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LETTER

An illicit artisanal fishery for North Pacific white sharks indicates frequent occurrence and high mortality in the Gulf of California

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Abstract

Large sharks shape ecosystems across their geographic ranges and have become a top research and conservation priority. Eastern North Pacific (ENP) white shark (*Carcharodon carcharias*) aggregations off the United States and Mexico are well described, but their population status is currently uncertain. Population assessments of ENP white sharks are complicated by migrations across international boundaries, vulnerability at aggregation sites, and undetermined mortality levels. While protective legislation exists both in the United States and Mexico, ongoing incidental and unreported catch may undermine assessments and management. Here, access to a clandestine artisanal fishery provides evidence for white shark abundance and mortality in the Gulf of California that has been underestimated by other methods (e.g., satellite telemetry, [by]catch data). Shark size estimates based on tooth measurements suggest abundance of both juvenile and mature sharks in the region, and updated population models indicate the potential for substantial impacts of this fishery on ENP population viability. The data here, fisher-provided information, and anecdotal evidence suggest potentially high abundance at two specific regions, making directed future research efforts feasible in the Gulf. These data demonstrate that cryptic life histories and geopolitical boundaries can still limit fundamental understanding of megafauna distribution, necessitating international cooperation for both research and management.

KEYWORDS

Carcharodon carcharias, conservation, population dynamics, Sea of Cortez

1 | INTRODUCTION

White sharks (*Carcharodon carcharias*) make long-distance migrations and form seasonal aggregations,

making them ecologically important predators across a range of pelagic and coastal habitats (Bonfil et al., 2005; Domeier & Nasby-Lucas, 2008; Duffy et al., 2012; Hammerschlag et al., 2019; Jorgensen et al., 2010; Skomal

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et al., 2017). Movements across geopolitical boundaries complicate management efforts (Barkley et al., 2019; Harrison et al., 2018) and create vulnerability at aggregation sites (Domeier & Nasby-Lucas, 2007) due to dichotomies in protection status, management measures, and enforcement across developed and developing nations (Harrison et al., 2018). Identifying high abundance regions and critical habitats across the geographic ranges of migratory species is thus a challenging priority but is fundamental to management of fisheries interactions and associated mortality (Huveneers et al., 2018).

Electronic tagging technologies have revolutionized migratory marine predator research (Hussey et al., 2015) and have characterized white shark movements in the Pacific, Atlantic, and Indian Oceans (Huveneers et al., 2018). Movements of eastern North Pacific (ENP) white sharks are the most described globally, comprising the majority of all tracked white sharks (53%) (Madigan et al., unpubl.). Tracking studies show seasonal migrations between ENP aggregation sites in coastal (off central California, USA and Guadalupe Island, Mexico) and offshore (the white shark Café, or shared offshore foraging area [SOFA]) waters (Boustany et al., 2002; Domeier & Nasby-Lucas, 2013; Jorgensen et al., 2010; Weng et al., 2007). Genetic and migration studies in the ENP have suggested either a single population (Jorgensen et al., 2010, 2012b) or two sub-populations (Oñate-González et al., 2015), with limited connectivity between aggregations off central California (Anderson & Pyle, 2003; Anderson et al., 2011; Klimley, 1985; Klimley & Anderson, 1996) and Guadalupe Island (Domeier & Nasby-Lucas, 2008; Hoyos-Padilla et al., 2016; Jorgensen et al., 2012b). However, individuals from both regions perform consistent migrations between these coastal regions and the offshore aggregation region (Domeier, 2012; Domeier & Nasby-Lucas, 2012; Jorgensen et al., 2010, 2012a; Weng et al., 2007).

White sharks in the ENP also use the proximate Gulf of California, but use of the Gulf has been demonstrated in relatively few individuals compared to the coastal aggregation sites and offshore region. Satellite telemetry studies have shown Gulf entry by two adult females (Domeier & Nasby-Lucas, 2013) and a juvenile male (176 cm TL at ~2 months before Gulf entry) (Weng et al., 2012), though there have been no observations of tagged white sharks entering the Gulf use in other extensive ENP tagging studies (Domeier & Nasby-Lucas, 2008 [$n = 56$], Weng et al., 2007 [$n = 20$], Jorgensen et al., 2010 [$n = 68$ satellite tags, $n = 78$ acoustic tags]). Catch and sighting data reveal occasional white shark presence in the Gulf, but not consistently high abundance (Galván-Magaña et al., 2010). A recent historical synthesis (Galván-Magaña et al., 2010) reported 38 sightings and incidental captures over a 47 year period (1964–2010; 0.8 observations yr^{-1}), with

other reports of single observations (Kato, 1965; Márquez-Farías & Lara-Mendoza, 2017). A synthesis of artisanal fisheries data (1939–2014) reported capture of 38 shark species, with no mention of white sharks (Saldaña-Ruiz et al., 2017), and a thorough survey of northern Gulf elasmobranch fisheries (1998–1999) also reported no white sharks captured (Bizzarro et al., 2009). Additional mortality of adult females has been reported in the Gulf (Castro, 2012), largely through personal communication (Dewar et al., 2013). Collectively, these reports suggest occasional or infrequent presence and an overall minor role of the Gulf in ENP white shark life history.

Robust estimates of white shark abundance and mortality are crucial for population assessments and management (Chapple et al., 2011; Kanive et al., 2015, 2019; Sosa-Nishizaki et al., 2012). White shark populations generally are considered vulnerable due to fisheries interactions and low intrinsic rebound potential (Rigby et al., 2019; Smith et al., 1998), and international trade has been banned under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix II since 2004. In the United States, bans on nearshore gillnets and white shark take were enacted in 1994 (Heneman & Glazer 1996 et al., 1996), demonstrably reducing bycatch (Dewar et al., 2013; Lowe et al., 2012; Lyons et al., 2013). In Mexico, all shark fishing in the Gulf has been seasonally banned (May–July) by the Mexican government since 2012 (DOF, 2012). White shark-specific legislation has moved from a listing as “threatened” (DOF, 2002), to illegal targeting/trade (DOF, 2007), to illegal possession and mandatory release of incidental catch (DOF, 2014). Lack of reporting and monitoring is an ongoing challenge (Arreguín-Sánchez & Arcos-Huitrón, 2007; Cisneros-Montemayor et al., 2013; García-Rodríguez & Sosa-Nishizaki, 2020; Hernandez & Kempton, 2003), and incidental catch still occurs in American and Mexican fisheries (Oñate-González et al., 2017). A recent white shark status review under the Endangered Species Act by the National Oceanic & Atmospheric Administration (NOAA) (Dewar et al., 2013) recognized that additional mortality of adult females may occur in the Gulf, but at uncertain levels (García-Rodríguez & Sosa-Nishizaki, 2020) which precludes incorporation in population assessments.

Here, artisanal fishers provided harvested white shark teeth and local knowledge (LK; here, multi-generational fishing experience and observations) from a site-specific targeted fishery in the Gulf of California. Using tooth size and allometric relationships, we estimated the size distribution of white shark catch in the Gulf and applied updated mortality estimates to population viability models. Gulf-associated mortality may influence the population status of ENP white sharks, indicating the

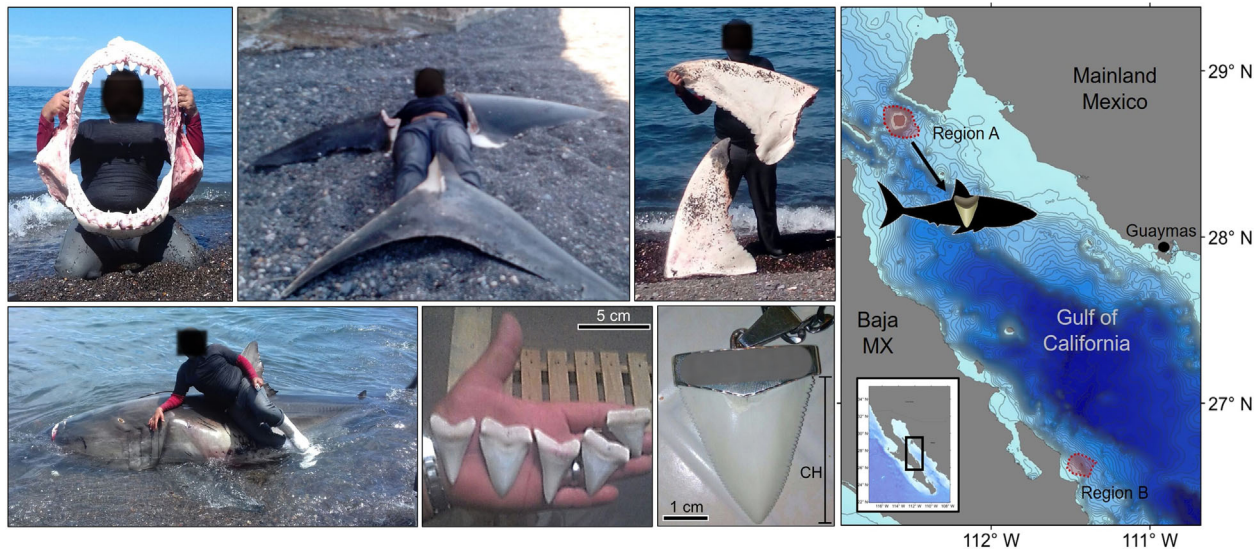


FIGURE 1 An illicit white shark fishery in the Gulf of California, Mexico. Fishers bring large white sharks to remote beaches, remove and discard fins, remove and retain jaws, and combine filleted meat with mixed species catch. Fishers provided teeth (bottom center panels) which were measured to reconstruct body size of harvested sharks, allowing for population viability analyses. Map shows study region, identifying the two undescribed regions of white shark abundance and harvest in the Gulf (red circles: Region A, Isla San Esteban; and B, Isla San Ildefonso). Images of shark parts were provided by local fishers; images of teeth were taken by the lead author

region's importance and the need for further research efforts.

2 | RESULTS AND DISCUSSION

Local fishers indicated high catches of white sharks in two regions in the Gulf of California (Regions A and B; Isla San Esteban and Isla San Ildefonso; Figure 1). Over a 1-year period (2017–2018), fishers provided teeth from individuals captured at Region A, photographs and video of white shark capture, and information of fishing methods and locations (Figure 1 and Video S1). Tooth measurements and jaw position assignment (see Supporting Information Methods) allowed for allometric body size reconstructions of harvested sharks (Shimada, 2002).

From Region A, teeth ($n = 13$) and one full jaw (total $n = 14$ individuals) were provided by fishers in the Mulegé municipality of Baja California, Mexico (Figure S1). Each tooth was reported to represent a distinct individual, indicating a minimum mortality rate of 14 sharks from June to December 2017 by this group of eight individual fishers alone. Peak white shark sightings and catch were reported as seasonal (June to September), with occasional sightings and catch throughout the year. Estimated shark lengths (TL) were mostly between 350 and 550 cm (Figure 2), consistent with fisher estimates of 400–600 cm. Depending on sex ratio of captured sharks, up to 72% could have been mature based on size at maturity (Bruce & Bradford, 2012) (Figure 2; Francis, 1996). Given larger length-at-maturity

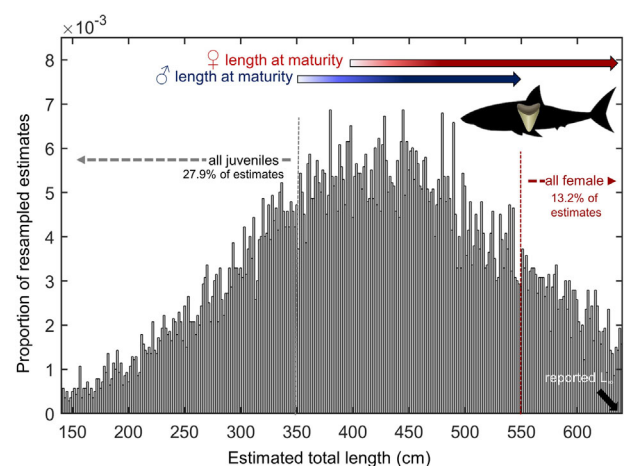


FIGURE 2 Bootstrapped size estimates of harvested white sharks in the Gulf of California, reconstructed from tooth measurements. Teeth were provided from individual white sharks, and allometric relationships were used to estimate shark size. Length estimates were resampled (10^3 shark $^{-1}$) to account for error in allometric calculations and variability in tooth position assignments. Male and female sizes at maturity and bounds for minimum (140 cm) and maximum (640 cm) size are taken from the current literature

estimates for females (Francis, 1996), up to 56% of harvested sharks could be mature females (>400 cm) and 13% are almost certainly mature females (>550 cm; Figure 2). Overall, 14 sharks yr^{-1} represents a conservative minimum for harvest at Region A, as additional groups were reported to target white sharks at that site.

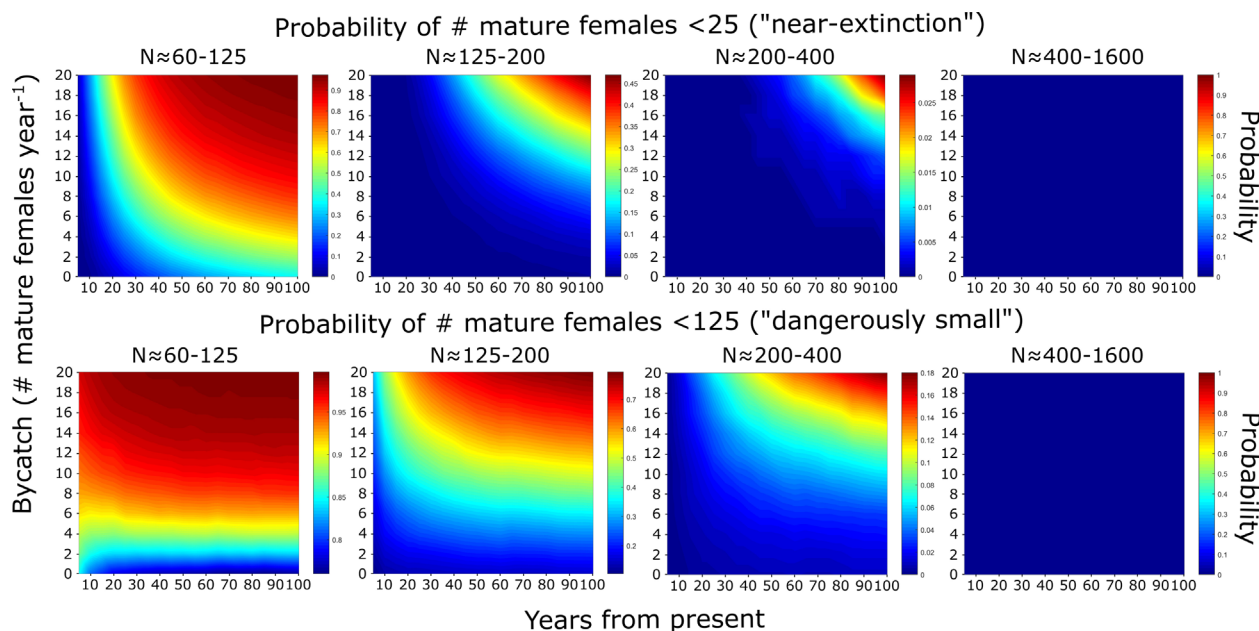


FIGURE 3 Population models of adult female white shark abundance across mortality and abundance scenarios. Panels show effects of mature female mortality on mean population projections, increasing from left to right from lowest estimated current abundance of mature females ($N = 60\text{--}125$) to highest abundance ($N = 400\text{--}1600$). Bycatch of ≤ 20 mature females yr^{-1} had no predicted effects in the largest female abundance scenario (rightmost blue panels). Note different probability scales on color bars across panels

Local knowledge and web-based media reports were used to further inform information regarding shark sizes, prevalence, and catch. Fisher reports and publicly available observations suggest adult white shark prevalence and mortality at region B (Isla San Ildefonso; Figure 1 and Table S1). Observers reported 13 sharks with visually estimated lengths of $\sim 490\text{--}670$ cm harvested over a period of several weeks in 2012 (Table S1). A report from 2014 indicates an electronically tagged individual captured at Region B, supporting connectivity between Gulf sharks and individuals tagged around Guadalupe Island and/or central California. These reports corroborate Region B as a high abundance area, with an associated targeted artisanal fishery. The same reports also indicate catch of a large white shark (~ 600 cm) around the Guaymas region in 2012, in the eastern Gulf along mainland Mexico (Figure 1). Adult white sharks have historically been caught around Guaymas (Galván-Magaña et al., 2010) indicating broader white shark occurrence, but less information is available for the broader Gulf.

Population trajectories for adult female ENP white sharks were modeled in the National Oceanic & Atmospheric Administration (NOAA) white shark status review (Dewar et al., 2013), using variable abundance estimates (60–125 to 400–1600 mature females) and mortality rates (0–10 mature females yr^{-1}) (Dewar et al., 2013). Most plausible mortality and abundance scenarios were estimated to be 2 adult females yr^{-1} and >200

females, respectively, (Dewar et al., 2013), with modeled population trajectories varying widely across abundance and mortality scenarios (see Methods section for details of estimates). Trajectories ranged from population declines to “dangerously small” or “near extinction” for low abundance scenarios (60–125 mature females) to no declines in high abundance scenarios (400–1600 mature females). We re-evaluated the NOAA population viability models by increasing the upper limit of modeled adult female mortality to 20 yr^{-1} based on observations here (see Methods section). Our models, incorporating Gulf mortality, demonstrated immediate population effects in the lower female abundance scenarios and population effects within several decades for moderate abundance scenarios (Figure 3). Trajectories for the latter (200–400 mature females) differed markedly from the previous NOAA assessments once Gulf mortality was included (Figure 3). No mortality estimates substantially affected population trajectories for the maximum female abundance scenario (400–1600 adult females; Figure 3), though this level of abundance has been deemed unlikely (Burgess et al., 2014; Dewar et al., 2013). Thus, while our mortality estimates are preliminary and data limited, fisheries-related mortality in the Gulf could significantly influence population trajectories for ENP white sharks. Discrepancy across modeled scenarios makes clear that both female mortality and abundance require more rigorous quantification.

Quantifying Gulf white shark sex ratio would inform the region's life history functions and improve estimates of the impacts of artisanal fisheries. Unfortunately, few data were available on the sex of harvested sharks. Fishers reported most as females (assessed by lack of claspers), with one pregnant individual reported, from which pups were removed and added to bulk catch. Historical records offer some sex information, indicating both adult males and females in the Gulf (Galván-Magaña et al., 2010). Of seventeen potential adults reported in Galván-Magaña et al. (2010), sex was reported for one female (~500 cm) and two males (~346 and ~500 cm); two individuals >550 cm (600, 650 cm) can be inferred as mature females based on size (Mollet et al., 1996), leaving the majority ($n = 12$; ~350–500 cm) of unidentified sex. Electronic tagging studies at Guadalupe Island tracked a single tagged female in the Gulf (Domeier & Nasby-Lucas, 2012), and a subsequent study, using data from some of the same tagged animals, revealed two large females (498 and 508 cm at time of tagging) entering the Gulf 2–3 years post-tagging (Domeier & Nasby-Lucas, 2013). Satellite-linked radio-telemetry (SLRT) tags with multi-year battery capacity allow ongoing tracking of tagged sharks from the above studies (www.expeditionwhiteshark.com) and may provide further supportive data for Gulf use by large adult females.

The influence of Gulf white shark mortality on ENP white shark population dynamics will depend on connectivity to central California and Guadalupe Island populations. Given low rates of exchange observed between these regions (Hoyos-Padilla et al., 2016; Jorgensen et al., 2012b) and genetic similarity of Gulf sharks to those at Guadalupe Island (Oñate-González et al., 2015), data here could indicate dispersal of sharks from Guadalupe Island, potentially caused by an increasing ENP population. In this case, the Gulf fishery would have a region-specific impact, with less influence on the central California population. Estimating impacts on the overall ENP population may be complex, depending on long-term movement dynamics, connectivity, and genetic exchange across ENP aggregation regions. Regardless, our results show that ENP-wide fishing mortality likely has been underestimated, possibly substantially, due to unobserved and unreported Gulf mortality. Importantly, it is also unknown how long the targeted Gulf fishery has been active and how catch trends have fluctuated therein. Our models indicate that mortality levels in the Gulf alone may negatively influence the overall ENP white shark population. Quantifying further potential mortality across the ENP white shark range, including exposure to offshore commercial fishing fleets where minimal observer coverage occurs (White et al., 2019b), will allow for improved estimates of total ENP mortality rates.

The level of mortality observed here in the Gulf would require harvest of a large-bodied, protected species that has been largely hidden from researchers and managers. The illegality of harvest drives clandestine fishing practices, including methods to make capture undetectable upon landing. Fishers use a single large float tethered to a large single hook baited with dolphin (*Delphinus* spp.; harvested specifically for use as shark bait) or yellowfin tuna (*Thunnus albacares*), then harpoon sharks with additional floats until mortality occurs (Video S1). Large sharks are then towed to remote beaches (see Figure 1) where fins are removed and discarded, jaws are removed, and muscle is added to overall catch. While gillnetting for other shark species, fishers report observations of >10 large white sharks visible at the surface and actively avoiding gillnets (DJM, personal communication; Table S1). This potential evasion ability would make incidental gillnet catches (Galván-Magaña et al., 2010) inadequate to reflect local white shark abundance. We also observed artisanal fishers providing local research groups with access to other shark species (*Sphyrnidae*, *Alopiidae*, and *Carcharhinidae* spp.) for measurement and biological sampling; however, no collection of white shark data was observed. Finally, satellite tracking studies in other ocean basins have shown that white shark presence can be underestimated by observational methods (Bastien et al., 2020). Any of these dynamics may have limited regional white shark observations in the Gulf.

The role of the Gulf in white shark life history is speculative. Based on observed 2-year migration patterns in females (Anderson & Pyle, 2003; Domeier, 2012; Domeier & Nasby-Lucas, 2007), a presumed 18-month gestation cycle (Christiansen et al., 2014; Mollet et al., 2000), and data for two tagged mature females (Domeier & Nasby-Lucas, 2013), the Gulf has been proposed as a potential pupping and nursery area (Domeier & Nasby-Lucas, 2013). However, young-of-the-year (YOY) white sharks (<175 cm TL; Bruce & Bradford, 2012) have not been documented (Galván-Magaña et al., 2010; Saldaña-Ruiz et al., 2017), though individuals near this size have been reported (183 cm: Márquez-Farías & Lara-Mendoza, 2017; ~200 cm: Galván-Magaña et al., 2010; 176 cm: Weng et al., 2012). If YOY were present in the Gulf, targeted and incidental fishing pressure should result in high catch levels similar to those observed off the Pacific Coast of Baja California (García-Rodríguez & Sosa-Nishizaki, 2020; Oñate-González et al., 2017; Santana-Morales et al., 2020). Combined with continuously evolving knowledge of white shark size-at-age (Santana-Morales et al., 2020), the potential of the Gulf as a pupping and/or nursery area requires further investigation. An ecological function of the Gulf can be hypothesized; for juveniles, habitat suitability models indicate the Gulf as favorable, though

for fewer months than the Pacific side of Baja California (Weng et al., 2012; White et al., 2019a). The Gulf is one of the most productive marine ecosystems in the world (Mercado-Santana et al., 2017), and hosts many known prey species for white sharks, including sea lions (*Zalophus californianus*), pelagic teleosts, and elasmobranchs. Isla San Esteban and Isla San Ildefonso share common characteristics to other ENP aggregation sites, as islands descending to steep bathymetric gradients (see Figure 1) with associated pelagic currents and large marine fauna. White sharks feed on sea lions, dolphins (*Tursiops truncatus*), sharks, and pelagic rays in these regions (Galván-Magaña et al., 2010; author personal observation), and stable isotope analysis has suggested that Gulf prey may contribute to the diet of Guadalupe white sharks (Jaime-Rivera et al., 2014). Thus, the Gulf may provide valuable foraging habitat for juveniles and adult sharks.

Temporal trends of white shark abundance at these sites and throughout Gulf waters are difficult to estimate with historical data. A broad size range (~200 to ~600 cm) has been reported sporadically since 1964, including six juveniles (~200 to ~300 cm) in 1 year (1991; Galván-Magaña et al., 2010). More recent abundance could be driven by an increasing ENP population, which has been suggested (Lyons et al., 2013; Tinker et al., 2016) though estimates of population size vary widely (Burgess et al., 2014; Chapple et al., 2011). This has been observed in the North Atlantic, where increasing population size and/or prey recovery has been linked to increased regional abundance, which was cryptic and underestimated prior to satellite tracking (Bastien et al., 2020; Skomal et al., 2017). While studies combining PSATs and acoustic tags have revealed crucial new information for ENP white sharks (Boustany et al., 2002; Chapple et al., 2016; Del Raye et al., 2013; Domeier & Nasby-Lucas, 2008; Jorgensen et al., 2010, 2012a, 2012b; Weng et al., 2007; White et al., 2019b), only sharks tagged with SLRT (e.g., SPOT) tags have provided continuous movement information over multiple years (Nasby-Lucas & Domeier, 2019), including movements into the Gulf (Domeier, 2012; Domeier & Nasby-Lucas, 2013). For a species with multi-year migration cycles, endurance of applied telemetry technology that matches their spatiotemporal ecology will be required to fully characterize horizontal movement dynamics.

Effective regulation in Gulf of California fisheries will likely rely on a combination of ecosystem-based approaches and improved regulatory compliance (Ainsworth et al., 2012). Artisanal fisheries comprise the majority of the Mexico fisheries fleet (Fernández et al., 2011; Saldaña-Ruiz et al., 2017) and have been targeting sharks since the 1940s in a multi-gear, multi-species fishery (Applegate et al., 1993). Artisanal fisheries operating in regions identified here use gillnets, hook-and-line,

and longlines (Moreno-Báez et al., 2010), resulting in occasional white shark bycatch (Galván-Magaña et al., 2010; see reports in Table S1). Mexico's seasonal closure of all shark fishing (DOF, 2012) overlaps with reported white shark abundance, and has been partially effective by suspending targeted white shark fishing from May to July due to higher regulatory monitoring (D. Madigan, personal observation). However, prohibition of white shark catch (DOF, 2007, 2014) has made the targeted fishery clandestine, not inactive. Increased enforcement has been a challenge in the Gulf, making monitoring, data collection, and enforcement difficult (Ainsworth et al., 2012; Cinti et al., 2010; García-Rodríguez & Sosa-Nishizaki, 2020; Hernandez & Kempton, 2003; Lluch-Cota et al., 2007); regular monitoring with fishermen involvement may improve conservation efforts (García-Rodríguez & Sosa-Nishizaki, 2020). Based on effective gillnet restrictions off California (Lowe et al., 2012), gear modifications or restrictions may reduce white shark bycatch (García-Rodríguez & Sosa-Nishizaki, 2020), while allowing adaptable artisanal fishers to utilize alternative gear and/or adjacent regions. Economic opportunities that incentivize conservation may include ecotourism, which has limited illegal fishing, contributed to research, and provided economic incentives at Guadalupe Island (Becerril-García et al., 2019; Torres-Aguilar et al., 2015), but also must consider impacts such as altered shark behaviors (Bruce & Bradford, 2013; Huveneers et al., 2013; Meza-Arce et al., 2020). Engaging fishers in financial incentive programs that include monitoring, and collection, and/or safe release of bycaught animals could also be considered (Leduc & Hussey, 2019), though these measures require better understanding of white shark abundance in fishing regions.

Limitations should be considered for interpretations of demographics and mortality of Gulf sharks. Tooth description as individual-specific was supported by a broad estimated size distribution (Figure 2), but we could not independently validate that each tooth represented a single individual. Moreover, rigorous methodologies for synthesizing LK could not be applied to an illicit, secretive fishery, and how such information should be approached and defined remains an open question. CITES and domestic restrictions prohibited tooth possession, precluding further analyses of teeth that potentially could yield genetic information (Ahonen & Stow, 2008) to assess connectivity to other aggregation regions (Oñate-González et al., 2015). Finally, the scope, timeframe, and opportunistic nature of this initial study involved only international researchers, risking "parachute science" (e.g., Hart et al., 2020); future efforts could be led by Mexico-based researchers. Despite these limitations, data here should motivate future, collaborative study efforts to address knowledge gaps for white sharks in the Gulf.

The analyses presented here are a conglomerate of opportunistically collected samples, LK, and nonscientist observations (i.e., citizen science). These data strongly indicate higher abundance of white sharks in the Gulf than has been described, with associated high mortality from targeted artisanal fisheries. Data were only obtained by interaction with a group operating an illicit fishery; this is not easy territory for scientific efforts to access. However, such efforts may be necessary to utilize LK in a mutually productive and beneficial manner (e.g., Leduc et al., 2021), especially when species migrate between developed/developing nations with disjunct management and enforcement. Directed white shark studies in the Gulf will clarify the importance of the region to life history and mortality of ENP white sharks, and research efforts that consider the cultural and economic drivers of white shark harvest will likely be most successful with scientific outcomes and longer term reduction of future white shark harvest.

3 | METHODS

3.1 | Collection of fishing information and tooth measurements

Information regarding white shark fishing practices, photographic and video evidence, and tooth measurements were obtained by the lead author (DJM) from artisanal fishers in the Mulegé municipality of Baja California Sur, Mexico, from October 2017 to May 2018. Local fishers outlined the two general fishing areas using regional maps provided by the author (see Figure 1) and provided anecdotal information on white shark abundance and behavior, photograph files of shark capture and post-capture processing, and video files of capture.

Teeth were voluntarily offered to the lead author by several fishers. Fishers reported that each tooth came from a different individual. Sex information was requested and general observations reported, but sex could not be assigned to any individual tooth. Teeth were immediately photographed (Figure S1) and measured for tooth crown height (CH; Figure S2) to the nearest mm. The author could not retain teeth for further analyses due to the white shark listing in CITES Appendix II and domestic regulations. Teeth were consequently returned to fishers after being photographed and measured.

3.2 | Tooth measurements and estimates of shark size

White shark tooth CH was used to estimate total body length (TL) based on reported allometric relationships for

upper and lower teeth at different positions in the jaw (Shimada, 2002). Since teeth provided by fishers were from different jaw positions, teeth were first assigned to a jaw position based on tooth morphology and identification criteria detailed in Shimada (2002). We used a Structured Expert Decision Making (SEDM) process in which all authors independently assigned jaw positions to each tooth; K. Shimada was consulted as an external expert for a total of five assigners. Assigners identified one or several classifications for each tooth, depending on their level of certainty. When individual teeth were assigned multiple jaw positions (due either to individual assigner uncertainty or discrepancy across assigner classifications), each assignment was weighed equally in generating size estimates. For example, following the assignment nomenclature in Shimada (2002), if an individual tooth was assigned L1 by three assigners, L2 by one assigner, and A1 by one assigner, calculated length estimates were generated using regression equations for L1 (60% of estimates), L2 (20% of estimates), and A1 (20% of estimates), for a total of 600 length estimates based on position L1, 200 length estimates based on position L2, and 200 length estimates based on position A1.

To generate a distribution of probable sizes for the white sharks harvested, we generated 10^3 size estimates for each shark, using the jaw position-specific regression equations in Shimada (2002), and incorporating the standard error reported for each regression equation. To avoid unrealistic outlier estimates, we set lower and upper bounds for shark size (140 cm and 640 cm, respectively) based on neonate and maximum reported size in the literature (Francis, 1996; Mollet et al., 2000).

Each shark was represented equally (10^3 length estimates shark⁻¹) in overall size distribution estimate of catch (see Figure 2), but the range of size estimates for individuals varied based on the variability across jaw assignments by the five assigners (see above). Since only one tooth position assignment can be truly correct, the SEDM allowed for uncertainty to be incorporated into our estimated shark length distribution (i.e., Figure 2), but may unrealistically skew shark size estimates to larger or smaller lengths depending on the degree of classification error (which is unknown). To assess the potential extent of shark size bias due to tooth classification error, we also generated (1) a distribution of shark sizes based on the tooth assignments that resulted in the smallest size estimates for each shark and (2) a distribution of shark sizes based on the tooth assignments that resulted in the largest size estimates for each shark. These distributions can be compared to assess the most extreme extent to which tooth classification error drove under- or overestimates of shark length in the overall catch size distribution (Figure S3).

3.3 | Models of white shark population viability

We generated population viability models for mature female abundance over time (100 years) with varying levels of adult female mortality (0–20 females year⁻¹). Our models adopted the same statistical modeling framework used in the National Oceanic & Atmospheric Administration (NOAA) white shark status review under the Endangered Species Act (Dewar et al., 2013). The NOAA population viability modeling framework was provided directly by the authors of that review (NOAA's Biological Review Team, BRT) in the form of code written for R (v 2.15). Below is a brief description of the modeling framework, followed by a description of our slightly modified analyses. The full description of the basic model used in the NOAA ESA review and here, associated equations, and justification for parameter value selection can be found in Dewar et al. (2013).

Briefly, Monte Carlo simulations i were performed for each abundance and bycatch scenario to project ENP white shark female population trajectories over 100 year. These population trajectories were calculated according to a stochastic density dependent model (Dewar et al., 2013):

$$N_{t+1} = N_t \lambda_t, \quad (1)$$

$$\lambda_t = \{\lambda_{\max} \exp \left[-\log(\lambda_{\max}) (N_t/K)^\theta \right] - \Delta\lambda_{\text{byc}} \exp(\varepsilon_t), \quad (2)$$

where N_t is adult female abundance in year t and λ_t is the annual population growth rate in year t . λ_{\max} is the population's maximum potential growth rate, K is carrying capacity, and θ is a theta-logistic growth model parameter. Maximum population growth rate λ_{\max} was estimated using a Monte Carlo randomization approach, solving for λ_{\max} using a version of the Euler method that assumes constant annual survival and fecundity at maturity (Skalski et al., 2008):

$$0 = \lambda_{\max}^{\alpha-1} (S_{\text{adult}} - \lambda_{\max} \alpha) + 1_\alpha F \quad (3)$$

where S_{adult} is the adult survival rate, 1_α is the probability of surviving to reproductive age (α), and F is fecundity (average number of pups born female⁻¹ year⁻¹). Carrying capacity K is unknown for ENP white sharks, and was calculated for each Monte Carlo simulation i as

$$K = N_0/\kappa, \quad (4)$$

where N_0 the abundance estimate at $t = 0$ and κ expressed as $\kappa \sim \text{Uniform}(0.1, 0.9)$, corresponding to a current abundance that is between 10% and 90% of what the environment can currently support (Dewar et al., 2013). Parameter θ is also unknown, but the lower bound is informed by models for long-lived, late maturing species ($\theta > 1$) (Fowler, 1988) and the upper bound ($\theta = 10$) is a value that corresponds to population production being maximized at $N = 0.8K$, resulting in θ being expressed as (Dewar et al., 2013):

$$\theta \sim \text{Uniform}(1, 10). \quad (5)$$

$\Delta\lambda_{\text{byc}}$ is defined as the difference between λ_{\max} and λ_{\max}^* , where λ_{\max}^* is a calculated maximum potential population growth rate that incorporates bycatch mortality of young-of-the-year and age-1 white sharks in the population, i.e., $\Delta\lambda_{\text{byc}}$ represents the decrease in maximum potential population growth rate caused by bycatch of YOY and age-1 sharks. Parameter ε_t represents annual stochastic variation in population growth rate (λ_t) and is described as

$$\varepsilon_t \sim \text{Normal}(0, \sigma = 0.10), \quad (6)$$

where σ represents an estimate of interannual variation in annual abundance. The value for σ was based on photo-ID data from Guadalupe Island white sharks and from other vertebrate species with relatively long generation times (i.e., 15–30 years) (Regan et al., 2009). Interannual variation of adult female white shark abundance at Guadalupe Island from 2001 to 2011 resulted in $\sigma \approx 0.15$, though this was deemed likely to be an overestimate of true variation due to sampling error and unknown emigration and immigration of adult females from the study area. The value of σ was further informed by vertebrate populations with similar generation times, and associated values of $\sigma \approx 0.1$ – 0.2 (Regan et al., 2009). Upper values of this range were also deemed likely overestimates, due to sampling error and population abundance estimates that include juveniles, for which σ is likely to be more volatile than for adult age classes due to lower survivability of youngest age classes (Dewar et al., 2013). As such, a conservative value of 0.1 was selected for σ following Dewar et al. (2013).

In the NOAA ESA review, different levels of annual adult female bycatch (C_{adult}) were assessed for their influence on population viability over time. Values for C_{adult} were based on minimum ($C_{\text{adult}} = 0$), maximum ($C_{\text{adult}} = 10$), and most likely values ($C_{\text{adult}} = 1, 2, 5$) based on a “Structured Expert Decision Making” (SEDM) process, in which members of the BRT use data on adult mortality (which is sparse) and other information regarding potential bycatch in more obscure fisheries

and unreported bycatch. The SEDM process resulted in a most likely scenario (based on SEDM voting process by BRT members) of $C_{\text{adult}} = 2$, with reasonable support for $C_{\text{adult}} = 1$ and $C_{\text{adult}} = 5$ and little support for minimum and maximum estimates ($C_{\text{adult}} = 0$ or $C_{\text{adult}} = 10$). Values of C_{adult} were incorporated into the stochastic density-dependent model (Equations 1 and 2) by changing the value of $\Delta\lambda_{\text{byc}}$ according to following equations. The adult female bycatch mortality rate ($M_{\text{adult},b}$) is expressed as

$$M_{\text{adult},b} = C_{\text{adult}}/N_{\text{adult}}, \quad (7)$$

and a modified value for adult female survival rate (S_{adult}), taking different levels of annual female bycatch (C_{adult}) into account, is expressed as

$$S_{\text{adult}} (1 - M_{\text{adult},b}). \quad (8)$$

To generate population models using different values of C_{adult} , the modified value of S_{adult} above (Equation 8) was used in each Monte Carlo simulation using the Euler method (Equation 3) to calculate a new value for $\lambda_{\text{max}*}$ for each simulation. Each new $\lambda_{\text{max}*}$ value resulted in a new calculated value of $\Delta\lambda_{\text{byc}}$ in each iteration:

$$\Delta\lambda_{\text{byc}} = \lambda_{\text{max}} - \lambda_{\text{max}*}, \quad (9)$$

and that new value for $\Delta\lambda_{\text{byc}}$ was used in the stochastic density-dependent model (Equations 1 and 2) to generate new population trajectory estimates for the different values of C_{adult} . In the NOAA ESA review, Monte Carlo simulations using the stochastic density-dependent model above were run for each of the four adult female abundance (N) categories ($N \approx 60$ –125, 125–200, 200–400, 400–1600) defined by the NOAA Biological Review Team in Dewar et al. (2013) for each selected value of C_{adult} (0, 1, 2, 5, 10).

For population models calculated here and reported in this manuscript, we used the same equations and framework above. For direct comparison to NOAA models, we used the same four adult female abundance (N) categories ($N \approx 60$ –125, 125–200, 200–400, 400–1600) selected by the NOAA BRT. However, based on the high observed mortality in our data, we increased the values of adult female mortality C_{adult} , deeming NOAA's most likely estimate ($C_{\text{adult}} = 2$) unrealistically low and using a value of $C_{\text{adult}} = 20$ as a reasonable upper limit based on our estimated mortality of 14 sharks yr^{-1} from our data from the Gulf alone. To better estimate the effects of adult mortality across the range of C_{adult} values, we ran a set of Monte Carlo simulations for each C_{adult} estimate across the range

assessed ($C_{\text{adult}} = [0, 2, \dots, 20]$), for each of the four female abundance categories. For each combination of C_{adult} and N , we ran 500,000 iterations over a timeframe of 100 yr ($t = [5, 10, \dots, 100]$). For each iteration, for a given combination of C_{adult} and N , the value for C_{adult} was fixed at the selected value, while the value for N was randomly selected for each iteration from a uniform distribution of the range of values represented by each abundance category.

Due to built-in model stochasticity and variable values for N_0 (due to random selection of N_0 from the range of values in each of the four female abundance scenarios), population trajectories varied for a given C_{adult} value and abundance category. These values were bilinearly interpolated across the range of C_{adult} (0–20 females yr^{-1}) and time (0–100 yr) to allow better visualization of scenario-based population risk over time. For assessment of population risk, we calculated the mean probability of the population reaching two categories, “Near-extinction” and “Dangerously small,” as defined in Dewar et al. (2013). “Near-extinction” was defined following Regan et al. (2009) as “a population that has declined to a size at which the probability of extinction in the near future (50 years or the lifespan of the species, whichever is longer) is extremely high.” The IUCN criterion of ≤ 50 mature individuals as qualification for a Critically Endangered Species (IUCN, 2001) was used, resulting in an adult female white shark abundance of ≤ 25 used as a threshold for “Near-extinction,” assuming a male:female ratio of 1:1. “Dangerously small” is defined as “a population that is sufficiently small that density depensation may occur and that variability in population size resulting from fluctuations in the environment could result in reaching near-extinction” (Mollet et al., 1996). The IUCN criterion of ≤ 250 mature individuals as qualification for Endangered (IUCN, 2001) was used, resulting in an adult female white shark abundance of ≤ 125 used as a threshold for “Dangerously small,” assuming a male:female ratio of 1:1. Our population models thus report the mean probability of “Near-extinction” and “Dangerously small” as a function of the proportion of population trajectories i , for a given combination of C_{adult} and N , that resulted in $N_t \leq 25$ or $N_t \leq 125$ at any given time t over a timeframe of 100 yr ($t = 0$:100).

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AUTHOR CONTRIBUTIONS

Daniel J. Madigan and Natalie S. Arnoldi conceptualized the project; Daniel J. Madigan performed fieldwork and sampling; Aaron B. Carlisle and Daniel J. Madigan performed statistical analyses; Daniel J. Madigan, Natalie S. Arnoldi, Aaron B. Carlisle, and Nigel E. Hussey performed tooth classifications and wrote the manuscript.

ETHICS STATEMENT

This manuscript was prepared following the guidelines of the Committee on Publication Ethics (COPE). Biological materials were briefly measured and photographed, but never held in possession, physically altered, or transported, to assure compliance with domestic and international regulations. Information and materials from human participants were provided voluntarily and under conditions of anonymity.

DATA ACCESSIBILITY STATEMENT

Data can be made available upon request from the corresponding author.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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