FACULTAD DE CIENCIAS MARINAS

UNIVERSIDAD AUTÓNOMA DE BAJA CALIFORNIA

FACULTAD DE CIENCIAS MARINAS
INSTITUTO DE INVESTIGACIONES OCEANOLÓGICAS

CARACTERÍSTICAS POBLACIONALES DEL TIBURÓN BLANCO (*Carcharodon carcharias*) DEL NOROESTE MEXICANO: ESTRATEGIAS PARA EL MANEJO DE UN DEPREDADOR TOPE

T E S I S

QUE PARA CUBRIR PARCIALMENTE LOS REQUISITOS NECESARIOS PARA OBTENER EL GRADO DE

DOCTOR EN CIENCIAS EN OCEANOGRAFIA COSTERA

PRESENTA

M. en C. OMAR SANTANA MORALES

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RESUMEN

El Tiburón Blanco (*Carcharodon carcharias*) es un depredador tope con una distribución amplia y en estado de protección a nivel mundial. En México, está considerado como especie amenazada, por lo que esta prohibida su captura o retención. En el Pacifico Nororiental la distribución del Tiburón Blanco es diferente por estadios de vida. Por ejemplo, los sub adultos y adultos muestran una agregación en Isla Guadalupe, México y California central, EUA. Los recién nacidos y juveniles, son más abundantes a lo largo de la zona costera del sur de California y Baja California. Por lo tanto, se requiere integrar las características poblacionales, el comportamiento y la variabilidad ambiental para manejar eficientemente los recursos. En México, la captura incidental de individuos sucede durante las actividades de pesca artesanal que se desarrollan en la zona costera de Baja California. Con base en diversos análisis realizados a un individuo recién nacido, capturado incidentalmente en la zona costera de Tijuana, se logró determinar que era el Tiburón Blanco de vida libre más pequeño hasta ahora reportado a nivel mundial. Así mismo, se pudo determinar que el individuo presentaba los haplotipos más comunes de los dos sitios de agregación de adultos (Isla Guadalupe y California central), sugiriendo la presencia de un área de crianza compartida entre México y Estados Unidos. Por otro lado, existe un aprovechamiento no extractivo de la especie durante las actividades turísticas de observación en jaula de tiburón blanco en Isla Guadalupe. Utilizando a esta industria como plataforma, durante el periodo 2014-2019 se realizó el monitoreo biológico del tiburón blanco en donde se registraron tanto datos biológicos como

de comportamiento. En este documento, presento el desarrollo y resultados de tres preguntas de investigación enfocadas a la generación de información para promover mejores prácticas de manejo del tiburón blanco en el Pacifico Nororiental. Como principales resultados, presento el registro del incremento gradual de individuos, indicando una recuperación de la especie derivado de los esfuerzos de conservación. Además, utilizando un programa de monitoreo sin precedentes, informamos que durante las temporadas 2016 y 2019 aumentó considerablemente el número de individuos juveniles en Isla Guadalupe, coincidiendo con anomalías oceanográficas documentadas en la zona costera de California y Baja California. La presencia de individuos juveniles durante las actividades turísticas tuvo implicaciones importantes debido a que los protocolos de seguridad e instrumentos de manejo del Tiburón Blanco en la Reserva de la Biosfera Isla Guadalupe están basados en individuos adultos. Con base en los resultados de este monitoreo se observó que los individuos con tallas entre 4-5 m de longitud total (LT) son los que presentan una mayor interacción con las embarcaciones turísticas. Con base en este resultado, se realizó el seguimiento acústico de 12 Tiburones Blancos (4-5.5 LT), acumulando un total de 330 horas. Con esto se logró caracterizar el uso de hábitat de la especie, dentro del polígono delimitado para las embarcaciones turísticas. Se encontró que el Tiburón Blanco utiliza esta área de forma diferente a lo largo del día (24 horas), con una mayor presencia durante las horas con luz de día como respuesta a los métodos de atracción de las embarcaciones turísticas. Con esta investigación se actualizó el estudio de capacidad de carga de las embarcaciones turísticas, recomendando 6 embarcaciones realizando actividades turísticas al mismo tiempo. Estas tres preguntas de investigación ya pasaron por el riguroso proceso de revisión por pares. Los detalles de cada uno de estos casos los encontrarán adjuntos en su versión original de cada una de las revistas científicas donde fueron publicados los resultados.

ABSTRACT

The White Shark (*Carcharodon carcharias*) is a top predator with a wide distribution and in a protected status worldwide. In Mexico, it is considered a threatened species, so its capture or retention is prohibited. In the Northeast Pacific the distribution of the White Shark is different by life stages. For example, the sub-adults and adults show an aggregation in Guadalupe Island, Mexico and central California, USA. Newborns and juveniles are most abundant along the coastal area of southern California and Baja California. Therefore, it is necessary to integrate population characteristics, behavior and environmental variability to efficiently manage resources. In Mexico, bycatch of individuals occurs during artisanal fishing activities that take place in the coastal zone of Baja California. Based on various analyzes carried out on a newborn individual, incidentally caught in the coastal zone of Tijuana, it was possible to determine that it was the smallest free-living White Shark reported to date worldwide. Likewise, it was determined that the individual presented the most common haplotypes of the two adult aggregation sites (Guadalupe Island and central California), suggesting the presence of a shared breeding area between Mexico and the United States. On the other hand, there is a non-extractive use of the species during the tourist activities

of observation in the White Shark cage on Guadalupe Island. Using this industry as a platform, during the 2014-2019 period the biological monitoring of the White Shark was carried out, where both biological and behavioral data were recorded. In this document, I present the development and results of three research questions focused on generating information to promote better management for White Sharks in the Northeast Pacific. As main results, I present the record of the gradual increase of individuals, indicating a recovery of the species derived from conservation efforts. In addition, using an unprecedented monitoring program, we reported that during the 2016 and 2019 seasons, the number of juvenile individuals increased considerably on Guadalupe Island, coinciding with documented oceanographic anomalies in the coastal zone of California and Baja California. The presence of juvenile individuals during tourist activities had important implications because the safety protocols and management instruments for the White Shark in the Guadalupe Island Biosphere Reserve are based on adult individuals. Based on the results of this monitoring, it was observed that individuals with sizes between 4-5 m in total length (TL) are those that present a greater interaction with tourist boats. Based on this result, 12 White Sharks (4-5.5 LT) were monitored acoustically, accumulating a total of 330 hours. With this, it was possible to characterize the habitat use of the species, within the polygon delimited for tourist boats. It was found that the White Shark uses this area differently throughout the day (24 hours), with a greater presence during the hours of daylight in response to the attraction methods of tourist boats. With this research, the study of carrying capacity of tourist boats was updated, recommending 6 boats carrying out tourist activities at the same time. These three research questions have already gone through the rigorous peer review process. The details of each of these cases will be found attached in their original version of each of the scientific journals where the results were published.

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DEDICATORIA

Este trabajo está dedicado a mi madre Irene del Carmen Morales Gil† y a los guardaparques de la RB Isla Guadalupe Miguel A. Escobedo-Olvera†, René† y Pajarito†

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INDICE

INTRODUCCIÓN GENERAL

El tiburón blanco (*Carcharodon carcharias*) es un depredador tope conocido principalmente por su gran tamaño y naturaleza depredadora. A pesar de su popularidad y su amplia distribución, poco se sabe de su etapa reproductiva, sus áreas de nacimiento y primeras etapas de vida (Compagno et al., 1997; Bruce, 2007). Actualmente, el tiburón blanco se encuentra protegido por varias regulaciones internacionales y está enlistado en el Apéndice II de la Convención Internacional para el Comercio de especies protegidas de Flora y Fauna (CITES). Esta especie está enlistada en la Unión Internacional para la Conservación de la Naturaleza (IUCN) en donde se resalta la falta de información acerca del estatus actual de sus poblaciones (Dulvy et al., 2008). En México, el tiburón blanco está considerado como una especie amenazada en el Diario Oficial de la Federación (DOF), y se encuentra en permanente veda su captura o retención (DOF, 2012, 2014) con el fin de reducir el número de muertes de individuos durante las actividades de la pesca comercial o recreativa.

Dada la vulnerabilidad de las especies grande de tiburones a la sobreexplotación, y en el caso del tiburón blanco a la incógnita de su estatus poblacional, cualquier información con respecto a su historia de vida puede contribuir al mejoramiento de conservación y acciones de manejo de esta especie. Aunque existen recientes estudios biológicos y ecológicos y avances en las acciones de conservación de la especie, la localización, estacionalidad y características de las áreas de nacimiento y crianza del tiburón blanco continúan limitadas. Por otro lado, se sabe que tanto en la costa de California como en ambas costas de la Península de Baja California ocurren capturas incidentales importantes de la especie durante las actividades de la pesca comercial (Lowe et al., 2012; Santana-Morales et al., 2012). Con base en este tipo de registros, es que se han identificado y descrito áreas de crianza de la especie (Oñate-Gonzales et al., 2017; Tamburin et al., 2019). A pesar de que en los dos principales sitios de agregación en el Pacífico Oriental (Isla Guadalupe e Islas Farallón), se han desarrollado numerosos estudios de investigación, poco se sabe sobre su conectividad entre estas áreas y como es que son aprovechadas (apareamiento o alimentación) por el tiburón blanco (Domeier y Nasby-Lucas, 2006; Jorgensen et al., 2009).

Recientemente, anomalías térmicas importantes dentro del sistema de la Corriente de California han impactado a Isla Guadalupe. Estas anomalías incluyen procesos físicos muy bien documentados como El Niño y más recientemente El Blob (Hu y Fedrov, 2017; Wang y Hedon 2017). Actualmente sabemos que este tipo de eventos tienen influencia en los patrones de movimiento y migración de tiburones blancos juveniles en la costa de California (White et al., 2019), incluyendo a diferentes especies de mamíferos marinos como los pinnípedos, que forman parte de la dieta del tiburón blanco en su etapa adulta (Elorriaga-Verplancken et al., 2016; García-Aguilar et al., 2018; Gálvez et al., 2020). Por medio del monitoreo biológico del tiburón blanco en sus sitios de agregación, podemos conocer como estas anomalías impactan en sus características poblacionales y de esta manera se pueden proponer medidas de manejo de la especie con bases científicas.

Isla Guadalupe es administrada como Reserva de la Biosfera por la Comisión Nacional de Áreas Naturales Protegidas y en ella están permitidas determinadas actividades antropogénicas entre las que se encuentra el avistamiento de tiburón blanco en jaula. Esta actividad comenzó en 1999 con una embarcación, formalizándose en 2005 con 6 embarcaciones, aumentando a 10 embarcaciones hasta la actualidad (Meza-Arce et al., 2020). El avistamiento de tiburón blanco en jaula es una herramienta útil para disminuir el estigma y mala reputación que se le ha dado a los tiburones, en particular a esta especie. Esta actividad puede ser utilizada para generar una nueva ética de conservación para la especie mientras funciona como plataforma científica. Además, el buceo en jaula puede ser utilizado para asignar un valor económico a un tiburón vivo, el cual es mucho más alto que el de un tiburón muerto al ser comercializado. Sin embargo, se sabe que las actividades turísticas que se desarrollan en la vida salvaje son la mayoría de las veces lucrativas y modifican el comportamiento de la especie objetivo. Además, estas actividades se han culpado de degradar el hábitat y de generar disturbios ecológicos que reducen el fitnes de la especie objetivo.

Isla Guadalupe está considerada como el principal centro de agregación de tiburón blanco en el Pacífico Noroeste y también como el mejor lugar del mundo para el avistamiento del tiburón blanco en jaula. Bajo estas condiciones, es importante monitorear a la especie y regular las actividades turísticas de manera rigurosa. Asimismo, es importante conocer la procedencia de los individuos que aquí se reúnen año con año con la finalidad de proponer medidas de manejo integrales que aseguren la conservación de la especie. La presente tesis analiza información generada a partir de la colecta de un individuo recién nacido capturado incidentalmente en la costa noroeste de Baja California y del monitoreo de la población de tiburón blanco en Isla Guadalupe. Con ello presentamos un panorama general de la población de la especie en el Pacífico mexicano, y proponemos medidas para el manejo de una especie que en la actualidad está siendo aprovechada de forma intensa por un turismo internacional que genera una derrama importante para el país.

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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 overexploitation 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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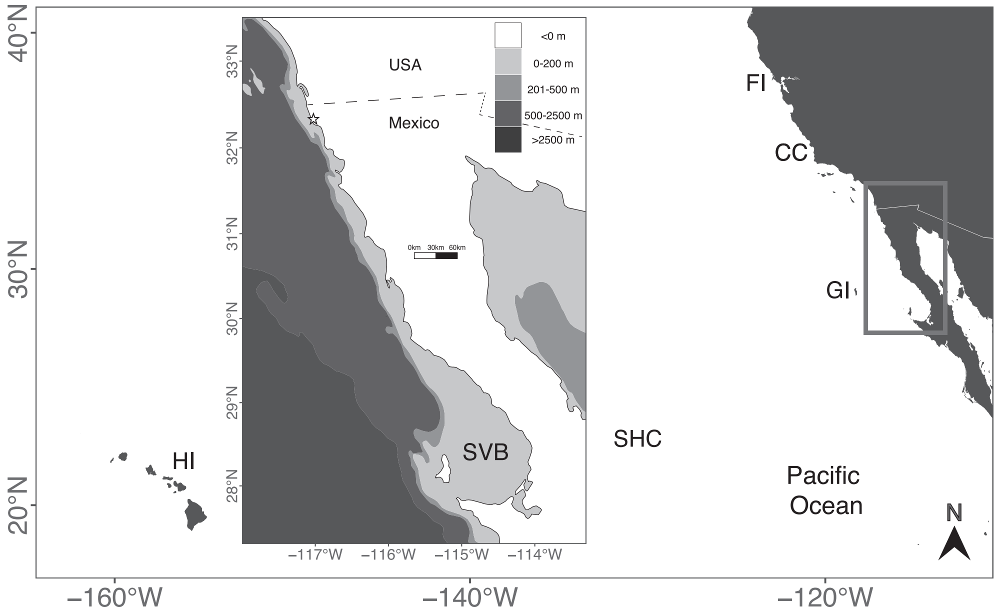

Fig. 1. Map depicting geographical and bathymetric characteristics where the 1066 mm total length newborn White Shark (*Carcharodon carcharias*) was caught. Inset map shows with a star the White Shark capture location and its proximity to the USA–Mexico international border. Depth contours are indicated 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 Cafe (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 approximately 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
Preanal 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

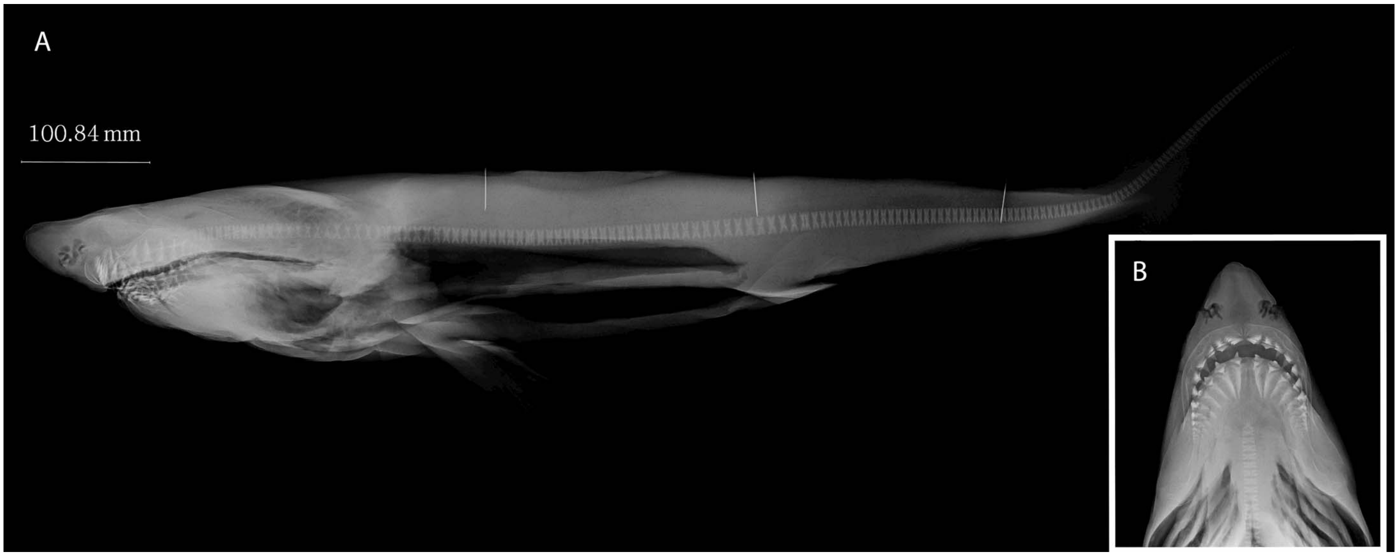

Fig. 2. (A) X-ray analysis of the newborn White Shark (*Carcharodon carcharias*). (B) The head in ventral view showing rows of teeth in the upper and lower jaws.

addition, we also identified 177 vertebral elements along the dorsal area of the body (Fig. 2).

Genetic characteristics.—The newborn White Shark in this study shares the most common haplotype found at both of the adult aggregation sites GI and CC (haplotype 3) with a frequency of 39% and 34%, respectively (Table 2). Our data suggest that individuals at both sites likely correspond to the same population ($F_{ST} = 0.0064$; $P = 0.216$).

DISCUSSION

This work provides biological information for a rare newborn White Shark specimen. Both the length and weight of the studied individual are smaller than any other free-living newborn White Shark or full-term embryo previously described to date (Francis, 1996; Uchida et al., 1996; Saidi et al., 2005; Kabasakal and Ozgur Gedikoglu, 2008; Table 2). The number of tooth rows quantified in this study was found to be similar to that reported for a 1420 mm TL newborn

Table 2. Summary results for both central California and Guadalupe Island White Shark (*Carcharodon carcharias*) populations. *n*: number of individuals; *A*: total number of haplotypes; *pA*: number of private haplotypes; %: haplotype frequencies. Bold indicates private haplotypes.

Population	*n*	*A*	*pA*	Number of haplotypes	Haplotype	Frequency	%
Individual shark	1			1	1	1	
Guadalupe Island (GI) (GenBank accession no. MN504425–MN504430)	29	6	2	6	1	10	34.48
					2	3	10.34
					3	10	34.48
					4	1	3.45
					5	4	13.79
					6	1	3.45
Central California (CC) (Jorgensen et al., 2009)	54	15	11	15	1	18	33.33
					3	21	38.89
					4	2	3.70
					5	1	1.85
					7	2	3.70
					8	1	1.85
					9	1	1.85
					10	1	1.85
					11	1	1.85
					12	1	1.85
					13	1	1.85
					14	1	1.85
					15	1	1.85
					16	1	1.85
					17	1	1.85

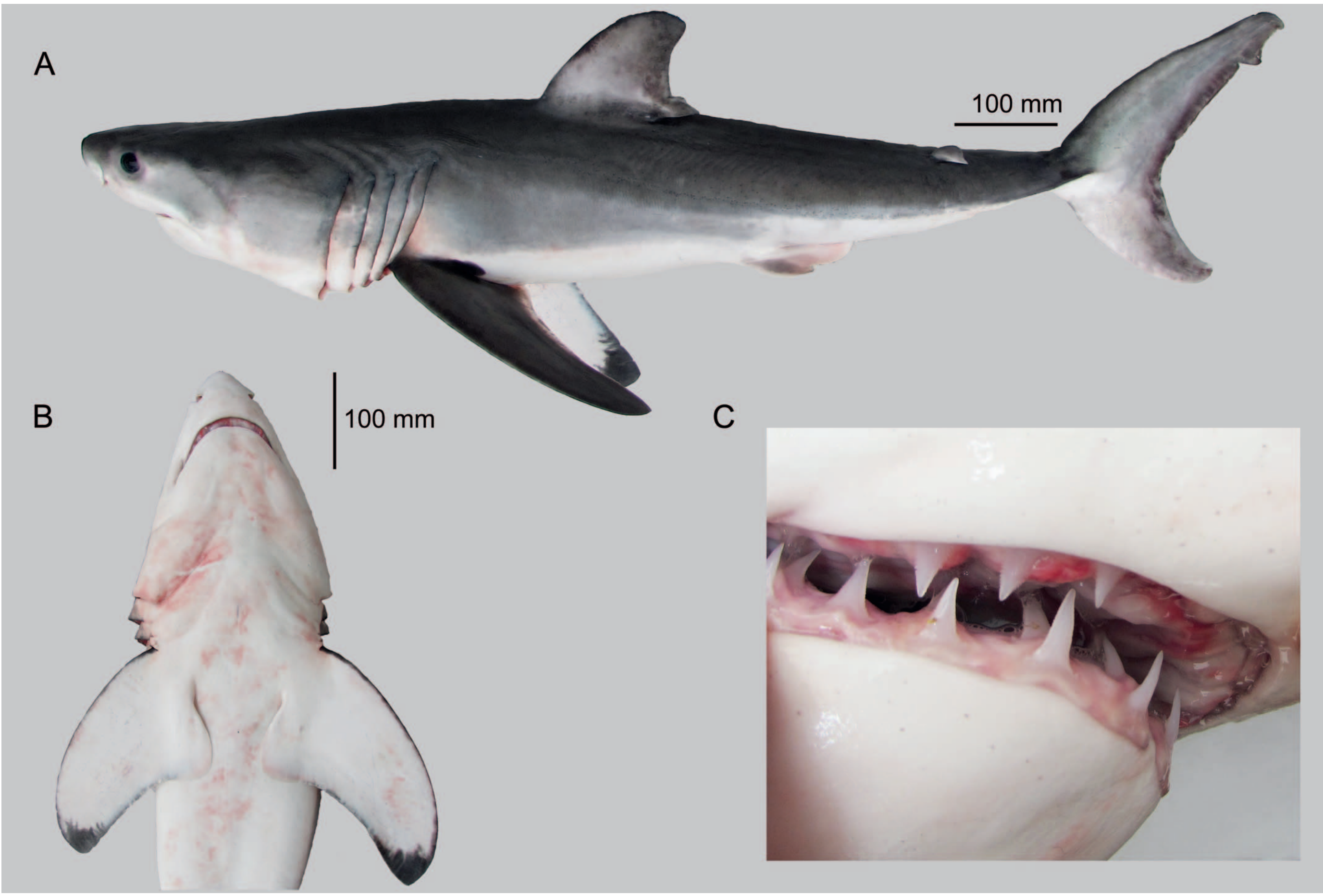

Fig. 3. (A) Whole body of the newborn White Shark (*Carcharodon carcharias*) male of 1066 mm of total length. (B) Ventral part of the individual showing a yolk sac scar above the origin of pectoral fins. (C) Snout and teeth of the individual.

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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RESEARCH ARTICLE

WILEY

An exploration of the population characteristics and behaviours of the white shark in Guadalupe Island, Mexico (2014–2019): Observational data from cage diving vessels

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Abstract

1. In the eastern North Pacific, the Guadalupe Island Biosphere Reserve (GIBR) is one of the most renowned white shark (*Carcharodon carcharias*) aggregation sites studied to date, and an important tourism activity has been developed in the reserve.
2. This study used tourist-based cage diving activities to biologically monitor white sharks from 2014 to 2019 within the GIBR.
3. The data indicated a gradual increase in the overall abundance of white sharks with an age-structure shift, as young of the year and juvenile sharks were more prevalent during the latter part of the study period (2016–2019).
4. The arrival of young of the year and juvenile white sharks coincided with regional changes in oceanographic conditions off California and Baja California.
5. The arrival of adult female white sharks coincided with the seasonal peak in elephant seal abundance.
6. Records of high-risk white shark behaviours, a shift to sharks of younger ages, and the high prevalence of small individuals during cage diving activities supports the need for the continued revision of tourism operational protocols.
7. This study highlights the importance of white shark biological monitoring to identify threats and challenges to the growing tourism industry and the management of the species in Guadalupe Island and in other aggregation sites.

KEYWORDS
behaviour, coastal, distribution, fish, island, threatened species

Omar Santana-Morales and Rodrigo Beas-Luna should be considered joint first authors.

1 | INTRODUCTION

The white shark *Carcharodon carcharias* (Linnaeus, 1758) is widely distributed (Ebert & Stehmann, 2013) in coastal and oceanic waters (Compagno, Marks & Fergusson, 1997). This species has been shown to aggregate in relatively high densities in several regions, especially around pinniped colonies (Jorgensen et al., 2012; Ebert & Stehmann, 2013). White shark aggregation sites constitute important areas for monitoring population dynamics and generating estimates of regional abundance (Domeier & Nasby-Lucas, 2007). Most of the known aggregation sites are also used by tourism operators for cage diving activities, as the repeated interannual presence of white sharks increases the probability of attracting individuals to the cages through baiting. Some of the most recognized sites worldwide are the Neptune Islands (Australia), Farallon Islands (USA), Guadalupe Island (Mexico), Cape Town–Port Elizabeth (South Africa), and Steward Island (New Zealand) (Bruce, 2015; Nazimi et al., 2018).

The Guadalupe Island Biosphere Reserve (GIBR) is recognized as one of the main white shark aggregation sites in the eastern North Pacific (Domeier & Nasby-Lucas, 2008). In this island, the cage diving tourism activity started in 1999 with one vessel, followed by a second in 2002. Subsequently, another four vessels began operations in 2004 (Guerrero-Ávila, 2011). Cage diving is confined to the north-western side of the island in what is known as Rada Norte Bay because of the safety concerns expressed by local fishers, which are heightened during the abalone season when divers must enter the water, and because the area contains suitable sea bottom characteristics for anchoring boats (Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT), 2013). In 2005, cage diving was formalized as an official tourist activity in Mexico (SEMARNAT, 2013) with six vessels in operation. Since 2014, the industry has grown considerably, and 10 vessels currently service an average of 2,800 divers each year (Meza-Arce et al., 2020; Santana-Morales et al., 2021). Despite the popularity of white shark cage diving operations and the published accounts detailing the presence and movements of white sharks within the GIBR (Klimley, 1985; Klimley & Ainley, 1996; Domeier, 2012), Rada Norte Bay remains poorly studied with regard to the impacts that both climatic conditions and human activities have on white sharks.

Recently, significant thermal anomalies within the California Current system (Freeland & Whitney, 2014) have impacted the GIBR. These anomalies include well-documented physical processes like the El Niño-Southern Oscillation and, more recently, the occurrence of a marine heatwave known as 'the Blob' (Hu & Fedorov, 2017; Wang & Hendon, 2017; Amaya et al., 2020). Previous studies have proposed that a better understanding of both prey availability and climate trends may improve efforts to track changes in white shark distributions and seasonal fluctuations (Klimley & Ainley, 1996; Hazen et al., 2012; White et al., 2019). Such events have influenced the movements and migration patterns of juvenile white sharks in California, along with those of other species, like pinnipeds, which form part of the adult white shark diet (Elorriaga-Verplancken et al., 2016; García-Aguilar et al., 2018a; García-Aguilar et al., 2018b; White et al., 2019; Gálvez, Pardo & Elorriaga-Verplancken, 2020). By monitoring white sharks in their aggregation sites, population trends may be detected, such as those related to changes in size structure and the life stages present.

To this end, the objective of this study was to characterize the white shark population that seasonally visits Guadalupe Island to generate information that may be used to improve cage diving regulations and white shark conservation efforts (Santana-Morales et al., 2021). In this regard, an analysis of white shark surface behaviour is presented, which can be used to improve current Best Practices manual and prevent wildlife–human incidents (Torres Aguilar et al., 2015; Becerril-García et al., 2020b). Finally, considerations and implications for the conservation and management of white shark cage diving in the GIBR are discussed, with recommendations for the future of this species in this marine protected area.

2 | METHODS

2.1 | Study area

The GIBR (29° 06′ 40″ N and 118° 19′ 12″ W) is located 240 km offshore of the Baja California Peninsula. The island, which extends ~35 km in length and ~15 km in width (Figure 1), is of volcanic origin and emerges over the mid-oceanic ridge of the eastern Pacific with a maximum elevation of 1,300 m asl (García-Gutiérrez et al., 2005). The maximum depth of the sea bottom around the island is ~2,500 m and occurs ~17 km from the coast. Given that Guadalupe Island is not located on the continental shelf, abrupt bathymetric changes are present within a kilometre of the coastline (Castro et al., 2005), resulting in a highly productive nearshore environment for several pelagic species (e.g. tuna, horse mackerel, yellowtail, and white sharks).

Owing to its semi-circular form and high bordering cliffs, Rada Norte Bay is a naturally sheltered embayment that offers protection to boats. This location is ideal for cage diving due to its calm waters, high visibility, and steep bathymetry (150 m depth) close to shore. For these reasons, Rada Norte Bay was designated for cage diving by the GIBR management programme (Figure 1; SEMARNAT, 2013; Torres Aguilar et al., 2015).

2.2 | Sampling effort

This study is limited to data obtained during the tourism season, which takes place between July–November. Data were collected by qualified observers who were trained and supervised by two of the authors (OSM and RZC). Observer training was conducted throughout all study periods to ensure standardized and systematic data collection.

Photo identification, biological (i.e. sex and total length (TL)), and behavioural data were obtained during the 2014–2019 field seasons

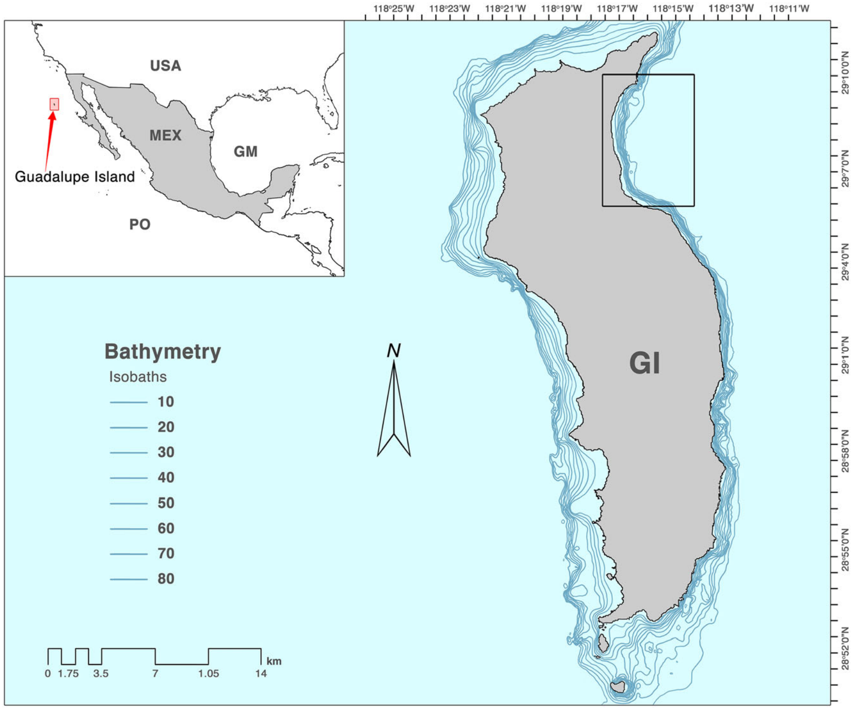

FIGURE 1 Map of Guadalupe Island with Rada Norte Bay indicated by the rectangle showing where white shark data were collected. Inset (upper left) shows the position of Guadalupe Island (small box) with respect to the mainland

through the White Shark Biological Monitoring Programme (WSBMP), which is coordinated by the Federal Commission of Protected Natural Areas (CONANP) in collaboration with cage dive operators. The sampling activities and data collection were sanctioned by research permits granted by the General Office of Wildlife and Ministry of Environment (DGVS) under the SEMARNAT (permit numbers SPGA/DGVS/07052/16, 06673/17, 004284/18, and 6949/19).

Once a vessel arrived in Rada Norte Bay, the observer immediately collected information and continued to observe while the cages were in the water. A total of 10–12 monitoring hours were logged each day. A white shark sighting was defined as the uninterrupted presence of a shark within a 30 m radius surrounding the vessel (Figure 2). If the individual white shark left this area for more than 10 min and later returned, it was considered a new sighting. To compare between years, the sightings per hour effort (SPHE) was calculated using the following equation:

$$\text{SPHE} = \frac{\text{Number of sightings per day}}{\text{Hours of observation effort per day}}$$

A non-parametric Kruskal–Wallis test was performed along with a Bonferroni post-hoc test to evaluate monthly differences in the SPHE. The data obtained from each sighting included the TL of the shark (determined from comparisons with the known dimensions of the cages), sex (presence or absence of claspers), underwater photographs, and conspicuous body characteristics (e.g. scars, pigmentation patterns, and attached electronic tags). Using the estimated length data and the categories proposed by Bruce & Bradford (2012), the white sharks were divided into two main groups: (1) young of the year (YOY) and juveniles (<3 m TL), and (2) sub-adults and adults (>3 m TL).

Once the presence of a shark was registered within 10 m of the bait being used, the observer recorded its surface behaviours during the sighting period using a table generated by the CONANP programme (Appendix I) that was standardized with the behaviour patterns described by Klimley & Ainley (1996) and Becerril-García et al. (2019). The behaviour frequencies were standardized according to the effort based on the number of days per season. According to the Lilliefors test, the data did not meet the assumption of normality ($P < 0.05$), and non-parametric Kruskal–Wallis and Bonferroni post-hoc tests were used to detect possible differences between years. In this regard, the behavioural data from 2014 were not included in the analysis, given that the records were not consistent with those of the other years.

White shark photoidentification was conducted by one of the authors (RZ) at the end of each season, according to the methodology of Domeier & Nasby-Lucas (2007) and the *White Sharks of Guadalupe Island Photo Identification Guide* (Marine Conservation Science Institute, 2013; Marine Conservation Science Institute, 2014; Marine Conservation Science Institute, 2015; Marine Conservation Science Institute, 2016; Marine Conservation Science Institute, 2017; Marine Conservation Science Institute, 2018). The number of identified white sharks per year was standardized according to the effort based on the number of days covered per tourism period (similar to the behaviour analysis). Shark abundance and the life stages of the individuals present during and between years were compared. The sex ratio for each year was estimated with a Chi-square test. Lastly, to track the presence of photoidentified individuals (i.e. recaptures) between

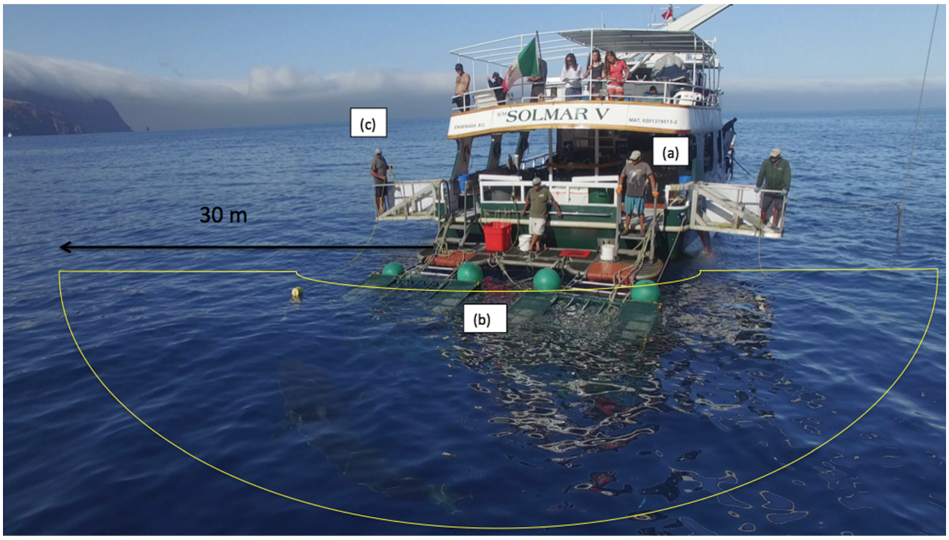

FIGURE 2 A white shark cage diving vessel in Guadalupe Island. Stern of the boat from which an observer (a) collects data within a radius of 180° up to 30 m from the boat; the position of the cages (b) and the crew that handles the bait (c) are shown. The yellow line indicates the 180° visual range of the observer. Photographer: Erick Higuera

TABLE 1 Monitoring effort

Year	Boats	Total trips	Covered trips (proportion, %)	Total days	SPUE	Observed days
2014	6	92	15 (16)	31	0.51	47
2015	7	110	22 (20)	47	0.58	64
2016	8	137	30 (22)	69	0.91	94
2017	9	133	20 (15)	45	0.69	60
2018	10	123	14 (11)	36	0.94	40
2019	10	143	18 (13)	39	0.9	60

Note: Boats: the number of boats performing cage diving activities per season; Total trips: the total number of trips made by each boat per season; Covered trips: the total number of trips covered by biological observers and their proportion in parentheses with respect to the total number of trips completed; Total day:s the total number of calendar days covered; SPUE: the sighting rate per hour of effort; Observed days: the number of accumulated days covered by at least one observer, given that two or three observers at times worked simultaneously on different vessels.

years, a record log for individual sharks was generated per year according to Nasby-Lucas & Domeier (2012).

3 | RESULTS

This study documented relevant biological information during six consecutive years from 119 different cage diving tourism trips (~20 trips per year, with a total observation effort of 267 days (~61 days per season); Table 1). The annual effort (number of trips and days of observation) varied by year and depended on sea conditions, space availability onboard the vessels, and research funding.

3.1 | White shark sightings

The number of sightings per hour of observation increased throughout the years from an average of 0.5 sharks per hour of effort in 2014 (0–1.8) to 1 shark per hour of effort in 2019 (0–2.3) (Figure 3). In this regard, there were significant differences between the SPHE values among years ($H_{5,\,421} = 65.09158$; $P < 0.01$). According to the Bonferroni test results, it was observed that 2014, 2015, and 2017 had similar SPHE values, whereas 2016, 2018, and 2019 presented significantly higher SPHE values that were also similar to each other ($P < 0.05$). During most years, the number of observed sharks was higher during September and October. Overall, the highest variability (i.e. zero to more than two individuals per hour) was recorded in 2016 and 2019, whereas 2018 presented the least amount of variability, with an average of one individual observed per hour throughout the entire year (Figure 3). However, no significant monthly differences were observed between the SPHE values throughout the study period ($H_{3,\,421} = 2.946992$; $P > 0.05$).

From 2014 to 2019, there were 50, 84, 138, 96, 119, and 113 photo-identified individuals registered respectively, with significantly different abundances recorded among years ($\chi^2 = 45.3$, $P < 0.05$; Figure 4). However, these differences were related to the number of covered trips. There were 160 individuals repeatedly observed or 'resighted' based on published photoidentification guides (Marine Conservation Science Institute, 2013; Marine Conservation Science Institute, 2014; Marine Conservation Science Institute, 2015;

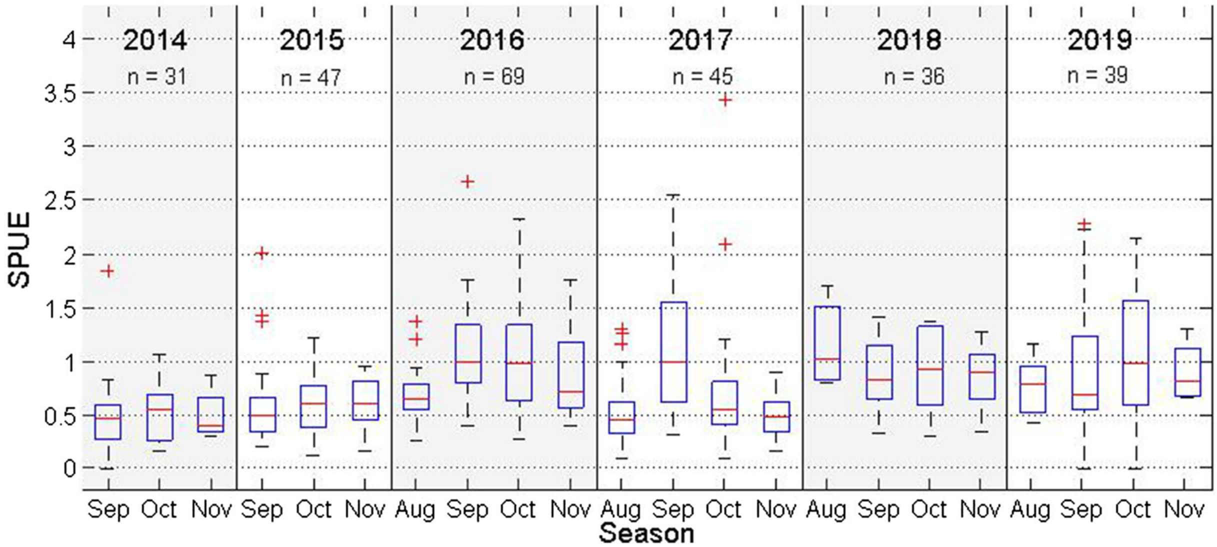

FIGURE 3 Sighting rate per hour of effort (SPHE) for white sharks during 2014–2019. The bottom and top of each box indicate the 25th and 75th percentiles respectively. The distance between the bottom and top of each box indicates the interquartile range. The red line in the middle of each box represents the sample median. Notches display the variability of the median between samples

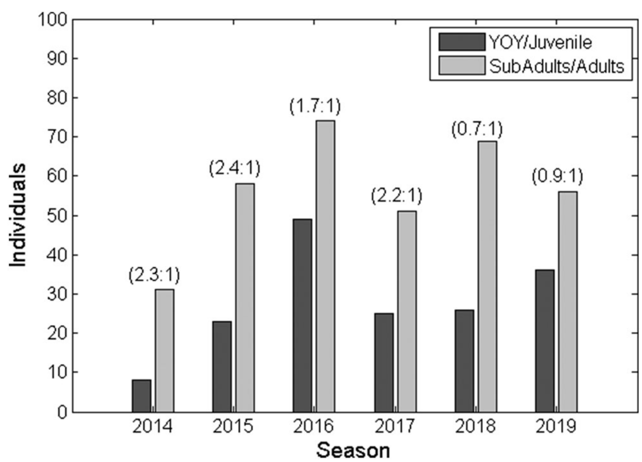

FIGURE 4 Frequency of the age classes of photoidentified white sharks by season. Each bar represents a year during the 2014–2019 study period. According to the life stages proposed by Bruce & Bradford (2012), the dark grey in the bar indicates the proportion corresponding to young of the year (YOY) and juvenile (<3 m total length (TL)) sharks, and the light grey colour corresponds to sub-adult and adult (>3 m TL) sharks. Above each bar, the male:female sex ratio is indicated in parentheses

Marine Conservation Science Institute, 2016; Marine Conservation Science Institute, 2017; Marine Conservation Science Institute, 2018). From the resighting data, seven individuals (4%) were identified during all six years of this study; eight individuals (5%) were identified in five years; 13 individuals (8%) were identified in four years; 26 individuals (16%) were identified in three years; 37 individuals (22%) were identified in two years; and 74 individuals (45%) were identified in one year.

Males were more abundant than females ($\chi^2 = 15.54$, $P < 0.05$), although mainly from 2014 to 2017 (Table 2). However, the sex ratio was close to 1:1, with a slightly higher prevalence of females during 2018 and 2019 ($\chi^2 = 3.36$, $P = 0.06$ and $\chi^2 = 0.14$, $P = 0.70$ respectively). Sex determination was not possible for approximately 16% of the individuals.

Once the data were standardized by days of sampling effort per year, a general increase was observed in the number of sharks identified per day over the 6 years, with a maximum of 3.31 sharks observed per day in 2018 (Figure 5). Moreover, the sub-adult/adult group was the dominant size class throughout the study period. However, there was a gradual increase in YOY and juveniles overall, and this was most prevalent during 2016 and 2019 (36%; Figure 5).

3.2 | Observed behaviours

A total of 65,440 behavioural events were recorded from 2015 to 2019. The median number of behavioural events was significantly different among years, with an increase in surface activity registered since 2018 ($H_{4, 386} = 101.63$; $P < 0.01$). The lowest median (25 events per day (SE ± 12.63)) was observed during 2015. An increase was recorded in 2016 and 2017 with medians of 127 (SE ± 13.19) and 111.5 (SE ± 9.00) events respectively. Nonetheless, the highest frequencies were observed towards the end of the study, with a median of 262.5 (SE ± 23.92) events in 2018 and 210 events (SE ± 25.57) in 2019 (Figure 6).

Slow swimming was the most frequently observed behaviour (22.6%, $n = 14{,}804$; see Appendix II). Other common behaviours included surfacing (17.9%; $n = 11{,}732$), horizontal strikes (16.4%; $n = 10{,}760$), or close inspections (15.8%; $n = 10{,}358$). The types and frequencies of the behaviours recorded per day varied within years

TABLE 2 Total number of white sharks recorded in each season in Rada Norte Bay at Guadalupe Island

Year	Total sharks	Resight (proportion, %)	Sight (proportion, %)	Male	Female	YOY-Juv (<3 m TL)	Sub-A. & adult (>3 m TL)	No size data
2014	50	46 (92)	4 (8)	35	15	8 (16)	31 (62)	11 (22)
2015	84	57 (68)	27 (32)	59	25	23(27)	58 (69)	3 (4)
2016	138	76 (55)	62 (45)	87	51	49 (35)	74 (54)	15 (11)
2017	96	54 (56)	42 (44)	66	30	25 (26)	51 (53)	20 (21)
2018	119	60 (50)	61 (50)	49	70	26 (22)	69 (58)	24 (20)
2019	113	67 (59)	46 (41)	54	59	36 (32)	56 (50)	21 (18)

Note: Resight: sharks registered in previous seasons, with percentage in category in parentheses; Sight: new records with percentage of category in parentheses. YOY-Juv: young of the year and juvenile sharks, defined as individuals less than 3 m total length (TL); Sub-A. & adult: sub-adult and adult sharks, defined as individuals bigger than 3 m TL.
Life stage shark classifications were carried out based on the methodology of Bruce & Bradford (2012).

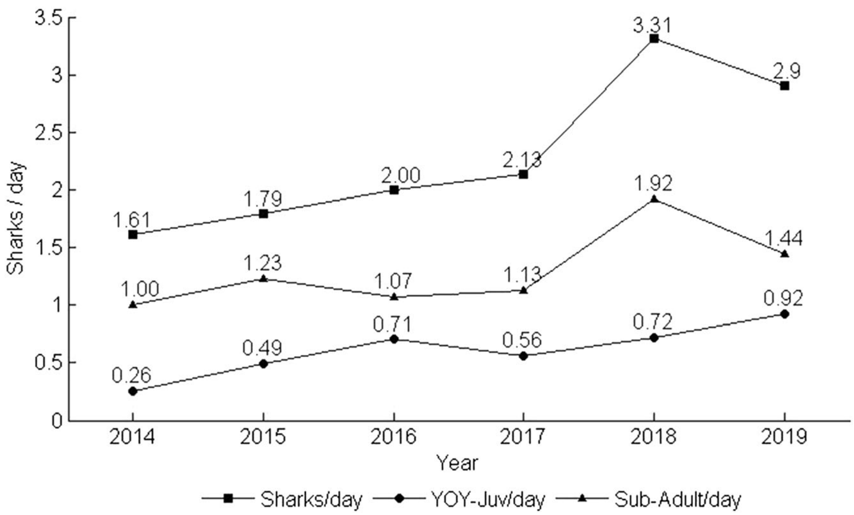

FIGURE 5 Trends of the different life stages of the photoidentified white sharks during 2014–2019

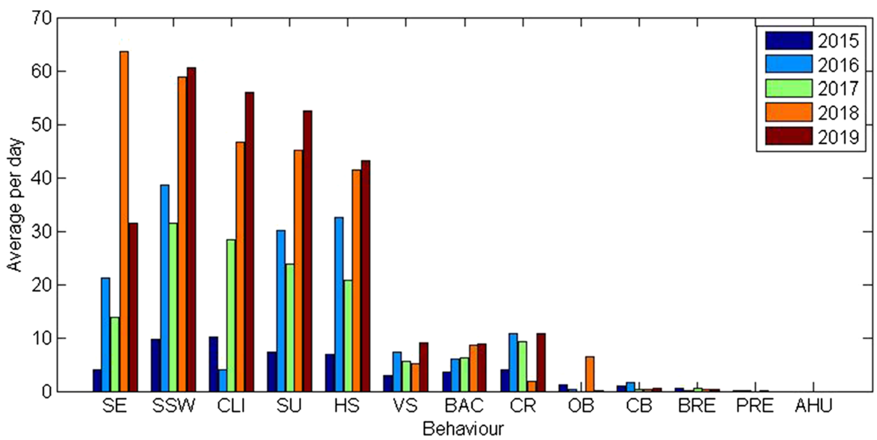

FIGURE 6 White shark individual behaviour frequencies by season (2015–2019) in Guadalupe Island. See Appendix I for behavioural event coding and classification

(Figure 6; see Appendix II). Searching ($H_{4,\,386} = 91.57$), surfacing ($H_{4,\,386} = 89.26$), horizontal striking ($H_{4,386} = 89.51$), and bait catching ($H_{4,\,386} = 35.91$) behaviours were significantly higher ($P < 0.05$) during 2018–2019 compared with what was observed in the other years of the study. Similarly, the occurrence of slow swimming ($H_{4,\,386} = 67.73$) and close inspection ($H_{4,\,386} = 186.17$) behaviours were higher after 2015, with the highest frequencies recorded in 2019. In contrast, the frequency of cage banging was highest during 2015–2016 ($H_{4,\,386} = 29.02$), and the cruising behaviour presented the lowest frequency during 2018 ($H_{4,\,386} = 75.44$).

4 | DISCUSSION

This study offers data for improving the management of white shark cage diving activities and provides insights into recent and future population trends within the GIBR (Becerril-García et al., 2020c). Information generated from the biological monitoring efforts in this study have been presented in workshops at Guadalupe Island at the start of the last five tourism seasons. These efforts have allowed the authorities, boat owners, fishers, and scientists to discuss current challenges and threats to review the incidents of previous seasons. The results of these efforts come in the form of collective agreements reached to limit the number of cage diving vessels, the intensity of tourism activities, and baiting times, as well as a seasonal assessment of white shark conditioning (Heupel & Simpferdorfer, 2005; Hughes et al., 2017; Becerril-García et al., 2020c; Santana-Morales et al., 2021).

A gradual increase in the number of white sharks observed around the GIBR has been recorded, which has been mainly driven by YOY and juveniles and may be related to recent oceanographic conditions (White et al., 2019). This increase in YOY and juveniles was also reflected in the behaviours recorded in this study. According to Domeier & Nasby-Lucas (2007), white sharks in the GIBR vary in TL from 2.5 to 5.5 m with most being >3.5 m in TL. Hoyos-Padilla et al. (2016) reported the presence of individuals smaller than 2.5 m TL that seemed to remain around the island for up to 14 months. In addition, Becerril-García et al. (2019) reported a greater proportion of younger individuals (63% juveniles and YOY) within the GIBR compared with those of previous studies.

These studies clearly show that the population dynamics of the white sharks of the GIBR are dynamic; however, the origins and basis of these changes are not yet clear. The potential implications of this observation are worthy of future research efforts, especially those concerning any conditioning that may be occurring as a result of the tourism activity. For example, it has been shown that juvenile sharks are more likely to develop apprenticeship behaviour towards bait or boats (Wright & Jackson, 1964). In this sense, greater control over the intensity of baiting and interspersed baiting schedules may be required to curb this tendency, in addition to restricting the interactions with juvenile individuals who show signs of bait or boat conditioning (Becerril-García et al., 2020c).

Younger sharks showed different behaviours compared with those that have been reported for larger individuals. Hoyos-Padilla et al. (2016) suggested that a size-based partitioning of nearshore waters is present in Guadalupe Island, with YOY and juveniles predominantly occupying a narrow coastal strip (<100 m from the coast) with a depth range of 5–80 m, and adults displaying more general and diffuse distributions (Santana-Morales et al., 2021). This difference was observed from more than 300 h of acoustic monitoring performed with sub-adult and adult individuals from 2015 to 2019 (Santana-Morales et al., 2021) and was previously confirmed from 2012 to 2014 by Becerril-García et al. (2020a) using statistical modelling. Given that Guadalupe Island is of volcanic origin with a rapidly descending shelf, the preferred habitat for juveniles is limited to this narrow coastal strip (Castro et al., 2005; García-Gutiérrez et al., 2005; Becerril-García et al., 2020a), which represents a critical habitat for juvenile white sharks due to the protection offered from adult sharks and the overlapping distributions of forage species around the island (Hoyos-Padilla et al., 2016; Becerril-García et al., 2020a). Similar findings and juvenile foraging patterns have been reported along the coasts of the southern California Bight and Vizcaino Bay (Santana-Morales et al., 2012; Oñate-González et al., 2017; White et al., 2019; Santana-Morales et al., 2020).

Cage diving management instruments include the Best Practices manual and the reserve management programme, which are based mainly on adult individuals that were characterized in 2007, with the latter regulating cage dimensions and the use of attractants (SEMARNAT, 2013; Torres Aguilar et al., 2015). However, an increase in the abundance of both YOY and juvenile white sharks and their particular behaviours coupled with their distinct habitat use, make it necessary to update the aforementioned management instruments to reflect regulations that take into account white sharks of small size (Meza-Arce et al., 2020; Kanive et al., 2021). For instance, the minimum size for cage windows, as well as bait use and handling procedures, should all be periodically reviewed to minimize injury to both humans and sharks during cage diving activities (Tanno, 2019).

4.1 | Sightings and photoidentification observations

The increase in the number of sharks identified within the GIBR throughout the study period may be related to the monitoring intensity or to the increase in tourism activities (see Table 1), which also agrees with the results of other observational studies performed in Australia (Bruce & Bradford, 2012). However, the general increase in white shark abundance observed in the last years of the study was related to the higher presence of YOY and juvenile white sharks (Figure 5).

From 2001 to 2009, Nasby-Lucas & Domeier (2012) identified 113 individuals (67 males, 46 females) within the GIBR. From 2012 to 2014, Becerril-García et al. (2019) identified 106 individuals (75 males, 31 females). During the present study, 165 different sharks (90 males, 75 females) were recorded. Per year, an average of 60% of the photoidentified white sharks had been previously identified. From 2001 to 2019, the increase in the number of juvenile sharks in the GIBR may have been related to recent and regional changes in oceanographic conditions (Amaya et al., 2020) and conservation efforts in the eastern North Pacific (i.e. the permanent capture and sale ban; Becerril-García et al., 2020c). In California, white sharks have been protected since 1994 (Fergusson, Compagno & Marks, 2009), and Mexico imposed catch and possession restrictions in its fisheries in 2000 (Diario Oficial de la Federación (DOF), 2002; DOF, 2014). Given the potential impacts of these restrictions on the survival of white sharks, is not surprising that their population seems to be increasing off the California and Baja California coasts (Lyons et al., 2013; Huveneers et al., 2018a).

Bilateral efforts between Mexico and the USA to further white shark conservation should also include collaboration among the research communities of both countries. The observed increase in juvenile white sharks will require joint management and research initiatives, which will allow for strategies that meet regional needs to be developed (Malpica-Cruz et al., 2021). Similarly, this increase could imply changes in population structure and in the recruitment of individuals to the adult population, indicating that population estimates must be updated using data from both Mexico and the USA (Burgess et al., 2014; Becerril-García et al., 2020c; Kanive et al., 2021).

4.2 | Surface behaviour analysis

Although ethological techniques were not applied, this study provides general information regarding the frequencies of each behaviour recorded from 2015 to 2019. Of particular importance are those behaviours that could potentially cause harm or negatively impact both sharks and divers, particularly given the recent increase in tourism activities and the potential habituation of sharks to human presence. Some authors have previously addressed these issues (Laroche et al., 2007; Huveneers et al., 2018b; Becerril-García et al., 2020b), which continue to constitute a major concern for reserve managers (Meza-Arce et al., 2020).

Despite the increase in cage diving activities, and consequently the use of attractants, this study did not observe any increase in behaviours that could be considered harmful to either sharks or humans (e.g. cage banging, predation events, and attacks on humans). However, there was an increase in surface behaviours, such as surfacing, slow swimming, horizontal strikes, and bait catching. These observations agree with the findings of Huveneers et al. (2013), suggesting that cage diving and chumming could influence the vertical distribution of white sharks (i.e. maintaining the sharks mostly near the surface).

The interannual changes in the life stages of the sharks observed over the course of this study were also detected in the behavioural analyses. From 2018 to 2019, behaviours like horizontal strikes, stalking, and close inspections were registered when a higher abundance of sub-adult and adult white sharks were within the GIBR (Figure 6). These behaviours are likely related to an increase in the number of females, which attain the largest sizes and generally arrive at the end of the season (Hoyos-Padilla et al., 2016; Figure 5; Appendix II). The increase in searching, bait catching, and vertical strike (from depth) behaviours, which are common in juveniles (MH and OS personal observations), coincides with 2016, when the highest abundances of YOY and juveniles were recorded (Figure 6; Appendix II). This is because juveniles show behaviours that are more related to biting (Sperone et al., 2012; Becerril-García et al., 2019), which explains the increase in activity observed throughout the study period. One of the explanations for this increase is the type of attractant used, given that bony fish, like tuna, are an important part of the juvenile white shark diet and are frequently used as bait for cage diving (Jaime-Rivera et al., 2014). This activity has safety implications for sharks and tourists, as peaks in the abundance of YOY and juvenile sharks coincide with periods during which cage diving incidents have occurred (Graham, 2016; Tanno, 2019).

With regard to predatory behaviours, no observations of any events directed towards northern elephant seals were recorded. Instead, sharks displayed predatory behaviours towards fur seals, sea gulls, turtles, and bony fishes (e.g. jacks and tunas). Although difficult to interpret, this finding may suggest that the bait used during cage diving has a certain non-discriminatory effect on the sharks, which are mainly visual predators that show complex behaviours to acquire prey (Bruce & Bradford, 2012; Sperone et al., 2012).

4.3 | Predator–prey relationship

The northern elephant seals around Guadalupe Island are an important food source for adult white sharks (Jaime-Rivera et al., 2014). It has been hypothesized that the arrival of white sharks around Guadalupe Island is associated with the breeding season of the northern elephant seal colony (Hoyos-Padilla et al., 2016). This hypothesis has also been used to support the high abundance of white sharks in other aggregation sites, such as the Farallon Islands (Ainley et al., 1981; Klimley et al., 1992; Pyle, Anderson & Ainley, 1996; Brown et al., 2010; Jorgensen et al., 2019). In contrast to the white shark abundance estimates observed in this study, the population of northern elephant seals around the cage diving zone appears to have decreased since 2014 (Figure 5; unpublished data Figure 7). Furthermore, these results suggest that the peak of elephant seal abundance only aligns with the arrival of the largest white shark females (i.e. late November), when the WSBMP ends

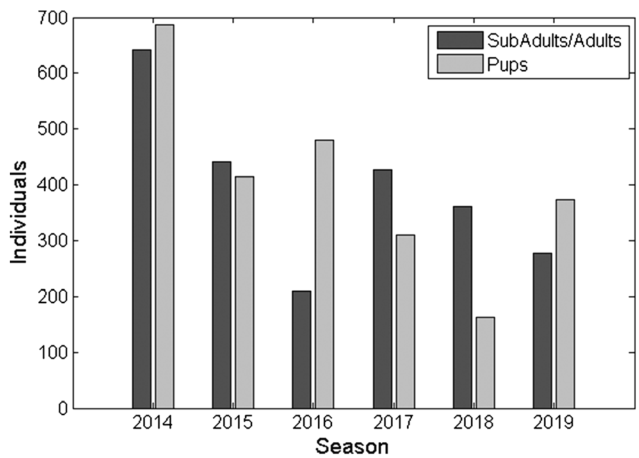

FIGURE 7 Preliminary data. Frequencies of the different maturity stages of the northern elephant seals (*Mirounga angustirostris*) recorded during the censuses carried out in the Rada Norte region of Guadalupe Island during the 2014–2019 winter seasons. Each bar represents a year during the 2014–2019 study period. The dark grey in the bar indicates the proportion corresponding to sub-adults and adults; the light grey colour corresponds to pups

(Hoyos-Padilla et al., 2016). Although small groups of elephant seals were observed on the beaches of Rada Norte Bay during the WSBMP (August–November), this period also coincides with peak white shark numbers (mostly YOY and juveniles that mainly feed on bony fishes; Klimley, 1985; Santana-Morales et al., 2012).

We expected to find a relationship between the abundance of white sharks and elephant seals on Guadalupe Island, as has been reported in other aggregation sites in the eastern North Pacific, such as the Farallon Islands (Brown et al., 2010). However, no evidence of this relationship was obtained. It is unclear how white shark hunting strategies and predation might influence the population dynamics of the elephant seals in the GIBR. However, recent studies suggest that white sharks around Guadalupe Island include other important food items in their diet, such as large cephalopods and other deep-sea species (Becerril-García et al., 2020d; Le Croizier et al., 2020).

4.4 | Management implications of cage diving tourism activities

As tourism activities around the GIBR continue to expand, it is also important to consider the impacts that tourism-based activities have on the local community with regard to commercial diving operations (e.g. abalone and lobster fishers; Meza-Arce et al., 2020). Abalone fishers do not use protective cages when diving; therefore, any increases in white shark abundance or the potential habituation to human activities could potentially impact this industry (Bruce, 2015).

The increase in the abundance of white sharks around the GIBR coincides with the oceanographic events observed in the eastern North Pacific and reflects the regulations implemented by Mexico and the USA in previous decades (White et al., 2019; Kanive et al., 2021). From the first year of this study, the predominant life stages observed were sub-adults and adults (>3 m TL). The behaviour of these white sharks (>4 m TL) has begun to be characterized by acoustic tracking methods to determine the degree of interaction between these sharks and the tourism vessels and to quantify critical white shark habitat (Santana-Morales et al., 2021). A maximum vessel carrying capacity of six vessels was determined based on this information (Santana-Morales et al., 2021). However, to date, 10 vessels have official permits to perform cage diving activities within the GIBR, with a limit of seven vessels simultaneously visiting the site due to the limited number of available anchoring spots (OSN, personal communication).

Despite the research and recent progress that has been made, it is important to assess other potential hazards to the white sharks of the GIBR, including potential pollution from vessels, engine noise, artificial light and seabed disturbances that result from repeated anchoring (Meza-Arce et al., 2020). Adequate procedures for monitoring activities, such as anchoring protocols, must be developed, as traditional surveillance is difficult given the remote nature of the GIBR (Cisneros-Montemayor et al., 2020). Additionally, it is important to consider annual oceanographic changes, especially given that few data are available for this ecosystem. For future management efforts to be effective, they should also consider the entire ecosystem, including the different species within the GIBR.

Given that Guadalupe Island is the only site in Mexico where consistent white shark monitoring is carried out, the results of this study may be used as a benchmark for assessing how well the white shark population is doing in Mexican waters and in the eastern North Pacific. Based on the results of the present study, it can be suggested that the population is increasing and is undergoing a spatial readjustment, which explains why sightings have become more frequent along the north-western coasts of Mexico (SEMARNAT, 2021). Oñate-González et al. (2015) found genetic connectivity between young white sharks from Bahia Sebastian Vizcaino and the GIBR based on a mitochondrial data analysis. Bahía Sebastian Vizcaino has been confirmed to be a nursery area for this species and is located inside one of the marine protected areas found along the western coast of Baja California (Oñate-González et al., 2017). In 2020, this connectivity was considered when updating the Action Programme for the Conservation of the White Shark in Mexico. The programme noted the importance of the connectivity between the coast and the GIBR and supports homogenizing white shark conservation efforts in all marine protected areas of the Baja California Peninsula.

Finally, addressing both ecological and social challenges may be the key to building a prosperous and healthy ecotourism industry that also meets the necessary conservation goals of the GIBR. First, it is important to update the Best Practices manual with the recent information on the abundance of juvenile white sharks around the GIBR. These data can help reduce potential threats, improving overall safety and management in the coming years. Standardized monitoring efforts must also continue (Santana-Morales et al., 2021), as they are necessary for detecting changes in population dynamics (Becerril-García et al., 2020c). These efforts should continue to involve local fishers in cage diving operations (e.g. participation in determining regulations and future management strategies) to strengthen the sustainability of this tourism industry, considering the welfare of the white sharks of the GIBR as well as that of other stakeholders (Cisneros-Montemayor et al., 2020; Meza-Arce et al., 2020).

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CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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APPENDIX I

White shark field behaviour form used by the biological observers during the 2014–2019 seasons during the biological monitoring of white sharks at Guadalupe Island. Key, patterns, and behaviour descriptions are based on those of Klimley & Ainley (1996) and Becerril-García et al. (2019).

APPENDIX II

Frequencies of the observed behaviours per day during the biological monitoring of the white sharks at Guadalupe Island from 2015–2019. Median, 25% and 75% percentiles, minimum, and maximum are shown (n = 386 days). Abbreviations: SE: Searching; SSW: Slow Swimming; CLI: Close Inspection; SU: Surfacing HA: Horizontal Strike; VA: Vertical Strike; BCA: Bait Caught; CR: Cruising; OB: Stalking; CB: Cage Bang; BRE: Breaching; PRE: Predation Event

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How much is too much? A carrying capacity study of white shark cage diving in Guadalupe Island, Mexico

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ABSTRACT

The Guadalupe Island Biosphere Reserve is one of the main aggregation sites for the white shark *Carcharodon carcharias* and is considered to be the best place in the world for white shark cage diving. From 2014 to 2019, the number of cage diving vessels in Guadalupe Island grew from 6 to 10, with an estimated 2800 tourists participating in white shark cage diving during the 2019 season. In 2016, the National Commission of Protected Natural Areas of Mexico requested a carrying capacity in which current regulations, white shark behavior, and the management capacity of the reserve were considered. To characterize the movement patterns of the white shark, 12 individuals were acoustically tracked. Based on the critical habitat of the white shark determined by an analysis of kernel densities, three carrying capacity scenarios (i.e., critical, optimal, and expanded) were calculated in which 1, 6 or 12 vessels, respectively, could operate simultaneously. It is important to consider that as the number of simultaneously operating cage diving vessels increases, the probability of sighting a white shark decreases [$>$ 0.9 (critical scenario), $>$ 0.5 (optimal scenario), and $>$ 0.1 expanded scenario]. The results of this study may act as a baseline for the management of other white shark tourism and aggregation sites in the world. However, future studies should also include other variables, such as the energy budget, due to the use of attractants in cage diving that may potentially affect individual behavior.

1. Introduction

Ecotourism and wildlife tourism are ecosystem services that allow human beings to come into close contact with the natural world [1]. In addition, these forms of nature-based tourism constitute important policy instruments that are used to help conserve biodiversity [2]. Wildlife tourism activities can often take place in remote, pristine, and ecologically important regions that have been established as protected areas to conserve biodiversity [3,4]. As such, the appropriate management of these activities will help to ensure the long-term conservation of the species that attract tourists as well as their ecosystems [4,5]. However, wildlife tourism activities are often lucrative and can modify the

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behaviors of target species to such an extent that their ecological and biological characteristics are negatively affected (e.g., diminished reproductive success) [6]. Moreover, wildlife tourism activities have been blamed for habitat degradation and ecosystem disturbances that have reduced the fitness of the species present [4,7]. For these reasons, it is necessary to implement precautionary and protective guidelines for wildlife tourism activities [8–10].

Worldwide, many wildlife tourism activities revolve around specific shark species (hereinafter referred to as shark tourism) [6,11]. The majority of shark tourism occurs in Oceania (22%) and North America and the Caribbean (16%), with a particular focus on reef sharks (33%), whale sharks (30%), hammerhead and requiem sharks (22%), and white sharks (13%) [12]. The use of attractants or bait is not necessary for all shark tourism activities, particularly those that are conducted in pristine sites in which sharks are highly abundant residents [13]. However, to ensure that tourists are satisfied with their wildlife experience, tourism operators often use attractants and/or provisioning techniques to keep sharks within the designated observation area. In these cases, different methods of supplying either bait or attractants may be employed, which mainly entail chumming, baiting, or feeding. Chumming consists of releasing fish fluids and tissues into the water to attract sharks over large areas, whereas baiting consists of using real or artificial bait to attract sharks passively or actively either visually or by smell [10,14,15].

In Mexico, there are many opportunities for diving with different shark species, and some of these activities do not require provisioning the animals with either bait or attractants. Examples of shark tourism that do not require provisioning include swimming with whale sharks (*Rhincodon typus*) and diving with bull sharks (*Carcharhinus leucas*) in the Cabo Pulmo National Park (in the Gulf of California) and diving with various shark species in the Revillagigedo Archipelago National Park (in the central Mexican Pacific) [5]. Shark tourism activities that employ provisioning techniques are carried out in Los Cabos and Bahía Magdalena (both in Baja California Sur) with pelagic species, such as the blue shark (*Prionace glauca*), short-fin mako (*Isurus oxyrinchus*), scalloped hammerhead (*Sphyrna lewini*), smooth hammerhead (*Sphyrna zygaena*), and silky shark (*Carcharhinus falciformis*). In Guadalupe Island, located off the western coast of Baja California, tourists can cage dive with white sharks (*Carcharodon carcharias*) [5]. The white shark is currently listed as vulnerable to extinction by the International Union for Conservation of Nature (IUCN) and is listed in Appendix II of the Convention on International Trade in Endangered Species (CITES).

Despite the popularity of cage diving, this activity has been associated with negative effects on target shark species. These negative effects are varied and include the transmission of diseases due to contaminated bait and natural predation being reduced as sharks become conditioned to artificial feeding [6,17]. Furthermore, the potential for negative interactions and accidents between tourists, cages, and the sharks themselves has been known to increase due to cage diving, and incidents have been observed in Guadalupe Island on several occasions [16,17]. For both reef sharks and the white shark, previous studies have also found negative effects on metabolic activity as a consequence of the elevated consumption of food items used as attractants [18,19]. Moreover, an increase in white shark residence times (from 11 to 98 days) and short-term changes in behavior have been registered within areas in Australia and Guadalupe Island [14, 20, this paper]. However, these effects have not been found to influence natural shark behavior in either the mid- or long-term, and attractants appear to function solely as distractors within the specific tourism area and do not appear to modify natural life cycle activities or result in behavioral conditioning to shark tourism [14,17,21,22].

White shark cage diving has been recreationally conducted in Australia since the 1970s [17,20]. Currently, this activity is carried out in the Farallon Islands (US), Guadalupe Island, South Africa, the Neptune Islands (Australia), and Stewart Island (New Zealand) [18]. Among these locations, the use of attractants is only prohibited in the Farallon Islands [23]. In Guadalupe Island, white shark cage diving involves the use of yellowfin tuna (*Thunnus albacares*) to maintain the white sharks in front of the observation cages [16]. Due to the visibility of the water (~ 30 m) and the size and abundance of the white sharks present, Guadalupe Island is now recognized as the best place in the world for white shark cage diving [5]. Due to the characteristics of the site, the number of white shark cage diving vessels operating in Guadalupe Island increased (i.e., from 6 to 10 vessels) from 2014 to 2019, reflecting a substantial increase in the number of tourists that visited the island [24]. In fact, more than 2800 tourists visited Guadalupe Island during the 2019 season [24,25].

Cage diving can be a great tool to remove the stigma and bad reputation that the white shark has been given. Moreover, this activity can be used to generate a new conservation ethic for this species while functioning as a scientific platform. Cage diving can also be used to assign an economic value to living sharks that is much higher than that of sharks that are caught for consumption or as trophies [5,19]. From an anthropogenic standpoint, shark tourism has proven to play a crucial role in conservation efforts, aiding in the development of local communities that value the exponential increase in profits that they obtain from the utilization of live sharks in a virtuous cycle called the blue economy [5,14,26].

Each year from July to December, white shark cage diving at Guadalupe Island constitutes one of the most economically important non-extractive activities [16,17,25]. In 2019, white shark cage diving in Guadalupe Island grossed US$ 8,000,000 with only 113 photo-identified white sharks, which breaks down to ~ US$ 70,795 per white shark [5, 24]. To put this in perspective, fishing studies that have been carried out along the west coast of the Baja California peninsula [27,28] have estimated that a white shark with a total length (TL) of 4 m (350 kg eviscerated weight with a set of dry fins) is only worth US$ 470. Nevertheless, the white shark is a protected species in Mexico and no retention of its products is permitted [29].

In Mexico, public policies of environmental matters are outlined in the *Ley General de Equilibrio Ecológico y Protección al Medio Ambiente* (LEGEPA; General Law of Ecological Equilibrium and Environmental Protection), which establishes that ecosystems must only be used in an optimal and sustained manner [30]. Moreover, the *Programa de Acción para la Conservación del Tiburón Blanco* (Action Program for White Shark Conservation) outlines a comprehensive strategy for white shark protection and conservation that is based on strengthening management measures that ensure sustainable, non-extractive uses that serve to prevent and mitigate the potential threats to this species and its habitat [31]. As such, the activities involving white sharks in Guadalupe Island must be sustainable while being founded on the premise that they will not alter or disturb the natural behaviors or habitat use of these sharks or those of the other species that make up the marine ecosystem of the protected area.

The term carrying capacity has been widely used in a variety of disciplines [32] and is frequently applied to populations and is defined as the number of individuals per unit area [33]. The carrying capacity of a marine environment is established based on the maximum number of tourists that the site can support [34–37]. In the LEGEPA, carrying capacity is defined as the estimation of the tolerance of an ecosystem to the use of its components, such that it does not exceed its short-term capacity for recovery without the implementation of restoration or recovery measures to establish ecological equilibrium [30].

In 2007, the carrying capacity for white shark cage diving at Guadalupe Island was determined based on the minimum permitted distance between vessels (i.e., 450 m) and the bathymetry of the area, and a carrying capacity of 10 simultaneously operating vessels was established [29]. In 2010, this carrying capacity was reviewed in an internal study that was not published but that employed the same parameters as those used in 2007. As a result of that study, the carrying capacity was reduced to 7 simultaneously operating large vessels. After a carrying capacity is determined, tourism activities may be regulated and possible negative impacts may be mitigated or limited [34,38]. However, it is crucial to also consider the current protection or conservation status of a site (a biosphere reserve in the case of Guadalupe Island), the management entities, and the tourism industry [7–9]. In addition, Cifuentes-Árias et al. [39] suggest that the biological factors of the species and the management capacity of a protected area should also be considered when estimating the effective carrying capacity of a site.

Given that white shark cage diving in Mexico only takes place at Guadalupe Island, this site is crucial for the management and conservation of this species [5,25]. In 2016 CONANP summoned expert white shark researchers to evaluate and update the carrying capacity for white shark tourism in this site, taking into consideration the criteria of Cifuentes-Árias et al. [39], the capacity of the authorities to manage the protected area, and white shark behavior, which is how this study was first conceived.

This study analyzes and integrates all of the available scientific information to date, including information generated by the authors themselves, to estimate a carrying capacity that adequately reflects current white shark regulations in Mexico [40], the behavior of the cage diving fleet, the movements and aggregations of white sharks and their aggregation zones, and the management capacity of the Guadalupe Island Biosphere Reserve. This study presents the first carrying capacity analysis for Guadalupe Island that takes into consideration white shark behavior and the authorized cage diving area management. The results of this study may serve as a basis for future management actions aimed at regulating white shark cage diving in Guadalupe Island and in white shark aggregation areas in other parts of the world.

2. Materials and methods

2.1. Study area

Guadalupe Island is located 240 km off the western coast of the Baja California peninsula (28° 52′ N, 118° 13′ W) and measures 35 km along its north-south axis while its width varies between 6 and 12 km (Fig. 1) [41]. The island is influenced by the California Current, one of the most productive ocean currents in the world, which is characterized by its cold and nutrient-rich waters that interact with local winds to foster high biological productivity [41,42].

The northeastern region of Guadalupe Island, also known as Rada Norte, is made up of a vestigial caldera composed of igneous rock with an approximate diameter of 10 km [43]. Insular topography protects this region from northwesterly winds, which predominate [44], while its

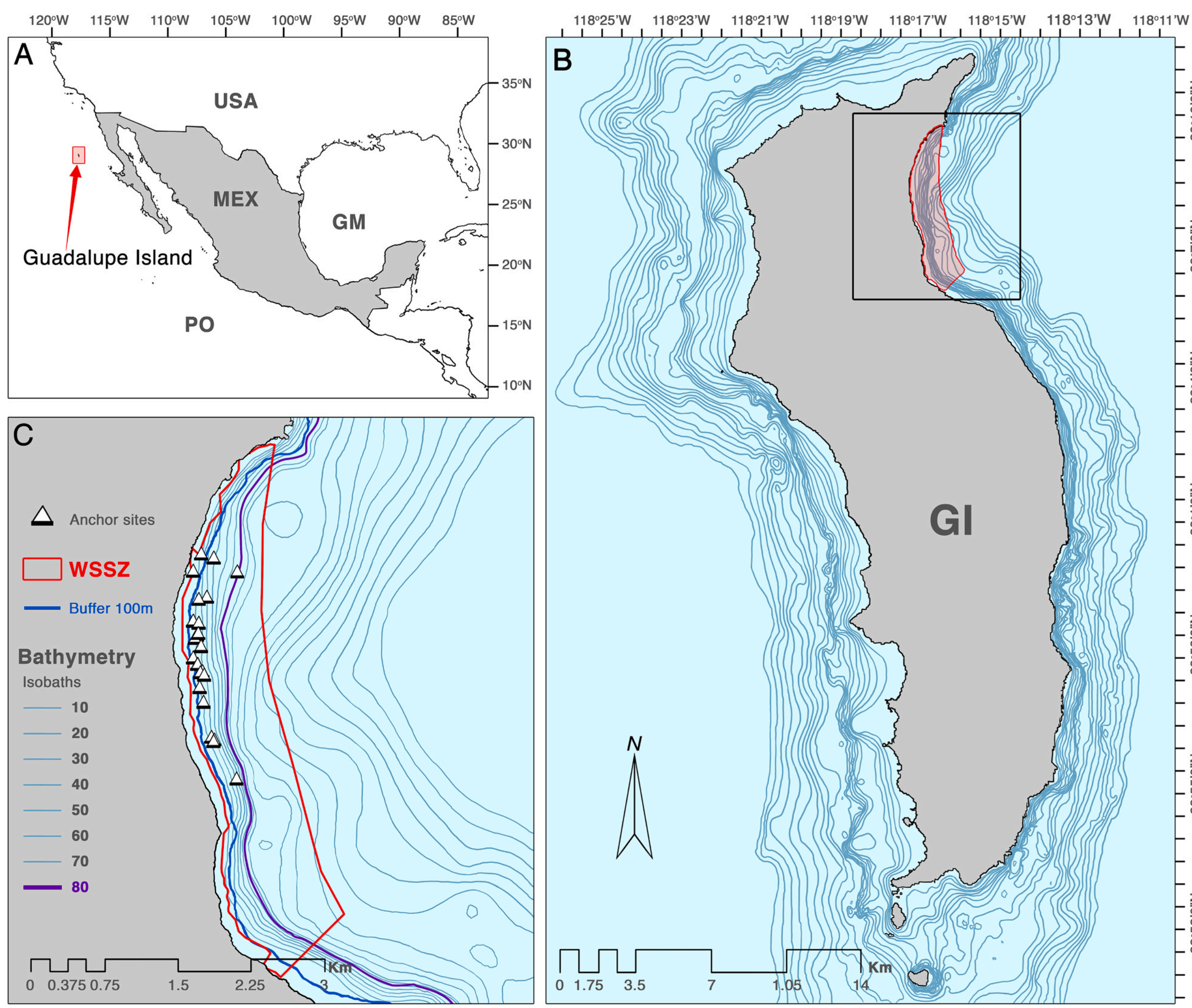

Fig. 1. The study area. A) The location of Guadalupe Island is shown in the red box. B) The designated cage diving area (red shaded region) and Guadalupe Island bathymetry. C) The black rectangular inset from panel B indicates the main aggregation area. The red polygon indicates the white shark sub-zone (WSSZ). The blue line shows the buffer zone or the maximum distance (100 m) at which the vessels can approach the coast. The purple line shows the 80-m isobath. The triangles indicate the anchor points recorded from 2014 to 2017. Abbreviations: GM, Gulf of Mexico; GI, Guadalupe Island; PO, Pacific Ocean; WSSZ, white shark sub-zone. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

abrupt bathymetry (0–200 m depth) prevents the resuspension of particulate organic matter [42]. Given that the northeastern region functions as a naturally formed roadstead, it has been designated as the area for white shark cage diving, which is carried out by surface-supplied diving using hookah [25].

2.2. Characterization of the white shark sub-zone

The white shark sub-zone polygon of Guadalupe Island was created using the coordinates referenced in the government management program of the Guadalupe Island Biosphere Reserve. Subsequently, a 100-m wide buffer zone was delimited that runs parallel to the coastline. This buffer zone serves to limit the approach of tourist boats to minimize disturbance to the resting pinnipeds that are found along the shore [45]. Within this zone, rules that have been agreed upon in the cage diving good practices must be followed, such as maintaining a minimum distance of 0.45 km between two vessels [46], which was fundamentally important for conducting this carrying capacity analysis. A total of 72 tourism vessel anchor points were recorded during the 2014–2017 seasons of the white shark biological observer program [24] and plotted to characterize anchoring dynamics within the white shark sub-zone.

2.3. Characterization of white shark movements

To characterize the area used by white sharks within the white shark sub-zone, a total of 21 white sharks were tracked by means of active acoustic telemetry using a small Robalo R220 boat (Georgia, United States) with an outboard motor equipped with a portable VR100 ultrasonic receiver (Vemco Ltd., Halifax, Canada) and a VH110 directional hydrophone (Vemco Ltd.). The sharks were fitted with V16TP-6x acoustic transmitters (Vemco Ltd.) attached with monofilament tethers and a plastic application dart. Tags were affixed to the sharks using a custom applicator and positioned on the dorsal musculature near the base of the dorsal fin. These transmitters were equipped with depth (0–680 m) and temperature (0–40 °C) sensors. Given that sub-adult (3–3.6 m TL for males, 3–4.8 m for females; Bruce and Bradford [47]) and adult white sharks interact with tourist boats more than sharks of other age classes [48], only individuals larger than 3 m TL were tagged. Ethics and tagging procedures followed an animal care protocol (Protocol number 16022, UC Davis Institutional Animal Care and Use Committee) and authorized by the research permits provided by the General Directorate of Wildlife (SEMARNAT; permit numbers SGPA/DGVS/6949/19, 07143/19, and 7913/19).

To detect and remove anomalies in white shark movements, spikes in the data were removed by low-pass filtering in MATLAB v. R2010a (Mathworks Inc., Natick, USA) using the community contributed script *despiking*. Temperature values lower than 0 °C and higher than 40 °C were eliminated from the acoustic data as well as all depths outside the range of 0–680 m. In addition, data with temperature values that did not correspond to acceptable values for a given depth based on the trend for the data series were eliminated. Finally, values that indicated speeds greater than 2.5 m/s (i.e., the average cruising speed of a white shark) were eliminated according to the variations in depth over time [49].

Geographic position data were plotted with ARC v.10.1 (ESRI Co., Redlands, USA) using the chronological representation of the coordinates and trajectories of the white shark movements recorded during each track. A kernel analysis was used to map the observation densities to determine the geographic areas in which the white sharks spent the most time. The kernel calculation was based on the distances between observations using the nearest neighbor method, and a 450-m bandwidth was used to estimate the probability density of encounters, which considered the established distance between boats. The kernel density results were associated with area measurements considering likelihood estimators and weight functions that were derived with a high degree of statistical reliability and reproducibility [50], and the frequency histograms were adjusted to reflect the probability of encounters per unit area [low (< 0.01) to high (1); 450 m]. Subsequently, a digital delineation was used to obtain the contour lines corresponding to each encounter probability contour interval and to evaluate overlapping areas. The contour lines were used to estimate the area that was most frequently used by tagged white sharks in three different scenarios: 1) when all data were pooled, 2) when only day or night data was included, and 3) when only the anchor points that were favored by cage diving operators were included. The area was calculated using two-dimensional cartesian mathematics with a precision of 1 m.

Finally, the accumulated interaction times between tourism boats and individual white sharks were determined for the 2015 and 2016 seasons. The interaction time was defined as the time during which an individual shark remained within a defined circular area (30-m radius) surrounding a given vessel. The times at which the individual shark entered this area (T1) and later left the area (T2) were used to determine the interaction time.

2.4. Monitoring and surveillance capabilities

To compare the management capacity of the Guadalupe Island Biosphere Reserve with those of other protected areas, the methodology proposed by Cifuentes-Árias et al. [39] was used, which indicates that this management capacity will depend to a great extent on the components of the protected area, such as its personnel, equipment, and infrastructure. In this sense, a comparative analysis of said components was conducted among the principal protected areas of the Baja California peninsula and northern Pacific region, namely the El Vizcaíno Biosphere Reserve; the Pacific Islands Biosphere Reserve; the Protected Area for Flora and Fauna Valle de los Cirios; the Cabo Pulmo National Park; the San Pedro Mártir National Park; the Revillagigedo National Park; and the Bahía de los Ángeles, Canales de Ballenas y Salsipuedes Marine Zone Biosphere Reserve.

Information on the personnel, infrastructure, and equipment of these protected areas was provided by their managing directors. Since the El Vizcaíno Biosphere Reserve presented the highest values for each of the three categories, it was considered as the base surveillance unit (i.e., percent coverage value of 100%) against which the percent coverage of each of the other seven protected areas was compared. The relative management capacity (MC) of each area was determined with Eq. (1):

$$MC = \frac{Infr + Eq + Pers}{3} \times 100, \quad (1)$$

where *Infr* is the infrastructure percentage, *Eq* is the equipment percentage, and *Pers* is the personnel percentage.

Finally, to characterize the percent coverage, the criterion of Cifuentes-Árias et al. [39] was used. In this categorization, a coverage percentage of $\leq$ 35% (0) was considered unsatisfactory, 36–50% (1) was considered not very satisfactory, 51–75% (2) was considered moderately satisfactory, 76–89% (3) was considered satisfactory, and $\geq$ 90% (4) was considered very satisfactory.

2.5. Carrying capacity calculation

In this study, the term carrying capacity was defined as the maximum number of vessels that could simultaneously be used for cage diving within the white shark sub-zone based on the available space, current regulations, tourism activities, and local white shark movements. Once data of the aforementioned variables had been gathered, a specific area was defined for the development of white shark cage diving, considering the relative management capacity of the Guadalupe Island Biosphere Reserve. To calculate the carrying capacity, this area was divided by the physical space required by each vessel, which was determined from the established courtesy distance between two vessels (i.e., 0.45 km diameter) [29], taking into consideration the core of the kernel distribution with encounter probabilities of $0.9 \geq 0.1$. For this, only data collected during the day (6 AM–6 PM) were used in order to exclude white shark use areas that were not affected by tourism activities (cage diving can only be performed during the day).

From the encounter probabilities, we established three different carrying capacity scenarios: 1) critical (encounter probability > 0.9), 2) optimal (encounter probability > 0.5), and 3) expanded (encounter probability > 0.1; Table 1). The area needed for each boat based on the courtesy distance was calculated from the area of a circle ($Area = \pi r^2$, where $r = 0.225$ km). The total area of physically available space was determined from the authorized observation area delimited by the 80 m isobath (maximum mooring depth) and the 100-m coastline limit established by the reserve.

3. Results

3.1. Characterization of the white shark sub-zone

The characterization of the white shark sub-zone aimed to identify the guidelines that should be used for white shark cage diving to ensure the protection of the species and the sustainable development of this wildlife tourism practice. The white shark sub-zone coordinates provided by the Reserve Management Program of CONANP, a polygon with an approximate area of 6.07 km^2 was generated (Fig. 2). The anchor points of the vessels allowed for a polygon to be generated that was used to identify a linear anchoring pattern that ran parallel to the coastline. This pattern was determined from the depth favored by boat operators (80 m), the locations of resting beaches for the different pinniped species [40], and the areas that were most protected from the wind. Considering the anchor points that were farthest from each other from north to south and those along the buffer line of the 80-m isobath, a preferential use polygon pattern for the vessels was recorded, which had an area of 1.1 km^2, a length of 3.4 km, and width of 0.34 km (Fig. 1).

3.2. Characterization of white shark movements

Data from 12 white sharks (7 females, 5 males) with TLs between 3 and 5.5 m (mean: 4.16 ± 0.61 cm SD) were obtained from 2015 to 2019. Taken together, these data were collected from a total of 21 active acoustic tracks with durations between 4 and 38 h (mean: 15.7 ± 9.36 h SD), yielding a total of 330 h of effective monitoring data (Table 1). These acoustic tracks provided 208,036 geo-referenced detections, which allowed for a kernel density calculation with observation percentages ranging from 1% to 100% [51]. In this way, a white shark use polygon was determined with a total area of ~ 160,073 km^2 and a critical area of ~ 3.49 km^2 in which the detections from all tracked sharks overlapped (Fig. 2). With regard to the interaction times between the sharks under observation and the tourism boats, the maximum and minimum accumulated interaction times, which ranged between 5 and 848 min (mean: 218 min), were recorded (Table 1).

3.3. Monitoring and surveillance capabilities

When comparing the relative management capacities of the protected areas evaluated in this study, it was found that the El Vizcaíno Biosphere Reserve presented the highest values in the personnel, infrastructure, and equipment categories. In particular, this protected area had 19 people in director (n = 1), deputy director (n = 1), department head (n = 1), social program operator (n = 4), and operational technician (n = 12) positions, in addition to land transport vehicles (cargo and personnel, n = 8), marine transport vehicles (small boats with outboard motors, n = 1), offices in the city closest to the reserve (n = 1), and stations within the reserve (n = 3; Table 2).

Considering that the El Vizcaíno Biosphere Reserve showed the highest management capacity, its relative management capacity was deemed to be 100% (very satisfactory), and the relative management capacities of the other areas were determined. The relative management capacity of the San Pedro Mártir National Park was determined to be 80.6% (satisfactory), followed by those of the Bahía de los Ángeles, Canales de Ballenas y Salsipuedes Marine Zone Biosphere Reserve (55%, moderately satisfactory), the Revillagigedo National Park (50%, not very satisfactory), the Pacific Islands Biosphere Reserve (48%, unsatisfactory), the Guadalupe Island Biosphere Reserve (34%, unsatisfactory), the Valle de los Cirios Flora and Fauna Protection Area (33%, unsatisfactory), and the Cabo Pulmo National Park (31.6%, unsatisfactory; Table 2).

3.4. Carrying capacity calculation

Considering the white shark sub-zone polygon, 100-m buffer, 80-m isobath, unsatisfactory relative management capacity, and central

Table 1
Acoustically tracked white sharks in the Guadalupe Island Biosphere Reserve (2015–2019). The code indicates the identification number of the tagged shark and the tracking year. Time indicates the total duration of the track. Interaction is the accumulated interaction time between the shark and tourism vessels.

Code	Date	TL (m)	Sex	Time (h)	Interaction (min)	Avg. Depth (m)	Avg. Temp. (°C)
T01-15	7–8 Sep-15	4	Male	14.3	175	17.2	21.8
	12- Sep -15			4	5	33	20
	14- Sep -15			7	38	24	21.7
	25- Sep -15			24	193	41.5	19.2
T02-15	13–14 Sep 15	4	Female	11.5	157	43	19.9
	13-Oct-15			24	464	14.1	22.5
T03-15	21- Sep -15	4.5	Male	24	329	47.9	19.6
T04-15	03-Oct-15	4	Male	16.3	476	46.9	18
	05-Oct-15			24	209	81	16.4
T05-16	24-Ago-16	4	Female	7.4	70	47.25	19.8
	3–4 Sep 16			14.8	105	22.39	20.8
	07- Sep -16			11.30	119	45.08	18.13
	18- Sep -16			4	45	5.7	21.28
	26–27 Sep 16			24.2	–	37.3	18.9
T06-16	14- Sep -16	4	Male	6.1	47	48.08	18.9
T07-16	28–30 Sep 16	5	Male	38	848	45	18.67
T08-17	15–17 Oct 17	4	Female	7	–	94	15.9
T09-18	16 Oct 18	4	Female	8	–	22	20
T10-18	14-Oct-18	3	Female	10	–	45	18
T11-19	26–28 Sep 19	5.5	Female	22	–	95	15.78
T12-19	4, 7–8 Oct 19	4	Female	28	–	16.05	20.22
Total 12		~ 4.16	7F/5M	330		~ 41.49	~ 19.37

Abbreviations: TL, total length; Avg. Temp, average temperature; Avg. Depth, average depth.

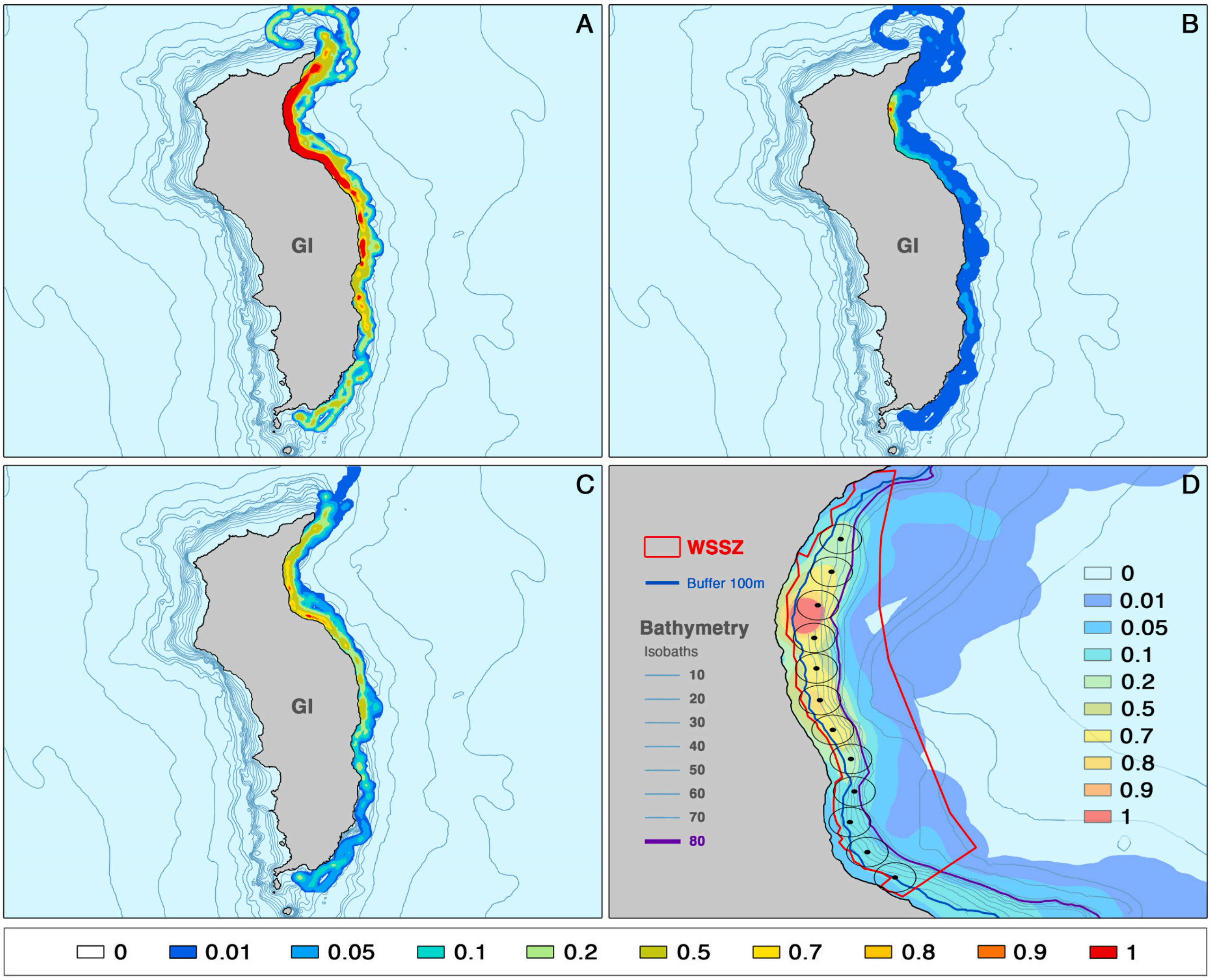

Fig. 2. Kernel densities showing the habitat use of the great white shark in the Guadalupe Island Biosphere Reserve. The color axes at the base of the graph and in panel D indicate the different contours and their respective probabilities. Panel A shows all acoustic tracking data; Panel B shows the data collected during the day (6 a.m.– 6 p.m.); Panel C shows the data collected at night. Panel D is an amplification of the white shark sub-zone (WSSZ) and shows daylight data and all the variables considered in the study. The WSSZ indicates the public use polygon decreed in the management program of the protected area. The blue line or buffer indicates a distance of 100 m from the coast, which is the maximum distance that tourist boats are allowed to approach. The purple line indicates the 80-m isobath, which is the maximum depth at which tourist boats can anchor. The black dots indicate the number of boats that fit within each contour, and the circle around each point indicates the 450-m courtesy distance that should be present between boats. What we wish to indicate visually with the circles (with center points) is the number of ships that could fit within each Kernel contour. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Relative management capacity of the eight principle protected areas of the Baja California peninsula. The main management components of the protected areas are presented based on the information provided by the different managing directors. The management capacity of the El Vizcaíno Biosphere Reserve was considered to be 100%.

PA	Terrestrial area (ha)	Marine area (ha)	Personnel	%	Infrastructure	%	Equipment	%	Management capacity
El Vizcaíno BR	2,259,002	287,787	19	100	4	100	9	100	100%
San Pedro Martir NP	72,910	0	10	52.6	4	100	8	88.9	80.6%
Bahía de los Ángeles, Canales de Ballenas y Salsipuedes Marine Zone BR	483	387,473	7	36.8	2	50	7	77.8	55%
Revillagigedo NP	15,518	14,793,261	10	52.6	3	75	2	22.2	50%
Islas del Pacífico BR	79,139	1,091,083	9	47.4	3	75	2	22.2	48%
Isla Guadalupe BR	26,276	450,694	4	21.1	1	25	5	55.6	34%
Protected Area for Flora and Fauna Valle de los Cirios	2,521,987	0	8	42.1	1	25	3	33.3	33%
Cabo Pulmo NP	38.86	7072	5	26.3	1	25	4	44.4	31.6%

Abbreviations: PA, protected area; BR, biosphere reserve; NP, national park.

contours generated by the kernel analysis (Fig. 2), three carrying capacity scenarios (i.e., critical, optimal, and expanded) were generated. Taking into account the mandatory courtesy distance of 0.45 km (total area of 0.15 km^2 per boat) and areas with different probabilities of shark encounters ranging from high to low based on the kernel analysis, it was determined that a critical scenario could allow for 1 boat with a sighting probability > 0.9, whereas the optimal and expanded management scenarios could allow for 6 and 12 boats with sighting probabilities of > 0.5 and > 0.1, respectively (Table 3).

4. Discussion

This study incorporates information on the bathymetry of the Guadalupe Island Biosphere Reserve, vessel anchoring points and operations, reserve regulations, white shark behavior, and management capabilities to generate a useful management tool for white shark cage diving [31]. Our acoustic tracking results suggest a critical white shark use area that clearly overlaps with the anchoring sites use by the cage diving vessels. Additionally, we provide a detailed comparison among the relative management capacities of the protected areas of Baja California, which highlights the current limited management capabilities of the Guadalupe Island Biosphere Reserve given its location, size, and complexity (i.e., having both terrestrial and marine protected areas). In addition, this study quantifies and strengthens the current working dynamics of the white shark cage diving tourism industry of Guadalupe Island. As of 2018, the operators of the cage diving vessels in this protected area have designed a travel calendar that prevents more than seven boats from simultaneously conducting activities [25].

4.1. The overlap of sharks and cage diving vessels

The observed trajectories of the acoustically tracked sharks were strongly related to the anchor positions of the tourism boats (even those within the white shark sub-zone). From the first acoustic tracking data collected during the 2015 season (4 sharks; 9 tracks; 149 accumulated h), it was observed that the area of greatest use overlapped with that of the polygon generated with the anchor points of the tourism vessels (white triangles in Fig. 1). As more acoustic tracking data were compiled, the total shark use area grew, covering a notable portion of the total area of the white shark sub-zone, the core of which was visited by all sharks (Fig. 2). This indicates the potential influence that tourism activities in the Guadalupe Island Biosphere Reserve may have on white shark behavior and the important overlap that exists between tourism activities and white shark home ranges [16,18,25,33].

With the acoustic tracking data, it was found that white sharks display different diurnal and nocturnal behavior patterns, which may be strongly influenced by cage diving activities. However, previous acoustic tracking studies that have ignored the influence of tourism activity have found the same pattern, namely that adult white sharks move offshore during the day and remain close to the coast at night [48]. This was the principle reason why only acoustic monitoring data collected during the day were included in our analysis. By excluding nighttime acoustic tracking data, we were able to exclude the areas that white sharks use at night, when the influence of tourist boats is minimal.

Table 3
Comparison of the carrying capacity scenarios based on all criteria.

Scenario/ Criterion	Shark encounter probability	Total area (km^2)	Area used per 1 boat (km^2)	Carrying capacity (# of boats)
Critical	> 0.9	0.13	0.15	1
Optimal	> 0.5	0.95	0.15	6
Expanded	> 0.1	1.95	0.15	12

4.2. White shark behavior in Guadalupe Island

From the acoustic tracking data, it was observed that not all sharks were equally attracted to each tourism boat. In particular, sharks showed different levels of interaction among the tourism vessels. While some sharks spent more time near the vessels, other showed only brief interactions (Table 1). This conclusion was corroborated by observations made during the concurrent biological observer program [see 25 for a detailed description of this program]. In particular, it was found that some sharks were only registered at certain vessels [24]. The same type of preferential behavior has been recorded in Australia, and it was concluded that the variation in the degree of interaction among individuals (e.g., presence, proximity to vessels, and bait attack) highlights the complexity of the effects that cage diving may have on white shark behavior [21]. In the case of Guadalupe Island, we believe that the abundance of individuals is such that a kind of micro-territorialism is generated that is based on the hierarchical status of each shark, with low-ranking sharks not being permitted to approach boats or areas by higher ranking sharks, as observed in previous behavioural studies [16].

The observations that have now been reported in two white shark aggregation sites indicate that it is necessary to better assess individual white shark preferences for particular cage diving attributes to determine those that serve to either attract or repel sharks, in addition to evaluating the often controversial provisioning approach to shark tourism. To some extent, these individualistic behaviors are beneficial to the white sharks of Guadalupe Island in that tourism activities may not necessarily affect all individuals equally [16,17]. However, future studies are required to evaluate the impacts of tourism activities on white sharks since cage diving has been shown to potentially affect the behaviors and energy budgets of individuals [18,25,31].

Although recent studies have suggested that tourism activities have a low impact on the behavioral conditioning of white sharks in Guadalupe Island [17], it is also important to assess white shark movements and behaviors in the absence of tourism activities. These comparisons are needed to fully assess how white sharks utilize the white shark sub-zone in the absence of attractants and humans. Moreover, the acoustic tracking data presented in this study were collected during periods when white shark cage diving activities were underway. In a previous study, Hoyos-Padilla et al. [48] observed individuals who also used the white shark sub-zone on a recurring basis during November in the absence of tourism activities. This study identified that the northern portion of the white shark sub-zone was used the most. This area also contains one of the main elephant seal (*Mirounga angustirostris*) colonies [45,46]. Despite these findings, the low number of individuals that were tracked and the time frame of this research precludes further speculation on white shark behavior and supports the need for future study.

4.3. Managing the cage diving activities at Guadalupe Island

In this study, three carrying capacity scenarios are proposed in which 1, 6, or 12 tourism vessels can simultaneously conduct their activities in the white shark sub-zone (Table 3), according to the management capacity of the protected area. Currently, 10 boats are authorized to conduct white shark cage diving in Guadalupe Island. However, an internally generated rotation schedule has been implemented so that no more than 7 boats are simultaneously operating within the white shark sub-zone. Based on this study, in which the management capacity of the protected area was found to be unsatisfactory, only one vessel should operate at a time. However, it is possible for the corresponding authorities and cage diving companies to work together to collaboratively finance the management and surveillance actions that are lacking within the white shark sub-zone and surrounding areas. Nevertheless, these scenarios should not be viewed as rigid, although they can function as useful reference points for future management decisions.

When answering the question we pose in the title of this paper, it is important to consider that as the number of boats that simultaneously conduct cage diving increases, the opportunity to see a white shark within a 450-m radius decreases, considering that sighting probabilities of > 0.9, > 0.5, and > 0.1 were found for the critical, optimal, and expanded scenarios, respectively. It is important to mention that white sharks arrive at Guadalupe Island in a staggered manner and that the period of September–November is when the greatest abundance of individuals has been registered [24,48]. As can be seen in Table 1, acoustic monitoring was carried out during August–October, and thus this study considers a period of peak abundance. Therefore, the probability of sighting a great shark before or after this period in each scenario is likely even lower than the value reported here. Given that this study does not consider the effects or impacts that white shark cage diving may have on the species in the mid- or long-term, it is useful to apply the precautionary principle when selecting the scenario as a preventive measure [9]. In this sense, the expanded scenario must be discarded, whereas the critical and optimal scenarios could serve as reference points to select an intermediate number of tourism vessels.

4.4. Management actions and conservation

The main objective of the action program for white shark conservation in Mexico is to develop strategies that generate information to conserve the species, including information on habitat use [31]. In this context, Guadalupe Island Biosphere Reserve managers have also expressed concern regarding the impact that cage diving activities could have on the white shark habitat and the other species present. In particular, there are concerns regarding the multiple anchor points that some vessels employ during a single trip, which may possibly affect the seabed and the associated benthic communities. In addition, the noise produced by the generators and engines onboard the cage diving vessels may be affecting the cetaceans in the area, while the night lights may be affecting the behavior of nocturnal birds, such as Leach's petrel (*Oceanodroma leucorhoa*) and the Mexican shearwater (*Puffinus opisthomelas*) [52]. From the results of this study, it is possible to determine fixed anchor points that will favor habitat protection and minimize the impacts of tourism activities on other species [5,22].

Shark tourism and its research at Guadalupe Island began nearly concurrently almost two decades ago [25]. Since then, managers at Guadalupe Island have strived to improve the management and sustainability of white shark cage diving [25,31], tour operators have incorporated environmental awareness in their tours [all authors, pers. obs.], researchers have aimed to assess the impacts of cage diving on white sharks [17,48], and members of the local community have begun to participate in the activity [25,45]. While several management challenges still exist, we consider that the combination of all of these efforts is taking white shark cage diving from a form of pure wildlife tourism to an activity with an ecotourism-focused approach, which not only benefits the conservation of this species but also the environment and the local community [2,3,5]. This study aims to provide valuable information that may eventually help white shark cage diving to become a form of ecotourism.

5. Conclusions and future research

The present study is the first carrying capacity assessment for white shark cage diving that incorporates encounter probabilities based on the spatial patterns of behavior at the Guadalupe Island Biosphere Reserve. These patterns revealed critical sites in which diving vessel regulations may be implemented to better manage this threatened top predator. The results of this study highlight the need to define a new vessel rotation schedule for the island and to designate fixed anchorage sites. These anchorage sites will not only favor tourism activities while reducing the impacts on white shark behavior but may also contribute to reducing the yet unevaluated potential damage to the seabed and associated fauna [45,53]. On the other hand, it is necessary to continue researching the white shark (e.g., energy expenditure studies) to help characterize the impacts that tourism activities could be having on this species [31]. In addition, when selecting a carrying capacity scenario, the precautionary principle should be considered as a measure to prevent irreversible negative impacts [8,10].

The analysis of the management capabilities of the protected areas evaluated in this study highlights the substantial lack of personnel and equipment. These are necessary to ensure the adequate preservation of marine and terrestrial resources of the Guadalupe Island Biosphere Reserve and of other key areas for marine conservation like the Cabo Pulmo National Park and Pacific Islands Biosphere Reserve. Improvements of the working conditions of the personnel of each protected area are urgently needed. Successful conservation actions depend on such factors and on effective responses to other threats like illegal fishing, unsustainable or damaging tourism practices, and natural or anthropogenic events related to climate change, forest fires, and pollution.

The present study represents an effort to integrate available scientific information on the spatio-temporal distribution and individual behaviors of the white sharks at Guadalupe Island. In addition, it provides information to improve the operational dynamics of cage diving to determine the carrying capacity of this marine ecosystem and the degree of compliance with the public policies for ecosystem protection and conservation delineated in Mexican laws. Likewise, the results of this study support the aims of the Action Program for White Shark Conservation [31] and may be used as a tool to define limits for the use of white shark habitat in Guadalupe Island. Finally, this study will contribute to improving the environmental management capabilities of the protected areas evaluated and possibly of other white shark aggregation sites in the world.

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Author statement

All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the concept, design, analysis, writing, or revision of the manuscript.

CRediT authorship contribution statement

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Declarations of interest

None.

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Glossary

acoustic tracking:: technique employed to follow animals tagged with ultrasonic transmitters using a unidirectional hydrophone to obtain fine-scale continuous movement data.
biological productivity:: amount and rate of production in a given ecosystem over a given time period, although this term may apply to a single organism, population, or entire community.
biological observer program (of the white shark):: long-term monitoring that focuses on photo-identification and recording white shark behavior during cage diving operations.
biosphere reserve:: a geographical area representative of the different ecosystems of the planet, which may be both terrestrial and marine, and that is part of the Man and Biosphere Program (MAB) that was initiated by UNESCO in 1970 with the aim of reconciling the conservation and use of natural resources and outlining the current concept of sustainability.
buffer zone:: an area surrounding or adjacent to the core area(s) of a reserve that is used for activities that are compatible with sound ecological practices related to scientific research, monitoring, training, and education.
carcharhinids:: any member of the shark family Carcharhinidae (also called **requiem sharks**), which includes ~ 12 genera and 50 species worldwide. Carcharhinids are found primarily in warm and temperate ocean waters, although a few species inhabit fresh or brackish water. Carcharhinidae is one of the largest shark families.
carrying capacity:: maximum number of people that may visit a tourist destination simultaneously without resulting in the destruction of the physical, economic, socio-cultural environment or an unacceptable decrease in the quality of visitor satisfaction
cartesian mathematics:: geometry describing every point in an n-dimensional space by means of n coordinates referred to within n-coordinate axes.
eviscerated weight:: fresh weight of an animal once it has been stripped of all of the internal organs of the abdominal cavity.
isobath:: line running connecting points with identical depth values.
kernel analysis:: a kernel density estimation, which is a non-parametric method to estimate the probability density function of a random variable.
protected area:: a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, aimed to achieve the sustainability and long term conservation of natural resources with associated ecosystem goods and services as well as social and cultural values [39].
national park:: a park that is used for conservation purposes and that is created and protected by national governments.
pinnipeds:: an infraorder of carnivorous mammals of the caniform suborder. Pinnipeds have long tails, short legs, flat hands, and clapped feet in the shape of flippers. They tend to be gregarious and feed on fish, mollusks, and crustaceans. Pinnipeds are present in all seas.
provisioning:: when an attractant, typically food-related, is used to aggregate target species and ensure consistent, up-close encounters for tourists.
reserve management program:: a plan to implement a set of rules in order to ensure good practices with regard to the activities that are carried out within the framework of the reserve.
white shark sub-zone:: the area in which white shark cage diving and observation is allowed.
wildlife (shark) tourism:: a set of tourism activities focused on observations and interactions with plant and animal life (sharks in the current study) in their natural habitat [54].

CONCLUSIONES GENERALES

En esta tesis, presento el reporte del Tiburón Blanco de vida libre más pequeño (107 cm LT) que se haya reportado hasta hoy a nivel mundial. Los resultados biométricos indican que contaba con pocos días de haber nacido, lo que sugiere que la zona de su captura incidental podría ser un área de nacimiento o de crianza extendida. Además, los resultados del análisis genético sugieren que individuos neonatos y juveniles que habitan la zona costera de Baja California pueden provenir de individuos adultos de California central o Isla Guadalupe. Estas observaciones sugieren la necesidad de una mayor coordinación internacional para el manejo y protección de especies compartidas.

También, mostramos el valor de un monitoreo innovador utilizando las embarcaciones turísticas que realizan la actividad de observación de Tiburón Blanco en jaula. Con esta plataforma pudimos llevar acabo un programa de monitoreo de Tiburón Blanco único en el mundo. Durante el periodo 2014-2019 registramos características poblacionales y de comportamiento importantes del Tiburón Blanco en Isla Guadalupe, observando una tendencia en aumento que coincide con los eventos oceanográficos registrados en el Pacífico Noroeste. También refleja las regulaciones de conservación de la especie implementadas en décadas previas en México y Estados Unidos. Los resultados que presento en esta tesis pueden ser utilizados como un punto de referencia para evaluar el estado de la población del tiburón blanco en México y en el Pacífico Noreste.

Así mismo, con base en los resultados del monitoreo biológico y utilizando la telemetría acústica pudimos caracterizar el comportamiento de los tiburones blancos alrededor de Isla Guadalupe. Con la información de comportamiento generada pudimos generar estrategias de manejo como el diseño de polígonos de uso público y la capacidad de carga del sistema. Esta información es relevante para el manejo adecuado de las actividades turísticas en la isla y para promover el uso sustentable de este recurso. Finalmente, concluimos que el aprovechamiento no extractivo de la especie, como es el avistamiento de Tiburón Blanco en jaula, se puede llevar acabo de forma sustentable y segura mientras sea regulado con bases científicas y con datos actualizados de su monitoreo biológico.