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Statistical modelling reveals spatial, temporal, and environmental preferences for white sharks at an oceanic aggregation site

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ABSTRACT: Guadalupe Island, Mexico, is one of the most important white shark (*Carcharodon carcharias*) aggregation sites in the Eastern Pacific. In the waters surrounding Guadalupe Island, cage diving has been carried out since 2001 during August–November; however, there is scarce information regarding the factors associated with this seasonal aggregation. The purpose of this study was to describe the probability of occurrence of white sharks relative to spatial, temporal, and environmental factors in Guadalupe Island. Generalized additive models (GAMs) were used to describe the effect of sea surface temperature, water visibility, tide, moon phase, cloud cover, time of day, and location on white shark occurrence. GAMs were generated from a data set of 6266 sightings of white sharks, classified as immature males, mature males, immature females, and mature females. A sexual segregation related to month was observed, where females arrived after males during late September. GAMs evidenced a segregation of white sharks according to the analysed variables, which is consistent with previous observations in this locality. Environmental preferences for each white shark category are potentially influenced by feeding habits, sexual maturation, and reproduction. This study constitutes a baseline of the effect of the environment on the occurrence of white sharks in Guadalupe Island, which can be used in further studies regarding management and conservation in future climatic and anthropogenic scenarios. Its relevance is related to the understanding of its ecology in oceanic environments and the presence of this threatened species during the ecotourism season.

KEY WORDS: Generalized additive models · Environmental factors · Protected species · Conservation · Ecology

1. INTRODUCTION

The white shark *Carcharodon carcharias* (Linnaeus, 1758) is a top predator that inhabits temperate coastal and oceanic environments around the globe (Compagno et al. 2005, Huveneers et al. 2018). Despite its wide distribution, this species is commonly observed at low densities, with the exception of nursery areas (White et al. 2019, Santana-Morales et al. 2020) and aggregation sites close to pinniped colonies where white sharks have shown site fidelity (Klimley et al. 1996, Domeier & Nasby-Lucas 2008). These aggregation sites are mainly located in both coastal and insular areas on the continental shelf

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(Huveneers et al. 2018, White et al. 2019). Nevertheless, there are oceanic aggregations such as Guadalupe Island, Mexico, or the 'shared offshore foraging area' in the Northeast Pacific Ocean where white sharks have also been seasonally registered (Domeier & Nasby-Lucas 2008, Hoyos-Padilla et al. 2016).

Aggregation sites are key areas for the survival of this threatened species, and are therefore relevant in terms of sustainable management, scientific research, and conservation (Huveneers et al. 2018, Rigby et al. 2019, White et al. 2019). Previous studies have shown that environmental factors can influence the white shark's distribution, reproduction, diving behaviour, and the probability of interaction with humans (Pyle et al. 1996, Hammerschlag et al. 2006, Robbins 2007, Weltz et al. 2013, Hoyos-Padilla et al. 2016). However, the majority of such studies has been carried out in coastal environments, so there is scarce information about the ecology of white sharks in remote oceanic areas (Huveneers et al. 2018).

In continental areas such as the Farallon Islands, California, environmental conditions such as high waves, low visibility, cloudy skies, new moon, and high tides have been related to an increase in the occurrence of white sharks, since these conditions are favourable for the predation of northern elephant seals *Mirounga angustirostris* (Anderson et al. 1996, Pyle et al. 1996). A similar effect has been observed in Seal Island, South Africa, by a significant increase of attacks on Cape fur seals *Arctocephalus pusillus pusillus* related to wind direction and intensity, low tides, and low sunlight (Hammerschlag et al. 2006).

Sea surface temperature (SST) is a key factor that influences the occurrence of white sharks. The presence of white sharks was related to a decrease in the SST during winter and early spring within a range of 14–23°C in Florida (Adams et al. 1994, Curtis et al. 2006). In the Mediterranean Sea, Fergusson (1994, 1996) reported the absence of white sharks when SST exceeded 25°C, which coincided with the movement of the sharks to cold, deep water with sporadic movements to the surface. In the Neptune Islands, Australia, a higher abundance of female white sharks was observed during warm SST (16–18°C) and high tide conditions, which was linked to a potential sexual segregation related to reproduction (Robbins 2007). Regarding the presence of white sharks in False Bay, South Africa, the probabilities of observing this species rise in the afternoon, with an SST of 14–18°C, and during nights with new moon (Towner et al. 2013, Weltz et al. 2013).

In the Mexican Pacific, the occurrence of white sharks has been reported in the Gulf of California (Galván-Magaña et al. 2010, Becerril-García et al. 2019a), the west coast of the Baja California Peninsula (Santana-Morales et al. 2020), the Revillagigedo Archipelago (Becerril-García et al. 2020a), and mainly in Guadalupe Island (Domeier & Nasby-Lucas 2007, Hoyos-Padilla et al. 2016). Since 2001, ecotourism activities have taken place from August–November in the northeast part of Guadalupe Island known as Rada Norte Bay, which is the official area for cage diving due to local wildlife regulations (Torres-Aguilar et al. 2015). This activity is carried out by national and foreign boats, and it generates economic benefits, provides extra vigilance against illegal fisheries, and is also frequently used as a platform for scientific activities (Cisneros-Montemayor et al. 2020).

Scientific research related to the ecology of white sharks in Guadalupe Island has focused on migration patterns (Domeier & Nasby-Lucas 2008, 2013), feeding habits (Jaime-Rivera et al. 2014, Alderete-Macal et al. 2020), and local movements (Domeier et al. 2012, Skomal et al. 2015, Hoyos-Padilla et al. 2016). Stable isotope analyses ($\delta^{13}C$, $\delta^{15}N$) of white shark dermis have provide evidence of the consumption of pinnipeds, tunas, and squid, although differences between maturity stages were not evaluated (Jaime-Rivera et al. 2014). Acoustic telemetry studies have shown that white sharks present spatial segregation on the island related to sex and maturity, with juveniles in shallow waters (<100 m) and adults in deep waters (>250 m; Hoyos-Padilla et al. 2016). However, studies of the effect of the environment on the presence of white sharks at this oceanic locality are still scarce, so the drivers of such segregation and environmental preferences remain unknown.

In this study, we aimed to provide information regarding the effect of spatial and temporal factors, as well as environmental conditions affecting the probability of occurrence of white sharks during cage diving operations in Guadalupe Island. These observations constitute one of the first descriptions of the ecology of white sharks in oceanic environments, which could be used for management decisions and as a baseline for future climatic and ecotourism scenarios in this marine protected area.

2. MATERIALS AND METHODS

2.1. Study area

Guadalupe Island is located within a marine protected area, 241 km west off Baja California, in the Mexican Pacific (29° 00′ N, 118° 26′ W; Fig. 1). In the

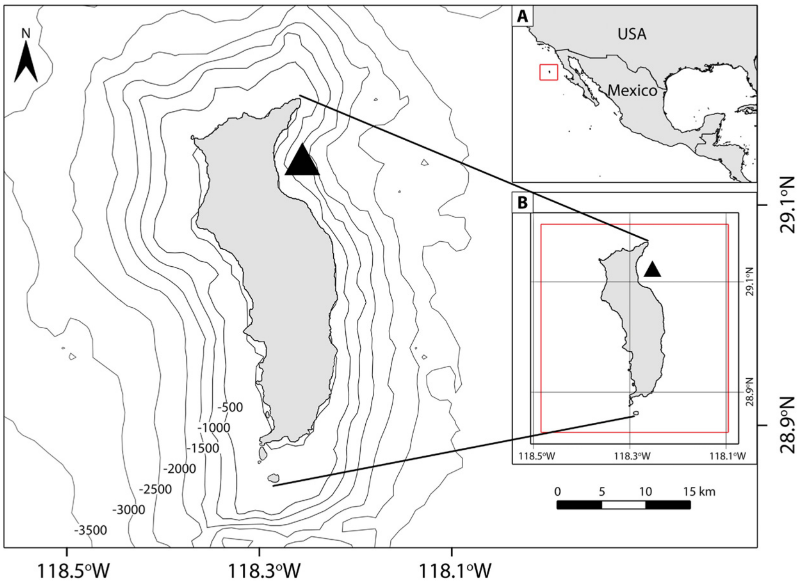

Fig. 1. (A) Guadalupe Island, Baja California, Mexico, including the boundaries (red square) of (B) the marine protected area and the location of Rada Norte Bay (▲). Bathymetric contours are expressed in m

marine protected area, oceanographic conditions are highly influenced by the California Current System, which generates local upwelling that provides cold, nutrient-rich waters to the island (Pierson 1987). Guadalupe Island is 35 km long and 9.5 km wide with a north–south orientation, with surrounding depths of more than 4000 m (Gallo-Reynoso & Figueroa-Carranza 2005). Wind from the north is predominant during the whole year (Strub et al. 1987). The waters surrounding the island have an average SST of 18°C that ranges between 16 and 20°C (Lynn & Simpson 1987, Gallo-Reynoso & Figueroa-Carranza 2005). Semidiurnal tides have an amplitude of 3 m, and water visibility of 25–30 m has been reported throughout the year (Gallo-Reynoso & Figueroa-Carranza 2005, Becerril-García et al. 2019b).

The cage diving season in Guadalupe Island occurs from August–November. The present study was performed onboard the 6 cage diving boats that visited Rada Norte Bay during the 2012, 2013, and 2014 seasons, for a total of 92 d from which the obtained data were pooled across sampling years. All the boats that participated in this study were equipped with 2 surface cages and were anchored 200–250 m off the coast at a depth of 70–80 m.

2.2. Biological data

The presence or absence of white sharks was recorded by the number of sightings during constant monitoring that lasted an average of 8 h d^{-1} between 07:00 and 17:00 h. However, the start of each day's monitoring was dependent on the schedule of the cage diving boats and their time of arrival to the island. A sighting was defined as the observation of one or more white sharks detected at the surface at an approximate distance of 10 m to the bait. All sightings were classified according to sex and maturity stage. Each sighting was reported as 1, while absences were reported as 0 for all analysed categories (immature males, mature males, immature females, and mature females). Total length (TL) was estimated by comparing the length of the cages with the length of each shark that approached horizontally, parallel, and close to the cage. Sex was determined by the presence or absence of claspers, confirmed through underwater photographs. Males of TL > 3.5 m and females of TL > 4.5 m were considered mature specimens (Compagno et al. 2005). In order to maintain the bias of estimations, all observations were carried out by one of the authors (E.E.B.G.).

General results of the occurrence of white sharks according to year and month were described using sightings per day and sightings per hour as a unit for preliminary statistical analyses. This data set did not meet the assumptions of normality according to Lilliefors test ($p < 0.05$). Therefore, significant differences were calculated using the nonparametric Kruskal-Wallis test and a Bonferroni post hoc test. The significance of monthly sex ratios was calculated with an exact binomial test using R v.3.6 programming software (R Core Team 2019). After these first analyses, presence and absence data were used for statistical modelling involving environmental data.

2.3. Spatial, temporal, and environmental data

The position of the cage diving boat (latitude, longitude) was recorded at the beginning of each day. Environmental conditions were registered every 30 min during cage diving activities along with the biological data. The analysed environmental factors included SST (ethanol-filled thermometer; 0.1°C); high or low tide using the software MAR V1.0 (CICESE 2020) and public data from the Center for Operational Oceanographic Products and Services

(NOAA 2020), moon phase according to data from the Astronomical Applications Department of the US Navy (US Naval Observatory 2020; considering 0 as new moon and 1 as full moon), *in situ* cloud cover percentage (binned in 4 categories: 0–25, 25–50, 50–75, and 75–100%), and water visibility through the use of a Secchi disk (m). The cut-off between high and low tide was defined according to the mean sea level (60 cm) for Guadalupe Island, as well as the reference values of mean lower low water (0 cm) and mean high water (120 cm).

The probability of white shark occurrence was examined relative to diverse environmental conditions to describe the factors that limit the presence of white sharks during cage diving activities. The assumption was that changes in the occurrence of white sharks are related to variables other than human activities, despite baiting being used to attract sharks during ecotourism activities in this area. This assumption was supported by the observation of a similar presence of white sharks regardless of bait, as reported by Becerril-García et al. (2020b) during the same study period.

2.4. Statistical modelling

Generalized additive models (GAMs) were used to evaluate the effects of spatial, temporal, and environmental factors on the probability of occurrence of white sharks at Guadalupe Island. GAMs were built using the 'mgcv' package in R v.3.6 (R Core Team 2019). These models are usually described as a generalized linear model with a linear predictor involving smooth functions of predictor variables (Wood 2006). The response variable was presence/absence for the 4 categories of white sharks: (1) immature males; (2) mature males; (3) immature females; or (4) mature females. Therefore, a binomial distribution with logit link function was used in the GAMs. For the modelling of the 4 categories of white sharks, the response variable was assigned a value of 1 if the shark belonged to a specific category, and 0 otherwise. Predictor variables were temperature, year, hour, cloud cover, lunar phase, visibility, tide, longitude, and latitude. Sighting data were reshaped for modelling, i.e. columns with presence/absence data for the 4 categories of white sharks were stacked row-wise according to hour and day across the 3 sampling years.

To avoid model overfitting, backward stepwise selection was used, which consisted of building the full model (all predictor variables) and then removing each predictor variable in each step. In the final step, the null model (overall mean) was obtained for each category. To assess if the deletion decreased model fitting, Akaike's information criterion (AIC) was used with the lowest AIC as the best-fitted model. Thus, up to 7 predictor variables with a low Pearson's correlation coefficient (<0.6, results not presented here) were used in the final models. The level of smoothing (i.e. number of basis in smoothing functions) for each predictor variable was restricted to 4 in order to avoid overfitting, except for the spatial term (longitude and latitude as interaction terms). Temporal autocorrelation was evaluated using the function corAR1() in the GAM for the 4 categories of white sharks; however, this did not improve the model fit and was therefore not included. The model's assumption of normality and homoscedasticity of residuals were evaluated using diagnostic plots ('gam.check' function). The GAM can be expressed as follows:

$$\text{logit}(\mu_i) = \alpha + f_1(\text{Lon}_i, \text{Lat}_i) + f_2(\text{Hour}_i) + f_3(\text{Lunar}_i) + f_4(\text{Visibility}_i) + \text{Year}_i + \text{Cloud}_i + \text{Tide}_i \quad (1)$$

where μ_i is the presence/absence of 4 categories of sharks (1: immature males; 2: mature males; 3: immature females; 4: mature females); α is the intercept; f_n is the smooth function (thin plate regression spline); year, cloud cover, and tide were used as categorical variables. Additionally, the results regarding spatial variables (latitude, longitude) of each GAM were used to create a figure that summarized the observations of the probability of occurrence of white sharks in Rada Norte Bay.

3. RESULTS

A total of 6266 sightings of white sharks were registered according to sexual maturity, of which 44% were immature males (n = 2740); 30% mature males (n = 1856); 5% immature females (n = 342); and 21% mature females (n = 1328). The median (±SE) number of records was 59 ± 5.96 sightings d^{-1} and 9.82 ± 1.22 sightings h^{-1}, with no significant differences in the number of sightings per hour related to year ($H_{2,90}$ = 6.35, p = 0.04), confirmed by a post hoc Bonferroni test (p > 0.05). Regarding month, the number of sightings per hour was higher during August ($H_{3,90}$ = 21.20, p < 0.01), with a lower and similar presence in the following months. Overall, a sex ratio of 2.8:1 (M:F; p < 0.01) was observed; however, this ratio changed according to the month of the year, given that only males were registered during August, and females were first observed at the end of September at 9.4:1 (M:F; $p < 0.01$). In the following months, the sex ratio was 1.6:1 (M:F; $p < 0.01$) in October and 1.2:1 (M:F; $p < 0.05$) in November.

3.1. Statistical modelling

Four GAMs were created to describe the probability of occurrence for each white shark category and explained 36–67% of the deviance according to the data set of each category. In this regard, only the significant factors (Table 1) were considered for each model since this avoided over-parameterization of the GAMs. Thus, spatial, temporal, and environmental variables affecting the occurrence of white sharks were described according to the analysed category. For modelling, a total of 3033 records for each category were used due to the reshape of the sightings data. In this regard, the arrangement of sightings with respect to time and day could have included more than one shark category; therefore, the total number of records was reduced for the GAMs. Diagnostic plots of residuals (results not shown) suggest that model assumptions of normal distribution and homoscedasticity of the residuals were not violated and were independent of the covariates values.

Table 1. Backward stepwise selection of generalized additive models for white sharks by sex and maturity stage (n = 3033 records). Dev. exp.: deviance explained (%); adj. R^2: adjusted R^2; AIC: Akaike's information criterion. The best-fitted models are in **bold**. Last row stands for null model (overall mean)

Model	AIC	Adj. R^2	Dev. exp. (%)
Mature male			
Full	1266	0.711	67.403
Year	**1264**	**0.711**	**67.404**
Cloud cover	1267	0.707	67.155
Tide	1269	0.705	67.047
s(Hour)	1281	0.701	66.538
s(Temperature)	1312	0.689	65.573
s(Visibility)	1337	0.686	64.706
s(Lunar)	1379	0.674	63.384
s(Lon, Lat)	3617	0.000	0.000
Mature female			
Full	**1551**	**0.536**	**54.331**
Year	1556	0.536	54.323
Tide	1566	0.529	53.831
Cloud cover	1644	0.500	51.182
s(Lunar)	1709	0.469	49.015
s(Visibility)	1753	0.453	47.458
s(Hour)	1809	0.425	45.501
s(Temperature)	1931	0.374	41.564
s(Lon, Lat)	3215	0.000	0.000
Immature male			
Full	**2538**	**0.465**	**41.270**
Year	2715	0.416	36.930
Cloud cover	2711	0.416	36.874
Tide	2710	0.415	36.860
s(Visibility)	2728	0.411	36.292
s(Temperature)	2784	0.387	34.794
s(Hour)	2843	0.371	33.244
s(Lunar)	3088	0.314	27.201
s(Lon, Lat)	4162	0.000	0.000
Immature female			
Full	525	0.516	63.886
Year	**522**	**0.516**	**63.875**
s(Lunar)	573	0.476	60.469
s(Temperature)	579	0.463	59.633
Tide	583	0.457	59.176
Cloud cover	604	0.450	57.130
s(Visibility)	781	0.274	42.834
s(Hour)	832	0.224	38.511
s(Lon, Lat)	1301	0.000	0.000

Mature males. According to the model, a higher probability of occurrence of mature males was observed along the entire bay and to the eastern area with depths >500 m (Fig. 2); during the morning before 10:00 h, with colder SST (<20°C), low visibility conditions (<15 m), low cloud coverage (0–25%), low tides, and after a crescent moon. The model involving the data of this category explained 67.4% of the deviance (Fig. 3).

Immature males. This model evidenced a higher probability of occurrence of juvenile male white sharks near the shore of the central part of the bay (<100 m; Fig. 2); before noon (12:00 h), during warm SST (>22°C), and high visibility conditions (>20 m), and after a half or full moon. Categorical variables suggest that the presence of juvenile males was higher in 2014, with cloud cover between 25 and 50% and high tide. The model involving the data of this category explained 41.3% of the deviance (Fig. 4).

Mature females. A higher probability of occurrence was related to the northern and southern part of the bay at depths <500 m (Fig. 2); after 14:00 h,

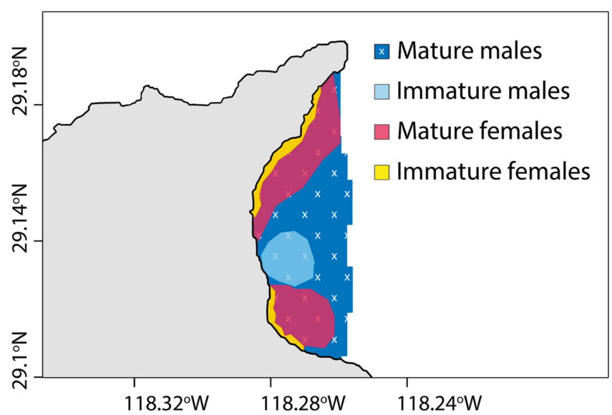

Fig. 2. Probability of occurrence of white sharks at Rada Norte Bay, Guadalupe Island, Mexico, according to the sexual maturity of the spatial variables of generalized additive models

during both cold (<21°C) and warm SST (>24°C) conditions, low visibility (<15 m), low tide, clear skies (<25% cloud cover), and after nights with less than 0.6 of moon light cover. This model suggests that probability of occurrence of mature females was similar during the study period. The model involving the data of this category explained 54.3% of the total deviance (Fig. 5).

Immature females. A higher probability of occurrence was related to the coast of the northern and southern part of the bay (<100 m; Fig. 2); after noon (12:00 h), during cold SST (<22°C), and low visibility (<15 m) conditions, high tides, cloud cover between 25 and 50%, and after a half or full moon. This model explained 63.8% of the total deviance (Fig. 6).

4. DISCUSSION

Statistical modelling revealed a spatial segregation of white sharks related to sex and maturity. This is similar to what has been observed in previous studies using passive and active telemetry, in which immature sharks remained close to the coast and mature individuals were found in deeper areas (Hoyos-Padilla et al. 2016). The probability of occurrence changed according to the location of the bay and the environmental preferences of each analysed group.

4.1. Spatial and temporal segregation

The arrival of mature and immature males was registered at the beginning of August, while females of both maturity stages arrived at the end of September. These results are consistent with the sexually segregated migration of white sharks that seasonally visit Guadalupe Island (Domeier & Nasby-Lucas 2008, Hoyos-Padilla et al. 2016). The effect of such migration patterns was evident in the monthly sex ratio, since this proportion was similar as the season progressed in October and November. Previous studies have shown that mature sharks remain until January (Domeier et al. 2012), so it is likely that the sex ratio could be similar throughout their time in the waters surrounding the island. The presence of mature individuals of both sexes highlights the importance of the area in terms of trophic ecology, with the acquisition of prey such as cephalopods, fishes, and pinnipeds (Jaime-Rivera et al. 2014, Hoyos-Padilla et al. 2016), but also for reproduction, by observing sexually mature individuals at the same period. Nevertheless, research on the reproductive biology of white sharks in Guadalupe Island is scarce, although it could be assessed in the future by analysing steroid hormonal profiles through minimally invasive techniques (Sulikowski et al. 2012, Domeier & Nasby-Lucas 2013, Becerril-García et al. 2020c). The higher probability of occurrence of juvenile males during the years 2013 and 2014 could be related to an increase in the proportion of this category of sharks, since some authors have suggested an increase in the number of juveniles due to the protection actions implemented by Mexico and USA since the late 1990s (Burgess et al. 2014, O. Santana-Morales unpubl. data). However, an increase in white sharks' occurrence could also be due to favourable environmental conditions or an increased prey availability in the area (Pyle et al. 1996, Hammerschlag et al. 2006, Weltz et al. 2013).

During the study period, the probability of occurrence of mature males was similar throughout the bay, with a higher occurrence in offshore areas; conversely, immature sharks were more likely to be found near the coast. This spatial segregation could be associated with prey availability for each group; the occurrence of mature males was higher in offshore areas, which could be related to the capture of prey such as yellowfin tunas *Thunnus albacares*, yellowtail jacks *Seriola lalandi*, and occasionally marine mammals (Reyes-Bonilla et al. 2010, Kim et al. 2012, Jaime-Rivera et al. 2014). In the case of immature sharks, their occurrence in shallow areas would be related to the capture of smaller prey, such as bony fishes and other elasmobranchs, as well as to avoid encounters with mature white sharks (Walther-Mendoza et al. 2013, Hoyos-Padilla et al. 2016, Becerril-García et al. 2019b).

The occurrence of mature females was related to areas that are close to the 2 northern elephant seal colonies *Mirounga angustirostris* located at the north and south of the bay (Gallo-Reynoso et al. 2005). The overlap of habitats for both female white sharks and northern elephant seals is related to trophic interactions between these taxa (Jaime-Rivera et al. 2014, Gallo-Reynoso et al. 2005). As potential prey, it is possible that northern elephant seals are an important element in the diet of mature females, since the presence of pregnant sharks has been suggested by other authors between October and December (Domeier & Nasby-Lucas 2013, Hoyos-Padilla et al. 2016). The income of energy for vitellogenesis and nutrition of embryos through means of oophagy could be substantially obtained by feeding on fat-rich prey such as cetaceans and pinnipeds (Klimley et al. 1996, Compagno et al. 2005, Jaime-Rivera et al. 2014).

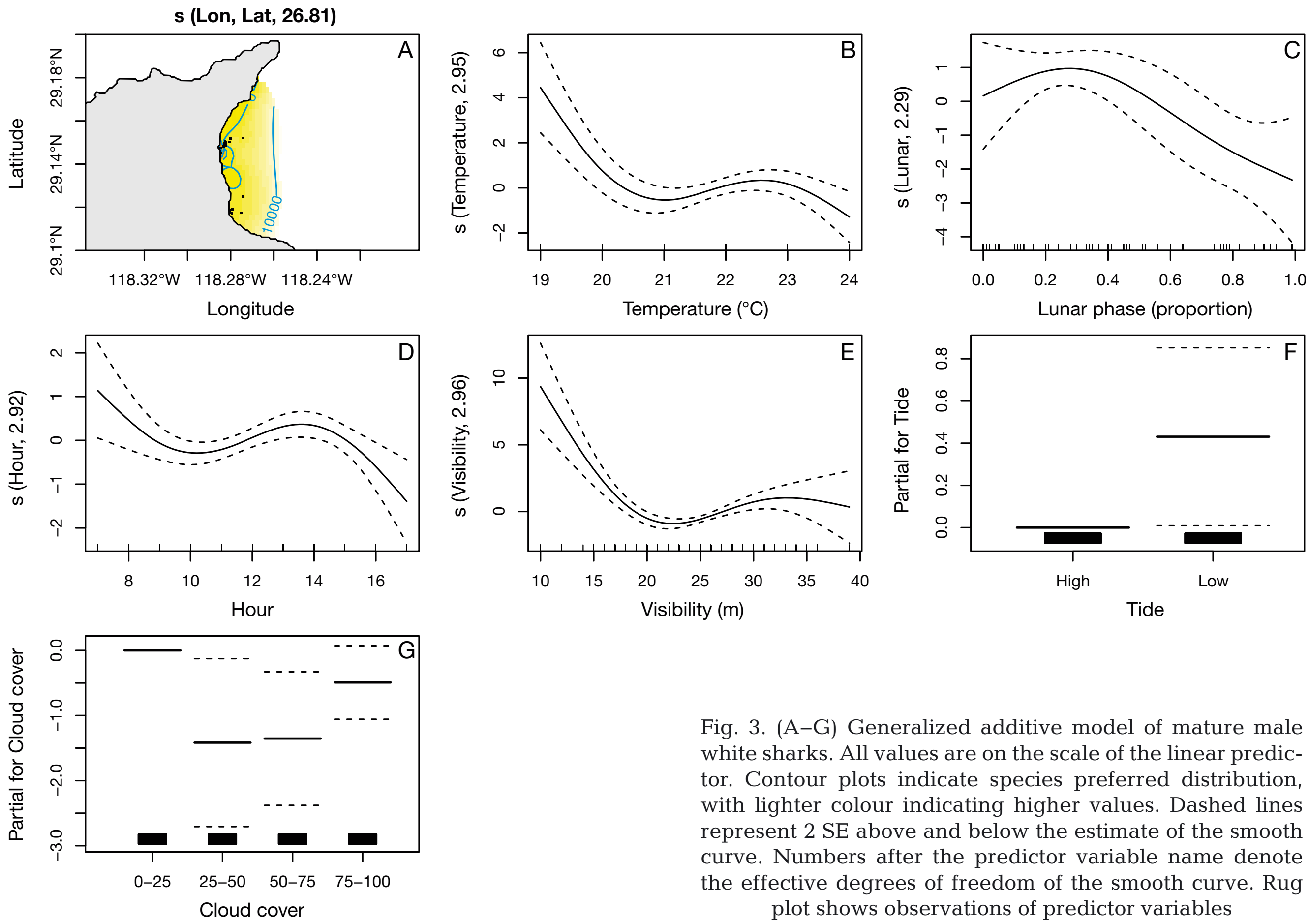

Fig. 3. (A–G) Generalized additive model of mature male white sharks. All values are on the scale of the linear predictor. Contour plots indicate species preferred distribution, with lighter colour indicating higher values. Dashed lines represent 2 SE above and below the estimate of the smooth curve. Numbers after the predictor variable name denote the effective degrees of freedom of the smooth curve. Rug plot shows observations of predictor variables

4.2. SST

The probability of occurrence of white sharks differed according to SST. The occurrence of mature sharks was higher during colder SST conditions (<21°C), while immature males were observed mainly during warmer SST conditions (>22°C). This observation could be related to thermal tolerance and heat regulation, since immature sharks have a smaller body and therefore a higher surface area to volume ratio compared to mature sharks (Block & Finnerty 1994). The lower thermal inertia compared to mature individuals could explain the preference of this group for warm water conditions, which could be beneficial for their metabolism in terms of higher growth rates and sexual maturation, as long as prey are available and the white sharks' energy requirements are met (Robbins 2007). However, this effect was not observed in the group of immature females, for which a higher probability of occurrence was observed during colder SST.

Although there is insufficient evidence to support this hypothesis and it is poorly understood in lamnoids, differences in SSTs between the occurrence of both immature males and females are likely due to potential sexual segregation during juvenile stages (Klimley 1987, Andrews et al. 2010, Hoyos-Padilla et al. 2014). The existence of sexual segregation during the early development of white sharks should be assessed in future studies through the use of telemetry, fatty acids, or detailed stable isotope analysis. This could provide evidence of differences in habitat use, prey preferences, and therefore ecological niche, which would lead to a better understanding of the ecology of this species (Jaime-Rivera et al. 2014, Huveneers et al. 2018, Becerril-García et al. 2019b, Alderete-Macal et al. 2020).

The generation of internal heat and its distribution in the body through the retia mirabilia could explain the increased occurrence of mature white sharks in colder waters (Goldman 1997, Compagno et al. 2005). In the Mediterranean Sea, mature white sharks showed vertical movements towards deep waters during warm SST conditions (Fergusson 1994, 1996), which could suggest diving behaviour

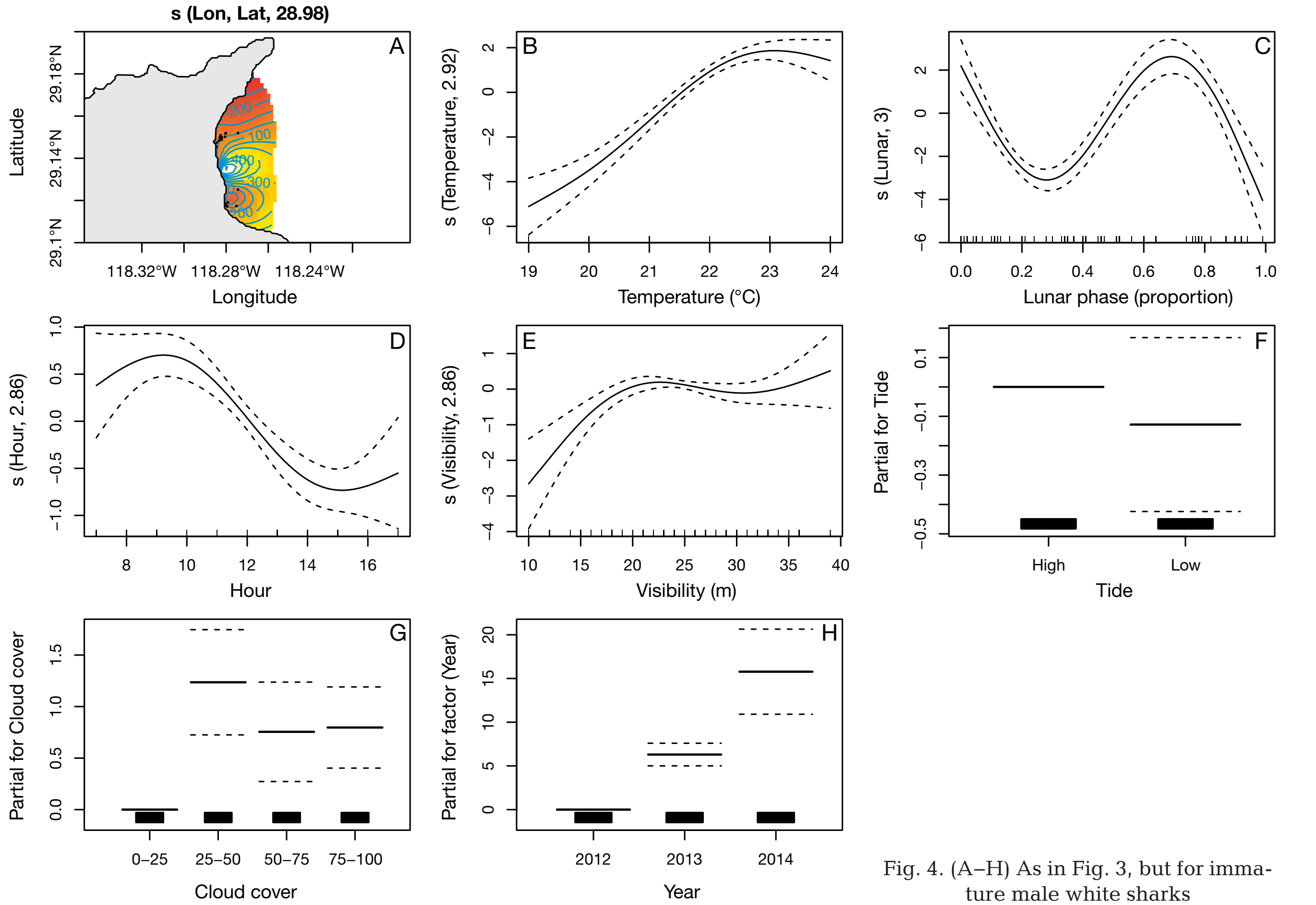

Fig. 4. (A–H) As in Fig. 3, but for immature male white sharks

for thermoregulation. In Guadalupe Island, mature sharks remain most of the time in depths of around 250 m, which could be related to their thermoregulation and the search for prey (Hoyos-Padilla et al. 2016). Future research concerning the thermoregulation of sharks would provide insights regarding this topic, in which differences between mature and immature individuals could be observed (Goldman 1997, Bernal & Sepulveda 2005). In contrast, some of the sightings related to mature females were registered during warm SST conditions (>24°C), which influenced the occurrence model of this category. If an 18 mo gestation period is considered (Domeier 2012, Domeier & Nasby-Lucas 2013), it is likely that pregnant females would visit Guadalupe Island to feed and for the inherent maintenance of embryos, which could also be favoured by warm waters that could increase the rate of embryo development (Hight & Lowe 2007, Robbins 2007). In this regard, Guadalupe Island could be considered an important area for the reproductive cycle of white sharks in the Eastern Pacific, although more research regarding their reproductive biology should be assessed in future studies (Sulikowski et al. 2012, Huveneers et al. 2018).

4.3. Visibility and tide

High visibility conditions (>15 m) favoured the probability of occurrence of juvenile males, which may be related to the ability to perceive larger sharks and evade probable encounters (Becerril-García et al. 2019b). In contrast, low visibility was related to the presence of mature sharks, which would favour the stalking and capturing of prey (Pyle et al. 1996, Hammerschlag et al. 2006). The minimum value of visibility was 9 m, so even under these conditions it was possible to register sharks at the surface (0–3 m). Other studies have shown that high tides favour the availability of pinnipeds in the water and therefore the frequency of foraging attempts from the white sharks to the seals (Anderson et al. 1996, Klimley et al. 1996). However, the effect of the tide on the white sharks of Guadalupe Island was different, since the

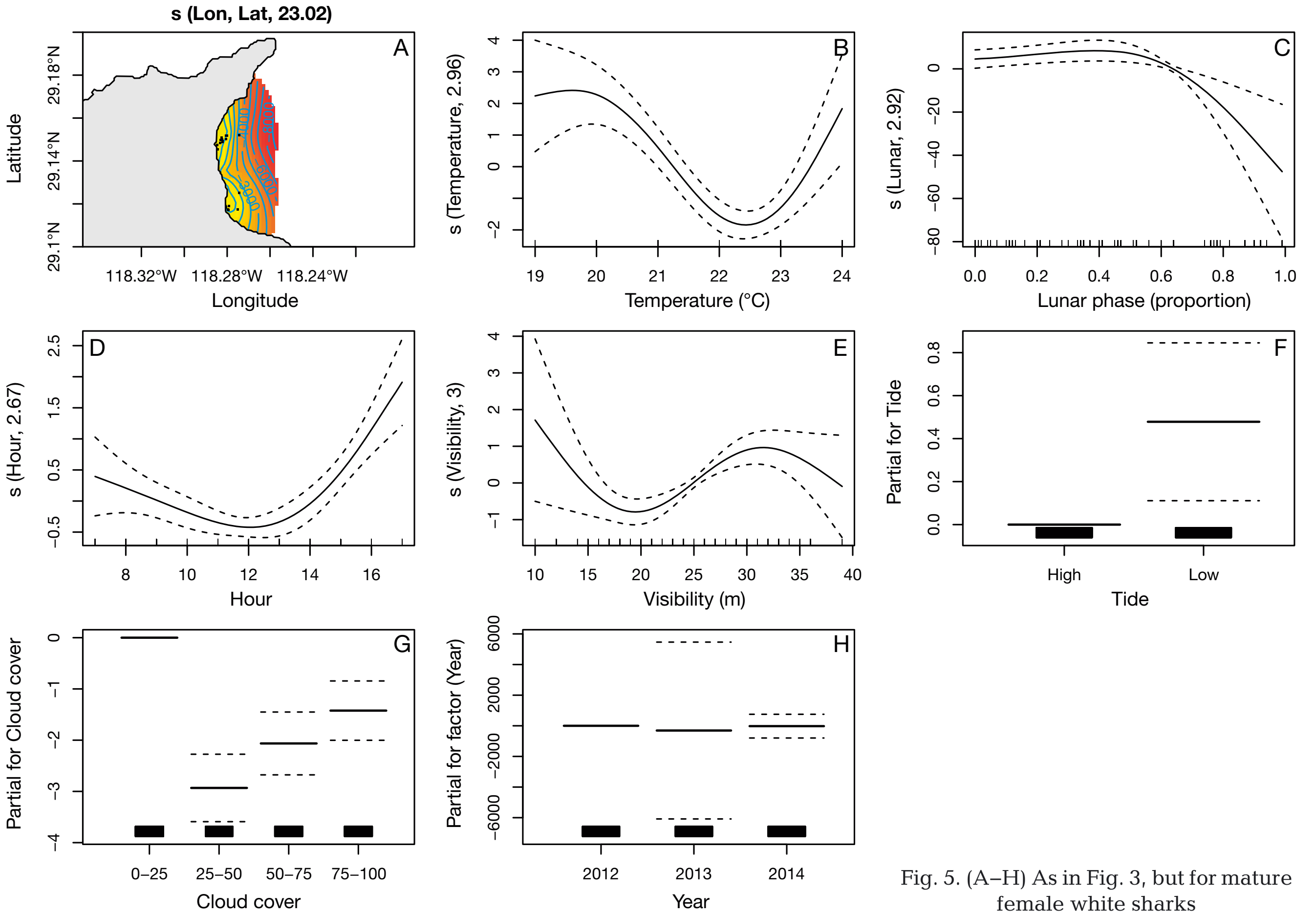

Fig. 5. (A–H) As in Fig. 3, but for mature female white sharks

probability of occurrence of mature sharks was greater during low tide. This could be related to the low abundance of northern elephant seals during the study period and therefore a lack of intraspecific competition for space in the coast that could lead elephant seals to the sea (Anderson et al. 1996, Gallo-Reynoso et al. 2005), in addition to the fact that predation in this environment occurs in deep waters (Skomal et al. 2015, Hoyos-Padilla et al. 2016). Nevertheless, the probability of occurrence of immature females was greater during high tide and in low visibility conditions, particularly in areas close to breeding colonies of the Guadalupe fur seal *Arctocephalus philippi townsendi* (Gallo-Reynoso et al. 2005, Hoyos-Padilla et al. 2016). This suggests that immature females may benefit from such conditions and feed on the offspring of the Guadalupe fur seal, which are born between June and July and are abundant in this coast during the following months (Gallo-Reynoso et al. 2005). Additionally, the intensity of the tidal cycles due to the effect of certain lunar phases could have influenced the presence of white sharks, since the probability of occurrence of immature males and mature males was higher during new and crescent moons, respectively.

4.4. Moon phase and cloud cover

Although knowledge concerning the effect of the moon or clouds on white sharks is deficient, some studies have sought to describe the relationship between this variable and the presence of sharks (Pyle et al. 1996, Dewar et al. 2004, Clarke et al. 2011). Lunar luminosity can provide the necessary light conditions to favour shark hunting strategies (Dewar et al. 2004, Clarke et al. 2011). The effect of the moon on their presence has been observed to persist during daylight hours, perhaps linked to the activity of their prey, as well as to a hierarchy of temporal territoriality (Pyle et al. 1996, Dewar et al. 2004, Towner et al. 2013). The probability of occurrence of mature sharks was higher on days with clear skies and crescent moon. In contrast, immature individuals were more likely to be found during cloudy skies, and after new or gibbous moon nights. Given that

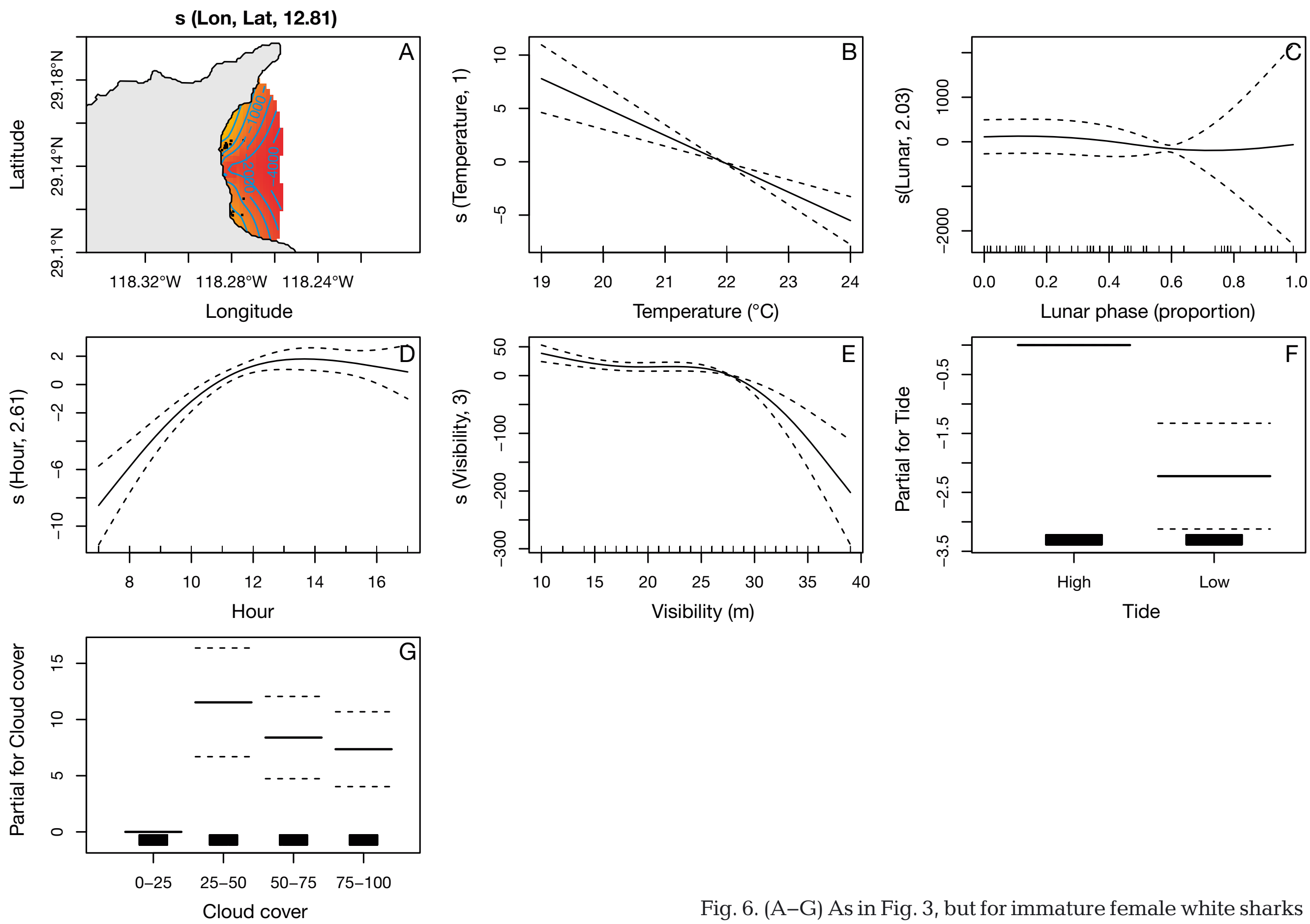

Fig. 6. (A–G) As in Fig. 3, but for immature female white sharks

juveniles are located near the coast, the light during gibbous moon could aid their vision to capture specific prey such as bony fishes or other elasmobranchs, while the predation of seal pups could be favoured during new moon and high tides (Pyle et al. 1996, Towner et al. 2013, Walther-Mendoza et al. 2013). In the case of mature individuals, the low lunar light could favour predation on species that carry out vertical migrations such as cephalopods (Jaime-Rivera et al. 2014), which would explain the higher probability of occurrence of mature sharks after nights with new moon (Skomal et al. 2015, Hoyos-Padilla et al. 2016).

4.5. Management and conservation

The use of non-invasive techniques such as visual monitoring and statistical modelling are useful for describing the ecology of threatened species such as the white shark. In addition to the effect of the environment and spatial preferences, the observed differences in occurrence of sharks according to time of day could be related to specific aspects of the ecotourism in Guadalupe Island (Torres-Aguilar et al. 2015). It has been suggested that immature sharks could be more vulnerable to negative effects from ecotourism such as energy loss, caused by changes in their surface behaviour and habitat use (Orams 2002, Cisneros-Montemayor et al. 2020). However, one of the main concerns is related to recent accidents involving immature sharks stuck in diving cages (Becerril-García et al. 2019b, Tanno 2019). Decreasing the intensity of baiting during the morning (10:00–12:00 h), as well as the avoidance of areas with a higher probability of occurrence of immature sharks could be positive management actions; specifically considering that the proportion of immature sharks seems to have increased in recent years (O. Santana-Morales unpubl. data). This proposal could be strengthened by studying the movements of white sharks with respect to cage diving boats, as well as science-based monitoring carried out by local authorities.

Implications for the conservation of white sharks are related to the understanding of climate preferences of this vulnerable species, which should be considered in future research involving the effects of climate change or heating events such as the 'Warm Blob' or El Niño–Southern Oscillation (Cavole et al. 2016, Gálvez et al. 2020). A proper assessment involving the potential increase of SST in terms of ecological and economical effects should be carried out in future studies (Cisneros-Montemayor et al. 2020), since the ecosystem of Guadalupe Island could change over the next several decades, and therefore affect prey availability for the white shark and impose physiological challenges on this species (Elorriaga-Verplancken et al. 2016, Gálvez et al. 2020). In this regard, management of cage diving and sport fishing would be necessary, since an important income is generated in Guadalupe Island by national and international companies that seasonally visit this marine protected area (Becerril-García et al. 2019b, Cisneros-Montemayor et al. 2020).

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