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The degree and result of gillnet fishery interactions with juvenile white sharks in southern California assessed by fishery-independent and -dependent methods

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ABSTRACT

Previous reports have documented juvenile white shark interactions with gillnet fisheries in southern California; however, there has been no quantification of the degree of this interaction using fishery-independent methods. We compared geopositioning data from juvenile white sharks fitted with acoustic ($n = 11$) or satellite transmitters ($n = 13$) to fisheries data to determine the degree and effect of white shark interactions with the gillnet fisheries in southern California. Between 2006 and 2008, set gillnet effort comprised a majority of the total gillnet effort (88%) and both set gillnet and inshore drift gillnet effort were significantly and positively correlated with incidence of white shark capture ($p < 0.0001$, $\tau = 0.34$ and 0.32) and number of satellite detections ($p < 0.0001$, $\tau = 0.34$ and 0.33). However, spatial and temporal overlap of white sharks with gillnet fisheries was limited. Approximately 18% of CDFW fishing blocks where white sharks were detected overlapped with blocks that were also heavily utilized by gillnet fisheries. Total gillnet effort tended to peak in the month of July before declining substantially whereas SPOT detections of tagged sharks were the most numerous in fall months. Although juvenile white sharks were shown to overlap with gillnet fisheries in their vertical, horizontal and temporal distributions, post-release survival of sharks retrieved live in gillnets was high (92.9%). Sharks were more often found live in gillnets when net soak times were low. Therefore, continued research is needed to further evaluate the potential benefit of reducing soak times to improve incidental capture survival of white sharks at this age class.

1. Introduction

Documented fishery-interactions with non-target species provide important information on species distributions, abundance, and seasonality through space and time. White sharks (*Carcharodon carcharias*) are a long-lived, slow to mature apex predator with their populations susceptible to fishing pressure (Dulvy et al., 2008). Juvenile white sharks have the highest interactions with entanglement nets (81% of total reported captures) compared to other fisheries in southern California (Klimley, 1985; Lowe et al., 2012). Due to their low reproductive output coupled with known fishery interactions (Heneman and Glazer, 1996), white sharks received protection as a prohibited species in 1994 and 2005 from the state of California and U.S. federal government, respectively (California Senate Bill 144, 1997).

Several types of gillnet fisheries (inshore set, inshore drift, and offshore drift) exist in southern California and their unique practices (i.e., type of gear utilized and temporal and spatial concentration of effort) may play a role in the extent of their interactions with juvenile white sharks. The inshore set gillnet fishery [herein "set"] primarily targets California halibut (*Paralichthys californicus*), white sea bass (*Atractoscion nobilis*), and will occasionally target thresher shark (*Alopias vulpinus*) and Pacific angel shark (*Squatina californica*). The set gillnet fishery (mesh size >8.9 cm) is focused inshore and nets (lengths restricted to 2743 m and net height ranging from 3 to 6 m) are deployed at fixed locations on the sea floor of shelf habitat with varying soak durations (CA Fish and Game Code [F.G.C.], sections 8680–8700, Larese, 2009). Similar to the set gillnet fishery, the inshore commercial drift gillnet fishery (mesh

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size 8.9–15 cm) mainly targets white sea bass (*A. nobilis*) that may be fished south of Point Conception, California year-round, except 15 March through 15 June (California Code of Regulations [C.C.R.], Title 14, §155). Both set and inshore drift gillnet effort tends to peak during the summer months. Unlike set gillnets, deployed gear in the inshore drift fishery is not fixed at specific locations or associated with the sea floor (e.g., drift gillnets targeting white seabass "drift" with the current for 4–12 h). Inshore drift gillnets are typically deployed relatively close to the surface with the top of the net within 2–12 m of the surface over sea floor depths of 20–100 m. This fishery occurs more inshore compared to the offshore drift gillnet fishery, which targets thresher shark (*Alopias* spp.) and swordfish (*Xiphias gladius*). Relative to the set and inshore drift gillnet fisheries, the offshore drift gillnet fishery is more highly regulated, with specific net soak durations, shorter net lengths (1828 m), larger mesh sizes >35.5 cm, and area restrictions that vary throughout the year (e.g., >75 nautical miles off the mainland although this varies by season and location; 50 F.G.C. §660.713). In addition, from 1990 to 2011 the offshore drift gillnet fishery has had consistent observer coverage ($17 \pm 5\%$, $n = 22$) compared to the inshore drift ($8 \pm 4\%$, $n = 5$) or set gillnet ($13 \pm 8\%$, $n = 11$) fisheries (NMFS, 2013). Offshore drift gillnets must be set a minimum of 12 m from the surface and are usually deployed over water 33–50 m in depth.

The passage of the inshore gillnet ban in 1994, which prohibited commercial gillnet fisheries in state waters (e.g., <3 nm off the mainland and <1 nm off offshore islands; California Proposition 132), caused a number of dramatic changes in fishing practices and overall resulted in a substantial decrease in total gillnet effort. Despite increased fishing regulations and lower effort decades prior to 1994, reported incidental YOY white shark captures have increased in recent years (Lowe et al., 2012). This apparent increase in YOY white shark-gillnet interactions is hypothesized to be indicative of increasing white shark recruitment and thus population growth. However, because fishing practices (i.e., locations and methods) have drastically changed since the ban on gillnetting in state waters and regulations in the offshore drift gillnet fishery have increased, it is difficult to determine whether the rise in white shark-fishery interactions is due to increasing juvenile recruitment or a shift in fishing location and effort.

Previous studies that utilized both fishery-dependent and -independent methods (e.g., satellite tagging technology) have provided a more holistic understanding of species interactions with fisheries (Horodysky et al., 2007; Teo et al., 2007; McClellan and Read, 2009; Baird et al., 2010) and may optimize fishing effort while reducing incidental bycatch of vulnerable species (Howell et al., 2008; Beverly et al., 2009; Campana et al., 2009). The objectives of the current study are two-fold: (1) quantify the degree of overlap between juvenile white shark movements and areas of high gillnet fishing effort to assess the extent of these interactions and (2) determine the post-release survival rate of sharks encountering gillnets. Young white sharks represent the most vulnerable age class of the species and are also the dominant age class encountered in these fisheries (Klimley, 1985; Lowe et al., 2012). Therefore, quantifying the extent and effect of this interaction may facilitate the implementation of appropriate practices and regulations to reduce the incidence of white shark bycatch and mortality.

2. Materials and methods

2.1. Shark captures

White shark bycatch captures were obtained from two data sources: California Department of Fish and Wildlife (CDFW) archive of logbook records (2006–2009), where reporting of incidentally captured white sharks is mandatory by commercial gillnet fisheries in southern California and white sharks that were targeted by researchers or incidentally caught by commercial gillnet fishermen participating in Monterey Bay Aquarium's (MBA) white shark research program during the years 2006–2012. MBA's juvenile white shark program conducts a variety of research on the sharks, including temporary public display. White sharks are opportunistically obtained through incidental gillnet catch but also through targeted efforts using purse seine and hook-and-line. Incidental bycatch captures from 2006 to 2009 were cross-referenced between the two sources to prevent duplication. Seven additional sharks were reported in the MBA research program by fishermen that were not found in CDFW logbooks. We limited white shark bycatch capture data to the years 2006–2009 to compare fishery-dependent (i.e., reported gillnet captures) and independent data (i.e., SPOT detections) on the same temporal scale. For confidentiality reasons, fishing locations in logbooks are provided as CDFW fishing block (10 min latitude by 10 min longitude); however, catch records from participating fishers were often provided as coordinates. While most records specified the location of capture there were a few instances where coordinates were not given. In those cases, the best possible position was estimated by referencing the fisher's notes that included estimated distances and bearings to fixed landmarks (e.g., oil rigs, breakwalls, etc.) from the capture with high-resolution maps of the area. Incidental white shark captures were separated by gillnet type (i.e., set gillnet and drift gillnet) and analyzed separately, where appropriate. Target species for all sharks caught by drift gillnets were reported; therefore, drift gillnet captures of white sharks were not separated between the inshore or offshore drift gillnet fishery.

Sharks incidentally caught by commercial fishermen participating in the MBA white shark research program were transported to the nearest port where researchers from California State University Long Beach (CSULB) Shark Lab and Southern California Marine Institute met participating fishers for processing. Responders assessed shark health (if alive), obtained morphometrics (e.g., sex, lengths, girth, etc.), capture information (i.e., gear type, target species, soak time, depth of net, etc.), and then tagged and released live sharks offshore. Deceased sharks where brought back to the laboratory for necropsy. Sharks were categorized as live or dead at the time of net retrieval and moribund sharks were considered captured as alive; however, in only one rare instance was a shark caught in this condition.

2.2. SPOT tagged sharks

From 2006 to 2009, 16 live white sharks were incidentally caught between Ventura and Oceanside, California, by commercial gillnet fishermen and Smart Position Only Tags (mini SPOT 5 AM-S182C and AM-S183E; Wildlife Computers) were externally attached to their dorsal fins. Sharks were released within several kilometers west of the port of landing and locations of capture and release sites were obtained from fishermen. An additional satellite tagged shark (#17; Table 1) was targeted using hook-and-line off San Onofre State Beach, California, as part of a juvenile white shark tagging study (M. Domeier, Marine Conservation Science Institute, Pers. Comm., Fallbrook, CA, 2009).

To test for movement/detection bias associated with the location of capture and/or release, we calculated the mean Euclidian distance from each SPOT detection of a tagged shark to (1) the mean center of detections, (2) the point of release, and (3) point of capture for sharks with sufficient detections ($n = 7$). We used a two-way ANOVA with individual sharks as a factor to test whether these distances were not significantly different (i.e., sharks remaining close to capture/release locations). Location of release or capture did not appear to bias the spatial distribution of detections of free-swimming tagged sharks toward those areas as SPOT detections

Table 1
Capture and detection data for SPOT tagged white sharks from 2006 to 2009 that were incidentally caught in commercial gillnets. "YOY" age class represents young of the year born sharks (i.e. <175 cm in total length; Cailliet et al., 1985); juvenile age class represents fish >176 cm and <375 cm TL. WSB, white sea bass; WS, white shark. Track duration is defined as the number of days between the first and last detection (ARGOS classes 1–3) in southern California.

Shark ID	TL (cm)	Sex	Date tagged	Age class	Gillnet type/target spp.	Class 1–3 detections	Total detections	Track duration (days)/date of last detection
1	140	F	14-July-06	YOY	Drift/WSB	3	38	10/24-July-06
2	149	F	21-September-06	YOY	Set/WSB	4	45	133/10-November-06
3	148	F	27-September-06	YOY	Set/WSB	1	8	–/12-October-06
5	170	M	12-July-07	Juvenile	Set/WSB	57	133	99/22-October-07
7	160	F	18-June-08	YOY	Set/WSB	24	41	87/7-September-08
8	135	M	20-June-08	YOY	Drift/WSB	53	87	113/15-October-08
9	154	F	26-June-08	YOY	Set/WSB	81	132	149/18-November-08
10	142	F	7-July-08	YOY	Drift/WSB	1	2	–/11-July-08
11	154	M	1-August-08	YOY	Drift/WSB	61	123	130/16-December-08
12	134	M	23-August-08	YOY	Set/WSB	40	82	108/11-December-08
13	150	F	30-June-09	YOY	Drift/WSB	7	29	22/28-July-09
14	168	M	16-July-09	YOY	Drift/WSB	15	45	48/5-September-09
17[a]	224	M	26-September-09	Juvenile	NA[a]/WS	4	12	37/29-October-09

[a] Shark 17 was obtained by M. Domeier via hook-and-line research collection.

were significantly farther away from the capture/release location (up to 120 km) than from the mean center of detections for five of the seven sharks analyzed (two-way ANOVA $p < 0.0001$).

Although 17 sharks were outfitted with SPOT tags, only 13 sharks were used for analyses (Table 1 and Fig. 1). The four removed sharks were excluded from subsequent analyses due to return of low-quality ARGOS positions, death with subsequent recapture, or lack of detections in southern California. ARGOS positions from SPOT reports (herein "SPOT detections" or "detections") were only analyzed for sharks while in U.S. waters. Furthermore, detections were filtered for only high quality ARGOS positions (i.e., class 3, <150 m; class 2, 150–350 m; class 1, 350–1000 m; www.argos-system.org); any detections occurring on land were removed from analyses (3 positions).

The geopositional accuracy of ARGOS positions in our data varied among the classes used (class 3 is more accurate than class 1) and the proportion of classes in our data was uneven (i.e., only 12% of detections were class 3, 28% class 2, 60% class 1). Using sea floor depth as a proxy of distance to shore, preliminary analyses demonstrated that location of SPOT detections between ARGOS classes ("2 and 3" versus "1") were evenly distributed throughout southern California ($D = 0.06$, $p = 0.85$). Thus, the more accurate positions were not located closer to shore than the other positional class and classes were pooled for subsequent analyses. In addition, we hypothesized that sharks detected in shallower depths may be detected more frequently than when they are offshore; thus, we tested for a time difference between detections when sharks were considered "inshore" (<200 m depth) and "offshore" (>200 m depth) using a Student's *t*-test.

Twelve of the SPOT tagged sharks were double-tagged with Mk10 Pop-up Archival Transmitting tags (PAT tags; Wildlife Computers). PAT tags were programmed to record light, depth, and temperature every 5 s, and to transmit summaries of these data to satellites upon release from the animals. Five of the 12 PAT tags were recovered and used in subsequent analyses since high-resolution time-series profiles could be obtained from these sharks upon the recovery of the tag which allowed for its complete data download (described below).

2.3. Fishing effort

Total gillnet fishing effort (e.g., set duration in hours, length of net in fathoms, target species, etc.) was obtained from gillnet logbooks for the years 2006–2009 for southern California (defined here as the region between Santa Maria and San Diego) and was reported by CDFW fishing block for confidentiality reasons. Southern California was chosen as the focus region to investigate juvenile white shark interactions with fisheries for two reasons: (1) From 1981 to 2008, 96% of all statewide gillnet fishing effort was concentrated in southern California and (2) juvenile white sharks tend to not utilize areas north of Point Conception (Weng et al., 2007) and have not been documented to travel further north of San Luis Obispo, California (C. Lowe, unpublished data), unless during El Nino events; therefore, southern California represents the area where California fisheries have the greatest potential interaction with juvenile white sharks.

Since gillnet length regulations vary among the fisheries, we attempted to normalize fishing effort data by dividing net soak hours by fathoms of net length for each fishery per year per fishing block (herein "effort" refers to standardized data unless otherwise noted). Effort was then summed over the examined years to obtain total effort (all three fisheries) by block as well as by their respective fisheries (i.e., summed set, inshore drift and offshore drift effort by block). Inshore and offshore drift effort was separated by examining the reported target species and fishing block location. The target species used to define the inshore drift gillnet fishery included white sea bass (*A. nobilis*), California barracuda (*Sphyraena argentea*), bottom sharks (i.e., Pacific angel shark, *S. californica*), yellowtail (*Seriola lalandi*) and "other species"; whereas swordfish (*X. gladius*), thresher shark (*A. vulpinus*), tuna (*Thunnus* spp.), and "miscellaneous fish" were used to define the offshore drift gillnet fishery. Due to inconsistencies in effort reports (i.e., disagreement between reported target species with net depth deployment and reported fishing block) three observations (0.08%) were removed.

2.4. Data analysis

2.4.1. Fishery interactions

Location of white shark bycatch captures (herein "captures"), SPOT detections, and total gillnet fishing effort were plotted using ArcMap 10 software (ESRI, 2003) and spatially joined to CDFW fishing blocks. All statistical tests were performed using R statistical package (R Core Development Team, 2011). Correlations were performed sequentially between total gillnet fishing effort (all fisheries combined) and (1) incidental gillnet white shark captures and (2) SPOT detections by fishing block. Assumptions regarding data normality and homoscedasticity were performed. If assumptions were not met, then Kendall's tau nonparametric correlations were used. The same correlations were also performed separately for each gillnet fishery to determine the relative degree of fishery interactions with white sharks. The number of white sharks caught per unit effort (CPUE; standardized effort) was calculated for all fisheries

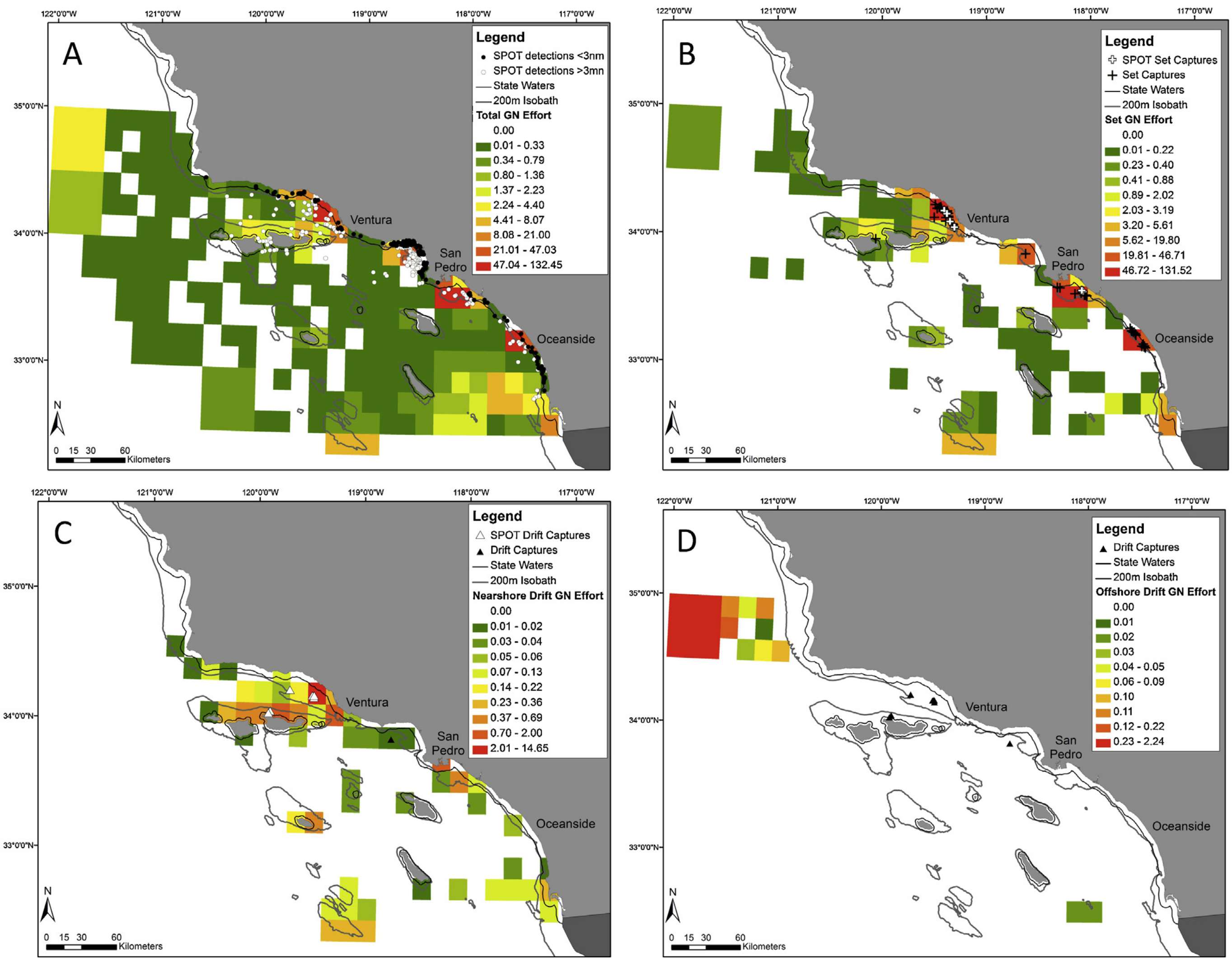

Fig. 1. Standardized gillnet effort (soak h/net length fathom) by CDFW fishing block, capture locations of white sharks, and white shark SPOT tag detections for (A) all gillnet fisheries combined and separately, by (B) set, (C) inshore drift, and (D) offshore drift gillnet fisheries. Warmer colors indicate higher effort. The 200 m isobath is depicted with respect to inshore drift gillnet fishing effort. Capture locations of sharks caught in the (B) set and (C)–(D) inshore and offshore drift gillnet fisheries are denoted by crosses and triangles, respectively, with open symbols representing capture locations of sharks that were SPOT tagged. SPOT tag detections in panel A that occur within (closed circles) and outside (open circles) state waters are compared relative to total effort.

combined per block and by fishery type (i.e., inshore drift and set gillnet) and also tested for a correlation with the number of SPOT detections per block. Blocks in which SPOT detections were absent and no effort was reported were removed from the correlation analyses. Our assumption was that a positive correlation would exist between CPUE and SPOT detections by block if fishermen are utilizing the same areas as free-swimming white sharks. In addition, set gillnet target species (i.e., halibut and white seabass) CPUE (effort in soak hours) was correlated to number of white sharks caught by set gillnets as an additional measurement of white shark-gillnet fishery interaction. We predicted white shark captures to increase concurrently with target species CPUE if sharks utilize the same areas that fishermen target for high product yields. Set gillnet target species CPUE data was obtained from fishermen logbooks for the years 2006–2008.

2.4.2. Depth distribution of tagged sharks

Since sharks may have a higher probability of being at the surface when they are in shallow water, and thus detected more often, there is potential for spatial bias in detections when sharks occur over deep or shallow water. To test for this bias, we examined Pearson correlations between the depth at a SPOT detection for double-tagged sharks whose PAT tag was recovered and compared it to the maximum depth recorded by PAT tags ±1 h at the time of the SPOT detection. This correlation was performed for all detections and for detections occurring in water <200 m deep ("shallow" habitat). The 200 m isobath was used as a cutoff given previous PAT tag depth profile analysis (Weng et al., 2007), which suggested a potential thermal barrier for juvenile sharks. In addition, we calculated the depth differences between the maximum depth recorded by the PAT and the depth of the sea floor at a SPOT detection location when sharks were in deep or shallow water. The distribution of these depth differences were compared using a two-sample Kolmogorov–Smirnov test and allowed us to test if sharks spend more time at the surface when they are in shallow water.

2.4.3. Spatial and temporal overlap of white sharks and gillnet fisheries

To investigate potential horizontal overlap of fishing grounds and habitat used by tagged white sharks, white shark detections and the number of unique individuals detected per block were superimposed on high fishing effort blocks to calculate their degree of coarse spatial overlap. Blocks were considered "high effort" if summed fishing effort exceeded 20 h/fathom net length, which comprised the top 20% of classes when effort per block was separated using a 10-class Jenks natural breaks optimization approach in ArcMap (Burdett et al., 2007). Using this function to set bin breaks allows for a better representation of data that is highly skewed or patchy by defining bin separation from natural breaks in the data as opposed to predefined bin classes that may over or underestimate effort in certain locations. In addition, since the exclusion of gillnet fishing from state waters (3 nm from shore and 1 nm from islands) functionally creates a *de facto*-MPA for white sharks, we examined the percent of detections occurring inside and outside state waters as another measure of white shark exposure to fishing pressure.

Potential vertical overlap between white sharks and gillnet fisheries was examined by comparing sea floor depth frequencies at SPOT detection locations to two fishery-dependent measures: (1) bathymetric depths where white sharks were caught in set gillnets and (2) bathymetric depths where set gillnet effort is concentrated. The areas of concentration of set gillnet effort were represented by the boundary extending 3 nm from shore at 1 km intervals in high fishing effort blocks as a proxy for where actual fishing effort occurs. Anecdotal reports from fishers suggest that a large portion of the effort takes place just outside state waters. Therefore, using depths along the 3 nm line in these high effort blocks would give a better indication of the depths fishermen may be utilizing that could potentially interact with white sharks as compared to using bathymetric information for the entire fishing block.

The set gillnet fishery was used since it accounted for a majority of the total fishing effort and more accurate fishing depth measurements could be obtained (fishing effort depth was inconsistently reported in logbooks) since nets are set on the bottom of the sea floor. We assumed that sharks had the potential to utilize the entire water column in places where they were detected, hence our use of sea floor depth at a SPOT tag location. Sea floor depths were determined using bathymetry data for southern California obtained from the US Geological Survey.[1] The depth frequencies at SPOT locations were compared to each of the two fishery-dependent measures using a two-sample Kolmogorov–Smirnov test.

Besides spatial overlap, fishery interactions with juvenile white sharks were also temporally examined. Total gillnet effort for all fisheries was summed across years (2006–2008) for each month and plotted against white shark captures from 2006 to 2012. Pearson correlations between total gillnet effort and white shark captures per month for these two fishery dependent methods were performed for all 12 months, all months which had a white shark capture, and the summer to fall months (i.e., purported pupping season for white sharks; Domeier, 2012). The number of SPOT detections per month was summed across years (2006–2009) and standardized to the number of individual sharks detected each month. Standardized SPOT detections per month were superimposed upon the fisheries-dependent data and examined to determine the extent of temporal overlap of white shark presence in southern California with peaks in fishing activity.

2.4.4. Capture and post-release survival

Condition indices (e.g., relationship of girth to length and liver weight to total weight; Bolger and Connolly, 1989; Jones et al., 1999) were compared between live and deceased sharks using an ANCOVA to evaluate external characteristics that may be indicative of capture mortality. Net soak time was compared between sharks categorized as alive or dead at net retrieval using a Mann-Whitney *U*-test (data were nonparametric). Additionally, the relationship between mortality and soak time was investigated using logistic regression analysis for binary response count data using the GLM function in R (R Core Development Team, 2011). To estimate the survival potential of sharks that are caught and released, we compared the post-release survival of sharks captured by two different methods, which subjects sharks to substantially different degrees of total captive time and handling stress. Sharks captured incidentally by commercial gillnets (i.e., "experimental" group) and sharks specifically targeted by purse seine fishing as part of MBA's white shark program (i.e., "control" group) were outfitted with either satellite or internal acoustic tags. Sharks were considered to have survived if (1) detections from satellite and acoustic tags were recorded or (2) the mortality function on the PAT tag was not activated. PAT tags were programmed to release if the tag recorded the same depth (±2 m) continuously for 96 h, which is indicative of mortality. We considered any activations of the PAT tag mortality function within two weeks of deployment to be related to stress incurred during capture and handling procedures as opposed to natural mortality (Campana et al., 2009; Hoolihan et al., 2011).

3. Results

3.1. Fishery interactions

Set gillnet fishing effort accounted for a majority of the total gillnet fishing effort (88.7%). Of the drift gillnet effort, the offshore fishery comprised 68.8% of this effort compared to the inshore fishery, which only made up 31.2%. Eighty percent of the total fishing effort was reported to occur in only nine (out of 241) CDFW fishing blocks. Areas of highest effort were located in proximity to nearby ports, such as those near Ventura, San Pedro, Oceanside, and San Diego (Fig. 1A–C). Total gillnet effort was higher during the first half of the year (January–July) with a peak in July and subsequently declined during the latter half (August–December; Fig. 2).

From 2006 to 2009, 56 incidences of white sharks captured in gillnets were reported (Fig. 1B–D). Approximately, 85% of these captures occurred in set gillnets, compared to drift gillnets (15%), with two captures without a defined net type, but were likely set gillnets given the primary gear type used by those fishermen. Average (±SD) CPUE for all fisheries combined was 0.32 ± 0.25 sharks caught/net length fathom/block. The set gillnet fishery had a lower CPUE (0.18 ± 0.11) than the inshore drift gillnet fishery (2.15 ± 1.81); however, inshore gillnet fishing effort was comparatively lower than the set gillnet fishery (0.52 ± 2.1 and 8.21 ± 23.33, respectively). Number of SPOT detections per block was not correlated to CPUE when fisheries were combined ($Z = 1.2$, $p = 0.23$, $\tau = 0.15$) or separated by gillnet type (Set GN $Z = 0.77$, $p = 0.44$, $\tau = 0.10$ and inshore drift GN $Z = 0.65$, $p = 0.51$, $\tau = 0.08$). Lastly, the number of white shark captures in set gillnets was not correlated to halibut or white seabass CPUE per block ($\tau = -0.08$, $p = 0.5$ and $\tau = -0.17$, $p = 0.2$), but rather dramatically decreased with increasing target species CPUE (Fig. 2A).

A majority (89%) of captured sharks were considered young of the year (YOY <175 cm total length [TL]) and the remaining were considered juveniles (>176 cm and < 375 cm TL; Cailliet et al., 1985). The size distribution of incidentally-caught sharks closely corresponded with the size distribution of satellite tagged sharks (85% YOYs, 15% juveniles). From 2006 to 2012, incidental white shark captures by commercial gillnets was highest during the summer months (June–August) and was only positively correlated to total gillnet effort between the months of June and November ($t_4 = 3.3$, $p = 0.03$, $r = 0.86$; Fig. 3).

Similar to white shark SPOT detections, white shark captures tended to occur over areas with higher fishing effort. There was a significant, strong positive correlation between incidence of

[1] http://coastalmap.marine.usgs.gov/regional/contusa/westcoast/pacificcoast/data.html.

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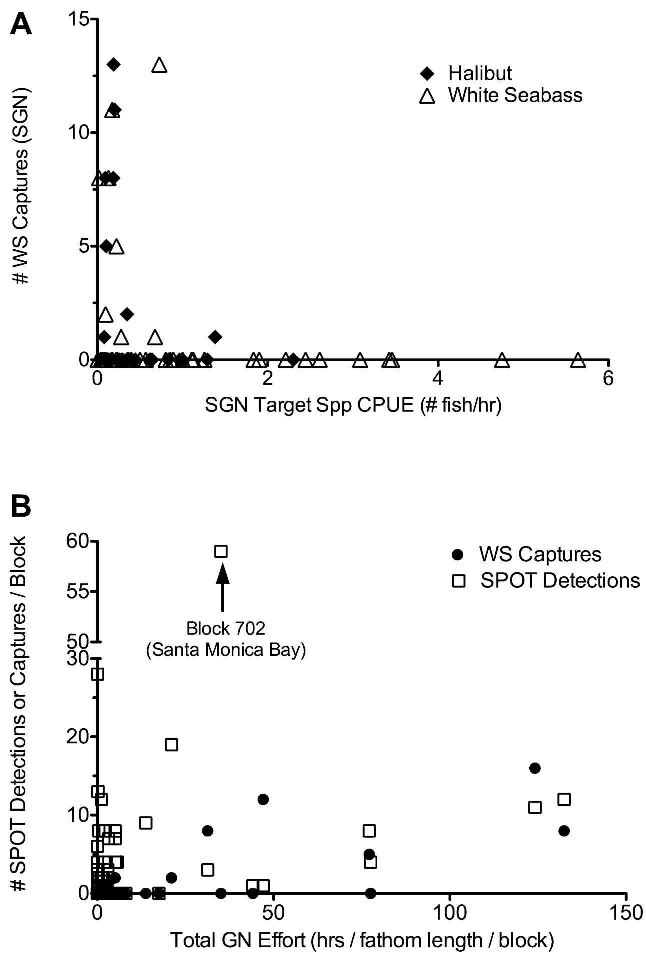

Fig. 2. Relationship between (A) target species set gillnet CPUE for halibut (closed diamonds) and white seabass (open triangles) and the number of white sharks captured in the SGN fishery (closed circles) and the relationship between (B) total gillnet effort and the number of white shark SPOT detections (open squares) and white shark captures (closed circles) per block. DFW block 702 had substantially greater SPOT detections relative to total gillnet effort compared to other blocks.

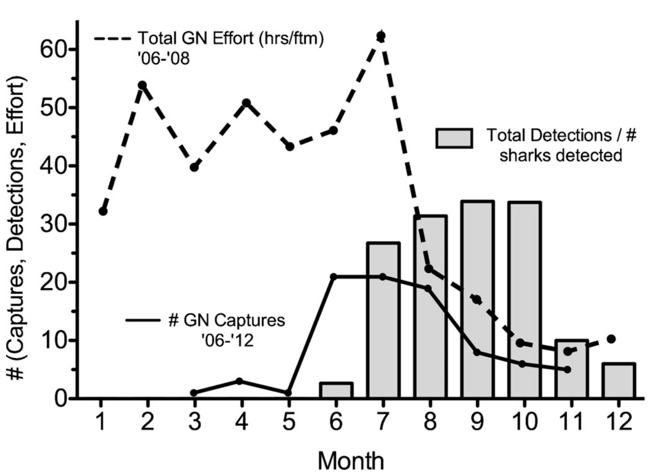

Fig. 3. Monthly trends in total gillnet effort (dashed line), numbers of incidental gillnet captures of white sharks (# GN Captures; solid line), and standardized number of SPOT detections (gray bars).

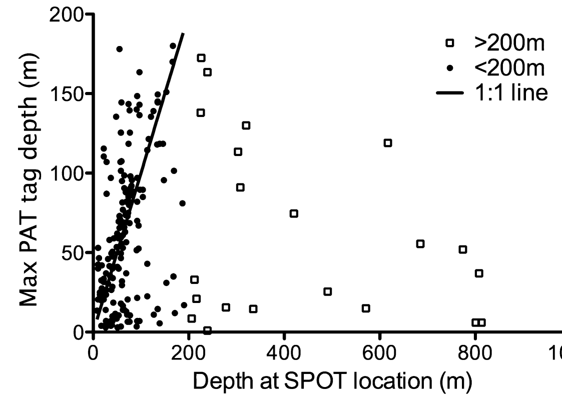

Fig. 4. Relationship between the sea floor depth at white shark SPOT detection location and the maximum associated PAT tag depth recorded within ±1 h of SPOT detection. Open squares represent sharks detected in water >200 m (n = 21) and closed circles sharks found in <200 m (n = 202) of water. The black line depicts the relationship when depth of the sea floor at a SPOT detection equals PAT tag depth; therefore, points above and below the line represent sharks with PAT tags that recorded the maximum depth as "deeper" or "shallower" than the sea floor depth at a SPOT detection, respectively. In waters <200 m, sharks utilized full water column, whereas in waters >200 m they did not.

white shark capture and total fishing effort by block (Z = 5.1, p < 0.0001, τ = 0.30; Fig. 3B), and a significant, weak positive correlation between the number of white shark SPOT detections and total fishing effort by block (Z = 2.8, p = 0.004, τ = 0.16). When separated by fishery, both set and inshore drift gillnet effort were significantly and highly correlated to set and drift white shark captures by block, respectively (Z = 5.2, p < 0.0001, τ = 0.34 and Z = 4.8, p < 0.0001, τ = 0.32). Effort from both of these fisheries was also significantly correlated to SPOT detections per block (Z = 5.3, p < 0.0001, τ = 0.33 and Z = 5.3, p < 0.0001, τ = 0.34). Neither white shark captures (total or drift only) or SPOT detections were significantly correlated to offshore drift gillnet effort (p = 0.40, τ = −0.03 and p = 0.09, τ = −0.1).

3.2. Depth distribution of tagged sharks

For the double tagged sharks, the linear relationship between the depth at SPOT detection was compared to the maximum depth recorded by PAT tags ±1 h of the detection (Fig. 4). When all detections were considered together, no relationship was found. However, for detections occurring in less than 200 m of water, a positive correlation was found between the depth at SPOT detection and maximum PAT tag depth (p < 0.0001, r = 0.43). When the differences between SPOT sea floor depth and maximum PAT tag depth were compared, 49% of the points were found shallower than depth at the SPOT location, 50% of the points were deeper than depth at the SPOT location and only 1% were equal to the depth of the sea floor at the SPOT location. No differences were found in the depth difference distribution of sharks classified as "shallower" or "deeper" than the sea floor for SPOT locations over isobaths <200 m (D = 0.33, p = 0.19). Thus, the depth distribution of sharks in the water column was similar regardless if sharks were detected in "shallow" or "deep" water.

3.3. Spatial and temporal overlap of white sharks and gillnet fisheries

The 13 tagged white sharks were detected a total of 777 times while in US waters. However, only 351 of these detections were of usable quality (ARGOS Classes 1–3) and were used in all subsequent analyses (Fig. 1A). SPOT detections per number of individual sharks detected (all years combined), increased

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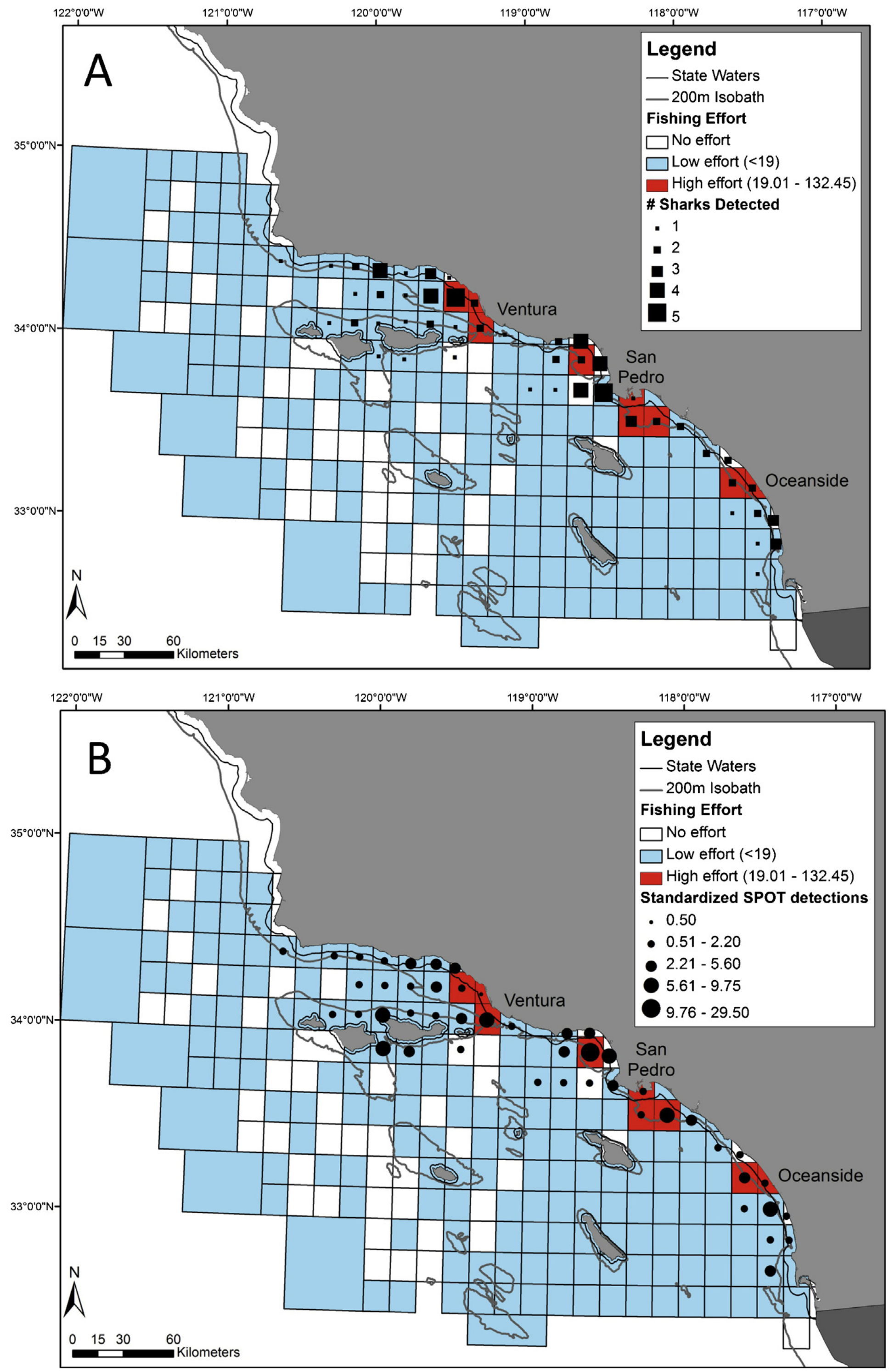

Fig. 5. Spatial distribution of the number of (A) SPOT tagged sharks sharks (graduated squares) and (B) the standardized number of SPOT detections (graduated circles) relative to high (red) and low (blue) gillnet fishing effort blocks (soak h/net length fathom). White shark SPOT detections were standardized to the proportion of individual tagged white sharks detected per block. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

from June to October after which they subsequently decreased (Fig. 3). Individual white sharks were detected in 49 southern California fishing blocks (~20%) with 18% of these blocks overlapping with blocks of high fishing effort (Fig. 5). Only a portion of these overlapping blocks had relatively high numbers of individual sharks and detections (22% and 44%, respectively). However, 100% of the high effort blocks coincided with blocks where individual sharks had been detected compared to 24% of low effort blocks. While there were only nine "high effort blocks" (~4%), they comprised 80% of the total fishing effort. White sharks were detected slightly more often outside of state waters; 44% of detections occurred inside state waters (Fig. 1A). Of the detections within state waters, the vast majority was between the mainland coast and the 3 nm line compared to detections in state waters surrounding the Channel Islands (1 nm designation; 151 versus 4 detections, respectively).

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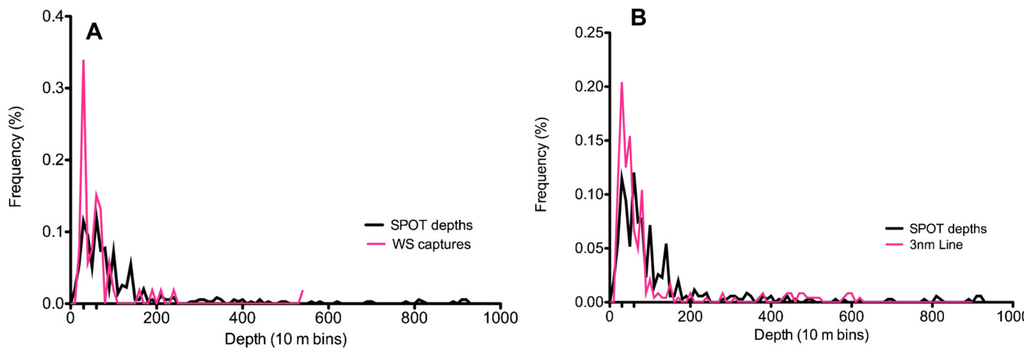

Fig. 6. Depth frequency distribution comparisons between SPOT tag detection locations (black line, $n = 351$) and (A) locations of incidental white shark captures (pink line, $n = 56$), and (B) along the 3 nm line in high gillnet fishing effort blocks (pink line, $n = 240$). The first and second tick marks indicate simultaneous peaks in depth frequencies at 30 and 60 m depths for both SPOT detections and the fishery-dependent metrics. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

The distribution of sea floor depths over SPOT detections was highly positively skewed with the peak occurring between 30 and 60 m depth (Fig. 6). Although a majority of detections occurred in water less than 200 m deep (~86%), there were no differences in time between detections when sharks were considered “inshore” or “offshore” ($t_{281} = -0.79$, $p = 0.42$). SPOT depth distributions were then compared to two fisheries-related depth distributions (Fig. 6). Sea floor depth distributions at SPOT locations were significantly different and shifted to the right compared to sea floor depth distribution at sites of white shark capture in set gillnets ($D = 0.2687$, $p = 0.012$, $n = 56$) but they were not significantly different from depths along the 3 nm line in high effort fishing blocks ($D = 0.1314$, $p = 0.38$, $n = 240$). However, the prominent mode in sea floor depths along the 3 nm line and in white shark capture depths coincided with the prominent modes in SPOT detection depths at 30 and 60 m, respectively (Fig. 6).

3.4. Capture and post-release survival

From 2006 to 2012, the average (±SD) number of incidental white shark gillnet captures per year by fishers participating in MBA's white shark project was 13 ± 5. No temporal trends were observed between the number of sharks caught or number of participating fishermen per year ($F_{1,5} = 0.26$ and 0.06, $p = 0.63$ and 0.80). The average annual proportion of sharks landed dead was 44 ± 24%.

Shark condition was hypothesized to be a potential factor influencing capture survival. However, no difference in condition index (total length versus girth) existed between sharks reported alive or dead at net retrieval ($F_{1,83} = 0.39$, $p = 0.53$; Fig. 7A). Liver weights were measured from sharks reported dead upon net retrieval and used to examine the relationship between liver and whole weight as well as total length, which are more traditional metrics used to assess fish condition. A positive linear relationships was present between liver weight and total length ($F_{1,14} = 86.03$, $p < 0.0001$; Fig. 7B) and no deceased sharks showed severe signs of starvation.

Factors related to fishing were also thought to influence the capture survival of sharks. Average net soak time for sharks reported as dead upon net retrieval was 37.8 ± 12.0 h ($n = 33$) whereas surviving sharks had significantly shorter average net soak times 21.1 ± 17.2 h ($W = 2601$, $p < 0.0001$; $n = 18$; Fig. 8A). However, set gillnet captures comprised 92% of the captures, and average net soak times for live and dead sharks were also significantly different 29.5 ± 22.6 and 40.7 ± 11.3 h; $W = 961$, $p < 0.001$). Set net soak durations for both live and dead sharks were significantly higher than sharks caught in the drift gillnet fishery where soak time was reported (11.4 ± 1.7 h, $n = 4$; $W = 1209$, $p < 0.0001$). The effect of soak time on juvenile white shark mortality for all gillnet fisheries combined was highly significant, where the probability of mortality increased 0.84% with every unit increase (h) in total soak time ($p = 0.00153$, Fig. 8B).

Of the 28 sharks caught, tagged with satellite or acoustic transmitters, and released alive by gillnet fisheries from 2006 to 2012, only two were confirmed dead (i.e., premature PAT tag release after four to ten days of tagging; 7.1%). Therefore, the post-release survival of tagged sharks incidentally caught in gillnet fisheries was very high and likely represents a conservative measure of survival since overall handling to support the tagging procedures, necessary for post-release survival estimation, inherently add additional capture time and stress. Therefore, we would expect survival rates of sharks immediately released upon capture to be higher.

Six sharks were targeted as part of the MBA research and exhibit program and caught by purse seine from 2010 to 2012, tagged with satellite and acoustic tags, and all were subsequently detected for weeks to months following release. Despite the considerable difference in handling time (defined as time of net retrieval to release) between gillnet (6.8 ± 2.6 h) and purse seine (0.8 ± 0.9 h) caught sharks, the post-tag and release survival of sharks caught by these two methods were the same (100% versus 92.9%).

4. Discussion

4.1. Fishery interactions

Juvenile white sharks have had historic interactions with the gillnet fisheries in southern California and as expected there was a significant positive correlation both spatially and temporally between white shark captures and fishing effort. However, the interaction of white sharks with gillnet fisheries was not equal among the three fisheries. The offshore drift gillnet fishery was found to have no interaction with white sharks as indicated from both fishery-dependent and -independent data during the years studied. This is likely due to its offshore concentration in areas not frequented by juvenile white sharks. As juveniles, white sharks are typically considered a coastal shark (Dewar et al., 2004; Weng et al., 2007; Domeier, 2012). In the current study, 80% of the SPOT detections occurred over areas in <200 m of water and, therefore, more inshore, which provides strong evidence that juvenile white sharks preferentially utilize inshore coastal habitats. Previous tracking studies suggested a habitat preference extending farther offshore (Dewar et al., 2004; Weng et al., 2007). However, these studies were limited either by short temporal period of active tracking, or by the coarse spatial resolution and potential biases associated with PAT tag geolocation error. Consistent with this study, however, these earlier works also noted that young sharks rarely dove deeper than 150 m, which may be due to thermal barriers that restrict juvenile white sharks to shallower waters (Dewar et al., 2004; Weng et al.,

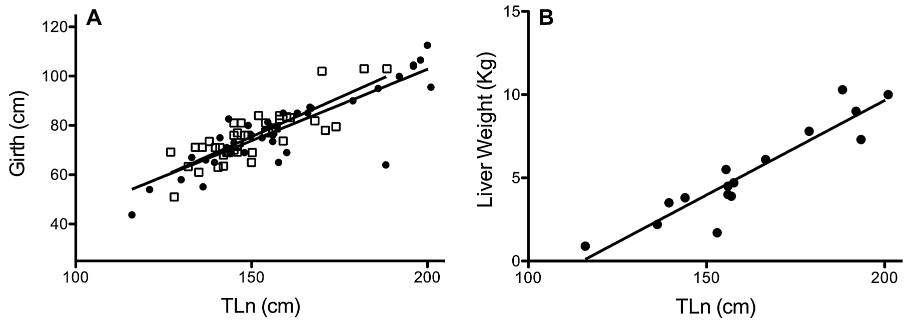

Fig. 7. Comparison of condition morphometrics, including (A) girth and total length for live (open squares, $n = 48$) and dead (closed circles, $n = 39$) white sharks incidentally captured in gillnets from 2006 to 2012, and a plot of (B) liver weight and total length for sharks suffering capture mortality.

2007). Therefore, since juvenile white sharks appear to use inshore habitats, it is not surprising that their interaction with offshore drift gillnets is limited.

Set and inshore drift gillnet fishery effort, however, was significantly correlated to white shark captures per block. Effort from these fisheries was also concentrated closer to shore than the offshore drift gillnet fishery. Although we found significant positive relationships between white shark captures and effort in the inshore drift and set gillnet fisheries, the set gillnet fishery constituted a large portion of white shark captures as well as total gillnet effort. Therefore, the interaction potential of the set gillnet fishery with juvenile white sharks is much greater than the inshore drift gillnet fishery. While there is a moderate degree of overlap in fishing areas between these two fisheries, differences in net mesh size and depth of net set may also influence these relationships. For example, greater incidences of captures in the set gillnet fishery may be related to the nets being set on the sea floor, and benthic associated prey items such as halibut and bat rays (*Myliobatis californica*) have been documented in the stomachs of juvenile white sharks (C. Lowe, unpublished data). This could lead to a greater overlap of the set gillnet fishery compared to the drift gillnet fishery, which tends to utilize mid-water depths.

We used SPOT detections as our fishery-independent method of locating YOY and juvenile white shark habitat in southern California and found a positive correlation between total fishing effort and the number of SPOT detections by fishing block. This suggests that free-swimming sharks utilize the same areas as fishers, to an extent, demonstrating that there is a potential for interaction. Both set and inshore drift gillnet effort were found to be significantly correlated to SPOT detections, but the offshore drift gillnet fishery showed no relationship. Interestingly, similar correlations were found for set and inshore gillnet effort with respect to both SPOT detections (e.g., fishery-independent method) and white shark captures by fishery (e.g., fishery-dependent method); however, the set gillnet fishery recorded significantly greater numbers of incidentally captured sharks than the drift gillnet fishery.

White shark CPUE with respect to total, set gillnet, and inshore drift gillnet fishing effort between 2006 and 2008 was relatively low and suggests that the number of sharks caught with respect to the amount of time nets were fishing was quite small. In addition, there was no relationship between the number of white sharks caught relative to the primary set gillnet fishery target species (i.e., halibut and white seabass) CPUE. Rather, white sharks were captured in greater numbers in blocks where target species CPUE was low. While white sharks do interact with gillnet fisheries, the extent of this interaction is likely less than once believed. We expected white shark captures to be greatest in blocks where target species catch is high relative to effort; however, the opposite was observed. Coupled with the lack of relationship between SPOT detections and white shark CPUE per block, our catch data indicate that the interaction potential of white sharks with the predominant gillnet fishery in southern California (i.e., set gillnet) is low, particularly in blocks that may be targeted by this fishery due to their high product yield.

4.2. Depth distribution of tagged sharks

Analysis of the five PAT tagged sharks demonstrated that the large portion of detections occurring inshore was indicative of actual shallow habitat use (i.e., real behavior) and not an artifact of the technology. Since the distribution of residuals for "deeper" and "shallower" sharks was not significantly different, sharks appear to utilize similar vertical distributions in the water column and do not greatly alter their behavior with respect to sea floor depth. Therefore, we deduced that the greater number of detections in shallow

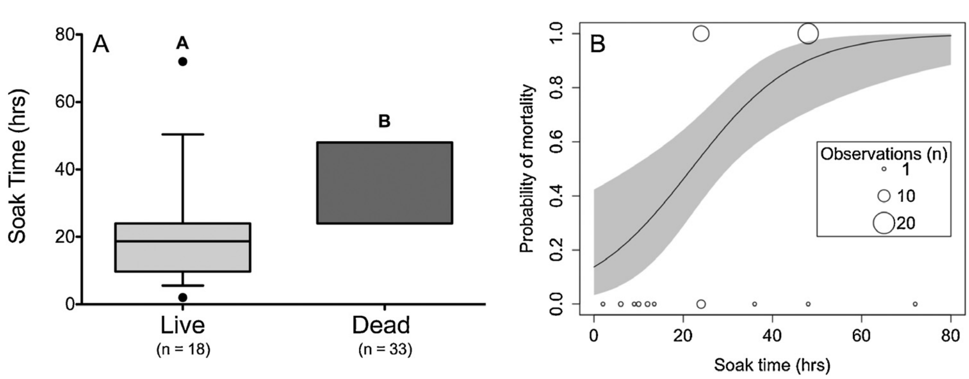

Fig. 8. The effect of gillnet soak time (all fisheries combined) on juvenile white shark bycatch mortality where (A) average gillnet soak times are compared for gillnet-caught white sharks landed live versus dead and (B) the probability of gillnet-caught white shark mortality relative to gillnet soak times. Panel A: Whiskers represent 10–90th percent quartiles; however, soak times for deceased sharks were only reported as either 24 or 48 h. Letters above bars indicate a significant difference at $p < 0.001$. Panel B: The probability of mortality increased significantly with increases in soak time ($n = 51$; $p = 0.00153$; shaded areas represent 95% confidence intervals).

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water (<200 m) areas was not due to sharks spending more time at the surface. Furthermore, if a "shallow water detection bias" were present, we would expect a greater proportion of detections to occur within state waters. On the contrary, a greater proportion of detections occurred outside state waters and less than half within (54% versus 44%). Additionally, sharks that were detected over deeper water (>200 m) only dove to average maximum depths of 61 ± 56 m and did not utilize the maximum possible depths and utilized depths that were comparable to sharks found in shallower water. Weng et al. (2007) have suggested that juvenile white shark avoidance of these deeper depths likely represents a thermal barrier to young individuals, which may limit their use of oceanic habitats if they cannot orient to the bottom and restricts their movements to coastal areas.

4.3. Spatial and temporal overlap of white sharks and gillnet fisheries

Significant interactions were discovered between white sharks and the set gillnet fishery regardless of the fishery-dependent or -independent metric used (e.g., white shark captures or SPOT detections); however, our data indicate that the potential interaction between white sharks and gillnet fisheries may be overestimated if only fishing-dependent methods are assessed. For example, only 18% of "white shark blocks" (i.e., fishing blocks where at least one individual SPOT-tagged white shark was detected) overlapped with areas of high fishing effort and these fishing blocks also comprised a substantial portion of the total effort. On the other hand, 100% of high effort fishing areas coincided with blocks where one or more white sharks had been detected. The most likely explanation for this pattern is that juvenile white sharks utilize a larger area than the fishery. If SPOT locations are representative of where sharks are spending their time, then these animals may not be interacting with the fishery as much as would be expected given their relatively wider area use compared to the few number of high effort fishing blocks.

Since a large portion of the SPOT detections (44%) occurred inside of state waters (i.e., restricted gillnet areas), this demonstrates that the nearshore gillnet exclusion measure has indirectly created an extensive protected region that significantly reduced overall spatial fishing interactions with white sharks in southern California. Prior to the State of California inshore gillnet ban, fishers heavily utilized the shelf area within 3 nm of shore (Holts, 1988; Lowe et al., 2012). After the ban, the remaining gillnet fishery was pushed further offshore, which removed a substantial portion of available suitable fishing area, especially for the set gillnet fishery. This area closure resulted in an increased abundance of several commercially important species previously impacted by gillnet fishing (Pondella and Allen, 2008). While our results demonstrated some overlap between YOY and juvenile white sharks and areas of high gillnet fishing effort (18% of blocks), a large portion of the white shark habitat occurs in areas where fishing effort is quite low or absent (Fig. 4). In particular, a large number of individual sharks were detected within or near Santa Monica Bay (SMB) area where limited shelf habitat beyond state waters limits suitable areas for gillnet fishing. Anecdotal reports over the years in this area also indicate an increase in YOY white shark sightings and hook and line captures by recreational fishermen from piers, which suggests SMB may be important for young sharks and limitation of gillnet fishery access to this area has been beneficial.

Furthermore, there is incomplete overlap between peak gillnet effort and the presence of juvenile white sharks in the SCB. Despite the relatively high effort during the first half of the year, there was a prominent absence of white shark captures during this time until June when captures substantially increased. From June to November, white shark captures were positively correlated to fishing effort by month. White sharks are thought to give birth starting in the spring and extending through the summer (Domeier, 2012); our data support this hypothesis as evidenced by the dramatic increase in captures with the onset of summer. The number of SPOT detections per month was highest during the late summer and fall during the time when notable decreases were seen in both fishing effort and captures (i.e., the peak in white shark utilization of southern California occurs when fishing effort is relatively low). This reduces their interaction potential beyond that due to the spatial separation.

The depth frequencies of sharks at their SPOT tag locations were heavily skewed toward shallow water, with the two highest peaks occurring over 30 and 60 m depth and substantially fewer detections occurring in water greater than 200 m. Since we found no difference in time between detections when sharks were considered "inshore" or "offshore", the pattern in depth distribution further indicates that YOY and juvenile white sharks prefer inshore habitat. Recent acoustic telemetry data for sharks tagged in Santa Monica Bay have shown some individuals spending a considerable length of time within a couple hundred meters of the shoreline; inshore habitats comprised largely of unconsolidated soft sediment and sand (C. Lowe et al., unpublished data). Other studies have documented similar behaviors with juveniles utilizing habitat that is relatively close to shore (Bruce and Bradford, 2011, 2012). However, more long-term tracking at finer scales is required to better determine the extent sharks use these shallow coastal habitats.

Substantial overlap was found between the depth distributions of free-swimming sharks and presumed areas of gillnet fishing. Depths over locations of white shark detections were significantly shifted to the right over deeper depths compared to depth distributions of white sharks that had been previously captured; however, SPOT tagged shark depth distributions were not different from areas of high fishing activity along the 3 nm state waters line. Interestingly, the frequency of sea floor depths at white shark capture locations had much less overlap with SPOT detection depths compared to the depths along the 3 nm line, areas that were presumed to be highly utilized by gillnet fishers. However, the actual locations of fishing spots may not lie along the entire 3 nm line within a block, especially if fishers consistently only utilize a small number of areas along the 3 nm line; this would then over-estimate the potential overlap of fishing depths at the 3 nm line and SPOT detection depths.

Although there was no temporal trend, we did observe high variability in the number of white sharks caught from year to year. This variability may be related to yearly environmental conditions or timing of white sharks reproductive cycles. While white sharks are hypothesized to reproduce on a three year cycle (Mollet et al., 2000; Domeier, 2012), asynchronous cycles among reproductive females in the population could be one factor accounting for the differences in YOY white shark catches among years. While catches of white sharks were not standardized by effort (data post-2009 was not available), anecdotal statements from fishers have indicated variation in environmental conditions (e.g., water temperature or surface conditions). Changes in these factors could influence yearly fishing effort or availability of suitable YOY habitat and, therefore, the number of sharks that are caught in a given year.

4.4. Capture and post-release survival

While there was no significant increase in the proportion of sharks dead at net retrieval over the course of the study, there was a relationship between probabilities of net mortality with soak time. When condition was compared between sharks found alive and those found dead upon net retrieval, no condition metrics indicated that dead sharks had been in poorer body condition. Previous work on deceased sharks has also shown that the lipid content in the livers of these animals is relatively high (average 63 ± 25% lipid content; Mull et al., 2012). Therefore, these animals are not in a state of starvation that might make them more susceptible to net mortality. Rather, it appears that the duration of net soak time may be a much more important factor determining whether sharks will be landed live or dead. Indeed, the difference in post-release survival between tagged sharks caught via purse seine (where handling time and entanglement within the net is low) and gillnet was surprisingly small, despite the fact that handling and transport times of gillnet sharks could be in excess of 10 h. Therefore, this species appears to be very robust to entanglement and handling, which is uncharacteristic of other lamnid species such as mako (*Isurus* spp.) and thresher (*Alopius* spp.) sharks (Hight et al., 2007; Heberer et al., 2010).

5. Conclusions

This study provides the first high-resolution geoposition data for juvenile white sharks in the Eastern Pacific, revealing that their preferred habitat is shallow inshore waters. Although the positive effect on white sharks was not anticipated at the time of regulation, the 1994 inshore gillnet ban in California likely reduced much of the potential overlap between white shark habitats and areas of high fishing effort by significantly reducing effort and shifting effort to areas less used by young sharks. Despite the continued interaction between juvenile white sharks and gillnet fisheries, their potential interaction was much less than expected after comparing our fishery-dependent and -independent sources of where juvenile white sharks occur in southern California. In addition, the high survival of sharks released from gillnets demonstrates that the impact of existing interaction within areas of overlap may be lessened with shorter net soak durations. The findings of this study are also significant in that fishers participating in MBA's white shark project had a direct and crucial role in collecting the data.

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