

The Smallest Known Free-Living White Shark *Carcharodon carcharias* (Lamniformes: Lamnidae): Ecological and Management Implications

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The White Shark (*Carcharodon carcharias*) is a top predator cosmopolitanly distributed and heavily protected worldwide. Identification and information pertaining to White Shark nursery areas is limited yet crucial for the protection of sharks during their most vulnerable life stages. Here, we present morphometric, skeletal, and haplotypic characteristics of the smallest free-living White Shark reported to date (1066 mm TL). These characteristics correspond to a newborn White Shark smaller than those previously reported in an embryonic state but displaying the same number of rows of functional teeth as an adult. The individual was caught incidentally by an artisanal fishery operating along the Pacific coast of Baja California, near the international border between Mexico and the United States (USA). We found no genetic divergence between Isla Guadalupe and central California, two aggregation sites that have been proposed as a possible source for newborn sharks in this area. The newborn White Shark displayed the most common haplotype present among individuals at both aggregation sites. These findings provide evidence suggesting the presence of an extended nursery habitat in the Northeast Pacific, a transnational region between Mexico and USA.

THE White Shark (*Carcharodon carcharias*) is an apex predator that is largely known for its great size and predatory nature. Despite its popularity and ubiquitous distribution, little information exists on the early life history of this species (Compagno et al., 1997; Bruce, 2007). Currently, the White Shark is protected by several international regulations and is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). These regulations limit commercial trade of the White Shark. In Mexico, the White Shark is listed as a threatened species in the Official Journal of the Federation (Diario Oficial de la Federación, DOF) since 2002 (DOF, 2002), and there is a permanent prohibition on capture and retention (DOF, 2002, 2014) to help reduce the number of sharks killed through commercial and recreational fishing activities. This species is listed as Vulnerable by the International Union for Conservation of Nature (IUCN) where it is noted that very little is known about the actual population status of the White Shark (Dulvy et al., 2008).

Given the vulnerability of large pelagic sharks to over-exploitation and the unknown population status of the White Shark (Dulvy et al., 2008; Ferguson et al., 2009), any life-history information can contribute to the improvement of conservation and management actions for this species.

Specifically, studies pertaining to reproductive biology and early life history remain scarce as access to specimens continues to be limited (Francis, 1996; Bruce, 2007; Tanaka et al., 2011). Thus, records of unusual sightings and fishery interactions/observations are extremely important and provide one of the few data sources for enhancing our understanding of this species.

Despite recent biological and ecological advancements and conservation actions that continue to protect this species, the location, seasonality, and characteristics of White Shark pupping and nursery areas continues to be limited. Although two of the nearby adult aggregation sites have received considerable study (Guadalupe Island, Mexico, and central California, USA), little is known regarding the connectivity of these areas and how they feed into nearby rookery areas (Domeier and Nasby-Lucas, 2006; Jorgensen et al., 2009). Of particular importance are the nursery areas along central and southern California, as well as the coastal areas off central Baja California. Commercial and recreational catch records have historically shown these areas to be potential aggregation areas for juvenile and early life stage White Sharks (Klimley, 1985; Lowe et al., 2012; Santana-Morales et al., 2012). Indeed, small individuals (1085 mm TL) as well as individuals with umbilical scars (1408 mm and 1414 mm TL)

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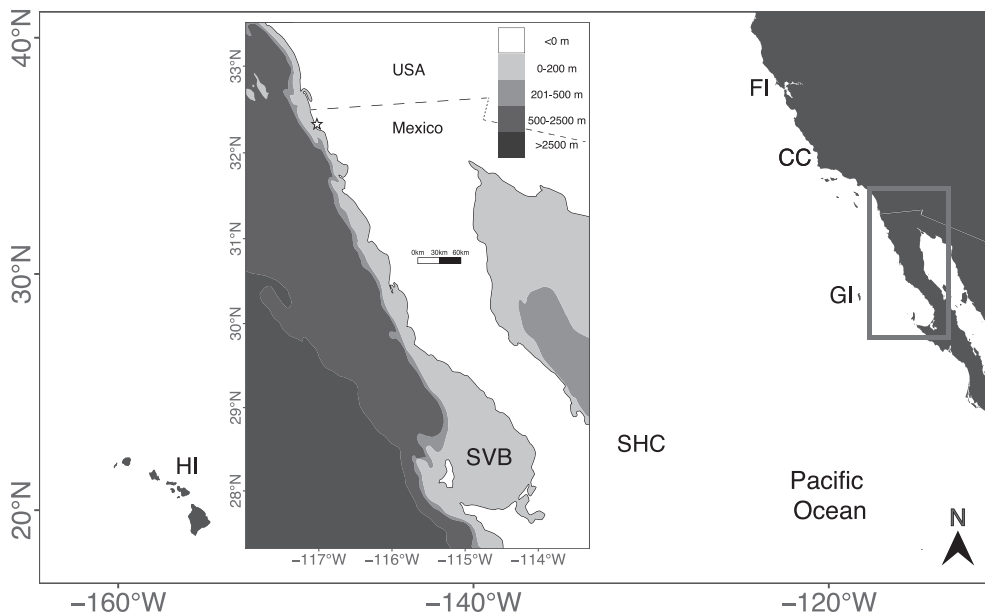


Fig. 1. Map depicting geographical and bathymetric characteristics where the 1066 mm total length newborn White Shark (*Carcharodon carcharias*) was caught. Inset map shows with a star the White Shark capture location and its proximity to the USA–Mexico international border. Depth contours are indicated by a gray scale from 0 to >2500 m. Relevant locations previously identified in the life history of Northeastern Pacific White Sharks (see text for details) are indicated as follows: Farallon Island (FI), central California (CC), Guadalupe Island (GI), Sebastian Vizcaino Bay (SVB), Shark Caffe (SHC), and Hawaii (HI).

have been reported off southern California, offering support for this region to be considered a White Shark nursery area (Klimley, 1985). Additionally, Sebastian Vizcaino Bay (SVB) and nearby Cedros Island, located off the west coast of the central Baja California Peninsula, have also been considered White Shark nursery grounds (Oñate-Gonzales et al., 2017; Tamburin et al., 2019).

To better understand how White Sharks aggregate and how local fisheries impact this vulnerable species, it is critical that we continue to collect biological information from all stages of development. Three main stages have been identified for White Shark early development: 1) newborn (NWS; 120–150 cm total length [TL]), 2) young-of-the-year (YOY; 150–175 cm TL), and 3) juvenile (JWS; 175–300 cm TL) (Bruce and Bradford, 2012). Individuals in the NWS stage are considered the most vulnerable due to a higher risk of predation (Benson et al., 2018), as well as incidental capture in nearshore fisheries (Santana-Morales et al., 2012; Lyons et al., 2013; Castillo-Geniz et al., 2016; Oñate-Gonzales et al., 2017).

Given the knowledge gaps that exist regarding White Shark early stages and pupping areas, this work describes the discovery of the smallest free-living newborn White Shark reported to date. The aim of this study is to document morphometric, skeletal, and haplotypic characteristics of this individual and to enhance our biological and ecological understanding of this species. We also discuss how this information should be considered for meeting future management and conservation objectives of this multi-national pelagic species.

MATERIALS AND METHODS

On 15 June 2018, a small White Shark was caught incidentally by artisanal fishers off the Pacific coast of Baja California, ~2 km offshore, 6.6 km south of the Mexico–USA international border (32°28'N, 117°8'W; Fig. 1). The shark was captured in a bottom set gillnet targeting California Halibut (*Paralichthys californicus*) and White Sea Bass (*Atractoscion nobilis*) that was positioned at approxi-

mately 28 m deep. The White Shark was landed and subsequently donated to the research team. Upon notification from the fisher, the shark was collected and processed under a scientific permit granted by the Mexican Natural Resources and Environmental Secretariat (SEMARNAT-DGVS; SGPA/DGVS/007180/18).

Morphological analysis.—For the description of the specimen, 42 morphometric measurements were collected based on Compagno (1984). All measurements were performed with the body in its natural position, to the nearest mm using a flexible measurement tape (precision: 0.01 cm), and the mass was obtained using a digital balance (Rhino, BARAG-40-01150; precision 0.001 kg). In addition, the skeleton and other hard or calcified structures of the individual were characterized using x-ray technology using a TXR Rotanode Linear MC150-C Toshiba x-ray machine, using an amperage of 50 ma, a voltage of 11 KVP, and an exposure time of 2.5 sec. The analysis of x-ray images allowed us to explore inner-body hard structures that can be used to differentiate stages of development or discern between species.

Genetic analysis.—We explored the genetic association of the studied individual relative to nearby White Shark aggregation sites in central California (CC) as well as Guadalupe Island (GI), to better elucidate connectivity between these geographically proximal but distinct locations. Total genomic DNA from the studied individual was extracted in duplicate using the rapid salt-extraction method developed by Aljanabi and Martinez (1997). Primers ProL2 (5'-CTGCCCTTG GCTCCCAAAGC-3') and PHeCacaH2 (5'-CTTAGCATCTT CAGTGCCAT-3') were used to amplify the mitochondrial DNA control region sequence according to polymerase chain reaction (PCR) conditions described in Pardini et al. (2001). The PCR product was sent for bi-directional Sanger sequencing at SeqExcel Inc. (San Diego, CA). Reverse and forward sequences were assembled and chromatograms visually examined using the software Geneious 10 (<https://www.geneious.com>). Control region sequences

Table 1. External and proportional morphometric measurements (% of total length) of the individual newborn shark, compared to embryos (*) and free-swimming White Sharks reported by different authors.

Authorship	This study		Kabasakal and Ozgur Gedikoglu, 2008	Saidi et al., 2005*	Francis, 1996*		Uchida et al., 1996*		
Total length (TL, mm)	1066		1352	1340	1430	1449	1350	1500	1400
Measurements	(mm)	%TL	%TL	%TL	%TL	%TL	%TL	%TL	%TL
Precaudal length	817	76.6	78	77.4	76.6	78.1	—	—	—
Fork length	920	86.3	—	85.6	88.1	88.1	—	—	—
Pre-first dorsal length	383	35.9	37.26	32.2	34.5	35.9	35	34	34.6
Pre-second dorsal length	707	66.3	66.4	63.5	66.5	66.8	—	—	—
Prepectoral length	271	25.4	27.57	22.8	24.5	24.2	24.6	22.7	22.9
Head length	300	28.1	27.91	25	24.8	26.6	—	—	—
Prebranchial space	222	20.8	22.14	17.8	19.7	20.6	20.4	17.7	18.6
Prespiracle length	140	13.1	—	10.3	—	11.3	—	—	—
Preoral length	64	6.0	6.76	4.8	—	6.3	—	—	—
Interdorsal space	230	21.6	20.36	21.6	21.3	22.1	21.8	21.7	22.9
Pelvic fin length	98	9.2	8.2	8.3	—	—	—	—	—
Second dorsal–caudal length	360	33.8	—	10.3	—	8.3	—	—	—
Prepelvic length	546	51.2	54.04	51.6	54.5	55.9	53.1	53.3	55
Preal anal length	712	66.8	69.09	66	69.3	68.4	—	—	—
Pelvic–anal length	114	10.7	10.27	10.5	—	9	—	—	—
Pelvic–caudal length	210	19.7	—	19	18.5	19	17.3	16.3	15
Snout–vent length	580	54.4	56	53.4	55.9	57	—	—	—
Vent–caudal length	470	44.1	—	46.6	43.4	43.3	—	—	—
Prenasal length	40	3.8	4.25	3.3	3.6	3.7	3.4	3.8	3.6
Intergill length	66	6.2	6.28	7.2	6.2	6.3	—	—	—
Eye width	20	1.9	1.25	1.2	1.5	1.4	1.5	1.5	1.5
Eye height	17	1.6	1.58	1.1	1.5	1.6	—	—	—
Internasal length	48	4.5	—	3.4	4	4.1	4	4	4
Mouth width	108	10.1	8.46	9.7	—	10.7	7.9	9.7	8.3
First dorsal height	93	8.7	8.17	8.3	9.3	9.3	9.5	9.1	9
First dorsal base	103	9.7	9.09	10.9	9.6	9.9	9.5	9.7	9.4
First dorsal inner margin	29	2.7	2.18	1.8	2.7	2.5	—	—	—
First dorsal anterior margin	146	13.7	11.75	12.8	13.6	13.6	—	—	—
Second dorsal height	16	1.5	—	1.3	1.3	1.5	—	—	—
Second dorsal base	16	1.5	1.36	1.6	1.5	1.6	—	—	—
Second dorsal inner margin	23	2.2	1.51	1.4	1.4	2.1	—	—	—
Second dorsal anterior margin	30	2.8	2.47	2.5	2.9	2.6	—	—	—
Pectoral height	230	21.6	—	14.2	—	19.7	—	—	—
Pectoral inner margin	52	4.9	5.5	3.8	—	4.1	5.7	5.7	5
Pectoral anterior margin	218	20.5	20.55	19.1	—	22.2	—	21.9	22.1
Caudal anterior margin	246	23.1	—	23.8	—	—	—	—	—
Caudal terminal lobe	55	5.2	—	4.5	4.7	5.1	—	—	—
Second dorsal insertion–anal insertion	15	1.4	—	2.7	—	—	—	—	—
Second dorsal origin–anal origin	8	0.8	—	2.5	—	—	—	—	—
Trunk height	150	14.1	—	12.3	19.2	21.7	—	—	—
Caudal peduncle height	30	2.8	—	2.6	2.9	2.9	—	—	—

from the two nearby White Shark aggregations sites at CC and GI were used as references. Sequences from CC ($n = 54$) were previously published (GenBank accession numbers GU002302–GU002321; Jorgensen et al., 2009). Sequences from GI ($n = 29$) were collected via whole mitochondrial genome target capture using protocols outlined in Li et al. (2013) and Li et al. (2015). Haplotype frequencies, number of haplotypes (A), private haplotypes (Ar) by population, and the fixation index F_{ST} were estimated using Arlequin ver. 3.5 (Excoffier et al., 2005).

RESULTS

Morphological characteristics.—The specimen examined in this study was a 1066 mm TL male newborn White Shark (Table 1). Body and organ mass measurements were as follows: whole body weight = 9.2 kg, eviscerated body = 7.86 kg, liver = 0.865 kg; esophageal stomach + intestine = 0.355 kg, heart = 0.040 kg, and kidneys = 0.080 kg. A small quantity of mucus was the only item found in the stomach. The x-ray images of the head region showed an average of 26 rows of teeth in the upper jaw and 24 in the lower. In

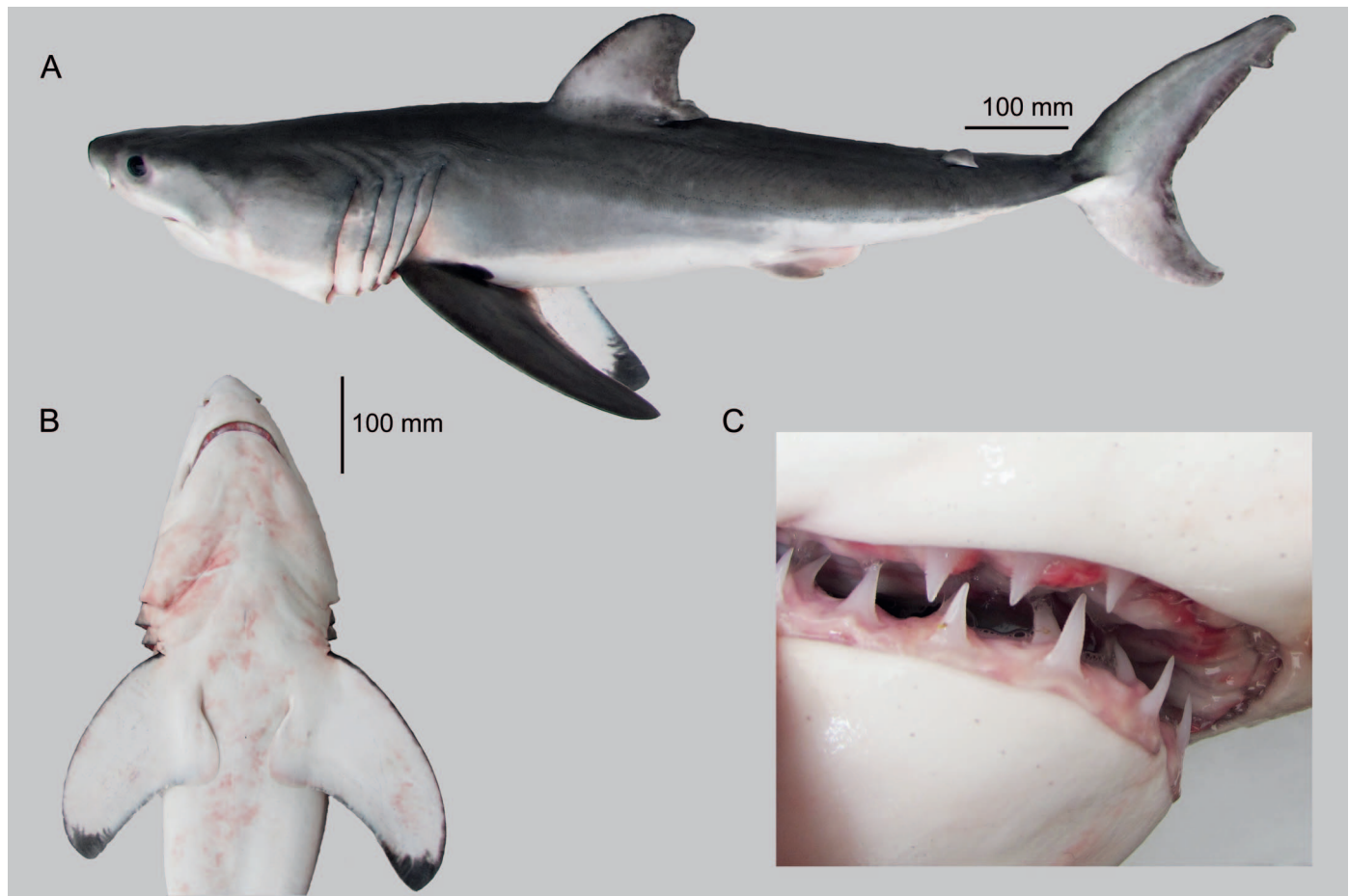


Fig. 3. (A) Whole body of the newborn White Shark (*Carcharodon carcharias*) male of 1066 mm of total length. (B) Ventral part of the individual showing a yolk sac scar above the origin of pectoral fins. (C) Snout and teeth of the individual.

White Shark as well as two adults (individuals of 3660 mm TL and 5180 mm TL; Hubbell, 1996; Fig. 3). The newborn specimen in this study shared three characteristics previously described only for White Shark embryos: 1) rounded apex of the dorsal fin (Fig. 3A; Saidi et al., 2005), 2) a healed and fully closed yolk sac scar in ventral area (Fig. 3B), and 3) teeth that were not all fully erect and covered by a thin membrane (Fig. 3C). However, the ventral part of the body was not distended (Fig. 3A, B) and there were no embryonic teeth or dermal denticles found in the stomach contents, which suggest that the shark was a free-living individual (Francis, 1996; Uchida et al., 1996). The small size of this specimen is noteworthy because it is important for demographic models and for those that use life history data. Moreover, based on Logan et al. (2018), the principal condition indices of the individual ($K = 1.18$; $M_T = 8.58$; and $M_H = 0.86$) are within the limits obtained for JWS from southern California (individuals from 1045–2480 mm FL; $K = 0.85$ – 1.94 ; $M_T = 9.7$ – 182.9 ; and $M_H = 0.9$ – 26.5), further supporting the hypothesis that the NWS of this study was a free-living individual.

Although the White Shark has been shown to have a cosmopolitan distribution, genetically distinct populations as well as localized aggregation sites have been described for this species around the globe (Pardini et al., 2001; Jorgensen et al., 2009; Tanaka et al., 2011; Blower et al., 2012; Oñate-González et al., 2015). Areas of increased localized abundance include seasonal inshore aggregation sites (Bruce,

2015), as well as offshore locations such as the Shark Cafe (SHC in Fig. 1; an area between Hawaii and the Baja California Peninsula; Jorgensen et al., 2009). Two of the most studied aggregation sites in the Northeast Pacific (NEP; GI and CC) are relatively near the capture site of the White Shark documented in this study. Based on the proximity of these areas and to better understand the source population of west coast juvenile White Sharks, we explored the genetic association of the newborn White Shark of this study relative to the nearby adult aggregation sites. The newborn White Shark shares the most common haplotype found at both GI and CC, a finding similar to that presented in a previous study performed within this same region (Oñate-González et al., 2015). The high degree of genetic similarity between CC and GI populations that we found suggests potential connectivity between the two aggregation sites. Although this level of connectivity supports previous telemetry studies (Jorgensen et al., 2012; Hoyos-Padilla et al., 2016), our findings differ from that reported by Oñate-González et al. (2015), which reported significant genetic divergence between the two adult aggregation sites. Additional work is needed to better understand the population dynamics and early life history of White Sharks in the NEP.

The timing of the capture of the newborn White Shark occurred within the pupping season described by Klimley (1985), and the location was only 6.6 km south from the US–Mexico border. Given that the shark was free-swimming prior

to capture, it is possible that the individual came from the southern California nursery area reported by Klimley (1985), or that the shark came from the more southern pupping grounds of SVB (Weng et al., 2007; Oñate-González et al., 2017). Given these uncertainties, we must also consider the possibility that the nursery area may be much larger than that previously proposed, or the possibility of an extended nursery region, one that spans the entire southern California/northern Baja California coastline. Given the rural coast off northern Baja California and the lack of catch monitoring for White Sharks in this region, it may be that these areas also play a nursery role but have yet to be documented. For this reason, it is important to extend White Shark sampling and monitoring efforts throughout the region, as it is an important part of understanding the population dynamics of this species.

Management implications.—Despite Mexico's ongoing harvest prohibitions, the only White Shark monitoring program in place is focused on the tourist cage diving activities around GI (SEMARNAT, 2013, 2015), where it is considered as an important economic resource (Santana-Morales, unpubl. data). The lack of biological monitoring of the juvenile cohorts is especially problematic given that previous work has highlighted the vulnerability of these stages to both predators and fishery interactions (Klimley, 1985). For example, bottom-set gillnet fishing gear contributes to more than 80% of the incidental catches of NWS and YOY White Sharks, both in southern California and Baja California (Cartamil et al., 2011; Santana-Morales et al., 2012; Lyons et al., 2013). In the Southern California Bight, fishers and researchers have initiated projects that record White Shark sightings and fishery interactions and also track shark movements using satellite-tagging technology (Benson et al., 2018). To date, this work has shown that incidental capture in nearshore fisheries continues to be the main source of juvenile White Shark mortality in the NEP. Studies along Baja California have also demonstrated the vulnerability of juvenile White Sharks to inshore gillnet operations (Santana-Morales et al., 2012; Castillo-Geniz et al., 2016; Oñate-González et al., 2017). Unfortunately, Mexico does not currently have an official monitoring program dedicated to enumerating incidental catch in artisanal fishing operations. The lack of such programs limits our understanding and mapping capabilities of nursery habitats, and supports the need for periodic reporting of unusual sightings and captures, like the one we report in this study. Given the vulnerability of the White Shark species and the lack of information available on the early life history, bi-national or multinational management coordination is necessary for the conservation of this shared resource.

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