form seasonally predictable adult aggregations, make them vulnerable to any anthropogenic mortality. Management and monitoring of aggregation sites is essential for the long-term survival of these populations, and modeling the populations should be an integral monitoring tool. However, both the analysis presented here and the analysis of Chapple et al. (2011) violate the assumption of equal probability of recapture and thus result in underestimates of the actual population; in our case, this fact has been empirically established by the raw photo-ID data from GI that provide a number of known individuals that is 8.5% higher than the modeled population (Chapter 25, this book). In our case we statistically failed this assumption while the sampling design of Chapple et al. (2011) creates a violation of this assumption. Chapple et al. (2011) used eight different models with similar results while stating that the presences of heterogeneity in recapture was limited; however, by excluding Año Nuevo and not considering the differing recapture probabilities relative to their study sites, their analysis may not be valid for the entire region. Furthermore, neither of the attempts to estimate adult and subadult populations attempted to develop a life history table that would provide population estimates for each age class of the overall White Shark population. Not all subadults visit adult aggregation sites, and virtually no juveniles visit these sites (Chapters 14, 15, and 16, this book), so the vast majority of the overall White Shark population is not included in either of these models.

Although efforts to estimate the number of individuals that visit adult aggregation sites are admittedly biased, they are valuable in establishing a baseline index of abundance for each of the sites. The White Shark is a protected species, highly mobile, and random sampling is very difficult to achieve (Cailliet, 1996). Until other methods that overcome these problems are developed, mark-recapture methods might be the only sources of estimation. However, considering the White Shark's multiyear migration patterns, and having access to long time series, such as the photo-ID data available from adult White Shark aggregations, the use of closed models is not justified. Furthermore, tagging studies have demonstrated that the northeastern Pacific White Shark adult aggregation sites are open populations (Chapter 13, this book); therefore we suggest standardizing population estimates at both sites by using a JS model that consider site and shark size as covariate (Pollock et al., 1990; Holmberg et al., 2009). Because the assumption of equal probability of recapture has been violated in several ways (resulting in underestimates of the true population), future modeling and/or sampling methods must be sought to increase the accuracy these population estimates. Although we identified bias in the application of photo-ID data to current efforts to model absolute population levels, our results, and that of Chapple et al. (2011), indicate that adult White Shark populations in the northeastern Pacific are small, highlighting the need for continued monitoring and precautionary management.

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