

**A critical analysis of the federal status review of the Northeastern Pacific population of white sharks (*Carcharodon carcharias*) under the Endangered Species Act.**

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December 18, 2013

***Abstract***

This document provides a critique of the federal status review report for the Northeastern Pacific population of white sharks (*Carcharodon carcharias*) (BRT, Dewar et al. 2013). This analysis brings into question the National Marine Fisheries Service's conclusion, which relied on the status review, that although the population was a distinct population segment, threatened or endangered listing was not warranted. There are significant flaws in the status review report. First, the BRT's evaluation of NEP white shark abundance was not substantiated by data. The BRT discarded as implausible the two lowest abundance categories (200 adult females or fewer) that are the most consistent with the best available data for young of the year bycatch mortalities and estimates of sub-adult and adult abundance at aggregation sites.

Second, contrary to standard scientific practices the BRT failed to adequately account for uncertainty, which likely led to underestimation of the severity of threats and risks to the population. The BRT failed to account for uncertainty in bycatch rates in its risk assessment, despite acknowledging that the numbers it used are probably underestimates. In addition, uncertainty in the intrinsic rate of population increase was not properly accounted for and risk criteria were narrowly defined. Adult female white shark abundances of 200 or fewer were found to correspond to medium to high risk of extinction by the BRT's assessment, which neglected major sources of uncertainty.

Accordingly, the status review report's conclusion that white sharks in the northeastern Pacific (NEP) are at low or very low risk of extinction and not likely to become endangered in the foreseeable future is unjustified because the BRT's evaluation was underpinned

primarily by beliefs about abundance and young of the year bycatch mortality rates, rather than data. Furthermore, the BRT's claim that the haplotypic diversity of NEP white sharks "*reflects a current adult female population size of at least a few hundred to a couple [of] thousand adult females*" is unsubstantiated. Additionally, the data sets presented by the BRT fail to provide evidence of a stable or increasing trend in white shark abundance, as the indices had major confounding factors that were not accounted for.

In light of the BRT report and the available data,, a high risk status appears to be highly plausible for NEP white sharks.

## ***Executive summary***

### *Background*

In June and August 2012, the National Marine Fisheries Service (NMFS) received two petitions for listing of the northeastern Pacific (NEP) population of white sharks (*Carcharodon carcharias*) as endangered or threatened under the Endangered Species Act (ESA). NMFS found the petitions to merit an ESA status review and formed a Biological Review Team (BRT) to conduct the review and report its findings on the risk of extinction to the NEP white shark population.

This document reviews the assumptions, methodology and findings of the BRT (Dewar et al. 2013) in the *Status review of the northeastern Pacific population of white sharks (Carcharodon carcharias) under the Endangered Species Act*. The BRT's conclusions regarding current abundance, bycatch mortality rates, trends in abundance and risk to the population are reviewed in the light of available information from the scientific literature.

The analysis finds that the status review inadequately supported its conclusions in several important respects. First, the conclusion that the most likely range for adult female white sharks is 400-1600 is unjustified and runs contrary to the best available science which is consistent with a much smaller population size. Second, the finding that bycatch mortality was below 20% is contradicted by tagging studies that show bycatch of young of the year to be a higher percentage. Third, Dewar's conclusion that the population may be increasing lacks a sound scientific basis. Finally, the team discounted the impact that uncertainty could have on its findings, which likely resulted in a biased risk assessment and overly optimistic appraisal of the population's outlook.

## *Current abundance*

The status review's conclusion that the most likely female population of NEP white sharks was above 400 individuals lacked scientific basis and is contrary to the best available science. Based on a series of structured expert decision making (SEDM) votes, Dewar et al. (2013) concluded that the most likely range for adult female abundance in the NEP is 400-1600 white sharks (i.e. 8.5 to 34 times the published estimates at aggregation sites). The BRT re-analyzed the mark-recapture (photo-identification) data of Chapple et al. (2011) and Sosa-Nishizaki et al. (2012) and estimated super-populations of 166 sub-adult and adult white sharks at Tomales Point and the Farallon Islands from 2006 to 2008 and 154 sub-adult and adult white sharks at Guadalupe Island from 2001 to 2011. The BRT's analyses corroborated published estimates (from open population models) of 156 sub-adult and adult white sharks for Tomales Point and the Farallon Islands and 120 at Guadalupe Island (Chapple et al. 2011; Sosa-Nishizaki et al. 2012).

The BRT's rationale for a much larger abundance for the NEP population as a whole than was estimated at the aggregation sites is primarily based on team members' opinions, rather than any hard evidence, about the number of white sharks that are not available to sampling at aggregation sites. To scale up abundance estimates at the aggregation sites to the whole NEP, Dewar et al. (2013) considered a number of factors affecting the sex ratio at the central California and Guadalupe Island aggregation sites and the proportion of adult females in the NEP population as a whole that does not visit the aggregation sites. Dewar et al. (2013) likely overestimated adult female abundance for several reasons:

- Several of the BRT's arguments for scaling up numbers at the aggregation sites based on under-sampling of females or the existence of separate parts of the population did not appear to be valid given information reported elsewhere (e.g. in Chapple et al. (2011)).
- The BRT posited the existence of numerous white sharks in other areas of the NEP that do not visit the aggregation sites. However, because white sharks are highly migratory and show strong philopatry, a high proportion of sharks that utilize other areas may be available to sampling at the aggregation sites. Dewar et al. (2013) were not able to demonstrate that white sharks in other areas of the NEP form separate parts of the population.

- There appeared to be overlap between arguments for scaling up mark-recapture abundance estimates related to average abundance at the aggregation sites and abundance in other parts of the NEP, which would lead to double counting of some parts of the population and overestimation of adult female abundance.

This is a key problem with the BRT's analysis, because their assessment of risk depends directly on abundance and the extrapolation of mark-recapture estimates to the whole NEP. Inflating the abundance estimates without sound empirical basis or reasoning is likely to result in underestimation of the extinction probability for NEP white sharks.

In support of their opinion that an adult female abundance of 400 or more (over 8 times the published estimates from the aggregation sites) is most plausible, Dewar et al. (2013) presented estimates of abundance (census population size) and data on haplotypic diversity for long-lived and slow-reproducing species (Table 2.2, p. 32). The BRT argued that the observed haplotypic diversity of NEP white sharks reflects a current adult female population size of several hundred to several thousand adult females, or that the population has recently undergone a dramatic decline from that level. However, the haplotype diversity data presented by Dewar et al. (2013) appear to contain only limited information about (past or current) abundance. The ratio of effective to census population size for the species they considered is unknown, and the census population sizes and measures of haplotypic diversity are weakly correlated.

The BRT evaluated the potential for a decline in adult female abundance from levels they considered to be consistent with the genetic data to numbers consistent with estimates at aggregation sites, accounting for bycatch mortality and concluded that *"the haplotypic diversity reflects a current adult female population size of at least a few hundred to a couple [of] thousand adult females."* This conclusion is unwarranted; even over the short timeframe of 41 years evaluated by the BRT, there appears to be fairly high probability of a current adult female abundance of "a few hundred" or less ( $\approx 40\text{-}50\%$ ) in 2011 with a starting abundance of 500 (Appendix B, Figure B1 top panel, Dewar et al. 2013). In addition, Dewar et al. (2013) used 500 adult females as the minimum number consistent with the genetic data in evaluating the potential for declines in abundance. However, given that they state that an abundance of a "several hundred" (p. 108, p. 127) adult females would be consistent with the genetic data, the potential

for decline for starting population sizes of 300 or 400 adult females should also have been evaluated, but was not. Given these issues, the genetic data presented by Dewar et al. (2013) do not comprise substantive support for adult female abundance abundances of several hundred or more, and do not detract significantly from the plausibility of the lower abundance categories considered (60 to 125 and 125 to 200 adult female white sharks).

### *Bycatch mortality*

Dewar et al. (2013) made assumptions about white shark bycatch mortality rates that are not consistent with the available data. Aside from expert opinion, the BRT considered the mortality rates implied by bycatch of young of the year (YOY) and juvenile white sharks to be “*one of the most important pieces of evidence*” for a low to very low risk of extinction (p. 108, Dewar et al. 2013), arguing that bycatch mortality rates over 20% are “highly implausible” considering estimated bycatch rates for marine mammals and turtles. However, observations from tagging studies with YOY white sharks suggest that the bycatch mortality rate may actually be much higher than 20% (Table 2). These observations provide estimates of the capture probability for YOY white sharks in fisheries as either 29% (2/7) or 43% (3/7), the latter assuming that the mortality rate of white sharks that were entangled and left their tag behind in the net was 0.49 (from Dewar et al. (2013), p. 48). Taking into account uncertainty in the bycatch mortality of YOY sharks and in vital rates, the YOY tagging data are most consistent with an adult female abundance less than 200 (Table 3). The reliance of the BRT on an inappropriate comparison with bycatch rates of marine mammals and turtles, and its omission to consider direct observations of YOY bycatch mortalities makes its claim that gill net bycatch mortality rates of 20% or higher would be “astonishing” (p. 106) difficult to defend. Since this was a key factor in the BRT’s decision (Dewar et al. 2013, p. 108), admitting the plausibility of higher bycatch mortality rates would likely result in a significantly higher evaluation of risk for NEP white sharks.

The BRT only considered low rates of bycatch mortality for adult females in its risk assessment; less than 2.5% for an adult female abundance greater than 400, the scenario judged most likely by the BRT. Given the high uncertainty about actual catches and available observations, a higher upper value for the bycatch mortality rate would have been more appropriate.

### *Trends in abundance*

Dewar et al. (2013) concluded (p. 109) that the available information is consistent with a stable or increasing population, but this is contradicted by their own admission (p.109) that “*population trend information is somewhat inconclusive.*” The trend in abundance does not appear to have been pivotal in their assessment, although they state that the data indicate “*an adult population size larger than what has been estimated based on photo-ID data for Guadalupe Island and Central California.*”

Dewar et al. (2013) considered several types of information (catch per unit effort data (CPUE), yearly abundance estimates from photo-identification and attacks on marine mammals) to assess whether the abundance of white sharks in the NEP is decreasing, stable or increasing. None of the data sets presented in Dewar et al. (2013) provide compelling evidence of a stable or increasing trend in white shark abundance. The available data for inferring trends in the abundance of white sharks are in many cases not straightforward to interpret owing to the presence of other, unaccounted-for confounding factors that can explain trends in observed catch or predation rates (e.g. changes in soak time, increasing density of prey species (functional response), changes in the foraging behavior of white sharks, etc.). Given this, the inclusion of unstandardized data on marine mammal attacks as a potential source of information about trends in white shark abundance is not justified.

In addition, the rate of change in all of the indices considered appeared to be too fast to reflect an increase in white shark abundance (Table 4). This indicates that an increase in white shark abundance alone cannot explain the observed trends, suggesting that other factors are partly or wholly responsible for them (e.g. shifts in foraging behavior or habitat use).

### *Assessment of risk*

The risk assessment was improperly weighted toward a lower risk of extinction classification due to inappropriate risk categories and because uncertainties in the data were not factored into the finding. Specifically, the BRT may have underestimated the severity of threats and thus risk to the population NEP white shark. Dewar et al. (2013) defined risk categories based

on the probabilities of decline to threshold population sizes of 25 “near extinction” and 125 “dangerously small” adult females (p. 97). The magnitude of decline was not considered as a separate component of risk, in contrast to the widely-used IUCN Red List criteria (IUCN, 2001). Using criteria based on both abundance and the rate of decline in abundance would have provided a more balanced summary of risks to the population.

The “near extinction” threshold population size of 25 adult females used by the BRT is inappropriately low, given that Dewar et al. (2013) reported bycatch mortality rates approaching 100% for YOY and age-1 white sharks for a population with 47 adult females. A threshold population size at which the extinction probability is roughly equal to one is arguably not suitable as a “near extinction” criterion; this is expected to lead to a significant underestimation of risk.

The approach taken by Dewar et al. (2013) appears to have under-represented uncertainty in a number of respects; overall, these are expected to lead to a less precautionary assessment of risk. Despite acknowledging that their results are conditional on the bycatch estimates used, and that those estimates are “*probably minimum bycatch estimates*” (p. 91), Dewar et al. (2013) did not account for uncertainty in YOY and juvenile bycatch mortality rates in their risk assessment. Since population risk assessment depends on a full treatment of uncertainty (e.g. Boyce 1992; Staples et al. 2004), this omission is a major flaw in their analysis and seriously undermines the credibility of their findings.

Uncertainty in the intrinsic rate of population increase ( $\lambda_{\max}$ ) also appears to have been understated by the BRT. The combined effect of these failures to account fully for uncertainty could lead to severe underestimation of risk.

### *Conclusions*

Dewar et al. (2013) concluded that the most likely risk category for NEP white sharks is “very low,” corresponding to an adult female abundance of 400 or more. However, the BRT offered little new information relevant to the abundance of white sharks in the NEP, instead using a strong assumption about the level of bycatch mortality of young of the year and juvenile white sharks to evaluate the plausibility of adult female abundance categories considered. The conclusion reached based on this assumption is largely circular, as mortality rates themselves depend on abundance. Observations of mortalities of tagged YOY white sharks suggest that the assumption made by the BRT was not appropriate.

Contrary to the assertion of Dewar et al. (2013), the genetic data do not appear to be inconsistent with a current adult female abundance less than “a few hundred.” Firstly, inferring a relationship between census population size and genetic diversity is problematic. Secondly, even if the BRT’s assertion was accurate, declines from a starting abundance of 300-500 adult females to less than “a few hundred” over 41 years would have a relatively high probability given the model in Appendix B (Dewar et al. 2013), whilst being consistent with the haplotype diversity data.

Failure to fully account for uncertainty in bycatch levels and demographic rates in concert with the questionable criteria and thresholds used to define risk is expected to have led to underestimation of risk for the NEP white shark population.

Taking these points into consideration, in addition to the available mark-recapture data and observations of YOY bycatch mortalities, the lowest two adult female abundance categories considered by the BRT (< 200) appear to be more parsimonious than the abundance found to be most plausible by the BRT (400-1600 adult females).

This review focuses on fishing mortality as the main threat to the population of white sharks in the NEP, as it was the only anthropogenic threat considered to be a “*potentially substantial risk factor*” by Dewar et al. (2013) (p. 107) and was the focus of their analyses in assessing extinction risk. The report begins with a critique of the use of structured expert decision making (SEDM) by Dewar et al. (2013). This is followed by sections that discuss arguments related to 1) current abundance 2) fishing mortality 3) trends in abundance and 4) risk assessment for the NEP white shark population. Additionally, this review references and addresses points raised in a draft version of the Burgess et al. (in review) study that was provided by NOAA Fisheries as part of their response to a Freedom of Information Act request. The Burgess et al. (in review) study included a critique of the Chapple et al. (2011) study, but has not been published as of the date of this review. While Dewar et al. (2013) claimed not to use this study as a basis of their conclusions, it was considered by the BRT and is relevant to issues raised in the BRT report, therefore, it is included in this review.

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### ***Critique of the BRT's use of structured expert decision making (SEDM)***

Dewar et al. (2013) made extensive use of structured expert decision making (SEDM) to express their beliefs on a number of factors that are critical to the assessment of the NEP white shark population's extinction risk. While elicitation of expert opinion is an accepted and valid methodology (e.g. see O'Hagan et al. 2006) to express expert knowledge and quantify uncertainty, Dewar et al. (2013) seem to have made inappropriate use of this method in several places. Perhaps foremost among the problems with the BRT's use of SEDM is the elicitation of plausibilities for point values for variables (e.g. abundance scaling factors) that are continuous-valued in real life. As an example, the BRT voted on the plausibility of abundance scaling factors of 1.0, 1.2, 2.0 and 10.0 (Appendix G, Table G2, Dewar et al. 2013), assigning 100 plausibility points among these values. In reality, the abundance scaling factor could also take any value intermediate between those considered by the BRT. It is unclear whether BRT members intended that intermediate values should have zero probability (which would be inappropriate) or if some kind of intervals were intended (none are stated). It is not clear whether the interpretation of the categories was clear to BRT members, or if they shared a common interpretation.

The BRT was also inconsistent in its use of SEDM. SEDM was not applied to all uncertain quantities in the BRT's assessment, for example, it was not applied to characterize the uncertainty associated with YOY and juvenile bycatch. In its SEDM process for the trend in abundance of white sharks the BRT included an "uncertain" category. The results of this voting exercise are difficult to interpret, since the distribution of plausibility points among categories which represent mutually exclusive states is itself an expression of uncertainty.

Finally, expert opinion is usually considered as an auxiliary source of information (e.g. it is often used to formulate priors which are later updated with data in a Bayesian context) (O'Hagan et al. 2006; Martin et al. 2012). However, the BRT appears to give precedence to expert opinion (e.g. about the YOY bycatch mortality rate, although this was not formally elicited) over

data (observations of bycatch mortalities of tagged YOY white sharks) without attempting to confront their judgment with the available data: this approach seems difficult to justify, particularly in a risk assessment context.

***The BRT's assessment of the current abundance of NEP white sharks is based primarily on expert opinion rather than actual evidence***

Based on a series of SEDM votes, Dewar et al. (2013) concluded that the most likely range for adult female abundance in the NEP is 400-1600 white sharks (8.5 to 34 times the estimated abundance at aggregation sites). These numbers were based primarily on expert opinion and a comparison of genetic diversity among long-lived species. However, the genetic diversity data presented by the BRT in support of its beliefs do not provide clear information about the abundance of adult female white sharks in the NEP. In this section, arguments relating to the current abundance of NEP white sharks based on mark-recapture studies, expert opinion and genetics are discussed.

The primary source of information about abundance is mark-recapture (photo-identification) data from three sites in the NEP. The BRT's own analysis of the mark-recapture data using open population models yielded (sub-adult and adult) abundance estimates that are consistent with earlier studies (Chapple et al. 2011; Sosa-Nishizaki et al. 2012). In the following text, the methods and reasoning used by the BRT to scale up adult female abundance estimates for the aggregation sites to the whole NEP are discussed. The section begins with a review of the mark-recapture estimates at the aggregation sites. This is followed by a critical analysis of arguments about the sex ratio at the sites and how to scale up average abundance at the aggregation sites to the whole NEP. Finally, the informativeness of the genetic data presented by Dewar et al. (2013) with respect to abundance is evaluated.

***Mark-recapture analyses***

Abundance at two central California aggregation sites (Tomales Point and the Farallon Islands) has been estimated as 219 adult and sub-adult white sharks using a closed population model or 156 adult and sub-adult white sharks using an open population model (Chapple et al. 2011). Abundance at Guadalupe Island has been estimated as 120 adult and sub-

adult white sharks (Sosa-Nishizaki et al. 2012). The closed population model estimate of Chapple et al. (2011) has been criticized (Burgess et al. in review) for violating the assumptions of a closed population and homogeneity of capture probability (i.e. that all tagged individuals have the same probability of recapture) that are standard in analyses of mark-recapture data (Pollock, 1981). The main concern of Burgess et al. (in review) was that not all white sharks return annually to the aggregation sites where sampling took place, although Chapple et al. (2011) reported that “*All animals that were passively detected in year one and three [with ultrasonic tags] were also detected in year two*”. Chapple et al. (2011) also presented estimates of sub-adult and adult abundance from an open population estimator (Jolly-Seber) and an estimator for a closed population that allows for heterogeneity in capture probabilities (Chao, 1987). Because the ideal of equal capture probabilities is difficult to attain in natural populations (Carothers, 1973), the estimate of 328 sub-adult and adult white sharks using Chao’s (1987) method might be the most robust of those provided by Chapple et al. (2011). However, in practice, this makes little difference, since estimates obtained using different methods did not differ significantly, based on overlapping 95% probability and confidence intervals; Bayes closed population [130, 275], Jolly-Seber [102, 322], Chao [222, 433] (numbers in square brackets are 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles for sub-adult and adult abundance).

Dewar et al. (2013) re-analyzed the mark-recapture data of Chapple et al. (2011) from Tomales Point and the Farallon Islands, with additional information on the sex and size of some of the individuals in the study. The data of Sosa-Nishizaki et al. (2012) from Guadalupe Island were also re-analyzed with 2 additional years of data and additional information on the number of days of sampling effort per month. The BRT’s estimate of the super-population at two central California sites between 2006 and 2008 using POPAN (a program to implement mark-recapture models of open populations: <http://www.cs.umanitoba.ca/~popan/>) was 166 white sharks. This is consistent with the estimate of 156 using an open population Jolly Seber model from Chapple et al. (2011). The BRT estimated a super-population size of 154 white sharks at Guadalupe Island over the period 2001 to 2011; Sosa-Nishizaki et al (2012) reported a super-population estimate of 120 for the years 2001 to 2009. These estimates are not directly comparable, as the BRT’s analysis used an additional 2 years of data (2010 and 2011). Nonetheless, estimates of the number of females in the super-population were not significantly different, while Dewar et al.’s (2013) estimate of the number of males was significantly higher

(based on reported means and standard errors or 95% confidence intervals). It is not clear whether the final model used by the BRT for the Guadalupe Island data used sex as a covariate for the probability of entry to the population; it is stated (p. 75) that the probability of entry/recruitment to the population was a constant value of 0.07 for both sexes. However, in Appendix F, Table F.1 (Dewar et al. 2013), the model selected by AIC is reported to be a model in which the entry probability was estimated by sex, suggesting that entry probabilities that differ by sex would have provided a better fit to the data. A further notable difference between the analyses of Sosa-Nishizaki et al (2012) and the BRT is the inclusion of sampling effort as a covariate for the capture probability (the models evaluated by Sosa-Nishizaki et al (2012) did not include of sampling effort as a covariate). Again, it is not clear whether the capture probability in the model selected by AIC in Dewar et al. (2013) used both sampling days per year and the proportion of sampling effort that occurred in November-December as covariates, as only “effort” is reported as a covariate for the capture probability in Appendix F (Table F.1, Dewar et al. 2013). This distinction is important since including the proportion of sampling effort that occurred in November-December as a covariate should help to account for seasonal differences in the availability of females.

### ***Assessment of bias in sex ratio and abundance estimates***

Dewar et al. (2013) considered the sex ratio at the aggregation sites and the proportion of the total NEP abundance at the aggregation sites as factors relevant to scaling up mark-recapture estimates of adult female abundance to the entire NEP. There are two reasons why the sex-ratio is of importance (although these are not clearly separated in Dewar et al. (2013)). Firstly, sex-ratios estimated using mark-recapture data might constitute biased estimates of the average sex-ratio at the sites (for reasons related to sampling). Secondly, the sex-ratio at the aggregation sites might not be representative of the sex-ratio in the whole NEP population. For example, if it was assumed that there are roughly equal numbers of adult male and female white sharks in the NEP, a lower sex-ratio of females: males at the sites than in the population as a whole might suggest applying some kind of upward correction when trying to enumerate females in the whole population.

The section of Dewar et al. (2013) dealing with sex ratios at the aggregation sites is made confusing by the use of “sex ratio bias” in many places where “sex ratio” seems to be the intended meaning (e.g. p. 81 “a sex ratio bias of 0.8 at Guadalupe Island”). In the section entitled “Quantifying bias in sex ratios using SEDM”, sex ratios, rather than biases appear to have been quantified. In this document, we use the terms “sex ratio” and “abundance scaling factor” throughout to refer to the sex ratios and the multiple of abundance at aggregation sites comprised by the entire NEP (referred to by the BRT as the “abundance bias”).

Dewar et al. (2013) used SEDM to capture expert opinion about the abundance of adult female white sharks in the NEP, splitting the process into 2 parts; an estimate of the true sex-ratio at the study sites and an abundance correction factor relating (sex-ratio corrected) abundance at the study sites to the larger population:

*“The first step in this process [of characterizing the representativeness of the mark-recapture adult female abundance estimate] was to characterize the bias in the observed sex ratios in order to estimate the total number of adult females at the two study sites. The second step was to characterize what proportion of adult females in the NEP population as a whole, do not visit the aggregation sites so that a total NEP population abundance could be estimated.”*

In considering how to scale up estimates of white shark abundance at the aggregation sites, it helps to define 3 sections of the adult female population:

- a) Adult females that are present at the aggregation site when sampling takes place (these individuals are potentially available to sampling).
- b) Adult females that are not present at the aggregation site when sampling takes place, but are present at other times of year or in other years.
- c) Adult females that do not visit the aggregation sites at any time.

The first two sections of the population need to be accounted for to arrive at the average adult female abundance at the aggregation sites (over a number of years), while the size of the third section will inform the ratio of abundance in the whole NEP to average abundance at the aggregation sites. Thus reasoning related to sections a) and b) of the population could be used to

inform the value of the actual sex-ratio at the sites, while reasoning related to section c) could be used to inform the abundance scaling factor.

Since the sex ratio corrected numbers of adult females at the aggregation sites are multiplied by the abundance scaling factors (Dewar et al. 2013, p. 81) to arrive at total female abundance, double counting will occur if arguments relating to any of a) to c) are used for both the sex ratio and the abundance scaling factor. In the following text, arguments related to 1) sex ratios and 2) the appropriate scaling factor for abundance considered in Dewar et al. (2013), are discussed in turn and allocated to one of categories a) to c) above, where appropriate.

### ***Sex ratio at the aggregation sites***

Dewar et al. (2013) considered the following factors related to the sex ratio at the aggregation sites:

- i) *The sex ratio in the NEP population of white sharks is truly skewed towards males.*

It seems plausible that the sex ratio in the NEP white shark population as a whole may depart from 1:1. Mechanisms for this could include differences in natural mortality, and/or fishing mortality between the sexes. An increase in natural mortality resulting from sexual maturity and reproduction has been described as one of the most fundamental trade-offs in life-history evolution (Kuparinen et al., 2011). Additional mortality associated with sexual maturity and reproduction may arise from allocation of energy to reproduction or through reproductive behaviors (Bell, 1980). White sharks are ovoviviparous, giving birth to live young and thus females make a considerable energetic investment in reproduction. It therefore seems possible that females may experience a higher survival cost of reproduction than males, which could contribute to a natural population structure with a sex ratio of less than 1:1 (females: males). The larger maximum body size of female white sharks (e.g. Tanaka et al. 2011) is consistent with a higher mortality cost of reproduction for females relative to males (Kuparinen et al. 2011).

Spatio-temporal segregation of the sexes could also lead to differential exploitation of the sexes by fisheries (Mucientes et al. 2009). Electronic tagging studies have shown that female NEP white sharks visit pupping sites in the Sea of Cortez and off the Pacific coast of Baja

California, Mexico (Domeier and Nasby-Lucas, 2013), spending more time in open oceanic water and traveling east and west over a broader area than males (Domeier and Nasby-Lucas, 2013). It is possible that they experience higher rates of fisheries exploitation over their lifetime as result of interactions with fisheries in areas that are not used by males. Domeier and Nasby-Lucas (2013) suggested that adult females may be at their most vulnerable when they return to Mexican coastal regions with active commercial fisheries. Male white sharks are exposed to “far less commercial fishery pressure than females” because they seldom move towards the coast of Mexico (Domeier and Nasby-Lucas, 2013). Such sex-specific differences in exploitation rates could also be expected to lead to a predominance of males in the population.

ii) *White sharks exhibit sexual segregation.*

Accumulated information from tagging studies indicates that female white sharks display differing patterns of seasonal and spatial habitat use to males. For example, sightings of female white sharks per day of effort at Guadalupe Island have been found to show a different seasonal pattern compared with males (Nasby-Lucas and Domeier, 2012). Sexual segregation might lead to females falling under category b) or c) above, i.e. these females could be unavailable to sampling at the aggregation sites.

iii) *Some females may arrive at the photo-identification sites after effort has ceased.*

This argument does not seem to be distinct from ii) in that it could be considered the product of sexual segregation, whereby females exhibit different spatial and temporal patterns of habitat use to males. It was stated that capture probabilities in the model for the Guadalupe Island photo-identification data varied by the proportion of annual sampling effort between November and December (Dewar et al., 2013, p. 75, although Appendix F is not clear on this), so this effect should have been accounted for in the estimate of adult female abundance at the Guadalupe Island aggregation site to some extent. Chapple et al. (2011) conducted sampling between September and January, thus this was likely not an issue in their study (95% of shark attack activity at South Farallon Islands occurs between September 1 and November 30, Ainley et al. 1985). These females fall under category b) above.

- iv) *Females are present at the aggregation sites but are not available to be sampled for behavioral reasons.*

Capture probabilities were estimated by sex in the open population models applied to the photo-identification data of Chapple et al. (Dewar et al., 2013, p. 77) and Sosa-Nishizaki et al. (2012). The estimated detection probability for females at the Guadalupe Island aggregation site was 17% lower and more variable than that for males (Dewar et al., 2013, p. 75). This effect should therefore have been accounted for to some extent in the estimates of adult female abundance for both aggregation sites (since the capture probability is inversely related to abundance (e.g. Seber, 1982)). These females belong to section a) of the population.

- v) *Mature females may not return to the aggregation sites every year.*

This would be expected to result in a lower average abundance of females at the aggregation sites over the years and would likely result in a lower estimate of the capture probability for females (since moving away from the study area for a year and returning the next may not be distinguishable from remaining there but not being observed). This should be accounted for to some extent owing to the inclusion of sex as a covariate for capture probabilities. These females belong to section b) of the population.

A further reason for the observed sex ratio at Tomales Point and the Farallon Islands was presented by Chapple et al. (2011) but not considered by Dewar et al. (2013): there is an identification bias because it is easier to confirm the presence of claspers (males) than their absence (females). The proportion of individuals of unknown sex that are females may therefore be higher than the proportion of females out of individuals of known sex.

### ***Assessment of the abundance scaling factor***

The following arguments for scaling (sex ratio corrected) abundance estimates at the aggregation sites to the whole NEP are presented by Dewar et al. (2013):

- i) *The central California abundance estimate does not include white sharks at other documented local white shark hotspots.*

The BRT's first suggestion for a white shark hotspot which may support white sharks that do not visit the aggregation sites is Año Nuevo, which supports a large breeding colony of Northern elephant seals (Dewar et al. 2013). However Chapple et al. (2011) reported in their supplement that omitting Año Nuevo data from their analysis resulted in a decrease in their abundance estimate of less than 3%, which corresponds to 6 or 7 individuals ( $219 \times 0.03$ ). Chapple et al. (2011) also reported that 6 out of 8 individuals identified at Año Nuevo were identified at other locations. This observation does not support the hypothesis of site fidelity to Año Nuevo, since the majority of white sharks identified at Año Nuevo were available to photo ID studies at other sites. In order to qualify as distinct female white sharks to those considered above under sex ratio arguments (i.e. to fall under category c)), adult females at Año Nuevo should not visit the aggregation sites. However, it seems more likely based on the observations of Chapple et al. (2011) that they would fall under a) or b) (i.e. white sharks at Año Nuevo visit the aggregation sites, but not necessarily at times when sampling takes place).

- ii) *White sharks may occupy unknown or previously unoccupied areas.*

The Channel Islands are proposed by the BRT as a potential previously unoccupied area. However, on p. 65 of Dewar et al. (2013), it is stated that *"In 2010 and in prior decades there were essentially no observed wounds on California sea lions"* with evidence of white shark attacks on pinnipeds at the Channel Islands appearing only in the last couple of years. This suggests that white sharks have only recently started to exploit this resource and have moved to the Channel Islands from other areas, as there were no signs of white sharks prior to 2011. Both the analyses of Chapple et al. (2011) and of Sosa-Nishizaki et al. (2012) include years prior to 2011, so it seems probable that the individuals that started to appear at the Channel Islands may have been available to sampling at the aggregation sites; there is no evidence to suggest that they form a separate part of the population in the NEP. These individuals could fall under category a), b) or c).

Reports of large white sharks around the Coronados Islands and Cedros Island are consistent with recorded locations of electronically tagged white sharks; one of four adult females tagged at Guadalupe Island was later located close to Cedros Island (Domeier and Nasby Lucas, 2013, Figure 2). It is therefore probable that at least some white sharks observed in these areas are available to the photo-identifications studies (i.e. these sharks could fall under categories a), b) or c)).

White sharks observed further away from the main aggregation sites might comprise a separate part of the population. However, it seems probable that individuals observed in Oregon and further north are visitors, as white sharks inhabit temperate and tropical waters (Weng et al., 2007); it is not known whether these individuals also visit the aggregation sites. Jorgensen et al. (2010) reported a tagged white shark at the mouth of the Columbia River (Oregon/Washington border), supporting the hypothesis that white sharks venturing farther north are from the same part of the population as those at aggregation sites. The BRT states that “some white sharks tagged at the two known aggregation sites have been observed to visit other coastal areas”, however, NEP white sharks have been found to be highly philopatric and tagged individuals tend to return to the site of tagging (Jorgensen et al. 2010). It therefore seems likely that these individuals would return to the aggregation sites, in which case they would have been accounted for above. These individuals could also fall under category a) or b) or c).

*iii) Some white sharks do not make the transition to feeding on marine mammals.*

White sharks that do not make the transition to feeding on marine mammals might form a part of the population that does not visit the aggregation sites, so these individuals could fall under category c). However, if white sharks aggregate for reasons other than feeding (e.g. Jorgensen et al. 2010), these individuals might still visit the sampled aggregation sites (i.e. they could also form part of sections a) or b) of the population).

*iv) Some white sharks do not undergo an annual offshore migration.*

The BRT suggests that there may be a further, separate component of the NEP population that remains near the coast. This suggestion is countered by the statement of Chapple et al. (2011)

that there is a low probability of many more white sharks in the vicinity of Central California than were encountered in their study, given the high human population density in the area and few reports of white shark sightings or historical attacks. This hypothesis could fall under category a), b) or c), depending on whether these individuals visit the aggregation sites at some point.

v) *Haplotypic diversity suggests a larger population than estimated by mark-recapture studies.*

See next section on “Genetics”.

Taking the factors listed above into consideration, Dewar et al. (2013) used SEDM to allocate plausibility points to actual sex ratios at sites where mark-recapture analyses have been conducted. Based on this process, the most plausible sex ratio (females: males) at Guadalupe Island was found to be 0.8:1.0 and at central California sites 0.6:1. These ratios imply that numbers of females present at the sampled sites during the year are 27% and 231% higher than the numbers estimated using the tagging data, at Guadalupe Island and central California sites, respectively (based on reported sex ratios of 0.63:1.0 and 0.26:1.0, Dewar et al. (2013), p. 72). Under-sampling of females as a result of the seasonal timing of sampling was cited as the main factor in assessing plausible sex ratios (females arrive later in the year). However, as noted above, it is unlikely that this had a large impact on the observed sex ratio at central California aggregation sites. A more in depth exposition of the arguments behind the sex ratios found to be most plausible was not given, for example, why the sex ratio (from mark-recapture analysis) is underestimated to a much greater extent at the central California aggregation sites compared with Guadalupe Island (if the BRT’s most plausible sex ratios are assumed to reflect actual sex ratios).

Sex ratio representativeness argument	Population section	Abundance representativeness argument	Population section
I	NA	i	a, b, c

li	b, c	ii	a, b, c
lii	b	iii	c, (a, b)*
liv	a	iv	a, b, c
v	b	v	implies b, c

Table 1. Assignment of arguments related to the sex-ratio and abundance scaling factor to sections of the adult female population. Letters in the columns “Population section” indicate that the argument proposes under-sampled or unavailable adult female white sharks in that section of the population. \*If white sharks aggregate for reasons other than feeding.

There appears to be some overlap between arguments for the sex ratio at the aggregation sites and the ratio of abundance in the whole NEP to that at the aggregation sites (Table 1). In order to constitute different individuals (and to avoid double counting), parts of the population considered relevant to the abundance scaling should not visit the aggregation sites. However, this was not always the case, e.g. abundance bias arguments i) and ii). This could lead to positively-biased abundance scaling factors from SEDM and overly-high estimates of adult female abundance in the NEP (after multiplying the sex ratio corrected abundances at the aggregation sites and the abundance scaling factors together). Dewar et al. (2013) were not able to convincingly demonstrate that white sharks in other areas of the NEP form separate parts of the population (i.e. that they are not available to sampling at aggregation sites). This is a key problem with their analysis, because the assessment of risk depends directly on abundance and the extrapolation of mark-recapture estimates to the whole NEP. Inflating the abundance estimates without sound empirical basis or reasoning risks underestimation of the extinction probability for NEP white sharks.

A further issue with the section on sex ratios and abundance is that the way in which the elicited sex ratios were used does not appear to correspond to their intended usage as described in section 4.4.3.1 (i.e. to account for the fact that the actual female: male sex ratios at the sites are higher than estimates from the mark-recapture data). Dewar et al. (2013) report that the estimated numbers of adult females from mark-recapture analyses were divided by the sex ratios elicited using SEDM (Dewar et al. 2013, p. 81):

*“For example, one of the 48 abundance estimates with a sex ratio bias of 0.8 at Guadalupe Island and 0.6 at central California and an abundance bias of 2 has an associated abundance estimate of ((27 females/0.8 sex ratio) + (20 females/0.6 sex ratio))\*2=134 adult females.”*

Using the sex ratios in this way does not account for the differences between mark-recapture estimates of the sex ratios and their actual value. Instead, one might expect that the sex ratios from SEDM would be used to obtain the ratio of the actual sex ratio to the observed sex ratio, and that the estimate of adult female abundance at the aggregation sites would be multiplied by this ratio, e.g.:

$$1. \quad N_F = 2 \left( 27 \frac{0.8}{0.6} + 20 \frac{0.6}{0.2} \right)$$

Where  $N_F$  is the number of adult females in the NEP and 0.6 and 0.2 are the observed sex ratios at Guadalupe Island and central California aggregation sites, respectively.

### **Genetics**

The BRT resorted to an argument based on genetic haplotypic diversity in several places in Dewar et al. (2013), and described this as another factor underlying its assessment of adult female abundance and risk in its “Risk Assessment Conclusions” (p. 108). Dewar et al. (2013) proposed that the genetic diversity contained in the NEP white shark population is consistent with either of two scenarios: 1) a current adult female abundance in the “high hundreds to low 1000s” (p. 32) or 2) a population that until recently was in the range of “high hundreds to low 1000s” of adult females but that suffered a precipitous decline in the last few generations (p. 31, 32). Based on an analysis aimed at exploring the potential for strong declines in the NEP white shark population, Dewar et al. (2013) concluded that *“the haplotypic diversity reflects a current adult female population size of at least a few hundred to a couple [of] thousand females”* (p. 108). However, this conclusion does not appear to be justified for a number of reasons discussed below.

In general, it is expected that populations with greater effective population size will lose their genetic diversity at a lower rate over time (Wright, 1969). Thus populations with a larger

effective size are expected to retain greater levels of standing variation. This relationship is the premise for the comparison Dewar et al. (2013) draw for the genetic diversity of long-lived and slow-reproducing species (Table 2.2, p. 32), given the observed haplotypic diversity for NEP white sharks (number of haplotypes=9, proportion of rare haplotypes =67%). This comparison and the conclusion reached by Dewar et al. (2013) that “*the haplotypic diversity reflects a current adult female population size of at least a few hundred to a couple [of] thousand females*” are problematic for reasons discussed below.

### 1) *Validity of the comparison*

Dewar et al. (2013) reviewed data from marine mammals and sharks with broadly similar life-histories to that of white sharks (long-lived and slow-reproducing species). It is not clear that the species and studies for which information on haplotypic diversity and abundance are presented are directly comparable to white sharks. The number of haplotypes in a population is expected to be related to the effective population size ( $N_e$ ). However, the abundance estimates presented in Table 2.2 of Dewar et al. (2013) appear to be census population sizes ( $N$ ). There is no direct relationship between effective and census population size (Portnoy et al. 2009). Rather, the ratio of  $N_e$  to  $N$  may vary between species and populations, depending on fluctuations in population size, variance in family size, definition of the census population, taxonomic group and sex ratio (Frankham, 1995). For example, the haplotypic diversity of mitochondrial DNA may depend on aspects of population structure, such as the level of female philopatry, which maintains unique genetic diversity within the population (Steibens et al. 2013). Female philopatry has been demonstrated in white sharks using genetic methods (Pardini et al. 2001). In summary, the biology and demography of NEP white sharks may differ in important ways, and this could undermine any inference on current or pre-decline population size.

### 2) *How informative are the haplotypic diversity data presented in Table 2.2 about abundance?*

There does not appear to be a strong relationship between abundance and the number of haplotypes or the proportion of rare haplotypes for the data in Table 2.2, and for a given abundance range, the number of haplotypes and the proportion that are rare are quite variable.

Using abundance estimates taken from the literature or midpoints of abundance ranges given in Table 2.2 of Dewar et al. (2013) where the original source was unavailable, and assuming that adult females comprise 25% of the population as in Dewar et al. (2013), correlations of 0.41 and 0.27 were obtained between abundance estimates and the proportion of rare haplotypes, and abundance estimates and haplotype number, respectively. These values result from the varying degrees of population decline and stages of recovery represented in Table 2.2, or may relate to other factors that cause variation in the ratio of  $N_e$  to  $N$ , as discussed above.

In the light of these problems, the genetic data appear to contain only weak information about abundance. To argue that they imply a current or pre-decline adult female abundance of “at least several hundred” as the BRT does (e.g. p. 127) thus overstates their information content.

#### *The observed genetic diversity of NEP white sharks may reflect pre-decline abundance*

As noted by The BRT, the haplotypic diversity of white sharks might not reflect current abundance if the population recently underwent a severe decline. Assessment of recent trends in the NEP population of white sharks is problematic owing to the lack of a complete record of removals from the population. White sharks display life-history characteristics that are associated with a low resilience to harvest and vulnerability to overexploitation (Hoenig and Gruber, 1990; Smith et al. 1998). The exact magnitude of declines in shark populations in the Atlantic and Gulf of Mexico has been the subject of debate. However, some studies have reported substantial declines (Baum et al. 2003, 2005) and it is generally agreed that overexploitation has led to population decline in several shark species (e.g. Baum et al., 2005, Burgess et al. 2005).

Some studies have presented information suggesting that unreported catches of NEP white sharks may have been substantial. For example, Castro (2012) reported seeing “*dried jaws of large juvenile white sharks (~3-4 m total length) hanging in fishermen’s huts and countless heads of small juvenile white sharks (<2m total length)*” in refuse piles surrounding fishing camps in Sonora and Baja California. Castro goes on to note that these white sharks are seldom examined by biologists. Santana-Morales et al. (2012) reported a white shark catch of 17 individuals recorded in the logbook of one commercial drift-gillnet fishing vessel based in Ensenada from 1,333 sets between April 1999 and December 2009. Four fishing trips on this

vessel with an observer yielded 3 white sharks from 46 sets. This translates to a CPUE of 0.013 white sharks per set for unobserved fishing trips and 0.065 white sharks per set for observed fishing trips, indicating that the logbook records likely represent an underestimate of the white shark catch. If unobserved trips had a similar CPUE to observed trips, the total catch for one vessel between 1999 and December 2009 could be as high as 86 white sharks. Depending on the number of drift-gillnet vessels operating at any one time, the total catch from these vessels may have been unsustainably high.

The BRT conducted a modeling exercise (Appendix B, Dewar et al. 2013) to assess the potential for decline in the NEP white shark population. Specifically, the BRT evaluated the potential for a decline of 90% or more starting from a population of adult female white sharks of 500 or 1000 between 1971 and 2011. It appears that the 90% criterion was used based on the estimated total adult female abundance at three NEP aggregation sites ( $\approx 50$ , Dewar et al., 2013), while the values used for the pre-decline population size stemmed from the BRT's assertion that the haplotypic diversity of NEP white sharks is within the range of that for species with populations of adult females in the high hundreds to low thousands (i.e. a decrease from 500 to 50 mature females would constitute a 90% decline). Dewar et al. (2013) concluded that the results of the analysis described in Appendix B "*suggest that the number of mature females still likely numbers at least in the low hundreds today*". This interpretation is difficult to justify for a number of reasons outlined below.

- 1) *The genetic diversity of NEP white sharks is consistent with a pre-decline adult female abundance of "several hundred" (Dewar et al. 2013).*

The BRT states (p. 108) that "*The available haplotype diversity for this population is consistent with a population consisting very recently (within the last few generations) of at least several hundred to several thousand females*", which suggests that the potential for adult female populations of e.g. 300 or 400 (in addition to 500 and 1000) in 1971 to decline to very low levels (e.g. less than 100) by 2011 should also have been evaluated, as these scenarios would not be inconsistent with the genetic data. This seems especially relevant given the problems associated with inferring abundance from the haplotype diversity data noted above.

2) *The potential for decline over 3 generation times was not evaluated*

Dewar et al. (2013) suggest that the haplotypic diversity of NEP white sharks is consistent with a population that has suffered a large decline in the “last few generations” (p. 31). This implies that 60 years (approximately 3 generation times) might be a more suitable timeframe for evaluation of the potential for decline than 41 years, as used in Appendix B (Dewar et al. 2013). All else being equal, a longer timeframe is expected to lead to a higher probability of decline to low levels of abundance by 2011.

3) *Historical catches are poorly quantified*

As noted above, historical white catches in the NEP are essentially unknown and are unlikely to be well-represented by reported catches. The BRT concedes that “*elasmobranch discards in the high-seas large-mesh drift gill net fisheries during the 1970s and 1980s were poorly documented and could have been substantial*” (Appendix B, p. 130 of Dewar et al. 2013). The BRT asserts that its model was “*conservative and precautionary*”, however the possibility that bycatch mortality rates for adult females were in fact higher than the values used in Appendix B cannot be ruled out. The possibility that the majority of adult white sharks killed historically in fisheries were females (owing to their tendency to utilize areas where commercial fisheries occur to a greater extent than males (Domeier and Nasby-Lucas, 2013)) is also relevant here. If bycatch rates were in fact higher than those assumed in Appendix B, the potential for decline will have been underestimated by Dewar et al. (2013).

4) *Current adult female abundances of 250 or less appear relatively plausible, even with a pre-decline abundance of 500 adult females*

The BRT focuses on declines of 90% or greater and in particular to the mark-recapture estimate of adult female abundance at aggregation sites by 2011. The potential for smaller (but still substantial) declines e.g. of 60% - 90% to adult female abundances in the lowest two abundance categories used by the BRT (i.e. fewer than 200) was not given much consideration, although the probability of population decline from 500 to 200 adult females was reported as 20% (Appendix B,

Dewar et al. 2013). This probability would increase for starting abundances of 300 or 400 in 1971 or using a time span of 3 generations ( $\approx 60$  years).

#### *SEDM vote on the abundance of adult females in the NEP*

Based on an SEDM vote, Dewar et al. (2013) concluded that the most likely range for adult female abundance in the NEP was over 400 white sharks (i.e. more than 8 times the number estimated at aggregation sites) (Table 4.11, p. 83). Numbers of adult females up to four times greater than the estimated number at aggregation sites (200 or fewer) were thought to be relatively implausible (16/100 plausibility points). Using information in Tables 4.11 and 4.14 (and taking 1600 as the upper limit of the highest abundance category from p. 81 of Dewar et al. (2013)), Dewar et al.'s (2013) implied estimate of abundance for all age classes is approximately 12,000 white sharks.

#### **Summary**

The BRT's analysis of the mark-recapture data corroborated the estimates of Chapple et al. (2011) (open population model) and Sosa-Nishizaki et al. (2012). To scale up mark-recapture abundance estimates to the whole NEP, the BRT considered a number of factors affecting the sex-ratio at central California and Guadalupe Island aggregation sites, and the proportion of adult females in the NEP population as a whole that do not visit the aggregation sites. Some of the BRT's arguments for scaling up numbers at the aggregation sites based on under-sampling of females or the existence of separate parts of the population did not appear to be valid given information reported elsewhere (e.g. in Chapple et al. (2011)). Dewar et al. (2013) did not provide convincing arguments that white sharks in other parts of the NEP form separate components of the population that do not visit sampled aggregation sites. There appeared to be overlap between arguments related to the sex ratio and the scaling of overall abundance, potentially leading to double counting of some parts of the population and overestimation of adult female abundance.

The genetic data presented by Dewar et al. (2013) appear to contain only weak information about (past or current) abundance (census population size) because of variability in the ratio of effective to census population size and the weak relationship between abundance and haplotype diversity for the data in Table 2.2. Given these data, it is not clear that the census

population size of mature female white sharks in the NEP would have to number at least several hundred, as Dewar et al. (2013) claim.

Dewar et al. (2013) evaluated the potential for a 90% decline in adult female abundance over 41 years, starting from 500 or 1000 females. They concluded that “*the haplotypic diversity reflects a current adult female population size of at least a few hundred to a couple [of] thousand adult females*”. This conclusion is unwarranted; there appears to be fairly high probability of a current abundance of adult females of 250 or less ( $\approx 25\text{-}30\%$ ) with a starting abundance of 500 (Appendix B, Figure B1 top panel, Dewar et al. 2013). Dewar et al. (2013) also state that an abundance of a “several hundred” (p. 108, p. 127) adult females would be consistent with the genetic data, but did not evaluate the potential for decline for starting population sizes of 300 or 400 adult females. Given these issues, the genetic data presented by Dewar et al. (2013) do not comprise substantive support of adult female abundances of several hundred or more, and do not detract significantly from the plausibility of the lower abundance categories considered (60 to 125 and 125 to 200 adult female white sharks).

Dewar et al.’s (2013) rationale for a much larger abundance than has been estimated is primarily based on expert opinion about the number of white sharks that are not available to be sampled at the aggregation sites. Their beliefs about abundance would require a portion of the population comprising a large multiple of numbers at known aggregation sites to exist in other areas of the NEP. No compelling evidence was provided in support of this thesis; furthermore, as white sharks are highly migratory and show strong philopatry, the proportion of sharks visiting other areas that were available to sampling at the aggregation sites may be high (i.e. many of these individuals may already be included in existing abundance estimates). This is a key problem with the BRT’s analysis, because the assessment of risk depends directly on abundance and the extrapolation of mark-recapture estimates to the whole NEP.

It has been proposed elsewhere (Chapple et al. 2011) that the abundance of sub-adult and adult white shark in the NEP may be around two times the estimated number at central California sites (i.e. 438 adult and sub-adult white sharks). Burgess et al. (in review) extended Chapple et al.’s (2011) abundance estimate for sub-adult and adult white sharks off central California to all age classes, obtaining a range of 2,148 to 2,819. However, it is not clear whether the assumption that the whole age distribution of white sharks is represented in central California is sound (e.g. young of the year and juvenile white sharks are likely to be associated with nursery

areas and may aggregate in different regions of the NEP). Burgess et al. (in review) did not report the number of adult females corresponding to this estimate, however given that it comprises all life stages, this still suggests a small population off central California (e.g. compared to the BRT's estimate of around 12,000 for the whole NEP).

The BRT's appraisal of adult female abundance is unjustified in the absence of compelling evidence; inflating the mark-recapture abundance estimates without sound empirical basis or reasoning is likely to have resulted in underestimation of the extinction probability for NEP white sharks.

***Empirical evidence indicates that YOY bycatch mortality rates greater than 20% are highly plausible, contrary to the belief of the BRT***

Dewar et al. (2013) concluded that the available bycatch data represent "One of the most important pieces of evidence for a low to very low risk of extinction" (p. 108) and this appears to have been a key factor in their decision. This section considers information about YOY and juvenile bycatch rates from tagging studies and reviews the arguments used by Dewar et al. (2013) to support the claim that bycatch mortality rates of more than 0.20 are implausible. Bycatch mortality rates for adult females considered by the BRT are also discussed.

***Bycatch mortality of YOY and juvenile white sharks***

The BRT conducted a second SEDM voting exercise (p. 82 of Dewar et al. 2013) for the abundance scaling factor because fishing mortality rates for young of the year (YOY) sharks based on the two lower abundance scaling factors (1 and 1.2) of 70% and 40% respectively were thought to be implausibly high. The BRT assembled estimates of fisheries bycatch mortality for several long-lived mammals and turtles (Appendix I, Dewar et al. 2013), and used them to reason about likely bycatch rates for NEP white sharks. However, this does not seem to be an appropriate comparison for a number of reasons. Bycatch mortality rates for a given species and fishing fleet(s) are likely to be highly case-specific and will depend on a number of factors, including abundance of the bycatch species, the level of effort in the fisheries, the extent of overlap

between the spatio-temporal distribution of the fishing fleet(s) and the species in question, the extent to which the species forms aggregations and the selectivity of the fishing gears used. There is no strong *a priori* reason to suppose that these would be similar for the disparate group of examples in Table I.1 and YOY white sharks in the NEP. As an example, white sharks are apex predators whose populations are naturally low in abundance (Domeier, 2012); this does not appear to be the case for all of the species listed in Table I.1. A further reason that the species presented in Table I.1 may not be comparable with white sharks is that those species are predominantly subject to fishing mortality as bycatch (i.e. they are not target species). Although white sharks are subject to bycatch mortality, there is additionally an economic incentive for targeted fishing. Santana-Morales et al. (2012) reported that the price of 1kg of dry fins was US\$100, while jaws can command up to US\$500. Duffy (2004) reported prices of between US\$1,350 to \$12,500 for white shark jaws. Commercial capture of white sharks is prohibited in Mexico (Mexican Official regulation NOM-ECOL-059), however, enforcement mechanisms are insufficient or not well implemented (Galván-Magaña et al. 2010).

A more relevant and direct source of information about mortality rates for YOY white sharks is tagging studies, which contain information about the proportion of tagged YOY sharks that were recaptured in fisheries. A summary of releases and recaptured of tagged YOY white sharks can be found in Table 2.

Tagged YOY white shark	Length at release	Time at large before recapture	Recapture in fishery	Survival of fishery recapture?	Reference
YOY 1 (female)	147cm TL	41 days	Commercial gillnet, Ventura, CA	Uncertain (escaped gillnet), tag left behind	Weng et al. (2007)
YOY 2 (female)	155cm TL	NA	No	NA	Weng et al. (2007)
YOY 3 (male)	156cm TL	NA	No	NA	Weng et al. (2007)
YOY 4 (male)	155cm TL	37 days	Commercial gillnet,	Assumed no –	Weng et al.

			Ensenada, Baja California	“recaptured by a gillnet fisherman”	(2007)
Female YOY	140cm FL	28 days	Net, Huntington flats, CA	Uncertain – only tag recovered in net	Dewar et al. (2004)
08-11 (female YOY)*	137cm TL	4 days	Commercial gillnet 35km south of Goleta, CA.	Yes- shark released alive with tag attached	Weng et al. (2012)
09-11 (female YOY)*	157cm TL	113 days	Set gillnet, Baja California	No	Weng et al. (2012)

Table 2. Fisheries interactions and mortalities of tagged YOY white sharks. \*Shark held in captivity; 08-11 exhibited for 11 days (released in Goleta), 09-11 exhibited for 70 days. Weng et al. (2012).

Of 7 tagged YOY sharks, 5 encountered net fishing gears and 2 died as a result, Table 2. Tag recaptures can be used to estimate fishing mortality rates when the tag recapture rate is known or can be estimated (Pollock et al., 1991, Hoenig et al., 1998, Punt et al., 2000). In this case, given that all the recaptured YOYs were captured within their first year at liberty, a simple estimate of the annual fishing mortality rate would be  $2/7$ , or 0.29. This can be viewed as a minimum value, as it is uncertain whether the female white shark from Dewar et al. (2004) and YOY 1 from Weng et al. (2012) survived following their entanglement in nets. The times at large until recapture are also very low for all but one of the recaptured YOY white sharks (41 days or less), implying a higher annual recapture rate. The 4 YOY white sharks tagged in Weng et al. (2007) and the YOY white shark in Dewar et al. (2004) were originally captured in net fisheries; Weng et al. (2007) stated that fishing mortality on juvenile white sharks may be significant, based on capture rates of juvenile white sharks in bottom set gillnet fisheries in US and Mexican waters.

The sample size of tagged YOY white sharks is small and it is possible that tagging and handling may have affected the sharks’ behavior. Nonetheless, these three separate studies point

towards a significant potential for YOY white sharks to interact with fisheries. In the light of this information, fishing mortality rates greater than 20% do not seem implausible, nor do there appear to be grounds to rule out a fishing mortality rate of 40% (corresponding to an abundance scaling factor of 1.2) for YOY white sharks. Following the second SEDM voting exercise, the BRT allocated only 9.4% of plausibility points to an abundance scaling factor of 1.2 or less (BRT, Table 4.10, p. 82).

Appendix 1 of this document presents a simple estimate of the abundance of adult female white sharks based on the tag recapture data, assuming that untagged individuals have the same capture probability as tagged individuals. This is not intended to be a full analysis of the tagging data (e.g. sex structure is omitted), but rather a back-of-the-envelope calculation to see what YOY recapture rates might imply about adult female abundance (taking into account uncertainty in the tag recapture rate and YOY catch). The example uses a lognormal distribution for the annual YOY catch, with mean 159 (from Dewar et al. 2013) and a coefficient of variation of 0.30. An estimate of the capture probability for YOY white sharks in fisheries was obtained as either 2/7 (29%) or 3/7 (43%), the latter assuming that the mortality rate of white sharks that were entangled and left their tag behind in the net was 0.49 (from Dewar et al. 2013, p. 48). These values were used as the means of beta distributions, while the standard error of the capture probability was used as the distribution's standard deviation (Appendix 1). An estimate of the abundance of YOYs can then be obtained by dividing the catch by the capture probability; adult female abundance was estimated by dividing the number of YOYs by the number of pups per female, using information from Table 4.13 of Dewar et al. (2013). Probabilities associated with the female abundance categories considered by Dewar et al. (2013) obtained using this simple model are presented in Table 3.

Mean fishery capture probability	≤ 125 adult females	>125 and ≤ 200 adult females	>200 and ≤400 adult females	>400 adult females
0.29	0.42	0.23	0.21	0.13
0.43	0.69	0.18	0.10	0.03

Table 3. Plausibility of adult females abundance categories implied by the YOY capture rate from tagging data. The relationship between YOY and adult female abundance is the same as that used in Dewar et al. (2013) (p. 91).

65% and 87% of the probability was associated with an adult female abundance of 200 or less (Table 3), with a mean YOY harvest rate of 29% or 43%, respectively. Thus despite the caveats noted above, at the very least, it appears that more data on the YOY capture mortality rate (e.g. from more tagging) would be needed to establish the implausibility of YOY harvest rates greater than 20%. The reliance of the BRT on an inappropriate comparison with bycatch rates of marine mammals and turtles, and its omission to consider direct observations of YOY bycatch mortalities makes its claim that gill net bycatch mortality rates of 20% or higher would be “astonishing” (p. 106) difficult to defend. Since this was a key factor in the BRT’s decision (Dewar et al. 2013, p. 108), admitting the plausibility of higher bycatch mortality rates would likely result in a higher evaluation of risk for NEP white sharks.

### ***Fishing mortality of adult female white sharks***

The BRT used SEDM to allocate plausibility points to the number of adult female white sharks (between 0 and 10) killed each year. The implied proportions of adult female white sharks killed each year corresponding to these numbers are very low, e.g. between 0.025 and 0.05 for an adult female abundance between 200 and 400, and less than 0.025 for an adult female abundance greater than 400. The BRT assigned the highest number of plausibility points to 2 female sharks dying annually as a result of fishing. This corresponds to 0.5% of adult females being killed each year for the abundance category given the highest weight (more than 400 adult females). The plausibility points allocated by the BRT for the number of adult females killed annually (p. 83 of Dewar et al. 2013) can be used to construct a probability distribution summarizing the BRT’s belief about the proportion of adult female white sharks killed by fishing each year. For example, taking the abundance category deemed most plausible (>400 adult females) a beta distribution with a mode of 0.005 (2/400) and 97.5<sup>th</sup> percentile of 0.025 (10/400) could be used to summarize the BRT’s belief about the annual proportion of adult females white sharks killed by fishing. Although there are few documented mortalities of female white sharks as a result of fishing, in one tagging

study (Domeier and Nasby-Lucas, 2013), the authors reported that fishing mortality was a reasonable explanation for the cessation of transmission for one out of four adult female sharks tagged with satellite-linked radio-telemetry tags. Domeier and Nasby-Lucas (2013) reported approximately 9 years of tracking data from the four white sharks, so their observation would correspond to an annual mortality proportion of around 0.1, if this tagged female was killed in a fishery. Although the sample size is small, this observation is very unlikely (probability $\approx$ 0) under the BRT's distribution for the annual proportion of adult female white sharks killed by fishing, based on the beta distribution described above (essentially because Dewar et al. (2013) use 10 as their upper limit (p. 147), assigning 0 probability to mortality rates greater than 10/400 or 0.025).

### **Summary**

Observations from YOY tagging studies (Table 2) suggest that the bycatch mortality rate may actually be higher than 20%. An estimate of the capture probability for YOY white sharks in fisheries was obtained as either 29% (2/7) or 43% (3/7). Taking into account uncertainty in the bycatch mortality of YOY sharks and in vital rates, the YOY tagging data are most consistent with an adult female abundance of less than 200 (Table 3). It is not clear why Dewar et al. (2013) chose not to consider these data, instead basing their judgment on bycatch mortality rate estimates for marine mammals and turtles. Harvest rates are likely to be highly case-specific, and assuming similarities across species, geographical regions and fisheries does not seem to be appropriate. The reliance of the BRT on an inappropriate comparison with marine mammals and turtles, and its omission to consider direct observations of YOY bycatch mortalities makes its claim that gill net bycatch mortality rates of 20% or higher would be "astonishing" (p. 106) difficult to defend. Since this was a key factor in the BRT's decision (Dewar et al. 2013, p. 108), admitting the plausibility of higher bycatch mortality rates would likely result in a different (higher) evaluation of risk for NEP white sharks.

Adult female bycatch mortality rates considered by the BRT were low; between 0.025 and 0.05 for an adult female abundance between 200 and 400, and less than 0.025 for an adult female abundance greater than 400 (judged most likely by the BRT). The BRT used 10 as the "*potential upper limit to the number of females that might be killed in a given year*". This would render a potential observation of fishery related mortality for a tagged adult female white shark

(Domeier and Nasby-Lucas, 2013) highly unlikely. Given the high uncertainty about actual catches, a higher upper value for the bycatch mortality rate is both plausible and appropriate. If adult female bycatch mortality rates are higher than those used in Dewar et al. (2013), the BRT will have underestimated risk to the population.

***The BRT's conclusion that NEP white shark abundance is stable or increasing is problematic given difficulties with interpreting the available data***

Dewar et al. (2013) concluded (p. 109) that the available information is consistent with a stable or increasing population. Despite their admission (p.109) that *“population trend information is somewhat inconclusive”* only 7% of plausibility points (of points that were not placed in the “uncertain” category, see below) were allocated to decreasing abundance. The trend in abundance does not appear to have been pivotal in their decision, although they state that the data indicate *“an adult population size larger than what has been estimated based on photo-ID data for Guadalupe Island and Central California.”* Dewar et al. (2013) evaluated several types of information to assess whether the abundance of white sharks in the NEP is decreasing, stable or increasing. These are reviewed here in the order in which they are discussed in Dewar et al. (2013); catch per unit effort data (CPUE), abundance estimates from photo-identification and attacks on marine mammals. The available data for inferring trends in the abundance of white sharks are in many cases not straightforward to interpret owing to the presence of other, unaccounted-for and confounding factors that can explain trends in observed catch or predation rates (e.g. changes in soak time, increasing density of prey species (functional response), changes in the foraging behavior of white sharks, etc.). These issues are discussed below.

***Catch per unit effort data***

Disentangling changes in the CPUE of U.S. fisheries with changes in reporting following the initiation of the Monterey Bay Aquarium's (MBA) observer program and shifts in the spatial distribution of effort following regulations in the mid 1990s is problematic; the increase in CPUE after 2002 coincides with MBA's program and the extent to which the observed increase in CPUE

is caused by increased reporting is uncertain. It is suggested that the mean logbook reporting rate may have increased by 34% (BRT, p. 44), based on changes in the ratio of MBA CPUE to the logbook CPUE data. An alternative way to calculate this increase would be to use the number of white sharks reported by observers that were also recorded in fishermen's' logbooks. This information can be found for set nets in Table 4.2 (p. 43 of Dewar et al. 2013). Between 1990 and 1994, 2/9 white sharks were reported, corresponding to a reporting rate of 0.22, while between 2002 and 2011, 40/74 white sharks were reported, yielding a reporting rate of 0.54. Using this information the change in the mean logbook reporting rate since 2002 is 143%.

The BRT chose to evaluate CPUE from the California set net fishery between 1994 and 2001 because of probable changes in the reporting of catches as a result of MBA's program. Attribution of the increase in CPUE between 1994 and 2001 to increasing abundance is problematic for a number of reasons:

- 1) Interpreting CPUE data to infer trends in abundance requires an understanding of the spatial distribution of fish and fishing effort through time (Harley et al. 2001). It seems likely that there would have been spatial changes in fishing effort following the 1994 ban on near shore nets i.e. fishing effort that was concentrated in near shore areas before 1994 may have simply been redistributed to other areas. White sharks are known to aggregate at certain sites, and on the strength of evidence gathered from tagging studies to date (Jorgensen et al., 2010, Domeier and Nasby-Lucas, 2013) do not appear to be uniformly distributed throughout the NEP. A shift of fishing effort to sites that have a higher use by white sharks is therefore a plausible alternative to increasing abundance. This possibility was also noted by an independent reviewer of the BRT report (Camilla McCandless), who suggested that the increase may be partially attributed to an area effect and raised the possibility of movement of set net effort into white shark nursery areas following regulatory changes.
- 2) The time scale and magnitude of increase in CPUE (8 years) do not appear to be consistent with the reproductive ecology of white sharks. CPUE is often assumed to be directly proportional to abundance (Harley et al. 2001). White sharks have a long generation time (22 years, Dulvy et al. 2008; Dewar et al. (2013) assume a generation time of approximately 20 years) and a low rate of intrinsic population increase (Dewar et al., 2013). It therefore

seems extremely unlikely that increase in abundance alone underlies the observed trend (approximately 7 fold increase in CPUE in 8 years, Figure 4.6, Dewar et al. (2013)).

- 3) *A priori*, one might expect that the total soak time across all nets would be a better measure of fishing effort than the number of nets, since a net that is in the water for longer could be expected to have a higher probability of encounter by sharks. Dewar et al. (2013) report that soak time increased over the time series i.e. there was a temporal trend in soak time. Based on a multiple linear regression to examine the effects of year and soak time on CPUE, the BRT concluded that soak time was not a significant factor (p. 63). However, as both were increasing there may have been collinearity between soak time and year; the BRT did not provide sufficient information (e.g. variance inflation factors for predictor variables included in the regression) to rule out this possibility. As an example, Pyle et al. (1996) found that a significant correlation between attacks of white sharks on elephant seals and the number of seals became insignificant after adjusting for year. If there was collinearity between soak time and year, it would be difficult to ascertain which was responsible for the increase in CPUE given the available data.
- 4) In addition, given the very small sample size of this analysis (number of years = 8), it seems probable that the statistical power to detect an effect of soak time on CPUE was low (i.e. lack of statistical significance may have resulted from low statistical power rather than lack of an effect in reality). Again, the BRT did not report the statistical power of the analysis.

### ***Photo-identification data from Guadalupe Island***

Interpretation of the trend in abundance estimates with respect to true abundance at Guadalupe Island is complicated by a number of factors. Possibly the main issue is that white sharks (particularly females) may not visit the Guadalupe Island aggregation site every year (e.g. Nasby-Lucas and Domeier, 2012). Female white sharks have been found to follow a two year migration cycle (Domeier and Nasby-Lucas 2013), and a large proportion of both male and female white sharks identified at Guadalupe Island were sighted in non-consecutive years (Figure 25.5, Nasby-Lucas and Domeier, 2012), which could arise from less frequent than annual visitation to

Guadalupe Island. Thus, for the first few years of sampling, one would expect that abundance estimates will increase as individuals that are not present at the site every year are progressively encountered (i.e. a discovery curve). The estimated population size would then start to level off with continued observation as the proportion of the population that has not been sampled decreases. This type of effect is consistent with the steady increase in estimated abundance during the first five years of the study (2001 to 2005) (Figure 4.11, Dewar et al. 2013). Abundance estimates for females leveled off after 2005 (Figure 4.11, Dewar et al., 2013). Abundance estimates for male white sharks at Guadalupe Island continued to increase from 2005 onwards at a lower rate; however, there do not appear to be any significant differences between abundance estimates for males between 2005 and 2011, based on confidence intervals constructed using 1.96 times the standard error (Figure 4.11).

In addition, the distribution of effort has shifted over the course of the study, such that in 2003 and 2004, sampling effort was highest in November to December, while from 2005 onwards, peak sampling effort occurred in September and October. It is not clear whether the capture probability in the model selected by AIC for Guadalupe Island used sampling days per year *and* the proportion of sampling effort that occurred in November-December as covariates, as only “effort” is reported as a covariate for the capture probability in Appendix F (Table F.1, Dewar et al. 2013). There are distinct seasonal patterns in the average number of sightings per day of effort for males and females (Nasby-Lucas and Domeier, 2012), which may be linked to the timing of arrival at Guadalupe Island – i.e. changes in sightings per unit of effort may reflect seasonal changes in the abundance of males and females at the site over the year. Transferring sampling effort between seasons with differing abundances over the course of the study could thus lead to spurious year to year trends in abundance.

### ***White shark attacks on marine mammals***

Inferring trends in white shark abundance from trends in attacks on prey species requires information about trends in the abundance of the prey species in question. The abundance of the prey species can be thought of as analogous to sampling effort, in that if the encounter rate of individual prey animals with white sharks remained constant, an increase in attacks proportional to prey abundance could be expected. An increase in the rate of

consumption of predators with increasing prey density is a well-studied ecological model and is known as a functional response (Holling, 1965).

Pyle et al. (1996) did account for increases in the population of northern elephant seals (*Mirounga angustirostris*) and increasing observation effort at the South Farallon Islands, and found a significant increase in white shark attacks between 1987 and 1993. They suggested that this increase may be a result of an increase in the white shark population at the South Farallon Islands. However, there was a seasonal element to the increase in attack rates, whereby a significant increase in the number of attacks per 100 hours of observation occurred in November, but not in September or October. The rate of white shark attacks per 100 hours of observation effort in November increased from approximately 9 in 1990 to approximately 16 in 1993 (Pyle et al., 1996, Figure 4). This corresponds approximately to an annual increase of 21% in the standardized number of attacks in November.

Dewar et al. (2013) report that bite marks consistent with white shark attacks on California Sea lions (*Zalophus californianus*) at San Miguel Island have increased from close to 0 in 2010 to 136 in 2011 and over 300 in 2012. However, observations of bite marks do not appear to have been standardized for increases in the California sea lion population at the Channel Islands. U.S. populations of California Sea lions have increased dramatically between 1975 and 2008 (National Marine Fisheries Service (NMFS), 2011); this increase needs to be accounted for to make inferences about predator abundance because of functional responses to increasing prey density. The rate of increase in observations of bite marks also appears to be too fast to be caused by population increase, given that white shark populations may increase by around 5% per year, under optimal conditions (Dewar et al. 2013) and have a low recovery potential (Smith et al. 1998). This was pointed out by a reviewer (Barry Bruce), who commented that the rate of increase suggested a shift or expansion of the population's distribution, rather than an increase in abundance.

Similar arguments apply to the observed increase in bite marks observed on southern sea otters (*Enhydra lutris nereis*) in central California. Sea otter populations have been steadily increasing during recent decades (NMFS 2008). The reported rate of increase in the proportion of sea-otter carcasses for which shark bites were responsible (3 to 4 fold in 5 years) is also incompatible with the maximum rate of increase of white shark populations. Again, this was

pointed out by a reviewer (Kevin Weng), who suggested that a change in foraging behavior by some sharks may be responsible for the increase in bite marks.

The BRT noted that establishing whether the rate of increase in observed white shark attacks is too fast to be explained by an increase in abundance could provide some insight into the underlying cause of trends in attack rates (p. 66). No such analysis was attempted because of a lack of information that would allow encounters to be related to shark numbers (Dewar et al. 2013). However, it should be straightforward to ask whether an increase in the white shark population could account for the entirety of observed increases by looking at the maximum potential increases in shark abundance, given the population dynamics modeling tools available to the BRT. Table 4 contains approximate values for the rate of increase in indices of abundance, marine mammal attacks etc. presented by Dewar et al. (2013), alongside the expected increase in white shark abundance under optimal conditions.

<i>Index</i>	<i>Number of years</i>	<i>Reported increase in index (%)</i>	<i>Maximum increase in white shark abundance (%)*</i>
CPUE from the California set net fishery between 1994 and 2001, Figure 4.6, p. 64 <sup>1</sup>	7	>600	41
Bite marks consistent with white shark attacks on California Sea lions ( <i>Zalophus californianus</i> ) at San Miguel Island, p. 65 <sup>1</sup>	2	>29900	10
Mean white shark attacks per 100 hours of observation effort in November 1990-1993 <sup>2</sup>	3	~78	16
Sea otter mortalities resulting from white shark attacks, p. 66 <sup>1</sup>	4	200-300	22
Guadalupe photo identification male white shark abundance	10	~137	63

estimates, 2001 to 2011, Figure 4.11, p. 75 <sup>1</sup>			
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Table 4. Comparison between reported rates of increase in indices of abundance and the maximal increase in white shark abundance over the same time frame (assuming population growth at the maximum potential growth rate,  $\lambda_{max} = 1.05$ ). Rates of increase in indices of abundance are only intended as an approximation of the actual rate (several are based on data presented in figures). All the reported increases (third column) are too fast to be explained by population growth alone (fourth column). *\*Based on population growth at a rate of 5% per year, corresponding to optimal conditions and low white shark density (Dewar et al. 2013).* 1. Dewar et al. (2013). 2. Pyle et al. (1996).

All the observed increases in indices of abundance, marine mammal attacks etc. were substantially greater than would be expected if an increase in white shark abundance was the only factor underlying the trend (Table 4). This does not rule out an increase in white shark abundance, but it suggests that there are some other mechanisms effecting changes in these rates (for example, shifts in distribution, foraging behavior, changes in effort etc.). It is therefore difficult to make conclusions from these data about trends in white shark abundance, since the relative contribution of increasing white shark abundance versus other factors is unknown.

Despite the issues related to the interpretation of these data sets described above, six out of eight members of the BRT assigned the majority of their plausibility points to increasing white shark abundance (i.e. this was ranked as the most likely true state of nature), Dewar et al. (2013). It is not clear why an “uncertain” category was used in the SEDM process for the trend in abundance of white sharks, but not for any of the other SEDM voting topics. The meaning of the “uncertain” category is not obvious, as the distribution of plausibility points among categories which represent mutually exclusive states is itself an expression of uncertainty (i.e. assigning 33.3 plausibility points to each of the categories “increasing”, “stable”, and “decreasing” would imply maximal uncertainty).

## **Summary**

None of the data sets presented in Dewar et al. (2013) provide compelling evidence of an increasing trend in white shark abundance. Raw CPUE data is seldom proportional to abundance over a whole time series and geographic range because multiple factors affect catch rates (Maunder et al. 2006); indices of abundance therefore need to be standardized for factors (other than abundance) that can affect the value of the index. This was not the case for most of the indices presented. Furthermore, in order to use observations of attacks on marine mammals as an index of relative abundance, the abundance of prey populations should be accounted for, since the abundance of the prey population could be regarded as analogous to fishing effort in CPUE data. Given this, the inclusion of unstandardized data on marine mammal attacks as a potential source of information about trends in white shark abundance seems unwarranted.

The rate of change in all of the indices considered appeared to be too fast to reflect an increase in white shark abundance (Table 4). This indicates that an increase in white shark abundance alone cannot explain the observed trends, suggesting that other factors are partly or wholly responsible for them (e.g. shifts in foraging behavior or habitat use).

Overall, given the difficulties associated with interpreting the data sets presented in Dewar et al. (2013), the BRT's conclusion that the available information is consistent with an increasing or stable population (p. 109) is unjustified.

### ***The BRT's risk assessment was not consistent with a precautionary approach as it failed to account fully for uncertainty***

Dewar et al. (2013) concluded that the NEP white shark population is at very low (50% of plausibility points) to low (36% of plausibility points) risk of extinction (Table 4.18, p. 107). However, their failure to account fully for uncertainty (in the YOY and juvenile bycatch and in the maximum intrinsic rate of population increase), in addition to the lack of evidence for adult female abundances of 400 or more discussed above casts significant doubt on their conclusions. In this section, the risk assessment for NEP white sharks conducted by Dewar et al. (2013) is reviewed.

The section deals with definition of risk categories and their thresholds, characterization of uncertainty by Dewar et al. (2013) and the analysis carried out by the BRT to assess risk.

### ***Definition of risk categories***

The criteria that are used to define risk categories by definition have an impact on the assessed risk (for example the set of criteria that a population must fulfill to be considered at high risk of extinction). Dewar et al. (2013) consider population decline as a risk only when it occurs to certain threshold abundance levels. The magnitude of any decline *per se* does not seem to have been considered. This is in contrast to the IUCN Red List criteria (IUCN, 2001), in which the magnitude of a population's decline is one of several factors (criterion A) that may qualify it for listing. A species is required to fulfill a minimum of one criterion (of criteria A to E) to qualify for the Red List, e.g. a decline in population size (of 80% for Critically Endangered or 50% for Endangered) alone is enough to merit listing. Although Dewar et al. (2013) present information about the probability of a decline of any magnitude over the course of 100 years (Table 4.17), this is not a very informative statistic for decision-makers. Declines of all magnitudes are not equal from a conservation perspective. No information is presented in section 4.5.2.3 of Dewar et al. (2013) about average rates of change in population size given current removal rates, nor are the probabilities associated with declines of differing magnitudes (e.g. 50% and 80%) given, despite the fact that this information is highly relevant to decision-makers. Some idea of the magnitude of decline for a population with 500 adult females over a 41 year period can be gleaned from Appendix B (Dewar et al. 2013, p. 127): the probabilities of declines of 60% and 75% are reported as 20% and 5% respectively, given the assumed historical bycatch rates. The probability of a 50% decline to 250 adult females or less appears to be substantial (Figure B1, top panel). It should be noted that in Appendix B of Dewar et al. (2013), a bycatch mortality rate of 20% was applied to YOY and age-1 white sharks and a bycatch mortality rate of 2% was applied to sub-adult and adults between 1971 and 1990. These rates are higher than those implied by most of the combinations of adult female abundance and YOY, age-1 and adult female bycatch mortality rates used in risk assessments in section 4.5.2 of Dewar et al. (2013). However, true catch rates are essentially unknown because reported catches may considerably underestimate actual catches for NEP white sharks (e.g. because white sharks are not a commercially targeted species and as a result of

protective regulation). Studies that have employed observers have found that catches may be under-reported by a factor of approximately 5 (Santana-Morales et al. 2012, Dewar et al. 2013).

In assessing risk, the BRT only considered the probability of declines in the NEP white shark population to or below the thresholds they chose to adopt for “near extinction” and “dangerously small” populations. Following the IUCN’S (2001) criterion D1 thresholds for Critically Endangered and Endangered populations, the BRT opted to use 50 mature individuals (25 mature females) as the threshold for “near-extinction” and 250 mature individuals (125 mature females) as the threshold for “dangerously small”. There are several issues with this approach.

The threshold population size for “near extinction” of 50 mature individuals or 25 mature females (p. 97) does not seem appropriate in the case of NEP white sharks, as a population size of 50 mature females was found to be unviable given current catch rates, with an age-1 bycatch mortality rate of 100% (Dewar et al. 2013). A mature female abundance of 50 or below thus corresponds to “imminent extinction”, rather than “near extinction”, based on current bycatch levels, as there would be no recruitment to the population of white sharks aged 2 and older. The probability of extinction in the near future, given current catch rates and assuming a population of 25 adult females is thus 1, instead of extremely high, as suggested in the definition from Regan et al. (2009), p. 87 of Dewar et al. (2013). A more appropriate threshold population size for “near extinction” based on Figure 4.15 would be in the range 60-125 adult females; this would correspond to a bycatch mortality rate that is high but not unity. Revising this threshold upwards would result in higher estimated probabilities of the population declining below the threshold within 60 or 100 years (values presented in Table 4.15 of Dewar et al. (2013)).

The declines required to reach the thresholds differ depending on the abundance category. For example, the lowest abundance category of 60-125 mature female white sharks would need to decline by 58-80% to reach the near-extinction threshold of 25, while the abundance category of 400-1600 mature female white sharks would need to decline by 94-98% to reach the near extinction threshold. Dewar et al. (2013) thus define risk in terms of larger declines for larger population sizes. This leads to some inconsistent evaluations of risk. For example, a population of 200 adult females declining by 90% to 20 over 60 years would be classified as high risk, while a population of 1000 undergoing a 97% decline to 30 in 60 years would not be. The rate of decline in a population’s abundance is arguably important in its own right: if the cause of decline is not removed, it becomes a matter of time before the abundance threshold is reached.

## ***Representation of uncertainty***

Population risk assessment depends on a full treatment of uncertainty (e.g. Boyce 1992; Staples et al. 2004). Failure to account for all relevant sources of uncertainty could lead to overly optimistic predictions about a species' persistence and potentially mis-classification of its conservation status. The approach taken by Dewar et al. (2013) appears to have under-represented uncertainty in a number of respects; these are listed and discussed in the following text.

The BRT took the approach of using a simulation study to obtain a distribution for the maximum annual rate of population growth ( $\lambda_{\max}$ ), which is the growth rate attained without limiting factors and at low population density (Dewar et al. 2013, p. 85). Distributions for vital rates used in the simulation are presented in Table 4.13 of Dewar et al. (2013).

The normal distribution that was used for litter size (Table 4.13, p. 86) appears to be overly precise, based on the range (4-14) reported in Mollet et al. (2000). The distribution used by the BRT has a 95% probability interval of [7.42, 10.36] and thus gives very low probability to litter sizes outside this range. A more realistic representation of the range of observed litter sizes would have been obtained by using a distribution with a larger standard deviation. For example, a normal distribution with a standard deviation of 2 would give a 95% probability interval of [4.98, 12.83].

The BRT used a distribution that gives equal probability to values of the ratio of YOY survival to juvenile survival between 0.5 and 0.99 (Table 4.13). The assumption that YOY survival is equally likely to be almost as high as juvenile survival compared with lower than juvenile survival seems over-optimistic. Juvenile sharks aged 2-5 will on average be considerably larger than YOYs, and natural mortality is often assumed to decrease with size (e.g. Lorenzen, 2000). The uniform distribution used by Dewar et al. (2013) for YOY survival rates assigns equal plausibility over the range 0.38 ( $0.89 \cdot 0.85 \cdot 0.5$ ) to 0.90 ( $0.96 \cdot 0.95 \cdot 0.99$ ). Again, it seems that YOY survival rates approaching or equal to adult survival (between 0.89 and 0.96) should have been assigned much lower plausibility. This type of mis-specification is expected to lead to over-estimation of  $\lambda_{\max}$  and underestimation of risk.

The BRT used a distribution for  $\lambda_{\max}$  based on a demographic invariant to update (shrink) the distribution from the simulation study (Dewar et al. 2013, p. 87 and Figure 4.12, p. 88).

Based on the information presented on pages 86 to 87 of Dewar et al. (2013), the distribution for  $\lambda_{\max}$  using the demographic invariant appears narrower than expected. An attempt to reproduce the process used to obtain the distribution for  $\lambda_{\max}$  based on the demographic invariant, using the information provided is presented in Appendix 2 of this document. Following the description of the findings of Dillingham et al. (in prep.) in Dewar et al. (2013), a value of  $a_k$  was drawn from a lognormal distribution with mean equal to 1 and standard deviation of 0.4. The standard deviation itself followed a lognormal distribution with a mean of 0.4 and CV of 0.35. Distributions for adult survival and age at first reproduction were taken from Table 4.13, and equation 2 (p. 87 of Dewar et al. 2013) was solved for  $\lambda_{\max}$ . This exercise resulted in a distribution for  $\lambda_{\max}$  that is considerably wider than the distribution of expected theoretical estimates in Figure 4.12 of Dewar et al. (2013), suggesting that one or more of the sources of uncertainty captured in Appendix B was not accounted for there. Based on the code in Appendix 2 of this document, a distribution for theoretical estimates of  $\lambda_{\max}$  with a 95% probability interval of 1.02 to 1.10 was obtained. Using this distribution (i.e. accounting for all the sources of uncertainty mentioned on pages 86 and 87 of Dewar et al. 2013) would be expected to lead to much less shrinkage of the distribution of life table estimates and a more uncertain final distribution for  $\lambda_{\max}$ . Failure to account for this uncertainty will tend to underestimate risk (e.g. the probability of the population declining below some threshold).

Observation error is a major source of uncertainty in fisheries assessment (Clark and Bjørnstad, 2004). Reported catches may deviate from actual catches for several reasons, including incomplete coverage of catches and non-reporting. The BRT stated that “*Consideration must be given to how the assessment would be affected by different catch estimates*” (p.106), and went on to note that existing bycatch estimates “*likely contain an unquantifiable degree of bias*” and are “*probably minimum bycatch estimates*” (p. 91). Considering this uncertainty, and the BRT’s acknowledgement that its results are conditional on the bycatch estimates used (p. 106), the treatment of YOY and juvenile bycatches as known by the BRT seems indefensible (values of  $159 \times 0.50$  and  $46 \times 0.50$  were used for the bycatch of YOY and juvenile female white sharks, respectively (Dewar et al. (2013), pp. 90-91). As a more robust alternative, the BRT could have considered a scenario based on observed rates of under-reporting (e.g. unreported catch around 5 times higher than reported catch, Santana-Morales et al. 2012, Dewar et al. 2013) or used SEDM to quantify uncertainty about rates of under- or over-reporting. The BRT did not offer an

explanation for omitting to use SEDM to characterize uncertainty in YOY and juvenile bycatch estimates. This approach was applied in many other instances in the report (e.g. to quantify bias in females abundance estimates and to produce a distribution for the number of adult females killed each year).

Treating bycatch estimates as known neglects a major source of uncertainty in the estimation of mortality rates for YOY and juvenile white sharks and in the assessment of risk to the population. Accounting for uncertainty about true bycatch levels could be expected to lead to more variability in the maximum annual rate of population growth accounting for fisheries bycatch mortality ( $\lambda_{\max}^*$ ), a greater spread of simulated population trajectories and a higher proportion of trajectories falling below thresholds corresponding to medium or high risk. Failure to address this uncertainty raises significant doubts about the reliability of the BRT's conclusions.

### ***Treatment of juvenile bycatch data***

The BRT states that it used a bycatch estimate of 46 juveniles between age 1 and 2 in its assessment of fisheries impact (p. 90). However, in the analyses that follow, it appears that only age-1 bycatch mortality is accounted for (estimated mortality rates for age-2 white sharks are not presented). The BRT goes on to rule out a total adult female abundance equal to the mark-recapture estimate ( $\approx 47$ ) on the grounds that the corresponding estimate of age-1 bycatch mortality of 100% is an “*unrealistic result*” (p. 92). However, this conclusion may be unjustified if bycatch mortalities for age-2 juvenile females and age-1 juvenile females were combined. Using the distributions for vital rates in Table 4.13 and the adult female abundance distribution with a mean of 47 in Figure 4.13, the approach described by Dewar et al. (2013) was applied to estimate  $\lambda_{\max}$  (without the shrinkage step). Bycatch mortality rate estimates greater than 100% were set to 100%. Assuming that all the juvenile females killed are age-1 ( $46 \times 0.5$  age-1 mortalities), 95% of age-1 bycatch mortality estimates were equal to 100% (a similar result to Dewar et al. (2013)). However, making the alternative assumption that half of the juvenile females killed in fisheries are age-1 and half are age-2 ( $46 \times 0.5 \times 0.5$  age-1 mortalities) resulted in a considerably lower proportion (63%) of age-1 bycatch mortality rates equal to 100%. This suggests that Dewar et al. (2013) may have done the former, which will tend to lead to an overestimate of the age-1 bycatch mortality rate, making an adult female abundance of around 50 white sharks seem less plausible that it

actually is. Moreover, age-1 mortality rates will be overestimated for all of the adult female abundance scenarios if the BRT assumed that all 23 juvenile female bycatch mortalities were age-1, further undermining the BRT's arguments that the estimated mortality rates render the lower categories of adult female abundance implausible (e.g. p. 106).

### ***Final estimates of abundance and risk from fishing mortality***

After evaluating the extinction risks associated with different scenarios for different levels of adult female abundance and mortality Dewar et al. (2013) return to arguments based on the plausibility of bycatch mortality rates for YOY and age-1 sharks implied by the different abundance scenarios (p. 106).

*“Catch and mortality rates informed the plausibility of the different abundances. For the lowest two abundance scenarios considered analytically plausible ( $N \approx 60 - 125$  and  $N \approx 125 - 200$ ), the corresponding annual catch rates for YOYs (means 0.49 and 0.27, respectively) are extremely and perhaps unrealistically high.”...“It would be astonishing if gill nets had the efficiency to capture  $>0.20$  of white shark YOYs each year...”*

However, as noted above, catch rates implied by tagging studies with YOY sharks suggest that an annual catch rate in the range 0.27 to 0.49 is not implausible. Of 7 tagged YOY sharks listed in Table 2, 5 (or over 70%) encountered net fishing gears, demonstrating that net gears do in fact have a high efficiency to capture YOY white sharks. Tagged white sharks encountered fishing gears in a variety of locations outside Sebastián Vizcaíno Bay (Table 2), including Ventura and Huntington flats in California, and Ensenada in Mexico. This information suggests that there may be unreported bycatch mortality of YOY and juvenile white sharks in addition to the reported bycatch from boats operating in Sebastián Vizcaíno Bay, thus assuming that all the bycatch is accounted for by the 6 boats operating there (e.g. Dewar et al. 2013, p. 82, p. 106) may be inappropriate.

## **Summary**

Despite acknowledging that their results are conditional on the bycatch estimates used, and that those estimates are probably underestimates, Dewar et al. (2013) did not account for uncertainty in YOY and juvenile bycatch mortality rates in their risk assessment. Since population risk assessment depends on a full treatment of uncertainty (e.g. Boyce 1992; Staples et al. 2004), this omission is a major flaw in their analysis, seriously undermining the credibility of their findings.

Uncertainty in the vital rates used in population projections appears to have been under-represented in a number of respects; overall, these are expected to lead to a less precautionary assessment of risk. Overly precise estimates of the intrinsic rate of population increase are expected to lead to fewer simulated population trajectories falling below the BRT's risk thresholds, underestimating risk.

Dewar et al. (2013) defined risk categories based on the probabilities of decline to threshold population sizes. The magnitude of decline was not considered as a separate component of risk, in contrast to the widely used IUCN Red List criteria. Using criteria based on both abundance and the rate of decline in abundance would have provided a more balanced summary of risks to the population. Use of abundance-based criteria only is expected to lead to lower estimates of risk because it does not consider whether the causes of population decline have been removed.

The threshold population size of 25 adult females seems inappropriately low, given that Dewar et al. (2013) reported a bycatch mortality rate of 100% for age-1 white sharks for a population with 47 adult females. In other words, given current bycatch rates, the population would have an extinction probability of one at a considerably larger number of adult females than 25. Again, this may have led to underestimation of risk to the population.

Strong prior assumptions about YOY and age-1 mortality were used to judge the plausibility of adult female abundance categories in the absence of supporting evidence. As mortality rates depend, among other things, on abundance, and mortality rates for a given species and population will vary case-by-case (see p. 29 of this review), this is an insufficient basis for denying protections to this white sharks.

## ***Response to the BRT'S conclusions***

In the following text, the conclusions of the BRT are reviewed in the light of the counter-arguments presented in this review.

Based on a final SEDM vote, the BRT concluded that the NEP white shark population is at very low (50% of plausibility points) to low (36% of plausibility points) risk of extinction (Table 4.18, p. 107). Noting that the risk categories (very low, low, medium and high) used by the BRT correspond approximately to the adult female abundance categories considered (400-1600, 200-400, 125-200 and 60-125, respectively), Tables 4.15 to 4.17 of Dewar et al. (2013), an approximate female abundance corresponding to the BRT's assessment of risk can be computed using the SEDM weights in Table 4.18 and the midpoints of the adult female abundance categories as  $0.50*1000 + 0.36*300 + 0.09*162.5 + 0.05*92.5$ , or around 630 adult female white sharks. Based on the relationship between adult female and total abundance in Table 4.14 (p. 90), this would correspond to a total population size (all ages) of 11,000-12,000 white sharks in the NEP. As discussed in this report, there were several problems with the way in which the BRT extrapolated mark-recapture abundance estimates to the whole NEP. Foremost among these was the BRT's failure to validate its opinions with observations of YOY bycatch mortalities. Inflating the abundance estimates without sound empirical basis or reasoning risks underestimation of the extinction probability for NEP white sharks.

Dewar et al. (2013) describe the bycatch data as "*One of the most important pieces of evidence for a low to very low risk of extinction*" since adult female abundances of 200 or less would correspond to removal of "*on the order of 20% to 70% of estimated annual pup production*". The BRT effectively uses a strong prior on the bycatch mortality rate with 0 probability for values above 0.20. This prior belief is based on a comparison with other species that may be inappropriate for reasons listed above. Above all, the bycatch mortality rate will depend on abundance, which itself is unknown. A more justifiable approach would be to estimate rates of bycatch mortality using tagging data. Available information from tagging studies suggests that bycatch mortality rates considered implausible by Dewar et al. (2013) are in fact quite likely. Based on studies to date where young of the year white sharks were tagged, bycatch rate estimates of 29% to 43% were obtained, depending on assumptions made about the fate of

individuals that encountered nets but were not retained. High uncertainty is associated with these estimates because of the low sample size of tagged YOY sharks (N=7) and uncertainty about the true level of YOY bycatch. Nonetheless, it appears that more data on the YOY bycatch rate (e.g. from further tagging experiments) would be needed to establish the implausibility of YOY harvest rates greater than 20%.

The BRT's second argument in support of its conclusion is that the haplotypic diversity of NEP white sharks "*reflects a current adult female population size of at least a few hundred to a couple [of] thousand adult females*". As established above, the haplotypic diversity data provided in Table 2.2 provide at best weak information about abundance (because of the large variability in haplotypic diversity at a given abundance and the unknown ratios of effective population sizes to census population sizes). The BRT omits to state results from the historical projection model with a starting population size of 500 adult females in its conclusions, under which depletion to a current population size of "a few hundred" adult females or less appears quite likely ( $\approx 40\text{-}50\%$ , Figure B.1, top panel, Dewar et al. (2013)). Starting population sizes of 300 or 400 adult females, which would also be consistent with the genetic data according to Dewar et al. (2013), were not evaluated by the BRT. The conclusion that "*the haplotypic diversity reflects a current adult female population size of at least a few hundred to a couple [of] thousand adult females*" is therefore unsubstantiated.

## **Conclusion**

Dewar et al. (2013) offered little additional data to assess the abundance of white sharks in the NEP, instead using a strong assumption (prior) about the level of bycatch mortality of young of the year and juvenile white sharks to evaluate the plausibility of adult female abundance categories considered. Observations of mortalities of tagged YOY white sharks suggest that the assumption made by the BRT was not appropriate.

Contrary to the assertion of Dewar et al. (2013), the genetic data do not appear to be inconsistent with a current adult female abundance of less than several hundred. For example, declines from a starting abundance of 300-500 adult females to 250 or less over 41 years would have a relatively high probability given the model in Appendix B (at least  $\approx 25\text{-}30\%$ , Dewar et al. 2013), whilst being consistent with the haplotype diversity data.

Dewar et al. (2013) likely underestimated the extinction risk to the NEP white shark population, through a failure to account for all the relevant sources of uncertainty (notably in YOY and juvenile bycatch levels) in their assessment. Their definitions of criteria and thresholds for different levels of risk are also expected to have led to an overly-optimistic assessment.

Taking these points into consideration, in addition to the available mark-recapture data and observations of YOY bycatch mortalities, adult female abundances in the lowest two abundance categories considered by the BRT (i.e. < 200) appear to be more parsimonious than the abundance range found to be most plausible by the BRT (400-1600 adult females). An adult female abundance of 200 or less would be classified as medium to high risk under the BRT's assessment, which likely underestimated risk because of a failure to properly represent uncertainty. A high risk status thus appears to be highly plausible for NEP white sharks.

## ***List of abbreviations***

BRT	Biological Review Team (Dewar et al. 2013)
ESA	Endangered Species Act
CPUE	Catch per unit effort
CV	Coefficient of variation
IUCN	International Union for Conservation of Nature
MBA	Monterey Bay Aquarium
NEP	northeastern Pacific
NMFS	National Marine Fisheries Service
SEDM	Structured Expert Decision Making
YOY	Young of the year

## ***List of symbols***

$\sim$	is distributed as
$C_{YOY}$	the ratio of the YOY survival rate to the juvenile survival rate
$\lambda_{max}$	maximum annual rate of population growth
$\lambda_{max*}$	maximum annual rate of population growth accounting for fisheries bycatch mortality

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Appendix 1:

Simple calculation for the number of YOYs based on tagging data

```
model{
```

```
#both YOY that left tags behind survived: 2/7 mortalities of tagged YOY white sharks SE  
(p) approx #0.17
```

```
#pcapt~dbeta(1.74,4.26)
```

```
#Nfem median 146, 95% 46-1157
```

```
#one YOY that left tag behind survived: 3/7 mortalities of tagged YOY white sharks SE (p)  
approx #0.19
```

```
pcapt~dbeta(2.57,3.43)
```

```
#Nfem median 93, 95% 36-416
```

```
yoy_bycatch~dlnorm(mu_c,tau_c)
```

```
N_yoy<-yoy_bycatch/pcapt      #YOY both sexes  
N_fem<-N_yoy/pups
```

```
litter~dnorm(8.9,1.778)      #standard deviation 0.75  
pups<-litter/2.2            #number of pups per year
```

```
mu_c<-log(159)-0.5/tau_c
```

```
CV_c<-0.3 #CV of YOY bycatch  
tau_c<-1/log(CV_c*CV_c+1)
```

```
}
```

## Appendix 2:

BUGS code to obtain a distribution for lambda max based on information provided on pages 86-87 of Dewar et al. (2013), based on results from Dillingham et al. (in prep.).

```
model{

m_a<-1 #mean of distribution for ak
mu_a<-log(m_a)-0.5/tau_a
tau_a<-1/pow(sigma_a, 2)

a~dlnorm(mu_a, tau_a) #ak (draw a value of a for white sharks from the inter-species
                        distribution, mean=1)

lambda_max<-exp(a*pow((alpha+S/(lamba_test-S)), -1)) #equation 2, p87

lamba_test<-1.049

sigma_a~dlnorm(mu_sigma, tau_sigma) #distribution for sigma a (mean=0.4)
mu_sigma<-log(0.4)-0.5/tau_sigma

CV_sigma<-0.35 #CV of sigma a
tau_sigma<-1/log(CV_sigma*CV_sigma+1)

S~dunif(0.89,0.96) #adult survival, from Table 4.13
alpha~dunif(12,15) #age at first reproduction, from Table 4.13

}
```