Received: 21 December 2017 | Accepted: 14 March 2018

DOI: 10.1111/1365-2664.13158

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Juvenile survival, competing risks, and spatial variation in mortality risk of a marine apex predator

John F. Benson[1] | **Salvador J. Jorgensen**[1] | **John B. O'Sullivan**[1] | **Chuck Winkler**[2] | **Connor F. White**[1,3] | **Emiliano Garcia-Rodriguez**[4] | **Oscar Sosa-Nishizaki**[4] | **Christopher G. Lowe**[3]

[1]Monterey Bay Aquarium, Monterey, California

[2]Aquatic Research Consultants, San Pedro, California

[3]Department of Biological Sciences, California State University, Long Beach, California

[4]Department of Biological Oceanography, CICESE, Ensenada, Mexico

Correspondence
John F. Benson
Email: benson.johnf@gmail.com

Present Address
John F. Benson, School of Natural Resources, University of Nebraska, Lincoln, Nebraska

Funding information
California State University Long Beach; CONAMP; Monterey Bay Aquarium; Reserva de la Biosfera El Vizcaino

Handling Editor: Andre Punt

Abstract

1. Reliable estimates of mortality have been a major gap in our understanding of population ecology for marine animals. This is especially true for juveniles, which are often the most vulnerable age class and whose survival can strongly influence population growth. Thousands of pop-up archival satellite tags (PAT) have been deployed on a variety of marine species, but analysis of these data has mainly been restricted to movement ecology and post-handling survival following fisheries bycatch. We used PAT data to provide empirical estimates of annual survival and cause-specific mortality for juveniles of a marine top predator.
2. We tagged and tracked juvenile white sharks in the northeastern Pacific Ocean to (1) estimate survival rates and competing risks and (2) investigate intrinsic and environmental influences on mortality risk. We also evaluated the use of PAT data with respect to meeting assumptions of known-fate survival models.
3. Annual juvenile survival rate was 0.632 ($SE = 0.15$) and annual natural mortality rate (0.08, $SE = 0.06$) was lower than the rate of gillnet interactions (0.48, $SE = 0.15$). Mortality risk decreased with greater body length and was significantly greater (hazard ratio = 9.05, $SE = 0.70$) for juvenile sharks in Mexican waters, relative to California waters.
4. The PAT data allowed for unambiguous determination of fate in most cases, aided by collaborative relationships with fishers and secondary tags deployed on a subset of sharks. Although caution must be exercised to establish whether assumptions are met, our work demonstrates that PAT data represent a widely available, untapped data source that could dramatically increase our understanding of marine population ecology.
5. *Synthesis and applications*. Our research shows fisheries bycatch to be the main source of mortality for juvenile white sharks in the northeastern Pacific Ocean, highlighting the need for best practices, such as releasing sharks quickly following incidental capture. Furthermore, mortality risk for juveniles was greater in Mexican

waters, such that survival may be lower in colder years when juveniles are likely to move south seeking warmer water. This could increase stochasticity in juvenile survival and negatively influence population growth for this apex predator.

KEYWORDS
bycatch, competing risks, cox proportional hazards, juveniles, mortality, pop-up archival satellite tag, sharks, survival

1 | INTRODUCTION

Juvenile survival is a critical demographic parameter that influences the fitness of individuals and the growth of populations (Mollet & Cailliet, 2002; Morris & Doak, 2002). Technology facilitating tracking of individually marked juvenile animals has become increasingly available for a variety of species, allowing for more direct estimation of juvenile survival and cause-specific mortality rates (e.g. Benson, Mills, Loveless, & Patterson, 2013; Moriarty, Whited, Sikich, & Riley, 2012). However, to date empirical estimates of juvenile survival have mainly been limited to terrestrial species. Thus, the lack of reliable estimates of mortality continues to be a major obstacle to understanding and modelling population dynamics of virtually all marine fish species (e.g. Hixon & Carr, 1997; Pauly, 1980; Tsai, Sun, Wang, & Liu, 2011).

Recently, Byrne et al. (2017) used satellite-tag data from Smart Position Only Transmitters (SPOT) to estimate annual fishing mortality of shortfin mako sharks *Isurus oxyrinchus* in the Atlantic Ocean. To our knowledge, this was the first study to use satellite-tag data of any kind from a marine species (aside from sea turtles) to estimate annual survival rates and model factors influencing fisheries mortality risk using known-fate models (Byrne et al., 2017). However, SPOT tags do not allow for reliable detection of natural mortality events and are only effective on certain fish species, such as sharks that surface regularly and have rigid dorsal fins (Byrne et al., 2017; Drymon & Wells, 2017). Heupel and Simpfendorfer (2002) estimated juvenile survival for blacktip sharks *Carcharhinus limbatus* in Florida using acoustic tags, but the passive nature of acoustic telemetry meant that survival monitoring was geographically restricted to a single bay. Several researchers have noted that data from pop-up archival satellite tags (PAT) would be effective for estimating mortality rates (Pollock & Pine, 2007; Skomal, 2007) and previous studies have used these data for estimating short-term survival following fisheries bycatch (e.g. Campana, Joyce, & Manning, 2009; reviewed by Musyl et al., 2011). However, despite wide and increasing availability of PAT data for numerous marine species (e.g. Block et al., 2011; Musyl et al., 2011), we are unaware of previous studies using these data to estimate annual survival and cause-specific mortality rates (natural and fisheries) with known-fate models.

Estimating survival is important for sharks because many species have experienced population declines, primarily as the result of mortality associated with commercial fishing (Dulvy et al., 2014). Apparent survival of adult and subadult white sharks *Carcharodon carcharias* in the northeastern Pacific (NEP) population was recently estimated using mark–recapture methodology (Kanive et al., 2015), but survival rates of white sharks during their first several years of life are not available. This is a critical knowledge gap because white sharks are believed to be most vulnerable to mortality early in life (Klimley, 1985; Lowe et al., 2012; Lyons et al., 2013; Oñate-González et al., 2017) and juvenile survival is thought to have the strongest influence on population growth for the species (Cortés, 2002; Mollet & Cailliet, 2002). Multiple studies have reported juvenile white sharks caught as bycatch in commercial and recreational fisheries in the NEP, highlighting this important cause of mortality (Dewar et al., 2013; Klimley, 1985; Lowe et al., 2012; Lyons et al., 2013; Oñate-González et al., 2017). The only known nursery area for the genetically distinct NEP white shark population (Jorgensen et al., 2009) straddles the coastal waters of southern California and Northern Baja, Mexico. Oñate-González et al. (2017) examined catch records and found that incidental capture of juvenile white sharks was higher in Mexican waters compared to California. However, the annual mortality rate is not known for white sharks, and spatial variation in juvenile mortality risk has not been quantified for any shark species. White sharks are protected internationally under the Convention on International Trade in Endangered Species (CITES, Appendix II) and listed as vulnerable under the World Conservation Union Red List (IUCN, Category VU A1 cd+2 cd; Dulvy et al., 2008). White sharks are also listed as a “threatened species” in Mexico (DOF, 2002). Unfortunately, there is limited information on population dynamics of white sharks in the NEP. Thus, estimating juvenile white shark mortality would inform conservation efforts and provide a key parameter needed to understand the population dynamics of this top predator, assess its population status, and inform conservation and management efforts.

We used PAT data collected from 37 juvenile white sharks captured off the southern coast of California, United States and Baja, Mexico from 2000 to 2016 with multiple objectives. First, we estimated rates of survival and competing risks. We hypothesized that the rate of interactions with fisheries would be greater than the natural mortality rate. Second, we investigated intrinsic (i.e. body size) and extrinsic (i.e. local environment) factors influencing mortality risk of juvenile white sharks. Given that bycatch appears to be more common in Mexico than California (Oñate-González et al., 2017), we hypothesized that mortality risk of juvenile white sharks would be higher in Mexican waters relative to California waters. We also evaluated the use of PAT data for known-fate survival estimation with respect to

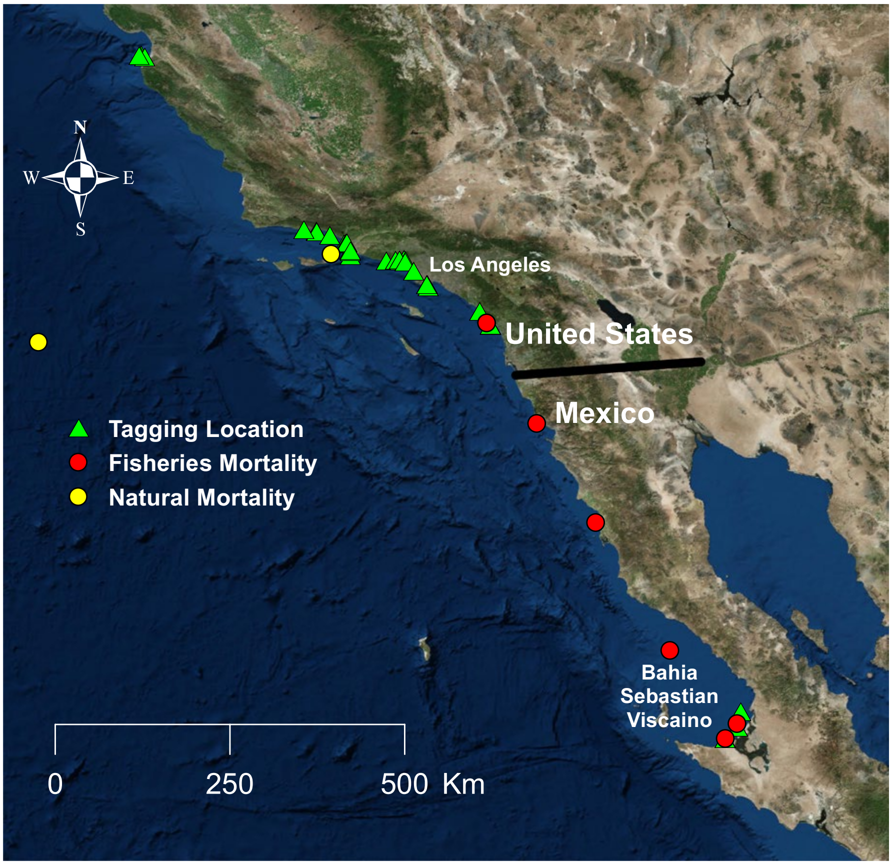

FIGURE 1 Locations where juvenile white sharks were tagged and subsequently died from fisheries or natural mortality along the coast of California and Mexico, 2000–2016

important model assumptions. Our work provides guidance to marine researchers interested in estimating survival and cause-specific mortality rates using satellite-tracking data, and begins to address a critical knowledge gap in the understanding of shark population biology. Practically, understanding spatial variation in juvenile mortality risk will facilitate developing and refining fisheries management practices that are compatible with white shark conservation.

2 | MATERIALS AND METHODS

2.1 | Capture and tagging

Juvenile white sharks were captured either through collaboration with fishers or by targeted fishing by researchers off the coast of southern California and Baja, Mexico from 2000 to 2016 (Figure 1, Table S1). Sharks not caught by researchers were captured as bycatch in commercial set-gillnet fisheries. We deployed PAT tags (PAT-2 and PAT-MK10; Wildlife Computers, Redmond, WA, USA) on 44 sharks and also used data from a single PAT deployment on a juvenile shark in our study area reported in the literature (PAT-2000; Wildlife Computers, Dewar, Domeier, & Nasby-Lucas, 2004). We programmed the PAT tags to record light, depth and temperature every 5–120 s, and to transmit summaries of these data to satellites upon release from the animals. We programmed tags to release from sharks after 40–270 days. We examined these data for evidence of mortality, which facilitated monitoring the survival of sharks on a daily basis. Three PAT tags never reported any data and we excluded these tags from the analyses. We also excluded data for four sharks that died immediately after release because survival data from these animals represented a clear violation of the important assumption that handling and tagging do not influence the survival of study animals (e.g. Pollock, Winterstein, Bunck, & Curtis, 1989). We also excluded data for a single shark because the transmitted data were very sparse and the tag was not recovered. All other tags reported upon scheduled pop-up ($n = 19$), reported upon premature pop-up ($n = 7$) or were involved in mortality events, gillnet interactions, or long-line interactions ($n = 11$). We also deployed SPOT tags on a subset of sharks ($n = 12$), which provided additional information on the fate of some sharks and aided our evaluation of PAT data with respect to meeting assumptions of known-fate models.

We sexed sharks and measured total length at time of tagging. Previous researchers have proposed that young of the year (YOY) are <175 cm, older juveniles are 175–300 cm, whereas sharks >300 cm are subadults or adults (reviewed by Oñate-González et al., 2017). Based on these classifications and their length at tagging, the sharks used in our analyses were mostly YOY ($n = 29$) with a small number of older juveniles ($n = 8$). Most sharks used in our analysis (86%, $n = 32$) were captured, tagged and released immediately ($n = 30$) or within 6 days ($n = 2$). However, five sharks tagged in California were brought into display at the Monterey Bay Aquarium (MBA) for periods of 22–223 days prior to release and tagging. However, we only included survival and mortality data for these sharks in our analyses for the periods following their release to the wild with a functioning

PAT tag. Additional details of capture and handling of juvenile sharks used in our study are available in Table S1 and elsewhere (Dewar et al., 2004; Lyons et al., 2013; Weng et al., 2007, 2012). All capture and handling of sharks in California was done under California Department of Fish and Wildlife collecting permit CDFG SCP #2026 and California State University, Long Beach IACUC protocol #274. Sharks in Mexico were tagged under permits SGPA/DGVS/06777/15 and 06294/16.

2.2 | Interpreting PAT data and determining mortality

We examined all PAT data received for evidence of mortality. In cases where previously tagged sharks were entangled or captured, the tags were retained by fishers and eventually returned. In some cases, detached tags were reported to be found in nets, but the shark was not present in the net at time of retrieval ($n = 2$) or sharks were released alive by fishers following interactions with gillnets ($n = 1$). For our analyses, only sharks known to have died from interactions with gillnets or long-lines were classified as mortalities. All other tag data were assessed by looking at the final hours of depth, temperature, and light data recorded before the tag released to determine the shark's fate using methods similar to those of Campana et al. (2009). Sharks were deemed to have survived unless the data provided a clear indication of mortality. Predation of a tagged fish resulting in PAT tag ingestion can be determined when tag sensors indicate a sudden change in behaviour, an increase in thermal inertia, and the extinguishing of light until the tag exits the predator's stomach and reports at the surface (Jorgensen et al., 2015; Polovina, Hawn, & Abecassis, 2008). Mortality can also be determined if a shark sinks to the ocean floor and remains there until the tag triggers the "mortality" release. We programmed PAT tags to release for this purpose if the tag recorded the same depth (±2 m) for >96 hr. Premature detachment can be concluded (and natural mortality ruled out) when tags sink to the bottom at a slower rate than would be possible if the tag was attached to a shark (Weng et al., 2012).

2.3 | Estimation of survival and competing risk rates

We estimated survival rates, standard errors, and 95% confidence intervals for juvenile white sharks captured in California waters using the nonparametric Kaplan–Meier product limit estimator and the Greenwood method for estimating variance (Therneau & Grambsch, 2000). Given that only four sharks were captured off the coast of Mexico, we did not pool these with the sharks tagged off California because it was possible that survival rates differed for animals tagged in the two locations. We did not estimate survival rates for these four sharks and instead simply present their monitoring times and fates. However, given that juveniles moved between waters of the two countries during the monitoring period, we were able to explicitly investigate the hypothesis that mortality risk varied spatially between US and Mexican waters using Cox proportional hazards models (see below), which allow for time-varying covariates.

For sharks tagged off the California coast, we used two time-scales and time of origins to estimate survival rates (Fieberg & DelGiudice, 2009). First, we used a time-since-release time-scale (Fieberg & DelGiudice, 2009) where all animals were entered into the model on day 0 (day of release with PAT tag) and survival rate was estimated across these monitoring periods (range 4–270 days). All animals exited the model upon mortality (coded 1) or were right-censored upon tag pop-up (coded 0). Next, we modelled survival using an annual recurrent time-scale (Fieberg & DelGiudice, 2009) to extend survival rates across the calendar year. With this approach, animals entered the model in a staggered manner (Pollock et al., 1989) on the day of the year (1 Jan—31 Dec, 0–364) on which they were released with a PAT tag, and exited upon death (coded 1) or were right-censored at the end of the monitoring period when the tag popped-up (coded 0). All animals still alive with a functioning PAT tag were censored on the last day of the year (31 Dec) and re-entered on the first day of the following year (1 Jan). Although we did not monitor any individual animal for a full calendar year, we monitored juvenile sharks during all months of the year allowing us to estimate annual survival rates and capture seasonal trends in mortality in our survival curves.

To evaluate the relative importance of different, mutually exclusive mortality and capture agents affecting juvenile white sharks tagged in California, we estimated the rate of competing risks for juvenile white sharks using the nonparametric cumulative incidence function estimator (CIF; Heisey & Patterson, 2006) with the annual recurrent time-scale. Specifically, we estimated rates of: (1) natural mortality (predation or unknown), or (2) interactions with commercial fisheries. We considered these rates to differ from one another if their 95% confidence intervals did not overlap. We did not consider competing risks for sharks tagged in Mexican waters because of the small sample size and the fact that all mortality events were from a single cause.

Implementing known-fate survival procedures using telemetry data requires that only events involving animals whose survival is reliably monitored with a working device are included in the analysis. Animals can exit the analysis (i.e. be right-censored) at any time if they can no longer be monitored, which in our study included tag failure or premature detachment. The critical assumption is that censoring is independent of fate (Fieberg & DelGiudice, 2009); i.e. animals that are censored are assumed to be no more or less likely to die than other animals in the study. There are two other important assumptions when using telemetry data for survival analysis. First, tagged animals are assumed to be a random sample of the study population (Pollock et al., 1989). Second, capture and tagging are assumed not to influence future survival of animals (Pollock et al., 1989). As noted above, we excluded four sharks that appeared to have died due to capture and handling to ensure this assumption was met.

2.4 | Modelling factors influencing mortality risk

We investigated intrinsic and environmental factors influencing mortality risk of juvenile sharks with semiparametric Cox proportional hazards regression modelling (Therneau & Grambsch, 2000). For these models, we used the annual recurrent time-scale described above which allowed us to account for seasonality in mortality with the baseline hazard (Fieberg & DelGiudice, 2009). Specifically, we investigated the potential influence of length at tagging (cm, continuous) on mortality risk of sharks captured in California. We also investigated whether mortality risk varied spatially between US and Mexican waters with a binary, time-varying covariate (California = 0, Mexico = 1) using the entire dataset of sharks captured in both countries. Although most of the sharks we tracked were captured off the southern California coast (89%), sharks moved between US and Mexican waters and approximately half (46%) spent some of the monitoring period in Mexican waters off the coast of Baja. When sharks left the waters of one country and entered those of the other, we censored them and re-entered them the next day after updating the binary spatial covariate (Therneau & Grambsch, 2000). We used previously described methods to estimate spatial locations from PAT data (e.g. Weng et al., 2007, 2012). White sharks are protected from targeted fishing in both the US and Mexico, but incidental catch of white sharks occurs in both areas and appears to be higher in Mexican waters (Oñate-González et al., 2017). Mexico implemented a complete fishing ban for white sharks and mandatory release of incidental captures in 2014 (DOF, 2014). Unlike Mexico, California prohibits gillnet commercial fishing within three nautical miles of shore (California Proposition 132), which appears to have helped reduce bycatch of juveniles in California waters (Lyons et al., 2013). Thus, we used the model to test the hypothesis that mortality risk was higher for juvenile white sharks in Mexican waters. Given our relatively small sample sizes (37 sharks, eight mortality events), we fit each covariate of interest separately in univariate models to avoid overfitting and potentially spurious results (Hosmer, Lemeshow, & Sturdivant, 2013). We compared the relative fit of models using Akaike's Information Criterion corrected for small samples (AICc; Burnham & Anderson, 2002). We also calculated AICc for a null model with no covariates and only made inference on univariate models that represented substantial information gain relative to the null model ($\Delta AIC_c > 2$; Burnham & Anderson, 2002).

Some individuals had >1 record in the input data (i.e. those tracked in multiple calendar years and those that crossed between international waters), so we estimated robust ("sandwich") standard errors and *p*-values for parameter estimates, clustered by individual, to account for the lack of independence of these records (Therneau & Grambsch, 2000). We examined parameter estimates for models with substantial information gain ($\Delta AIC_c < 2$) and present exponentiated beta coefficients (hazard ratios), robust standard errors, 95% confidence intervals, and robust *p* -values. We considered hazard ratios with 95% confidence intervals that did not overlap 1 to indicate significantly increased or decreased mortality risk. We conducted all survival and mortality analyses using the "SURVIVAL", "MASS", "AICCMODAVG", and "VISREG" packages in R version 3.3.1 (R Development Core Team, 2016; http://cran.r-project.org). The proportional hazards assumption is critical for model fit of Cox proportional hazards models (Fieberg & DelGiudice, 2009). Thus, we verified the proportional hazards assumption of Cox models by examining the distribution of Schoenfeld residuals with a Chi-square test using the cox.zph function in the "SURVIVAL" package (Therneau & Grambsch, 2000). We also visually inspected plots of Schoenfeld residuals for significant departures from a horizontal trend over time that would indicate a violation (Fieberg & DelGiudice, 2009; Therneau & Grambsch, 2000).

3 | RESULTS

We documented two natural mortalities of YOY white sharks tagged with PATs. One shark died and sank to the sea floor 63 days after tagging. The second was apparently consumed by a predator 36 days post-release along with the PAT tag. Indications of this predation event were (1) the extinguishing of light, (2) a marked change in vertical behaviour, and (3) thermal inertia characterized by a near constant temperature across a wide range of depths. This PAT tag remained inside of the predator for 19 days at which point the tag was expelled and once again began registering daylight prior to initiating transmission at the surface. We documented nine tagged YOY white sharks that interacted with gillnets (*n* = 8) or long-lines (*n* = 1). Of the sharks that interacted with fisheries, six died, one was released alive, and two were reported missing by fishers who retrieved the tag (but not the shark) from their nets. Thus, we considered the six sharks that died to be mortalities, whereas we censored the remaining three sharks that interacted with gillnets on the day the shark or tag was captured in the net. Sharks tagged in California resulted in all (*n* = 2) natural mortalities and three of the fisheries mortalities. Three of four sharks tagged in Mexico died of fisheries-related mortality. Five of six fisheries-related mortalities we documented occurred in Mexico.

3.1 | PAT data with known-fate models

Data from four sharks (11%) were potentially problematic for determining fate and meeting the assumptions of known-fate models without information beyond the PAT data (see Discussion and Appendix S1). However, information from secondary SPOT tags and assuming fishers always reported sharks that died in their nets removed this uncertainty and allowed us to determine fate in all cases. Our assumption with respect to fishers is reasonable given the collaborative relationship between fishers and researchers in our study areas, and because fishers were compensated for returning tags.

3.2 | Survival and competing risks

Survival rate for the monitoring period since release (4–270 days) for juvenile sharks tagged in California was 0.808 (*SE* = 0.079, 95% CI [0.666–0.979], *n* = 33, Figure 2a). We estimated annual survival of juvenile white sharks tagged in California to be 0.632 (*SE* = 0.146, 95% CI [0.403, 0.993], *n* = 33, Figure 2b). For sharks tagged in California, annual mortality rate from natural causes was 0.079 (*SE* = 0.058, 95% CI [0.00, 0.174], *n* = 2 events), whereas the

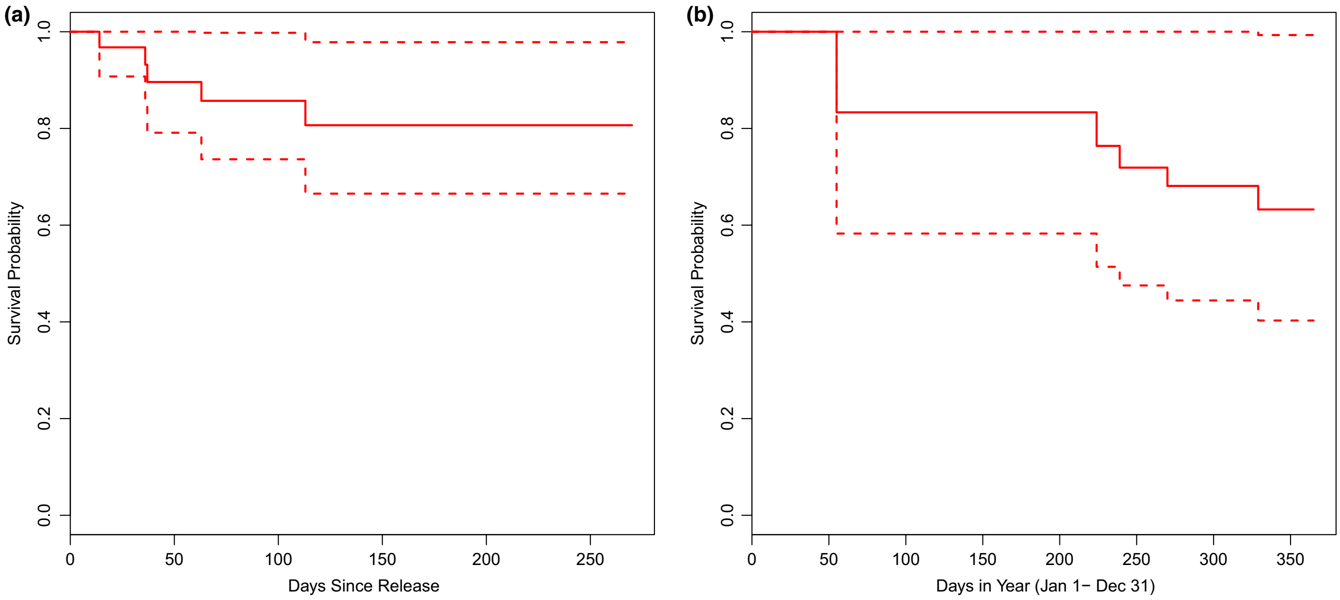

FIGURE 2 Estimated Kaplan–Meier survival probabilities and 95% confidence intervals for 33 juvenile white sharks satellite-tagged in California waters. Shown are (a) estimated survival probability for the monitoring period and (b) estimated annual survival probability

annual rate of interaction with gillnets was 0.469 (*SE* = 0.131, 95% CI [0.253, 0.685], *n* = 8 events). Given that not all sharks interacting with gillnets were known to have died, we estimated the fishing mortality rate as 0.289 (total mortality—natural mortality). We tagged four sharks in Mexico and three were killed in interactions with fisheries (two gillnets, one long-line) all within 27 days of tagging (range of monitoring 2–27 days). The remaining shark tagged in Mexico survived the entire 90-day monitoring period.

3.3 | Factors influencing mortality risk

The null models were inferior to the models including total length (for sharks tagged in California; $\Delta AIC_c = 3.14$) and location (for sharks tagged in California and Mexico; $\Delta AIC_c = 6.00$), indicating that these variables provided substantial information about mortality risk. There were no violations of the proportional hazards assumption in these models based on analysis of the distribution of Schoenfeld residuals (total length: $\chi^2 = 0.488$, $p = .485$; location: $\chi^2 = 0.803$, $p = .370$). Graphical evaluation of the residuals also indicated that the proportional hazards assumption was met (Figure S1). Mortality risk of juveniles tagged in California decreased with increasing total length at tagging (hazard ratio = 0.93, *SE* = 0.03, 95% CI [0.88, 0.98], *p* = .011, *n* = 33; Figure 3). Mortality risk was greater for juvenile white sharks when they were in Mexican waters relative to Californian waters (hazard ratio = 9.05, *SE* = 0.70, 95% CI [2.29, 35.78], *p* = .002, *n* = 37).

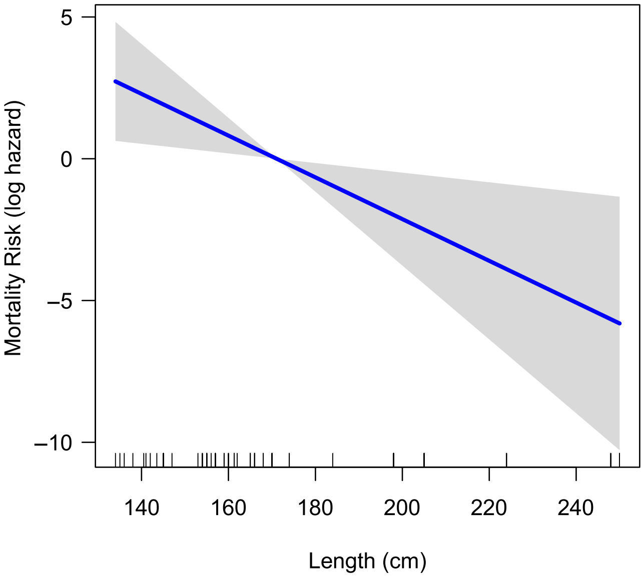

FIGURE 3 Relationship of instantaneous mortality risk (log hazard) and length at tagging of 33 juvenile white sharks satellite-tagged in California waters estimated with Cox proportional hazards model; 95% confidence interval shown with grey shading

4 | DISCUSSION

We believe our results provide the first empirical estimates of annual juvenile survival and spatial variation in mortality risk derived by satellite-tracking wild sharks. Our data suggest juvenile mortality of white sharks in the NEP mainly resulted from interactions with fisheries, whereas natural mortality was relatively rare. Large bodied, k-selected species in general (Pianka, 1970) and pelagic fish specifically (McGurk, 1986) tend to experience relatively low natural mortality. Interestingly, our empirical estimate of annual natural mortality (0.079) was similar to previously reported estimates derived through modelling approaches (e.g. 0.047–0.068, Cortés, 2016; Mollet & Cailliet, 2002). The increasing abundance of pinniped prey in the Pacific coast of North America during approximately the last 50 years (Wade et al., 2007) suggests food for adult white sharks in the NEP is relatively plentiful, which could help females provision young at birth. Less is known about the diet of juvenile white sharks in the NEP, but our documentation of low natural mortality and lower mortality risk for larger juveniles (when they were older and provisioning themselves) may indicate that food resources are sufficient to keep starvation rates low.

We acknowledge that sampling issues also could have influenced our results. First, our sample size is modest, resulting in large confidence intervals. Although we studied survival of juvenile sharks tagged in California over a 16-year period, our within-year sample sizes were quite low (range 0–9 sharks). Thus, our data should provide a valuable estimate of mean juvenile survival across that period, but they are clearly not sufficient to estimate mortality within years, or to understand inter-annual variation in juvenile mortality. Large, long-lived species in terrestrial systems often have highly variable juvenile survival rates (e.g. Derocher & Stirling, 1996; Gaillard, Festa-Bianchet, & Yoccoz, 1998). It is possible that juvenile white sharks experience similar fluctuations in natural mortality not captured by our estimates. If our estimates are used to parameterize future models of white shark population growth, the wide confidence intervals reported should be used to incorporate environmental stochasticity.

Second, although we tracked juvenile sharks from young ages (<1 year old), we acknowledge we could have missed some mortality of the youngest sharks prior to our most intensive tagging efforts. Parturition for white sharks in the NEP likely begins in May (Domeier, 2012; Oñate-González et al., 2017). Given that our tagging success was greatest in August, and that the median date of tagging for YOY sharks was 30 July, some YOY sharks may have died prior to the peak of our tagging season. Assuming juveniles are well provisioned at birth, they should have sufficient reserves that starvation would be relatively rare in the first several months, perhaps mitigating the problem. However, these first months could be a risky period for predation mortality and fisheries interactions, which could have resulted in underestimation of mortality. Indeed, mortality risk was greater for smaller sharks based on length at tagging, which should be approximately correlated with age. The single predation event we documented involved a shark captured in early July that was in the lowest quartile for length at tagging (142 cm).

Mortality was largely due to interactions with fisheries for sharks tagged in California and Mexican waters. Previous work has shown that juvenile white sharks have a high probability of survival when retrieved alive in gillnets and that mortality can be decreased by reducing the time that captured sharks spend in nets (i.e. soak durations; Lyons et al., 2013). Oñate-González et al. (2017) suggested that larger juvenile white sharks might be better able to free themselves from nets, which was consistent with our finding that mortality risk was negatively related to length at tagging. In Mexican waters, in addition to full protection for white sharks, a fishing closure between 1 May and 31 July for all sharks and rays was established beginning in 2012, which has probably helped protect juveniles since it coincides with the period when young white sharks are close to the Baja coast (Santana-Morales et al., 2012). In California waters, the 1994 inshore gillnet ban within three nautical miles of shore appears to have had a positive effect in terms of shifting gillnet effort to areas further offshore that are used less by young sharks (Lyons et al., 2013). However, our results also indicate that despite efforts to protect sharks by California and Mexico, and the potential for post-release survival, incidental gillnet capture continues to be the primary source of mortality for juveniles. The lower mortality risk we documented in California waters suggests that full closure of gillnet fishing close to shore is a more effective management strategy than simply banning targeted fishing to reduce mortality risk due to bycatch. Our results, combined with those of previous researchers, suggest that the following management regulations and fisheries practices are important to minimize bycatch mortality for juvenile white sharks in the NEP: (1) continued protection from targeted fishing, (2) prohibiting gillnet fishing close to shore in nursery areas, and (3) mandatory release combined with efforts to reduce soak duration for sharks caught in gillnets.

Mortality risk was substantially greater off the coast of Baja, Mexico compared with California. Juvenile white sharks captured and tagged in southern California waters often travel south into waters off the coast of Baja, especially during fall and winter (Weng et al., 2007, 2012). Juvenile white sharks select warmer temperatures than commonly occur in southern California during fall and winter, which likely provides at least a partial explanation for southward movements of juveniles in these seasons (White, 2016). These previous findings, combined with our current results, suggest that colder water temperatures in southern California, especially during non-El Nino years, could present an ecological trap for white sharks whereby juveniles seeking warmer temperatures during fall and winter could greatly increase their risk of mortality due to interactions with fisheries in Mexico. Water temperature in the Pacific varies between warm and cool as part of the 16–20-year cycle of the Pacific Decadal Oscillation. Highly temporally stochastic vital rates can strongly impact population growth, even for parameters with relatively low elasticity for mean values (Mills, Doak, & Wisdom, 1999). Previous elasticity analyses have suggested that mean juvenile survival actually has the strongest influence on population growth of white sharks. Thus, increased variation in juvenile survival due to the proposed interaction between water temperature and spatial variation in mortality risk could have important consequences for population growth of white sharks in the NEP where ocean temperatures vary annually due to climatic oscillations. Alternatively, increases in ocean temperatures (Levitus, Antonov, Boyer, & Stephens, 2000) associated with climate change could result in fewer juvenile white sharks moving south from California in future years, thereby reducing fishing mortality risk.

In terms of determining fate and meeting assumptions of known-fate models, several instances could have been ambiguous without additional information from fishers and secondary tags (see details in Appendix S1). There were two cases where sharks were captured and died in gillnets that may have been difficult to identify with certainty without information from fishers and secondary tags. There were also two cases where sharks survived, but with PAT data alone there may have been uncertainty. One case was resolved using secondary tag data (Appendix S1). With another shark, the tag detached from the shark and was not recovered such that we had to determine fate using only transmitted data. We censored this shark on the last date we knew the shark was alive, but acknowledge there is a slight possibility that the tag detached during a fatal gillnet capture. If so, this would violate the assumption of censoring being independent of fate. However, given that we documented only this single, slight potential violation of assumptions, we believe that known-fate survival modelling is an appropriate and valuable use of PAT data for marine organisms. Nonetheless, care is needed to ensure that assumptions are met and reliable estimates are obtained.

Use of PAT data to estimate natural and fishing mortality rates will provide valuable information to managers that is currently lacking. Specifically, our ability to estimate and separate natural and fisheries mortality is a clear advantage of PAT data relative to SPOT data (Byrne et al., 2017; Drymon & Wells, 2017). Empirical estimates of annual fishing mortality will be important for stock assessment and to set harvest regulations for sharks and a variety of other legally harvested fish species because these estimates could refine important biological reference points such as F_{MSY}, the fisheries mortality rate that produces the maximum sustained yield (Punt, 2000). Indeed, Tsai et al. (2011) noted the potential for incorrect assumptions about the effects of fishing when estimates of biological reference points are made without reliable data on important demographic parameters, such as fishing and natural mortality rates. PAT data also provide advantages over data from acoustic tags for survival estimation. Acoustic tracking requires that animals swim close enough to receivers to be detected, meaning that it is rarely feasible to continuously monitor survival with sufficient temporal and spatial scope for wide-ranging marine organisms like sharks. Heupel and Simpfendorfer (2002) provided useful estimates of juvenile survival for blacktip sharks within a nursery, but were forced to censor animals (43%) that left the bay where acoustic receivers were located. PAT data allowed us to monitor survival regardless of where sharks travelled, as evidenced by our ability to detect spatial variation in mortality risk across an international boundary. Furthermore, use of acoustic data requires the additional assumption that tag failure is non-existent as loss of signals were interpreted as fishing mortality (Heupel & Simpfendorfer, 2002).

Our results provide an important step towards filling a critical knowledge gap in the population dynamics of white sharks. Estimates of juvenile survival, combined with initial estimates of population size (Chapple et al., 2011; Sosa-Nishizaki, Morales-Bojórquez, Nasy-Lucas, Oñate-González, & Domeier, 2012) and apparent survival (Kanive et al., 2015) of adults and subadults are important components that could facilitate an empirically based population model for white sharks in the NEP. Empirical estimates of annual fertility are not available for white sharks. However, assuming previous elasticity analyses are accurate, fertility has minimal influence on population growth of white sharks relative to juvenile and adult survival (Cortés, 2002; Mollet & Cailliet, 2002). Estimates of juvenile white shark survival will also facilitate application of a recently developed method to derive abundance estimates referred to as close-kin population-estimation, which involves genetic parentage analysis and requires accurate estimates of juvenile survival (Hillary et al., 2018). Previously, satellite-tracking data have mainly been used to understand distribution and movements of marine organisms. Our work and that of Byrne et al. (2017) highlight the value of satellite-tracking data for advancing the understanding of population dynamics of sharks. Similar to telemetry data in terrestrial systems, the ability to track the fates of individual animals has the potential to revolutionize our capacity to study and model population dynamics for marine species.

ACKNOWLEDGEMENTS

This study was funded and supported by the Monterey Bay Aquarium (MBA), California State University-Long Beach, the National Commission for Protected Areas (CONAMP) and Reserva de la Biósfera El Vizcaíno. We thank K. Lyons, K. Weng, B. Block, M. Castleton, C. Perle, M. Blasias, C. Mull, K. Loke, K. Anthony, T. Farrugia, M. Espinoza, C. Martin, C. Mireles, E. Jarvis-Mason, T. Mason, B. Rogers, M. McKinzie, T. TinHan, B. Wolfe, R. Freedman, B. Ahr, D. Crear, A. Barilotti, J. Sawyna, R. Logan, L. Medranos, A. Flores, A. Fajardo, M. Pérez, C. Rodríguez, L. Saldaña, E. García, O. Hernández, E. Medina and Z. Mendoza for assistance with data management and collection. We thank collaborating gillnet fishers in southern California participating in the MBA's white shark project. We also thank E. Zepeda and R. Guzman for their help in tagging sharks in Mexico. We thank M. Murray for coordinating "best practices".

AUTHOR'S CONTRIBUTIONS

All authors designed the study. S.J.J., J.B.O., C.W., C.F.W., E.G.-R., O.S.-N. and C.G.L. collected the data. S.J.J., C.F.W., E.G.-R. and C.G.L. organized data and determined fate of sharks. J.F.B. analysed the data and wrote the manuscript. All authors contributed to drafting/revising the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository, https://doi.org/10.5061/dryad.2pp12mt (Benson et al., 2018).

ORCID

John F. Benson http://orcid.org/0000-0002-3993-4340

REFERENCES

Benson, J. F., Jorgensen, S. J., O'Sullivan, J. B., Winkler, C., White, C. F., Garcia-Rodriguez, E., … Lowe, C. L. (2018). Data from: Juvenile survival, competing risks, and spatial variation in mortality risk of a marine apex predator. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.2 pp12mt

Benson, J. F., Mills, K. J., Loveless, K. M., & Patterson, B. R. (2013). Genetic and environmental influences on pup mortality risk for wolves and coyotes within a *Canis* hybrid zone. *Biological Conservation*, *166*, 133–141. https://doi.org/10.1016/j.biocon.2013.06.018

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., … Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, *475*, 86–90. https://doi.org/10.1038/nature10082

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach* (2nd ed.). New York, NY: Springer-Verlag.

Byrne, M. E., Cortés, E., Vaudo, J. J., Harvey, G. C. M., Sampson, M., Wetherbee, B. M., & Shivji, M. (2017). Satellite telemetry reveals higher fishing mortality rates than previously estimated, suggesting overfishing of an apex marine predator. *Proceedings of the Royal Society B: Biological Sciences*, 284.

Campana, S. E., Joyce, W., & Manning, M. J. (2009). Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. *Marine Ecology Progress Series*, *387*, 241–253. https://doi.org/10.3354/meps08109

Chapple, T. K., Jorgensen, S. J., Anderson, S. D., Kanive, P. E., Klimley, A. P., Botsford, L. W., & Block, B. A. (2011). A first estimate of white shark, *Carcharodon carcharias*, abundance off Central California. *Biology Letters*, *7*, 581–583. rsbl20110124.

Cortés, E. (2002). Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. *Conservation Biology*, *16*, 1048–1062. https://doi.org/10.1046/j.1523-1739.2002.00423.x

Cortés, E. (2016). Perspectives on the intrinsic rate of population growth. *Methods in Ecology and Evolution*, *7*, 1136–1145. https://doi.org/10.1111/2041-210X.12592

Derocher, A. E., & Stirling, I. (1996). Aspects of survival in juvenile polar bears. *Canadian Journal of Zoology*, *74*, 1246–1252. https://doi.org/10.1139/z96-138

Dewar, H., Domeier, M., & Nasby-Lucas, N. (2004). Insights into young of the year white shark, *Carcharodon carcharias*, behavior in the Southern California Bight. *Environmental Biology of Fishes*, *70*, 133–143. https://doi.org/10.1023/B:EBFI.0000029343.54027.6a

Dewar, H., Eguchi, T., Hyde, J., Kinzey, D., Kohin, S., Moore, J., … Vetter, R. (2013). *Status review of the northeastern Pacific population of white sharks (Carcharodon carcharias) under the Endangered Species Act*. La Jolla, CA: NMFS Southwest Fisheries Science Center.

DOF (2002). Norma Oficial Mexicana NOM-059-ECOL-2001, Protección ambiental–Especies nativas de México de flora y fauna silvestres–Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio–Lista de especies en riesgo. In *SEMARNAT* (pp. 1–176). México, México: Diario Oficial de la Federación.

DOF (2014). ACUERDO por el que se establece veda permanente para la pesca detiburón blanco (*Carcharodon carcharias*) en aguas de jurisdicción federal de losEstados Unidos Mexicanos. In *SAGARPA* (pp. 1–3). México, México: Diario Oficial de la Federación.

Domeier, M. L. (2012). A new life-history hypothesis for white sharks, *Carcharodon carcharias*, in the Northeastern Pacific. In M. Domeier (Ed.), *Global perspectives on the biology and life history of the white shark* (pp. 199–224). Boca Raton, FL: CRC Press. https://doi.org/10.1201/b11532

Drymon, J. M., & Wells, R. J. D. (2017). Double tagging clarifies post-release fate of great hammerheads (*Sphyrna mokarran*). *Animal Biotelemetry*, *5*, 28. https://doi.org/10.1186/s40317-017-0143-x

Dulvy, N. K., Baum, J. K., Clarke, S., Compagno, L. J., Cortes, E., Domingo, A., & Martínez, J. (2008). You can swim but you can't hide: The global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *18*, 459–482. https://doi.org/10.1002/aqc.975

Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., … White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife*, *3*, 1–34.

Fieberg, J., & DelGiudice, G. D. (2009). What time is it? Choice of time origin and scale in extended proportional hazards models. *Ecology*, *90*, 1687–1697. https://doi.org/10.1890/08-0724.1

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, *13*, 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Heisey, D. M., & Patterson, B. R. (2006). A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management*, *70*, 1544–1555. https://doi.org/10.2193/0022-541X(2006)70[1544:AROMTE]2.0.CO;2

Heupel, M. R., & Simpfendorfer, C. A. (2002). Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 624–632. https://doi.org/10.1139/f02-036

Hillary, R. M., Bravington, M. V., Patterson, T. A., Grewe, P., Bradford, R., Feutry, P., … Bruce, B. D. (2018). Genetic relatedness reveals total population size of white sharks in eastern Australia and New Zealand. *Scientific Reports*, *8*, 1–9.

Hixon, M. A., & Carr, M. H. (1997). Synergistic predation, density dependence, and population regulation in marine fish. *Science*, *277*, 946–948. https://doi.org/10.1126/science.277.5328.946

Hosmer, Jr D. W., Lemeshow, S., & Sturdivant, R. X. (2013). *Applied logistic regression* (Vol. *398*). New York, NY: John Wiley & Sons.https://doi.org/10.1002/9781118548387

Jorgensen, S. J., Gleiss, A. C., Kanive, P. E., Chapple, T. K., Anderson, S. D., Ezcurra, J. M., … Block, B. A. (2015). In the belly of the beast: Resolving stomach tag data to link temperature, acceleration and feeding in white sharks (*Carcharodon carcharias*). *Animal Biotelemetry*, *3*, 1–10. https://doi.org/10.1186/s40317-015-0071-6

Jorgensen, S. J., Reeb, C. A., Chapple, T. K., Anderson, S., Perle, C., Van Sommeran, S. R., … Block, B. A. (2009). Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society of London B: Biological Sciences*, *277*, 679–688. rspb.2009.1155.

Kanive, P. E., Rotella, J. J., Jorgensen, S. J., Chapple, T. K., Anderson, S. D., Klimley, A. P., & Block, B. A. (2015). Estimating apparent survival of sub-adult and adult white sharks (*Carcharodon carcharias*) in central California using mark-recapture methods. *Frontiers in Marine Science*, *2*, 19.

Klimley, A. P. (1985). The areal distribution and autoecology of the white shark, *Carcharodon carcharias*, off the west coast of North America. *Memoirs of the Southern California Academy of Sciences*, *9*, 15–40.

Levitus, S., Antonov, J. I., Boyer, T. P., & Stephens, C. (2000). Warming of the world ocean. *Science*, *287*, 2225–2229. https://doi.org/10.1126/science.287.5461.2225

Lowe, C. G., Blasius, M. E., Jarvis, E. T., Mason, T. J., Goodmanlowe, G. D., & O'Sullivan, J. B. (2012). Historic fishery interactions with white sharks in the Southern California Bight. In M. L. Domeier (Ed.), *Global Perspectives on the Biology and Life History of the White Shark* (pp. 169–186). New York, NY: CRC Press. https://doi.org/10.1201/b11532

Lyons, K., Jarvis, E. T., Jorgensen, S. J., Weng, K., O'Sullivan, J., Winkler, C., & Lowe, C. G. (2013). The degree and result of gillnet fishery interactions with juvenile white sharks in southern California assessed by fishery-independent and-dependent methods. *Fisheries Research*, *147*, 370–380. https://doi.org/10.1016/j.fishres.2013.07.009

McGurk, M. D. (1986). Natural mortality of marine pelagic fish eggs and larvae: Role of spatial patchiness. *Marine Ecology Progress Series*, *34*, 227–242. https://doi.org/10.3354/meps034227

Mills, L. S., Doak, D. F., & Wisdom, M. J. (1999). Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology*, *13*, 815–829. https://doi.org/10.1046/j.1523-1739.1999.98232.x

Mollet, H. F., & Cailliet, G. M. (2002). Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. *Marine and Freshwater Research*, *53*, 503–515. https://doi.org/10.1071/MF01083

Moriarty, J. G., Whited, L., Sikich, J. A., & Riley, S. P. (2012). Use of intraperitoneal radiotransmitters to study mountain lion (*Puma concolor*) kittens. *Wildlife Society Bulletin*, *36*, 161–166. https://doi.org/10.1002/wsb.105

Morris, W. F., & Doak, D. F. (2002). *Quantitative conservation biology*. Sunderland, MA: Sinauer.

Musyl, M. K., Domeier, M. L., Nasby-Lucas, N., Brill, R. W., McNaughton, L. M., Swimmer, J. Y., ... Liddle, J. B. (2011). Performance of pop-up satellite archival tags. *Marine Ecology Progress Series*, *433*, 1–28. https://doi.org/10.3354/meps09202

Oñate-González, E. C., Sosa-Nishizaki, O., Herzka, S. Z., Lowe, C. G., Lyons, K., Santana-Morales, O., ... O'Sullivan, J. B. (2017). Importance of Bahia Sebastian Vizcaino as a nursery area for white sharks (*Carcharodon carcharias*) in the Northeastern Pacific: A fishery dependent analysis. *Fisheries Research*, *188*, 125–137. https://doi.org/10.1016/j.fishres.2016.12.014

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science*, *39*, 175–192. https://doi.org/10.1093/icesjms/39.2.175

Pianka, E. R. (1970). On r- and K-selection. *The American Naturalist*, *104*, 592–597. https://doi.org/10.1086/282697

Pollock, K. H., & Pine, W. E. (2007). The design and analysis of field studies to estimate catch-and-release mortality. *Fisheries Management and Ecology*, *14*, 123–130. https://doi.org/10.1111/j.1365-2400.2007.00532.x

Pollock, K. H., Winterstein, S. R., Bunck, C. M., & Curtis, P. D. (1989). Survival analysis in telemetry studies: The staggered entry design. *The Journal of Wildlife Management*, *53*, 7–15. https://doi.org/10.2307/3801296

Polovina, J., Hawn, D., & Abecassis, M. (2008). Vertical movement and habitat of opah (*Lampris guttatus*) in the central North Pacific recorded with pop-up archival tags. *Marine Biology*, *153*, 257–267. https://doi.org/10.1007/s00227-007-0801-2

Punt, A. E. (2000). Extinction of marine renewable resources: A demographic analysis. *Population Ecology*, *42*, 19–27.

Santana-Morales, O., Sosa-Nishizaki, O., Escobedo-Olvera, M. A., Oñate-González, E. C., O'Sullivan, J. B., & Cartamil, D. (2012). Incidental catch and ecological observations of juvenile white sharks, *Carchardon carcharias*, in western Baja California, Mexico. Conservation implications. In M. Domeier (Ed.), *Global perspectives on the biology and life history of the white shark* (pp. 187–198). Boca Raton, FL: CRC Press. https://doi.org/10.1201/b11532

Skomal, G. B. (2007). Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. *Fisheries Management and Ecology*, *14*, 81–89. https://doi.org/10.1111/j.1365-2400.2007.00528.x

Sosa-Nishizaki, O., Morales-Bojórquez, E., Nasy-Lucas, N., Oñate-González, E., & Domeier, M. (2012). Problems with photo identification as a method of estimating abundance of white sharks, *Carcharodon carcharias*, an example from Guadalupe Island, Mexico. In M. Domeier (Ed.), *Global perspectives on the biology and life history of the white shark* (pp. 393–404). Boca Raton, FL: CRC Press. https://doi.org/10.1201/b11532

Therneau, T. M., & Grambsch, P. M. (2000). *Modeling survival data: Extending the Cox model*. New York, NY: Springer Science & Business Media.https://doi.org/10.1007/978-1-4757-3294-8

Tsai, W. P., Sun, C. L., Wang, S. P., & Liu, K. M. (2011). Evaluating the impacts of uncertainty on the estimation of biological reference points for the shortfin mako shark, *Isurus oxyrinchus*, in the north-western Pacific Ocean. *Marine and Freshwater Research*, *62*, 1383–1394. https://doi.org/10.1071/MF11010

Wade, P. R., Burkanov, V. N., Dahlheim, M. E., Friday, N. A., Fritz, L. W., Loughlin, T. R., ... Black, N. A. (2007). Killer whales and marine mammal trends in the North Pacific – A re-examination of the evidence for sequential megafauna collapse and the prey-switching hypothesis. *Marine Mammal Science*, *23*, 766–802. https://doi.org/10.1111/j.1748-7692.2006.00093.x

Weng, K. C., O'Sullivan, J. B., Lowe, C. G., Winkler, C. E., Blasius, M. E., Loke-Smith, K. A., ... Ezcurra, J. M. (2012). Back to the wild: Release of juvenile white sharks from the Monterey Bay Aquarium. In M. Domeier (Ed.), *Global perspectives on the biology and life history of the white shark* (pp. 393–404). Boca Raton, FL: CRC Press.

Weng, K. C., O'Sullivan, J. B., Lowe, C. G., Winkler, C. E., Dewar, H., & Block, B. A. (2007). Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Marine Ecology Progress Series*, *338*, 211–224. https://doi.org/10.3354/meps338211

White, C. (2016). Quantifying the habitat selection of juvenile white sharks, Carcharodon carcharias, and predicting seasonal shifts in nursery habitat use (M.S. thesis), California State University, Long Beach.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Benson JF, Jorgensen SJ, O'Sullivan JB, et al. Juvenile survival, competing risks, and spatial variation in mortality risk of a marine apex predator. *J Appl Ecol*. 2018;55:2888–2897. https://doi.org/10.1111/1365-2664.13158