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Doctorado en Ciencias
en Ecología Marina

Importance of Ojo de Liebre lagoon and Vizcaino Bay in the early life stages of white sharks: ecological and fishery issues

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Resumen de la tesis que presenta **Emiliano García Rodríguez** como requisito parcial para la obtención del grado de Doctor en Ciencias en Ecología Marina

Importancia de la laguna Ojo de Liebre y de Bahía Sebastián Vizcaíno en los primeros estadios de vida del tiburón blanco: aspectos ecológicos y pesqueros

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Bahía Sebastián Vizcaíno (incluyendo la laguna Ojo de Liebre, LOL), está localizada en la costa oeste de la península de Baja California, y es un área de crianza para tiburones blancos inmaduros (TBI, *Carcharodon carcharias*) en el Noroeste mexicano. La utilizan comunidades pesqueras que interactúan con los TBI durante sus operaciones de pesca. Esta tesis exploró el rol ecológico de los TBI en la bahía y su interacción con las pesquerías artesanales utilizando diferentes metodologías. Se aplicaron 77 entrevistas a pescadores de la Bahía para describir sus actividades de pesca. De acuerdo a sus respuestas, las especies objetivo de la pesca (lenguado, curvina blanca y guitarra blanca) son presas potenciales de los TBI. Los TBI (<200 cm longitud total) se capturan mayormente en verano y las áreas de mayor interacción se encuentran en hábitats costeros cercanos a la boca de la LOL. Se utilizó telemetría acústica pasiva para entender cómo estos tiburones utilizan la LOL. Se detectaron 17 TBI (marcados localmente y en California, EU) en 11 receptores colocados dentro y fuera de la laguna; registrando un mayor número de tiburones en meses con capturas incidentales bajas. Empleando Modelos Generalizados Aditivos, se analizó el efecto de factores biológicos y ambientales en la presencia de los TBI. El mes (meses de otoño e invierno) y el lugar de marcaje (California) fueron las variables que mejor explican la presencia de TBI fuera de la laguna. La presencia dentro de la laguna se explica por el mes (invierno e inicio de la primavera) y la talla (tiburones >175 cm). Utilizando análisis de isótopos estables (SIA) de Carbono y Nitrógeno, en músculo de los TBI, se estimó una mayor contribución de presas demersales (44-48%), que son especies objetivo para los pescadores locales, en comparación con presas pelágicas (25-37%) y oceánicas (15-31%). También se compararon las dietas de especies simpátricas de tiburones que se alimentan en la Bahía usando los SIA. Se estimó un traslapo (45.27%) en el nicho isotópico entre TBI y tiburones martillo de tallas similares, sugiriendo que ambas especies se alimentan de presas parecidas o con composiciones isotópicas similares. Esta tesis confirma la importancia de la LOL y las áreas cercanas a su boca como área de crianza, donde se presentan individuos diferentes durante todo el año y donde encuentran una alta disponibilidad de presas. Las capturas incidentales son más frecuentes durante los meses con menos tiburones detectados, sugiriendo un traslapo temporal menor al pensado. Sin embargo, el traslapo espacial con las pesquerías artesanales parece ser alto y existe una competencia por las presas de los tiburones. De acuerdo al traslapo en dietas estimado, si las poblaciones de presas disminuyen por efecto de sobrepesca, la competencia entre especies simpátricas puede aumentar en el futuro, sumando una amenaza más para los TBI. Los resultados de esta tesis ayudarán a mejorar las medidas de manejo existentes para minimizar los impactos de las pesquerías artesanales sobre las poblaciones de TBI.

Palabras clave: tiburón blanco, pesquerías artesanales, áreas de crianza, Bahía Sebastián Vizcaíno

Abstract of the thesis presented **by Emiliano García Rodríguez** as a partial requirement to obtain the Doctor of Science degree in Marine Ecology

Importance of Ojo de Liebre lagoon and Vizcaino Bay in the early life stages of white sharks: ecological and fishery issues

Abstract approved by:

Dr. Oscar Sosa Nishizaki
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Vizcaino Bay, including its associated coastal lagoon Ojo de Liebre, is located on the Pacific coast of the Baja California Peninsula and has been confirmed as a nursery area for immature white sharks (IWS, *Carcharodon carcharias*) in Northwestern Mexico. This bay hosts several artisanal fishery communities that interact with early life stages during their fishing operations. This dissertation gave insights into the ecological role of IWS and the degree of interaction with artisanal fisheries in this nursery using several approaches. Semi-structured interviews were applied to 77 fishers along the Bay coast and helped to describe artisanal fishing activities. The main target species in the area (shovelnose guitarfish, white seabass, and California halibut) are potential prey of IWS based on fisher responses. Immature white sharks (<200 cm total length) are mostly caught during summer, and higher interaction areas are located in nearshore habitats close to the Ojo de Liebre lagoon's mouth. Passive acoustic monitoring was used to study how IWS are using the Ojo de Liebre lagoon. An array of 11 receivers was deployed inside and outside the lagoon, and 17 sharks (tagged locally and in Southern California, US) were detected inside the array, with a higher number of sharks detected during months with lower incidental catches. General Additive Models were used to analyze the effect of biological and environmental factors on the presence of white sharks. Month (belonging to late fall and winter) and tagging location (southern California) were the variables that better-explained the presence of sharks outside the lagoon. The presence of IWS inside the lagoon is better-explained by month (winter and early spring) and size (sharks larger than 175 cm). Carbon and nitrogen bulk stable isotope analyses (SIA) revealed a higher contribution of demersal prey (44-48 %) heavily targeted by local fisheries to IWS isotopic values from muscle tissue, compared to offshore (15-31%) and pelagic (25-37%) prey. SIA was also used to compare diet differences among sympatric shark species that feed in the bay. A partial overlap in the isotopic niche of IWS with hammerhead sharks (45.27%) of similar sizes was found. These results suggest that both species could be feeding on similar resources or prey with similar isotopic composition. This thesis confirms that Ojo de Liebre lagoon is an important nursery for IWS, where are individuals present year-round and found high food availability, mainly in areas near its inlet. Incidental catches are more frequent during months when fewer sharks were detected in the acoustic array, suggesting a smaller temporal overlap than previously thought. However, the spatial overlap seems to be higher, and competition for resources with local fisheries occur. Based on the diet overlap found in this study, if prey populations of IWS decrease due to local overfishing, competition among sympatric shark species could increase in the future, posing a new threat for this early life stage. Findings from this work could improve current management strategies to minimize local artisanal fisheries' impact on IWS populations.

Keywords: White sharks, artisanal fisheries, nursery areas, Vizcaino Bay

Dedication

“Fish," he said softly, aloud, "I'll stay with you until I am dead.”
— Ernest Hemingway, The Old Man and the Sea

“They were scientists enough to admit that they were wrong.”
— Isaac Asimov, Foundation

Por los caídos y por los que siguen en pie.

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A mis padres, mi hermano y a Luz. Por estar siempre, por darme fuerzas para seguir y por soportarme.

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Chapter 1. General introduction

The white shark *Carcharodon carcharias* (WS) is a top predator distributed worldwide (Figure 1) in temperate and subtropical waters (Compagno, 2002; Ebert et al., 2013). White sharks are large predators that can measure up to 6 m (Castro, 2011). Recent studies have reported that white sharks live longer than previously thought, with ages of some adults estimated as older than 40 years and with a maximum registered age of 73 years (Hamady et al., 2014; Andrews & Kerr, 2015; Natanson & Skomal, 2015; Christiansen et al., 2016). Age and size of maturity differ between sexes, with females maturing between 450-500 cm total length (TL) at 12-15 years, while males mature between 360-380 at 8-10 years (Cailliet et al., 1985; Francis, 1996; Pratt, 1996; Wintner & Cliff, 1999; Malcolm et al., 2001; Tanaka et al., 2011). However, age at maturity estimations have been challenged by recent studies reporting that males and females mature at ages > 16 and 26 years, respectively (Christiansen et al., 2016; Natanson & Skomal, 2015). White sharks exhibit yolk-sac vivipary with oophagy and histotrophy as supplemental forms of matrotrophy, with a relatively low fecundity of between 2 to 14 pups (Compagno 2002, Sato et al. 2016). Due to their late maturity, low fecundity, extended longevity, and low population size, white sharks are considered vulnerable to anthropogenic activities (Ebert et al., 2013; Rigby et al., 2019).

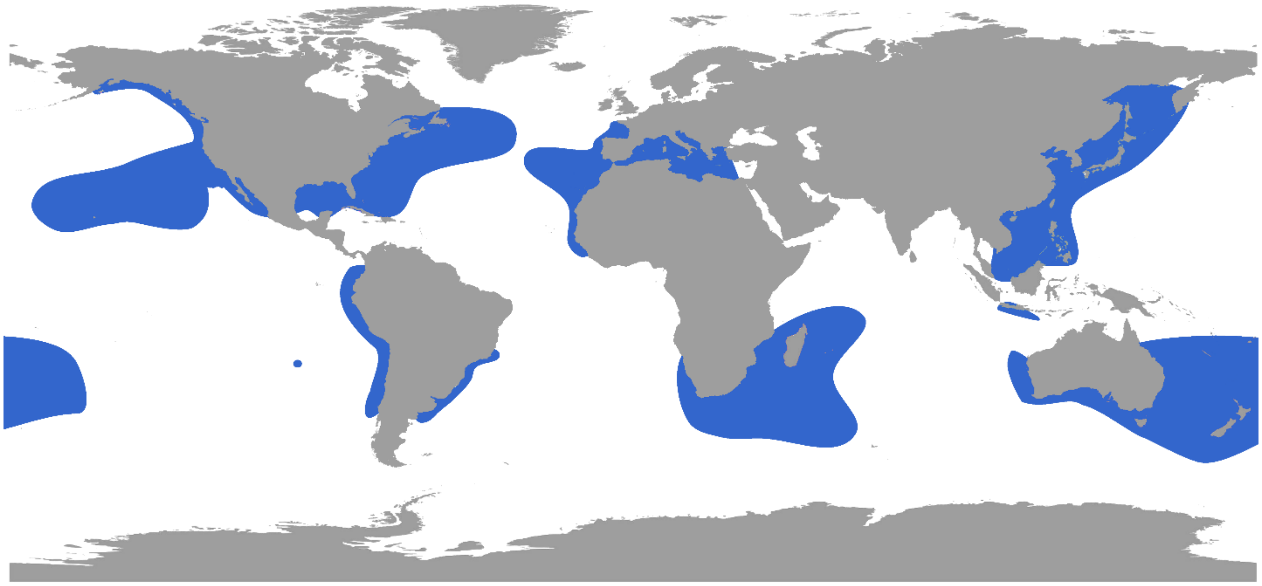

Figure 1. Global distribution of the white shark. Modified from Huveneers et al., 2018.

Based on their size, white sharks can be classified to five life stages: newborn sharks (NB, between 120-150 cm TL), young of the year (YOY, between 151-175 cm TL), juveniles (JUV, between 176-300 cm TL), sub-adults (between 300 cm and maturity size) and adults (Cailliet et al., 1985; Francis, 1996; Pratt, 1996; Wintner & Cliff, 1999; Bruce & Bradford, 2012). While the early life stages (newborns, YOY and juveniles) are distributed in productive coastal waters, including inside estuaries and lagoons (Harasti et al., 2017; Curtis et al., 2018; Bruce et al., 2019), adults aggregate at different ocean regions, including the waters of Australia, New Zealand, the Mediterranean Sea, South Africa, the northwestern Atlantic, and in the Northeastern Pacific (Klimley et al., 1992; Domeier & Nasby-Lucas, 2007; Bruce & Bradford, 2012; Francis et al., 2015; Boldrocchi et al., 2017; Skomal et al., 2017; Moro et al., 2019). The movements and ecology of adults are relatively well understood, but information about early life stages is still scarce (Huveneers et al., 2018). It is unclear as to how white sharks use different habitats throughout their ontogeny. Moreover, the study of how changes in diet, prey availability, environmental conditions and predation influence habitat use, space use and migration patterns have been proposed as research priorities for the species, and are considered essential for quantifying the current threats (Huveneers et al., 2018). Understanding these topics will help understand the role of white sharks' ecosystems and define proper management and conservation strategies.

Genetic analyses have shown that white sharks from the Northeastern Pacific (NEP) are a distinct population separated from the South Africa and Australia/New Zealand populations (Jorgensen et al., 2010). In the NEP, adult white shark aggregate near seal colonies of Farallon and Año Nuevo islands in Central California, USA, and near Guadalupe island in Mexico. It has been reported a limited connectivity between these two regions (Jorgensen et al., 2012). After aggregation near these islands, adults move to a shared offshore area off Hawaiian waters, and then migrate back to their original aggregation sites (Boustany et al., 2002; Domeier & Nasby-Lucas, 2007; 2008; Weng et al., 2007; Jorgensen et al., 2010; 2012). Domeier (2012) proposed that Guadalupe island serves as a mating area and that pregnant females move to offshore area during the gestation phase. After been in this offshore area, they migrate to parturition areas in the coastal waters off the Baja California Peninsula and the Gulf of California

Early life stages of the white shark are distributed in coastal waters from Point Conception in California to the Baja California Peninsula, and within the Gulf of California (Dewar et al., 2004; Weng et al., 2007; 2012; White et al., 2019). Immature white sharks use coastal areas as nurseries, where they spent the first years of their life and interact with coastal fisheries (Galván-Magaña et al., 2010; Cartamil et al., 2011; Lowe et al., 2012; Santana-Morales et al., 2012; Lyons et al., 2013; Ramírez-Amaro et al., 2013; Oñate-González et al., 2017). Vizcaino Bay (BSV) has been confirmed as one of these nursery areas for white sharks based on the analysis of incidental catches of neonates, YOY and older juveniles by the local artisanal fishery (Oñate-González et al., 2017). As a nursery area for white sharks, BSV is used by those born there, as well as immature white sharks that migrate south from the Southern California Bight (Weng et al., 2007; 2012; Oñate-González et al., 2015; White et al., 2019).

Although it is illegal to target and catch white sharks in both US and Mexican waters (DOF 2007; 2010; 2014), immature white sharks are caught incidentally in both California and Mexico, and they have a lower probability of survival when captured in Mexican waters (Benson et al., 2018). Specifically, artisanal fishers from BSV catch them incidentally throughout the bay and within Ojo de Liebre lagoon (OLL; Cartamil et al., 2011; Santana-Morales et al., 2012; Oñate-González et al., 2017). Deficiencies in Mexican fisheries statistics due to a poor reporting system and data collection process inhibit the assessment of the degree and location of white shark-fishery interactions. Besides, this lack of official statistics prevents the evaluation of the post-release survival for those sharks that are being released by local fishers to comply with existing regulations forbidding their catch. The assessment of where these interactions occur, their magnitude, and how white sharks use BSV is needed to define proper temporal and spatial management actions to increases juvenile survival (one of the most critical elements for population growth) and to ensure their recruitment to adulthood (Mollet & Calliet, 2002).

Immature white sharks feed mostly on demersal fishes and small elasmobranchs (Tricas & McCosker, 1984; Santana-Morales et al., 2012). Moreover, as their size increases, sub-adults and adult white sharks shift their diet to feed on squid, larg- sized pelagic fishes and eventually marine mammals (Carlisle et al., 2012; Jaime-Rivera et al., 2014; Malpica-Cruz et al., 2013). Understanding the role of BSV foraging habitat for young white sharks, as well as the trophic relationships with specific prey groups that may also be subject to fisheries exploitation are essential for their management and conservation.

In this thesis, I analyzed the interactions of immature white shark with BSV local fisheries, and characterize the main locations where this interaction occurs. Since immature white sharks are caught in fisheries that target their potential prey, I am also investigating the feeding ecology and habitat use in this nursery area. The results will help to better understand the ecological importance of Vizcaino Bay and the Ojo de Liebre lagoon for immature white sharks, including those born locally and those migrating from Southern California.

1.1 Study area

Vizcaino Bay (Figure 2) is a bay located in the southern portion of the California Current System, between Punta Canoas to the north and Punta Eugenia to the south (Cartamil et al., 2011; Hernández-Rivas et al., 2000). The bay covers 35,678 km^2 and is relatively shallow (average depth is 75 m) with a broad continental shelf (maximum width of 140 km) (Cartamil et al., 2011). BSV has marsh ecosystems, coastal dunes, three islands (Natividad, Cedros, and Benitos), and three coastal lagoons: Manuela, Guerrero Negro, and Ojo de Liebre lagoon (DOF, 2000).

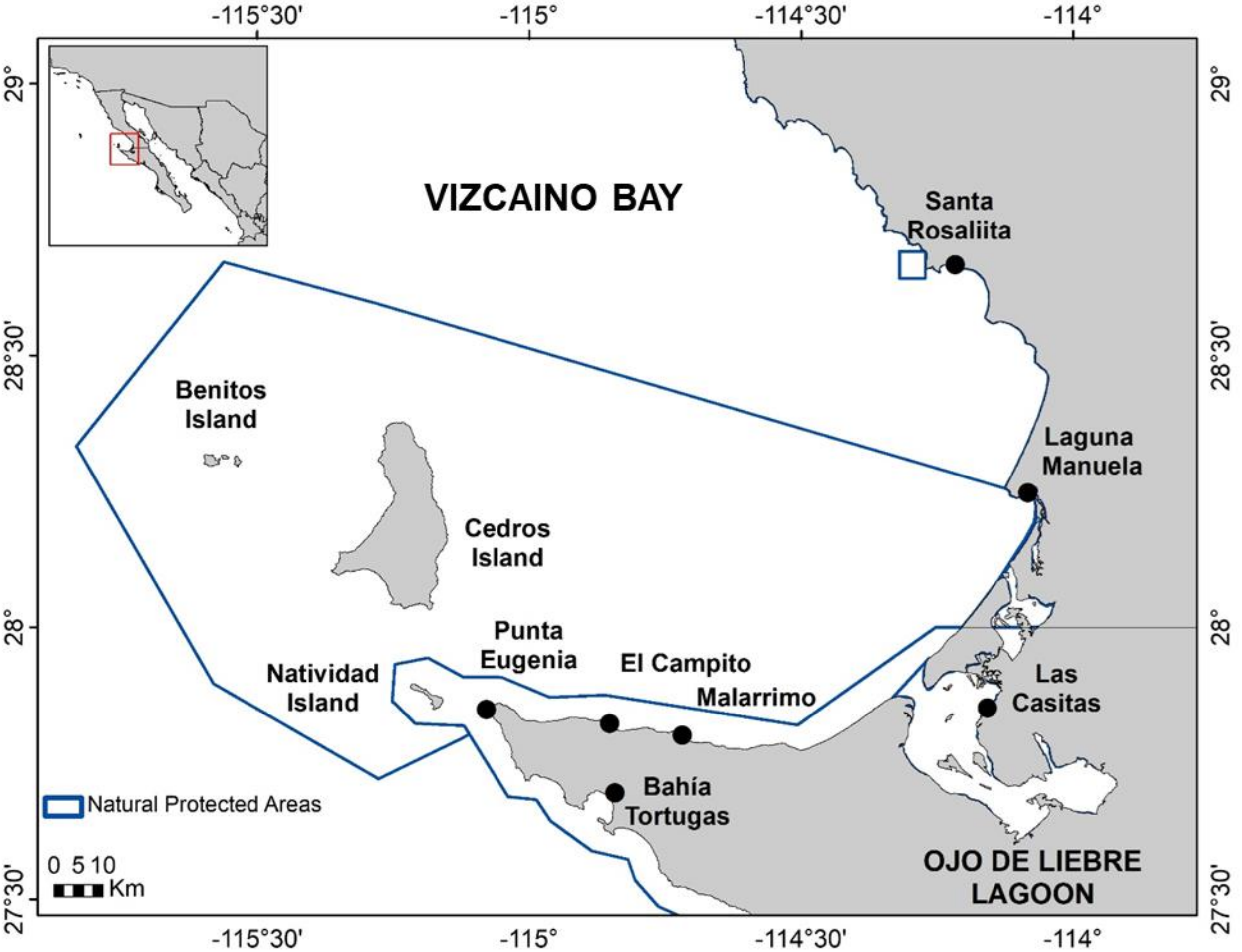

Figure 2. Location of Vizcaino Bay, Mexico and main fishing camps. Black dots represent main fishing camps in the region. Blue polygons represent the limits of the Natural Protected Areas.

Among the different bays within the California Current System, BSV is one of the most productive due to the oceanographic dynamics present, such as upwelling and gyre activity (Amador-Buenrostro et al., 1995; Mancilla-Peraza et al., 1993). The Bay also provides retention, feeding, and nursery opportunities for various species and has been defined as a Biological Activity Centre (Hernández-Rivas et al., 2000). Moreover, BSV is located at the boundary between the San Diegan and Panamic Biogeographical Provinces and is considered a bioregion transition for the distribution of tropical and temperate species (Hernández-Rivas et al., 2000; Horn et al., 2006). Two federal marine protected areas within the Bay: El Vizcaíno Biosphere Reserve and Islas del Pacífico de la Peninsula de Baja California Biosphere Reserve, were established in 1988 and 2016, respectively (DOF, 2000; 2016)

The Ojo de Liebre lagoon is a 366 km^2 coastal lagoon 40 km long and6 km wide (average). This lagoon has channels with a maximum depth of 30 m, and it has five islets (DOF, 2000; Gutiérrez de Velasco, 2000). Its circulation is dominated by tidal currents and receives no freshwater input from continuous rivers or streams (De la Cruz Agüero et al., 1996; Gutiérrez de Velasco, 2000). This lagoon supports one of the more prominent salt companies in Mexico and also constitutes important fishing area. Because of its size, this lagoon also serves as important birthing and nursery habitat for the gray whale *Eschrichtius robustus* and some migratory birds (De la Cruz-Agüero et al., 1996; DOF, 2000).

1.2 Research questions

1. Which areas along the coast of BSV have higher interaction between fishing activities and immature white sharks in Vizcaino Bay?

2. How are immature white sharks from Vizcaino Bay and Southern California using (spatially and temporally) the Bay and the Ojo de Liebre lagoon?

3. Are immature white sharks reflecting the isotopic signature of potential prey from Vizcaino Bay?

4. Does the isotopic niche from immature white sharks overlap with those from other sharks?

1.3 Objectives

1.3.1 General objective

Describe the importance of Vizcaino Bay and Ojo de Liebre lagoon for the first life stages of WS from the standpoint of the spatiotemporal use, their trophic ecology in the area, and their interaction with fishing activities.

1.3.2. Specific objectives

- Describe the fishing activities inside Vizcaino Bay: fishing gears, duration of fishing trips, target species.
- Describe the sizes of white sharks incidentally caught in each fishing camp.
- Identify areas (including fishing camps) with higher interaction with WS.
- Describe the movements of white sharks caught along the shoreline near the inlet of the Ojo de Liebre lagoon using acoustic telemetry.
- Determine the months with a higher presence of white shark in Vizcaino Bay.
- Estimate residence time of white sharks in Vizcaino Bay and Ojo de Liebre lagoon.
- Describe the effect of size, sex, origin, and temperature on tagged shark residency inside and outside the Ojo de Liebre lagoon.
- Compare the isotopic values of muscle between life stages and between areas inside and outside Vizcaino Bay for white sharks.
- Estimate the contribution of potential prey to the isotopic values of white sharks.
- Estimate the isotopic overlap between white sharks and sympatric species that could have similar isotopic niches.
- Quantify the trophic position of white sharks in Vizcaino Bay.

Chapter 2. Artisanal fishing activities and their documented interactions with juvenile white sharks inside a nursery area

2.1 Introduction

Protected areas and sanctuaries have proven to be useful elements that aid in the protection and conservation of vulnerable marine species, especially when coupled with other management strategies (Hillborn, 2017; Ward-Paige & Worm, 2017). For highly mobile species, like sharks, the identification of areas where individuals spend most of their time, like nursery areas, coupled with life-history information is essential for the development of specific conservation strategies aimed at reducing fishing mortality (Heupel & Simpfendorfer, 2005; Knip et al., 2012). Furthermore, the identification of areas where the interaction with fishing activities is higher is necessary to focus proper management strategies and protocols within the protected areas to conserve vulnerable marine species.

Nursery areas are crucial for juvenile survival (Heithaus, 2007; Heupel et al., 2007), and constitute an essential element for the population growth of white sharks (WS) (Mollet & Cailliet, 2002). Newborn (i.e. WS up to 150 cm), young of the year (YOY) (i.e. WS between 150-175 cm total length), and juvenile white sharks (i.e. WS between 175-300 cm total length) inhabit coastal waters where interactions with nearshore fisheries occur (Cailliet et al., 1985; Francis, 1996; Pratt, 1996; Wintner & Cliff, 1999; Weng et al., 2007; Lowe et al., 2012; Lyons et al., 2013; Oñate-Gonález et al., 2017). In the Northeastern Pacific, WS have been classified as “Vulnerable” by the IUCN and have been included in CITES Appendix II since 2004. In Mexico, WS are listed as “Threatened” by the NOM-059-SEMARNAT, and their catch or the possession of any of their parts was deem illegal in 2006 (DOF, 2007). These measures were reinforced in 2014 with the institution of a total fishing ban for WS and the mandatory release of any individual incidentally caught in fishing gears (DOF, 2014). Despite the regulations currently in place, incidental catches still occur in Mexican waters, especially in BSV (Oñate-González et al., 2017; Sosa-Nishizaki et al., 2015).

Vizcaino Bay (BSV) is located in the middle of the western coast of the Baja California Peninsula, Mexico (Figure 2). This bay has been identified as a nursery area for WS, including sharks born in BSV or sharks born in the Southern California Bight, US, that move into BSV mainly during autumn and winter (Oñate-Gonzalez et al., 2017; White et al., 2019). The southern portion of the Bay is part of the marine buffer zone of two protected areas: the El Vizcaíno Biosphere Reserve, that was established in 1988 to protect grey whales, and the Archipiélagos de San Benito y Cedros Natural Protected Area of the Islas del Pacífico de Baja California Biosphere Reserve, that was established in 2016 mostly to protect the habitats of seabirds

(DOF, 2000; 2016b). Artisanal fishing is allowed only to residents in the buffer zone of both protected areas (Figure 2).

Small-scale fisheries (artisanal fisheries), provide food security and are essential for the local economies of many coastal communities (Moreno-Báez et al., 2010) given that they require a low level of capital investment, due in part to the use of manual and labour-intensive harvesting practices (Salas et al., 2007). Generally, artisanal fisheries are multi-gear and multi-specific and contribute to national and international trade of fishing products (Cartamil et al. 2011). Despite the economic importance of the fishing activities in BSV (Álvarez et al., 2015), no formal description of the fisheries in the area is available that includes information on the target species, fishing areas, or how all these elements vary throughout the year. This information gap prevents an understanding of the interactions between artisanal fisheries and WS. Most incidental WS catches come from artisanal fisheries (Galván-Magaña et al., 2010; Santana-Morales et al., 2012; Oñate-González et al., 2017); however, because of the poor reporting and monitoring system for fishery data in Mexico (Castillo-Géniz et al., 1998; Hernández & Kempton, 2003; Arreguín-Sánchez & Arcos-Huitrón, 2007; Cisneros-Montemayor et al., 2013), reliable incidental catch data required for the formulation of management guidelines are not available. Gathering this information would result in better-informed conservation decisions for this species, as well as for other endangered species in the area. One way to overcome this lack of information is to capitalize on the accumulated local knowledge of artisanal fishers (Moreno-Báez et al. 2010).

Fishers's knowledge has proven to be a valuable source of information for vulnerable or endangered species in data-poor areas (Moore et al., 2010; Leeney & Poncelet, 2015). Also, it is essential to gather information from scientific sources to understand the impacts of fishing activities on local populations and to develop management and conservation strategies that benefit the entire community. These approaches can also offer opportunities to engage local communities in scientific studies and management activities through the development of relationships based on mutual trust that help to develop a sense of partnership and representation (Moore et al., 2010; Moreno-Báez et al., 2010; Carruthers & Neis, 2011; Jabado et al., 2015; Leeney & Poncelet, 2015).

This chapter aims to describe the activities and dynamics of the fisheries that interact with immature white sharks in BSV, to evaluate their impacts and identify the areas with the highest levels of interaction. This information will help inform the development of improved management strategies that could reduce the incidental catch of white sharks in BSV.

2.2 Methods

Between June and December 2015, semi-structured interviews were conducted with fishers from the following permanent BSV fishing camps (Figure 2): Santa Rosaliita, Laguna Manuela, Las Casitas, Malarrimo, El Campito, Punta Eugenia, and Bahía Tortugas (Cartamil et al., 2011; Ramírez-Amaro et al., 2013). Even though Bahía Tortugas is not inside BSV, it was included in the surveys because of its closeness to the bay, because fishers from there fish inside BSV and due to reports of incidental white shark catches from other studies at this fishing camp (Ramírez-Amaro et al., 2013). Only fishers using fishing gears that could interact with WS (gillnets or longlines) were interviewed, even if they only participated in fishing activities for part of the year. Surveys were conducted at landing sites, most commonly when fishers returned from their fishing trips. The duration of the interview was designed to be short (<40 mins) so as not disturb landing operations. Before initiating the interviews, fishers were informed of the goal of the project and that this study was part of an independent scientific research project. They were also informed that data obtained from the surveys could be used as a potential source of information for the development of management plans.

The questionnaire consisted of four general sections: demographic information and experience; fishing operation type, boat, and gear information; fishing sites; and incidental white shark catches. The first section included demographic information such as the age of the fishers, fishing experience, sources of income, number of dependents, and fishing cooperative information. The second section included questions regarding fishing gear and boat characteristics, fishing seasons, fishing trips, as well as the names of the target and incidental species caught in gears. The third section was focused on obtaining information on fishing sites, and fishers were asked to indicate on a map of BSV the main sites where they usually carried out their fishing activities. The last section consisted of gathering data regarding WS incidental catches, including the sites where incidental catches occurred or animals were spotted, their knowledge of shark regulations, their opinions of WS conservation, and their disposition to participate in a monitoring program.

The data obtained were analyzed using the response frequencies for all questions, and the results were compared between fishing camps and demographic groups. Fishing area polygons were constructed and were compared with WS sightings and incidental catch records to identify the areas with the greatest interactions between WS and fishing activities.

2.3 Results

Seventy-seven fishers were interviewed in six different fishing camps along the coast of BSV (Figure 2; Table 1). At the Punta Eugenia fishing camp, only one interview was conducted. Punta Eugenia has one of the largest fishery cooperatives in the area and targets mainly invertebrates, including abalone and lobster, which are fished for by diving and with traps baited with fish caught in gillnets. The results of the interviews at El Campito and Malarrimo were pooled due to their closeness.

Table 1. Number of fishers interviewed by fishing camp in Vizcaino Bay

Fishing camp	ID	Number of interviews
Bahía Tortugas	BT	14
El Campito-Malarrimo	CM-ML	10
Las Casitas	LC	29
Laguna Manuela	LM	13
Santa Rosaliita	SR	11

2.3.1 Fishers

The age of the fishers ranged from 18 to 64 years (mean= 41.93 ± 10.53 SD) (Table 2). Around 55% of the fishers belonged to middle-age groups (30-39 and 40-49 years), while older groups (>50 years) were represented by 30% of the fishers. Only 13% of interviewees were younger fishers (<30 years). Almost 60% of the respondents had fished for 20 or more years (Table 2), ranging from 1 to 50 years of experience (mean = 23.09 ± 10.84 SD). Around 85% of fishers indicated that they began to fish because a family member was involved in fishing activities.

Table 2. Demography of fishers interviewed in Vizcaino Bay

Age group	Number of fishers	Mean years of experience
<20	1	1.00
20-29	9	12.33
30-39	24	16.04
40-49	19	25.16
50-59	22	31.95
>59	2	50.00

Most of the fishers (97 %) listed fishing as their primary economic activity, and for 78 % of respondents, fishing was their only source of income. The most common alternative occupations were animal breeding and bricklaying. Fishing activities are essential for the economies of fisher families because 97% of fishers stated that at least one person depends upon their income, with 66 % and 23 % of the fishers supporting between 2-3 and 4-7 people, respectively. Around 17% of the fishers worked independently while 83% were part of a fishing organization that could either be a fishing cooperative or a group of independent fishers not legally constituted.

2.3.2 Fishing operations, fishing gear, and target species

For all fishing camps, 83% of fishers indicated that they engaged in fishing activities throughout the year, with the greatest activity occurring from July to October. The most common vessel size was 8 m length (6-12 m) with 2 t of declared storage, while engines ranged between 40 HP and 155 HP, the latter being the most commonly used engine size. Half of the respondents declared that they were not the owners of the fishing vessel that they operated; however, all boats were either owned by fishing cooperatives or by other fishers. Twelve fishers responded that they owned more than one boat and that they typically used one fishing permit to cover all of their fishing vessels.

Gillnet operations in the BSV area are most prevalent from March to August, with the largest number of active gillnet operations occurring in August (Figure 3). The most frequently-used gillnet length was 1000 m, ranging from 200 to 6000 m (mean = 1584 ± 1291.43). Respondents mentioned that they use several net mesh sizes, including 11.5, 15, 20, and 25 cm, that are used to target smooth-hounds, guitarfishes, white seabass, and California halibut, respectively. The use of gillnets in Las Casitas appears to be more constant when compared with the other fishing camps, although increased use was observed between June and August, which coincides with the period of increased use in the fishing camps of Campito-Malarrimo and Bahía Tortugas. Laguna Manuela and Santa Rosaliita showed greater use of gillnets during the spring months. Aside from Las Casitas and Bahía Tortugas, the use of gillnets in the autumn and winter months was very low (Figure 3; Supplementary material, Figure 21).

Fishers indicated that they use longlines less frequently than gillnets, although periods of higher use were observed at the end of summer and autumn months (Figure 3), mainly in Laguna Manuela and Las Casitas. In Bahía Tortugas, longlines were used from summer to winter (Supplementary material, Figure 22.). Most longlines were 1000 m, but the length varied between 200 m and 4800 m (mean = 1.50 ± 1.36 SD). Longlines were set with 15 to 500 hooks (mean = 226.77 ± 105.83 SD).

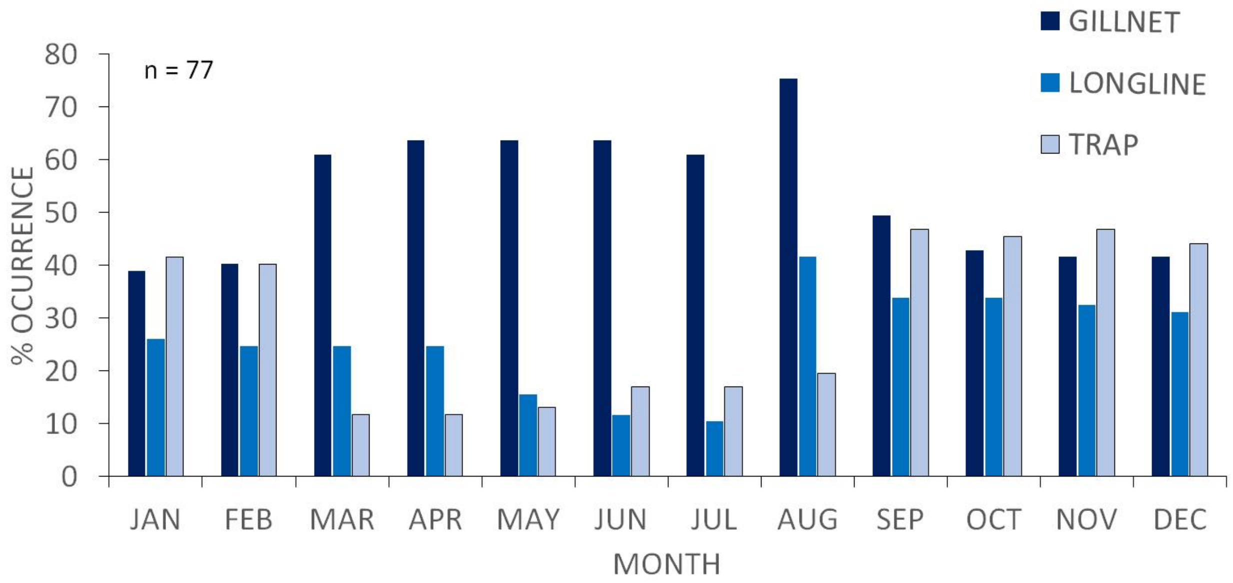

Figure 3. Fishing gear used in Vizcaino Bay by month. The period between May and July correspond with the yearly elasmobranch fishing ban.

Respondents indicated that they use traps mainly for fishing for lobster, but that in recent years, fishes have also been targeted with this fishing gear. Most of the trapping operations are carried out between September and January (Figure 3) during the lobster season, primarily in the fishing camps of Santa Rosaliita, Laguna Manuela, and Campito-Malarrimo (Supplementary material, Figure 23).

Approximately 80 % of the fishers responded that the duration of fishing trips was usually 8 hours, although durations ranged from 4 to 24 hours (mean = 9.45 ± 4.86). Shorter trip durations corresponded to trips in which fishers went to retrieve their nets, while longer trips were related to longline setting operations. Weather permitting, most of the fishers (85%) tended to go out fishing more than four days per week. The most common soaking time for both gillnets and longlines was 24 hours, but soaking times ranged from 4 to 48 hours. Shorter soaking times corresponded to fishing trips using set gillnets targeting white seabass and guitarfishes and to longline fisheries targeting sharks and giant seabass. Due to the fact that fishes could spend long periods in the fishing gears without decreasing its quality to be marketed, fisher prefer to let the gillnets for two days before getting them off, to maximize their catch.

Artisanal fishing in Vizcaino Bay is multi-specific. Twenty-one species were identified as target species (Table 3). These species are also incidentally caught when fishers target other species. The three main target species in BSV were white seabass (*Atractoscion nobilis*), California halibut (*Paralichthys californicus*), and shovelnose guitarfish (*Pseudobatos productus*) (Figure 4). These three species were mainly caught with bottom gillnets. Differences between the main target species were found between fishing camps (Supplementary material, Figures 24-28). The highest number of target species (21) was recorded for Las Casitas (Supplementary material, Figures 26), while Santa Rosaliita (Supplementary material, Figures 28) recorded the lowest number of target species (7). Fifteen other species were stated as incidental species in the area.

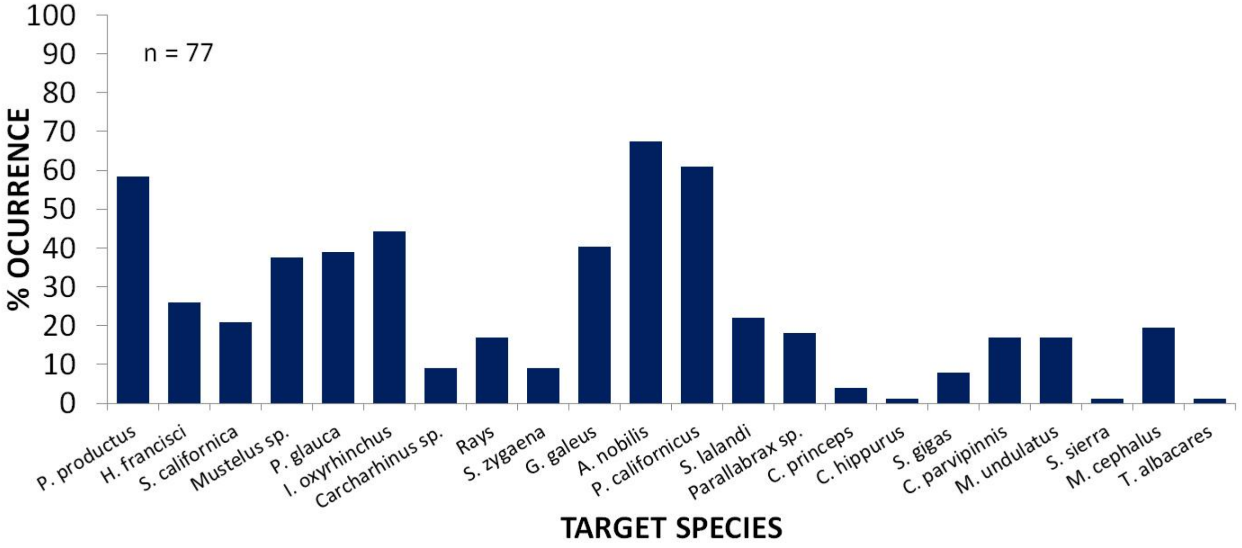

Figure 4. Major target species from artisanal fisheries in Vizcaino Bay.

Sharks were found also to be important fishery resources in BSV, and six shark species were included among the 21 target species (Table 3). Pacific angel shark (*Squatina californica*) was very important in Bahía Tortugas (Supplementary information, Figures 24), smooth-hound sharks (*Mustelus* spp.) in Campito-Malarrimo and Las Casitas (Supplementary material, Figures 25, 26), horn shark (*Heterodontus francisci*) was one of the main target species in Las Casitas (Supplementary material, Figures 25), blue sharks (*Prionace glauca*) and mako sharks (*Isurus oxyrinchus*) were important for Bahía Tortugas, Las Casitas, Laguna Manuela and Santa Rosaliita (Supplementary material, Figures 24, 26, 27, 28), while tope shark (*Galeorhinus galeus*) was important in Bahía Tortugas and Santa Rosaliita (Supplementary material, Figures 24, 28).

Table 3. Target and incidental species caught by fishing gears in Vizcaino Bay (T = target species; I = incidental catch; BG = bottom gillnet; SG = set gillnets; SN = seine net; L = longline; TR = traps).

Common name	Species	Type of fishing	Fishing gear
White seabass	*Atractoscion nobilis*	T, I	BG, SG, SN,
California halibut	*Paralichthys californicus*	T, I	BG
Yellowtail	*Seriola lalandi*	T, I	SG, SN
Shovelnose guitarfish	*Pseudobatos productus*	T, I	BG, SG, SN,
Horn shark	*Hetorodontus francisci*	T, I	BG, SG
Pacific angel shark	*Squatina californica*	T, I	BG, L
Barred sand bass	*Parallabrax nebulifer*	T, I	SG, TR
Sand bass	*Parallabrax* sp.	T, I	SG
Ocean whitefish	*Caulolatilus princeps*	T, I	SG
Smooth hound shark	*Mustelus sp.*	T, I	BG
Blue shark	*Prionace glauca*	T, I	L
Mako shark	*Isurus oxyrhinchus*	T, I	L, SG
Requiem sharks	*Carcharhinus brachyurus* *Carcharhinus obscurus*	T, I	BG, SG, L
Common dolphinfish	*Coryphaena hippurus*	T, I	SG
Rays	*Hypanus dipterurus* *Urobatis halleri* *Gymnura marmorata* *Myliobatis californica*	T, I	BG
Giant seabass	*Stereolepis gigas*	T, I	BG, L
Shortfin corvina	*Cynoscion parvipinnis*	T, I	SG
Smooth Hammerhead	*Sphyrna zygaena*	T, I	BG, SG, L
California kingcroaker	*Menticirrhus undulatus*	T, I	SN
Pacific sierra	*Scomberomorus sierra*	T, I	SG, SN
Flathead Mullet	*Mugil cephalus*	T, I	SG, SN
Yellowfin tuna	*Thunnus albacares*	T, I	SG
Tope shark	*Galeorhinus galeus*	T, I	SG, L
Thresher shark	*Alopias sp.*	I	SG, L
Pacific sardine	*Sardinops sagax caeruleus*	I	SG, SN
Eastern pacific bonito	*Sarda chiliensis*	I	SG

Leopard shark	*Triakis semifasciata*	I	BG
California sheephead	*Semicossyphur pulcher*	I	BG
Giant electric ray	*Narcine entemedor*	I	BG
Skipjack tuna	*Katsuwonus pelamis*	I	SG
Bacoco	*Anisotemus sp.*	I	BG, SG
Paloma pompano	*Trachinotus patiensis*	I	SN, SG
Pacific porgy	*Calamus brachysomus*	I	SN, SG
California killifish	*Fundulus parvipinnis*	I	SN, SG
California scorpionfish	*Scorpaena guttata*	I	BG, SN, SG
California lizardfish	*Synodus lucioceps*	I	BG, SG
Spine tail devil ray	*Mobula japanica*	I	SG
Swell shark	*Cephaloscyllium ventriosum*	I	BG

2.3.3 Fishing areas.

Fishers indicated that their main fishing areas were primarily located nearshore and close to their fishing camps, but that they do go into offshore waters to catch pelagic species (Figure 5). Most of the fishing areas were found to be within the two Natural Protected Areas (Figure 2). However, fishers mentioned that, at times they move to other areas in search of their primary target species. Fishers from Bahía Tortugas travel approximately 100-120 km to fishing areas near Cedros and Natividad islands, while fishers from Campito and Malarrimo only fish in areas less than 10 km from the coastline. In Las Casitas, some fishers set their nets very close to the islets and the shore inside the Ojo de Liebre Lagoon, but other fishers go out of the lagoon and travel around 40 km to set their fishing gear, and at times moving into waters 100 km offshore. The fishing areas from Laguna Manuela and Santa Rosaliita are relatively close to the fishing camps (<35 km), with some of these areas located outside the Natural Protected Areas (Figure 5).

2.3.4 White shark incidental catch information.

Around 95% of respondents indicated that they could identify WS, and 75% stated that they had incidentally caught at least one WS during their fishing careers. Most of the fishers from the Las Casitas fishing camp indicated that they had caught a white shark (82%, n=24), followed by fishers from Laguna

Manuela (71%, n = 10) and fishers from Campito-Malarrimo (70%, n = 7). According to 68% of the fishers, mainly from the Las Casitas and Laguna Manuela fishing camps, the most common WS size was less than 2 m (Figure 6). Fishers from the Santa Rosaliita fishing camp reported that the most common WS size was 2-3 m. Even though it was not asked directly, many of the fishers commented that they do not incidentally catch WS every year (n = 52), and most of the comments indicated that 1-3 WS are caught every year in each fishing camp (n = 40).

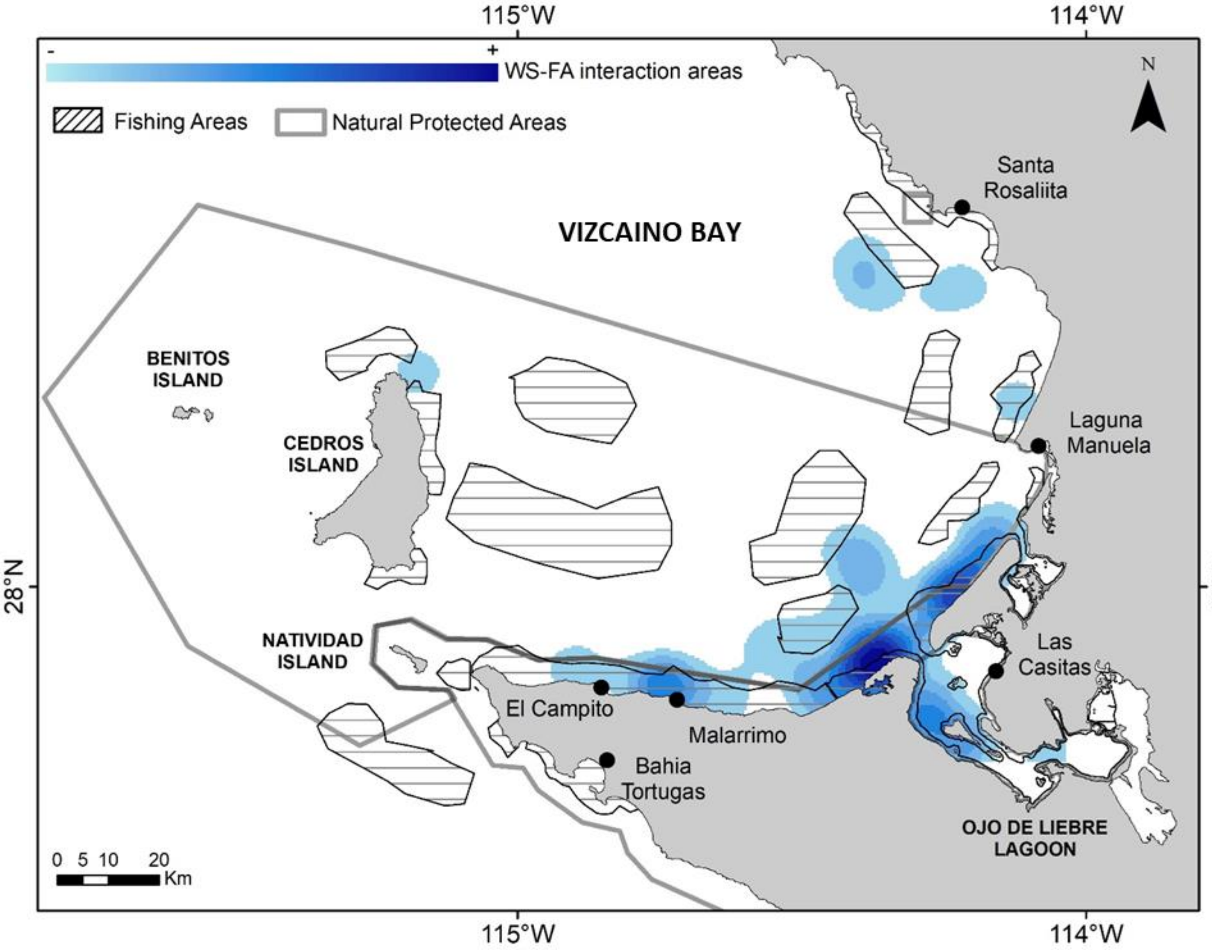

Figure 5. Areas of greater interaction between white sharks (WS) and fishing activities (FA) in Vizcaino Bay.

Fishers indicated that WS are more commonly caught in bottom gillnets (75%) than on longlines (16%) during the late spring and summer months (Figure 7). These results were consistent between fishing camps, although some white shark incidental catch peaks during the winter months in Las Casitas, Laguna Manuela, and Santa Rosaliita were observed (Supplementary Material, Figure 29). Although fishers indicated that the incidental catch of WS occurs along the entire coast of the bay, the most commonly reported areas were located very nearshore, near the mouth of the Ojo de Liebre lagoon, as well as on both sides outside the mouth of the lagoon (Figure 5). Other important areas where the incidental catch of white sharks occurs were indicated along the coast near Malarrimo, as well as inside the Ojo de Liebre Lagoon (Figure 5).

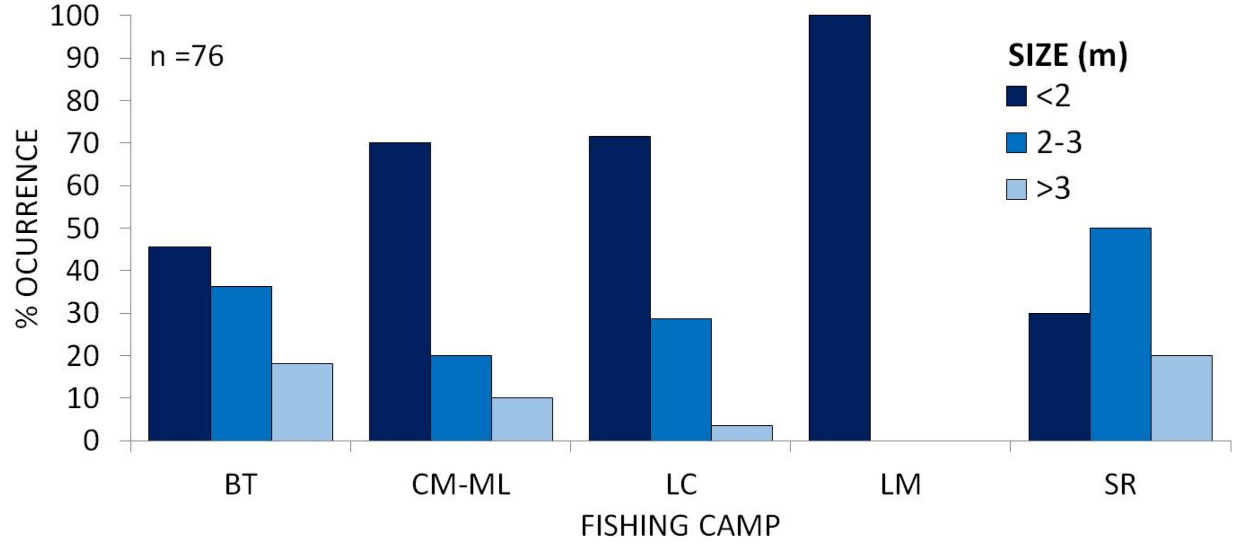

Figure 6. Sizes of juvenile white sharks incidentally caught in fishing camps from Vizcaino Bay (BT: Bahía Tortugas, CM-ML: Campito-Malarrimo, LC: Las Casitas, LM: Laguna Manuela, SR: Santa Rosaliita).

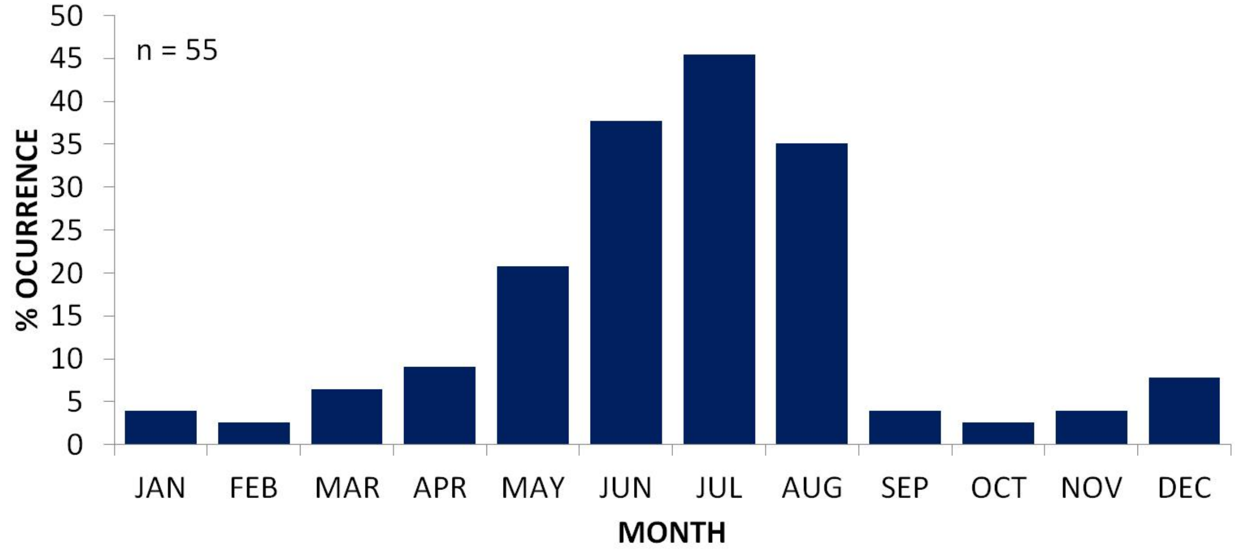

Figure 7. Incidental catches of juvenile white sharks by month in Vizcaino Bay.

Fishers were asked their opinion regarding the presence of WS in the area, and most answered that these sharks likely use the area to feed. About 66% of the fishers declared that WS do not have any economic value, while the other 34% stated that when white sharks are incidentally caught dead, they are sometimes sold as low-value meat. When asked what they know about the regulations surrounding white sharks, 85% of the respondents answered that they understand that white sharks are a protected species and that their catch is prohibited. When fishers were asked if they thought that WS needed protection, 74% answered "yes," and 61% indicated that WS protection benefits the entire community of BSV fishers. The most cited reason for this benefit was that adult white sharks prey on the pinnipeds that directly interact and interfere with fishing operations. Most of the fishers (64%) indicated that they would help to conserve WS and that they were already helping by releasing incidentally caught live white sharks. A high proportion (80%) of the respondents mentioned that they are willing to take part in specific WS monitoring programs.

2.4 Discussion

In this study, the majority of fishers had more than 20 years of personal experience in addition to the experience gained through relatives. The fishers were more than sufficiently experienced to provide accurate information regarding the topics raised in the interviews. In previous studies, fishers have been fearful of answering interview questions because of the potential effects that their answers could have on the development of regulations, especially when a protected species was involved in the surveys (Silver & Campbell, 2005; Leeney & Poncelet, 2015), which may influence the accuracy of their responses. In this study, fishers were enthusiastic about participating in the survey and were very open with their responses, indicating that the results presented are reliable.

Artisanal fisheries can account for 97% of the marine fleet in Mexico, highlighting their importance for coastal communities (Castillo-Géniz et al., 1998; Fernández et al., 2011; Álvarez et al., 2015). Our results are consistent with the aforementioned studies given that fishing is the main economic activity for the fishers of BSV and is often the primary (or even the only) source of income for their families, underscoring the socio-economic importance of artisanal fisheries.

Fishing activities are practiced throughout the year in BSV, but the use of fishing gears that interact with white sharks (i.e. gillnets or longlines) changes between fishing camps. Fishers from Campito-Malarrimo and some of the fishers from Laguna Manuela and Santa Rosaliita use these gears seasonally because they have fishing permits for the most economically valuable resources in the area: i.e. lobster and abalone. These fishers switch to targeting lobster and abalone when their fishing seasons open, September - February for lobster (DOF, 2016c) and February - June for abalone (DOF, 2016a), so their use of gillnets and longlines is mainly restricted to the months of June, July, and August. Most of the fishers surveyed from Bahía Tortugas and Las Casitas did not have permits for lobster or abalone, and their use of gillnets and longlines is more consistent throughout the year.

The vessel characteristics in BSV were consistent with the descriptions of artisanal fishery vessels from other areas in Mexico (DOF, 2007; Sosa-Nishizaki et al., 2008; Bizzarro et al., 2009; Moreno-Báez et al., 2010; Cartamil et al., 2011;). As a result of the political push during the 1970s to industrialize Mexican fishing fleets and advance the development of technologies, artisanal fleets are relatively well-equipped (Cisneros-Montemayor et al., 2013) which has enabled fishers to travel further to fish. Fishers from Vizcaino Bay, who use powerful engines, may travel up to 100 km to reach particular fishing grounds. Also, the implementation of hydraulic net winches in Bahía Tortugas and Campito-Malarrimo to pick-up nets has allowed the length of these nets to increase in comparison to the lengths of nets from other camps where fishers have to pick-up their gears by hand. Comments from respondents indicated that some fishers use a single fishing permit for several vessels and that a lot of fishing permits are not in use by the owners. This practice makes it very difficult to estimate the real fishing effort that interacts with white sharks in BSV.

In BSV, fishing activities are multi-specific, and target species may change from one day to the next, depending on their availability (Cartamil et al., 2011). Six of the ten most important target species in the area are bottom-related species that dwell in habitats where immature white sharks often forage. Also, two other target species are fished with longlines, and reports of incidental white sharks catches due to the use of these gear types have been reported (Santana-Morales et al., 2012; Oñate-González et al., 2017). In addition, six target species were previously found in the stomachs of juvenile white sharks from the North-eastern Pacific (Santana-Morales et al., 2012). Most of these species are caught using bottom gillnets with mesh sizes between 15-20 cm, which pose an entanglement threat to smaller white sharks (Lowe et al., 2012; Santana-Morales et al., 2012; Lyons et al., 2013; Ramírez-Amaro et al., 2013; Oñate-González et al., 2017).

A high proportion (71%) of the fishers stated that they have incidentally caught white sharks, which agrees with incidental catches previously recorded in these fishing camps (Santana-Morales et al., 2012; ; Ramírez-Amaro et al., 2013; Oñate-González et al., 2017). In general, the sizes of white sharks incidentally caught in the area as indicated by fishers (<2m) are consistent with the sizes previously reported for incidental white sharks catches in the area, along with the reported months in which most incidental catches occurred (summer) and the fishing gears used (bottom gillnet) reported for the North-eastern Pacific (Cartamil et al., 2011; Lowe et al., 2012; Santana-Morales et al. 2012; Lyons et al., 2013; Oñate-González et al., 2017). However, responses varied between fishing camps. Fishers from the northern fishing camps reported catches of white sharks during winter months, which could be related with the migration of juvenile white sharks from the Southern California Bight when the waters along California get colder (Weng et al., 2007; White et al., 2019). Also, fishers indicated that incidental catches of white sharks larger than 3 m occurred near the islands of Natividad, Cedros, and San Benito, which could be related to the presence of pinniped colonies, as pinnipeds are common prey for sharks of that size (Hussey et al., 2012; Arias-del-Razo et al., 2016).

The number of WS incidentally caught per fishing camp in this study is lower than what was reported by Oñate-González et al. (2017), who state that the incidental catches for some years were >100 WS. In our research, fishers were very open in their responses and even with issues related to white sharks catches, and it seems unlikely that their responses were inaccurate. However, direct observations of incidental catches in the area after this study was carried out suggesting numbers closer to what was reported by the fishers, with <15 incidental white sharks caught per year (Sosa-Nishizaki et al., 2015). An elasmobranch fishing ban was implemented in 2012 (DOF, 2012), but it seems unlikely that this ban could affect the number of incidental white shark catches because fishers are still able to target white seabass and California halibut, the two fisheries that have the highest interaction rates with white sharks. One of the data sources from Oñate-González et al. (2017) were log books from people in the fishing camps that were not necessarily fishers, which might explain the higher number of reported catches. Also, it is entirely plausible that during the years when Oñate-González et al. (2017) carried out their study, white sharks may have been especially susceptible to fishing activities due to oceanographic or ecological reasons.

The white shark is protected in Mexico by the NOM-059-SEMARNAT (2010), and its catch is prohibited by the NOM-029-PESC (2007), in addition to a species-specific ban that was implemented in 2014 (DOF, 2014). However, the dissemination of legislative information in coastal communities can be difficult (Bonfil et al., 2017). The lack of knowledge about regulations was evident in this study, with some fishers (15%) declaring that they did not know the existing rules surrounding white sharks, which might, in part explain the number of incidental immature white sharks catches still occurring in BSV. Reducing juvenile white sharks incidental catch in BSV appears to be difficult given that these sharks are incidentally caught when fishers target high-value species (California halibut and white seabass), so the effect of strengthening existing regulations may have a high social impact. In California, USA, it has been reported that the survival of juvenile white sharks increases when the soaking time of gillnets is <20 hours (Lyons et al., 2013). Thus, there is a high probability that white sharks could be released from the nets alive if soaking time in BSV is decreased. So, even if incidental catches do not stop, by releasing white sharks alive, fishing mortality should decrease.

The entire coast of Vizcaino Bay was identified as an area where fishers have incidentally caught white sharks; however, areas very close to the shore were the most important with only a small number of incidental catches recorded from fishing grounds far from the coast. This could be due to the preference of immature white sharks for shallow nearshore areas (Weng et al., 2007; Lyons et al., 2013; Harasti et al., 2017; Curtis et al., 2018) or due to a lower susceptibility of white sharks to fishing activities in offshore areas. Las Casitas stands out among the fishing camps because most fishers mentioned catches of white sharks and because geographically, those fishers operate in all the areas that are critical for incidental white shark catches (Figure 5). People from that camp, fish inside and outside the Ojo de Liebre Lagoon, to the north and south of the mouth of the lagoon, and the Malarrimo area, while fishers from other fishing camps can only access one of these places because going to other areas to fish implies a higher investment (i.e., fuel costs). Almost all the critical areas for the incidental catch of white sharks are inside one of the two Natural Protected Areas, except for some areas in the northern portion of the bay. Protected areas are designed for the conservation of vulnerable species, the protection of critical habitats, and fishery management (Bonfil, 1999; Hillborn, 2017). Their effectiveness in areas where fishing activities are permitted relies on other factors, including the engagement of local communities in the decision-making process, which is particularly important in Mexico (MacKeracher et al., 2018; Ulate et al., 2018)

Fishers's knowledge proved to be a reliable source of information for fishing activities from BSV as well as for the interactions between white sharks and BSV fisheries. This demonstrates its usefulness for describing artisanal fisheries when existing data are limited (Moreno-Báez et al., 2010) or when information regarding vulnerable or endangered species and their interactions with anthropogenic activities must be gathered (Frans & Augé, 2016; Hashim et al., 2017). This information serves as the baseline for the description of fishing activities in this area. Lack of information from artisanal fisheries along the Pacific coast of Baja California, Mexico, has been reported (Cartamil et al., 2011), avoiding the comparison if fishing activities have changed trough time and, in consequence, if interaction with white sharks has increased or decreased. Despite the biological and fishing importance of the area (Hernández-Rivas et al., 2000; Cartamil et al., 2011; Ramírez-Amaro et al., 2013), this is the first concerted effort to gather this information. While there is no consistent data on the number of fishers in the BSV, comments of the fishers surveyed and the sample size of this study provides not only an estimated of fishing activity, but also the attitudes of the fishing community that interacts with white sharks.

Previous studies tried to assess the status of white sharks in the North-eastern Pacific and reported a low probability that the white shark population is currently in danger (Dewar et al., 2013; Burgess et al., 2014). However, the main uncertainty is related to the incidental catches of juvenile white sharks, especially in Mexican waters, so a proper monitoring program to effectively report those catches is needed and to evaluate if they have been underestimated. Even if incidental catches of adult white sharks have been reported (Galván-Magaña et al. 2010), it seems that they are not large enough to put the population at risk (Dewar et al., 2013; Burgess et al., 2014). However, most of these adult catches occur at fishing grounds inside the Gulf of California, which are isolated and poorly monitored, so the number of adult white sharks caught in the area also might be underestimated.

Based on the information gathered in this study regarding the socio-economic importance of fishing activities in the area, we believe that more drastic regulations in Mexico for white shark conservation and management are not necessary. However, a regular monitoring program that records the number of juvenile white sharks incidentally caught in the area is necessary to corroborate if levels of incidental catches in BSV are as declared by the fishers and to understand the effect of these incidental catches on white shark population dynamics. Also, it is necessary to identify the origin of the sharks incidentally caught in the area (i.e., Vizcaino Bay or the Southern California Bight, Oñate-Gonzalez, et al., 2017) to understand the effects on white shark recruitment from both nursery areas. The fact that not all fishers knew existing regulations for white shark indicates that the dissemination of this information should be strengthened. It also highlights the need for an education campaign with fishers related to the importance of fulfilling the regulations and strengthening the white shark conservation.

The white shark has no economic value for BSV fishers, making it an ideal species to obtain the involvement of fishers in monitoring and conservation efforts, as a majority of them were willing to participate in this study. Conservation actions for the fishing camp of Las Casitas must be developed due to the high degree of reported interactions with juvenile white sharks. Management actions should be focused on decreasing fishing mortality by reducing the soaking time of bottom gillnets to allow the release of sharks alive, along with a fishers training program for the correct release of the sharks. Also, strategies like limiting fishing effort during months with higher incidental catches or the use of modified or alternative, fishing gear could be explored.

Chapter 3. The use of a coastal lagoon by juvenile white sharks (*Carcharodon carcharias*) as part of a nursery area in the Northeastern Pacific

3.1 Introduction

Coastal areas are vital for many shark species because it provides food availability and refugee from predators. These habitats, including bays, estuaries, and coastal lagoons, are used as nurseries, feeding or resting areas (Heupel et al., 2007; Knip et al., 2012). In some cases, these habitats are important for only one life stage (Heupel & Simpfendorfer, 2011) or several life stages (Wells et al., 2018). Understanding how sharks use these habitats during their life cycle is crucial to define their role in ecosystems and to develop spatial management strategies (Heithaus, 2007; Espinoza et al., 2015; Crossin et al., 2017).

In recent years, passive acoustic telemetry has proven to be a useful tool for quantifying area residency and movement patterns of sharks (Heupel et al., 2004; Knip et al., 2010) in relationship to environmental conditions (Donaldson et al., 2014; Heupel and Simpfendorfer, 2015; Oh et al., 2017; Heupel et al., 2018). For example, this technique has been used to study the movements of highly migratory sharks like shortfin mako *Isurus oxyrinchus* (Sepulveda et al., 2004) and common thresher *Alopias vulpinus* (Cartamil et al., 2010). Also, it has been useful to describe coastal movements of vulnerable sharks like scalloped hammerhead *Sphyrna lewini* (Nalesso et al., 2019), the whale shark *Rhincodon typus* (Gunn et al., 1999; Cagua et al., 2015), and the white shark (Francis et al., 2015; Harasti et al., 2017; McAuley et al., 2017; Curtis et al., 2018; Bruce et al., 2019).

The white shark *Carcharodon carcharias* is globally listed as a "vulnerable" species and is protected in most waters where populations are common (Rigby et al., 2019). Movements of adults are relatively well studied (e.g., Weng et al., 2007; Jorgensen et al., 2010; Duffy et al., 2012; Domeier & Nasby-Lucas, 2008; 2013; McAuley et al., 2017), but for younger sharks, their movements are not fully understood in all regions where they are present, even if in the past years this knowledge has increased (Bruce et al. 2019, Spaet et al. 2020)there is a lack of knowledge on how juveniles move in each region of its distribution. Recently, movements through ontogeny, and especially for early life stages, has been proposed as a research priority for the species (Huveneers et al., 2018).

In general, juvenile white sharks are known to distribute in coastal nursery areas and could enter into estuaries (Dewar et al., 2004; Weng et al., 2012; Harasti et al., 2017; Curtis et al., 2018; White et al., 2019).

These areas are essential and suitable places to spend their first life stages, offering them protection from predators and high availability of food (Heithaus, 2007; Heupel et al., 2007). Two nursery areas have been proposed for the white sharks in the Northeastern Pacific: one in the Southern California Bight, USA (Klimley, 1985; Domeier 2012; Lowe et al., 2012; Lyons et al. 2013) and the other one in Vizcaino Bay (BSV), Mexico (Oñate-González et al., 2017). The later serves as a nursery area for sharks born in BSV and juvenile sharks from the other nursery area in California (Oñate-González et al., 2015; 2017). However, these areas are places where interaction between juvenile white sharks and fisheries is higher, causing incidental catches (Cartamil et al., 2011; Lowe et al., 2012; Santana-Morales et al., 2012; Lyons et al., 2013; Oñate-González et al., 2017; García-Rodríguez & Sosa-Nishizaki, 2020). These incidental catches might affect juvenile survival, one of the most critical elements for the population growth of white sharks (Mollet & Calliet, 2002). Despite its importance, the use of this nursery habitat by immature white sharks in the Northeastern pacific has not been fully explored.

The white shark is a protected species in both the USA and Mexico, but incidental catches of this species still occur, especially in BSV, where juvenile white sharks are more susceptible to fishing activities than in California (Benson et al., 2018). In BSV, juvenile white sharks are incidentally caught, mostly, in bottom gillnets targeting white seabass and California halibut in summer months (Santana-Morales et al., 2012; Oñate-González et al., 2017; García-Rodríguez & Sosa-Nishizaki, 2020). Incidental catches in BSV occur all along the coast of the Bay and inside the Ojo de Liebre lagoon (García-Rodríguez & Sosa-Nishizaki, 2020), which suggests the potential importance of this habitat for immature white sharks. To our knowledge, no previous work has focused on the use of coastal lagoons by juvenile white sharks in the Northeastern Pacific, and this type of information is needed to understand the ecological role that these areas play for juvenile white sharks and to understand the extent of interactions with anthropogenic activities.

In this study, we used an autonomous passive acoustic telemetry receiver array to understand better how immature white sharks are using the Ojo de Liebre lagoon and nearshore areas adjacent to the lagoon inlet. The main goals were to 1) describe the juvenile white shark's presence patterns inside and outside the lagoon in a temporal scale, and 2) and to understand which biological (size, sex, origin) and environmental factors (temperature, salinity) are influencing their presence or absence from these environments. Results from this work could aid to refine management strategies that help to diminish the risk of incidental catches.

3.2 Methods

3.2.1 Acoustic monitoring.

An array of 11 VR2W (VEMCO) acoustic receiver was deployed inside and outside the Ojo de Liebre lagoon (Figure 8), from November 2013 to November 2017, to monitor juvenile white shark movements and their use the lagoon. Temporal coverage of the receivers varied over time, as three receivers were deployed in 2013, and the other eight were deployed at new location in 2014 And 2015 (Table 4). Receivers were deployed between sand and rocky substratum areas to prevent removal by local artisanal fishers and were suspended in the water column 1 m above the bottom by a mid-water buoy.

Although environmental conditions varied between inside and outside the lagoon, which likely influence receiver performance, the nominal acoustic detection ranges of receivers were estimated to be 350 m throughout the array. For this estimation, we conducted range tests in three places of the study area: inner lagoon, near the inlet and outside the lagoon. Test were done at a maximum distance of 500 m from the VR2W receivers with three V16 tags lowered at 5 m depth set for 10 minutes intervals each 50 m.

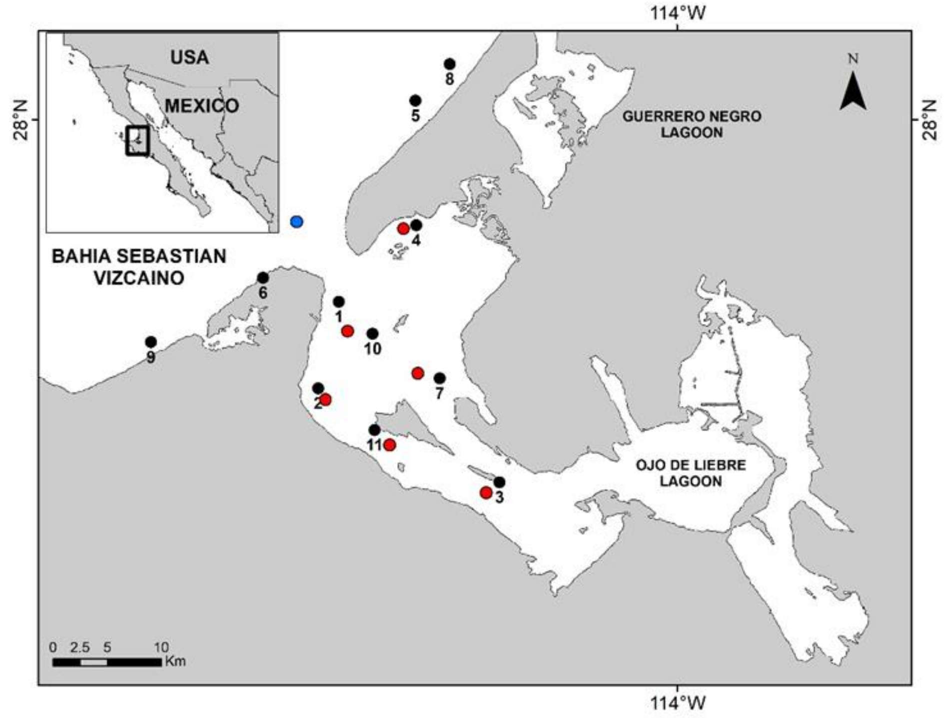

Figure 8. Location of the acoustic array deployed in Vizcaino Bay. Black dots represent the location of each receiver. Red dots are the locations inside the lagoon from where temperatures were taken and the blue dot is the station that represent the temperature outside the lagoon.

Table 4. Acoustic receivers deployed in Vizcaino Bay.

Receiver	Depth (m)	Month of deploy	Year of deploy
1	10	October	2013
2	8	October	2013
3	8	October	2013
4	20	June	2014
5	14	June	2014
6	6	June	2014
7	10	June	2014
8	18	June	2015
9	15	June	2015
10	10	June	2015
11	6	June	2015

3.2.2 Tagging of sharks.

With the help of local fishers, juvenile white sharks were caught, either with gillnets or longlines. Fishing gear sets were soaked for no more than 1 hour to reduce incidental mortality. All captured individuals were measured to the nearest centimeter of total length (TL) and sexed. For each tagged shark, an external acoustic transmitter (V16, 69 kHz; VEMCO; 159 dB power output, 3650 days battery life and transmission interval of 100 to 300 s) was anchored near the base of the first dorsal fin. On average, each shark was restrained for less than 10 min before its release. Also, presence of sharks tagged in California between 2011 and 2017 were monitored in the BSV array. Tagged sharks were categorized by size as newborns (NB) when smaller than 150 cm TL, young-of-the-year (YOY) between 150 and 175 cm TL, and juvenile (JUV) those larger than 175 cm TL. All sharks tagged in California before deploying the acoustic array in BSV were classified as JUV in this analysis.

3.2.3 Environmental data

Monthly surface water temperature data from several stations inside the Ojo de Liebre lagoon and from one station outside were obtained from the salt company based at Guerrero Negro. Temperature data from stations inside the lagoon were averaged to have a single temperature data inside the OLL.

3.2.4 Data analysis

Because of environmental noise and code collisions, a shark presence within the array was determine in at least two detections were recorded within 24 hours, all single detections were removed from the analysis based on Simpfendorfer et al. (2005). To quantify the temporal use of the area, we use the residence index (RI), calculated as the number of days a shark was detected within the acoustic array as a proportion of the number of days the tagged shark was monitored. Two RI were estimated: an overall RI and a monthly RI. These indexes were calculated for each shark detected in the array, and by areas: inside and outside OLL areas. General Additive Models were used to describe if age group (NB, YOY, JUV), sex (male or female), or origin (tagged at BSV or California) influenced the occurrence of white sharks within the monitored areas. The residence index per month for each shark was used as the response variable, and a Beta error distribution (commonly used for proportions) and logit link function were used. The backward selection was used to drop predictor variables (based on $p<0.5$ values), and the "best" model was selected based on the Akaike's information criterion (AIC). General Additive Mixed Models (GAMM) were used to determine the effect by age group, sex, origin, month, temperature, and salinity on the occurrence (RI) of white shark inside and outside OLL, with a beta error distribution and logit link. Cubic regression spline (Bs = "cr") was used to model predictor variables. Basis dimension ("k") was restricted to <4 to avoid overfitting. Pearson correlation coefficient (r) was used to eliminate correlated variables to avoid over-fitting the model. All models were runs using the *mgcv* and *gamm4* packages in R (R Foundation for Statistical Computing, 2020).

3.3 Results

A total of thirteen immature white sharks were tagged at BSV, but only eight were detected in the acoustic array. From the 13 sharks, four (30.7%) were subsequently incidentally caught and reported as dead in the nets, while the other two were never detected, and their mortality was not confirmed. Additionally, another seven sharks tagged at California, USA, were detected at the BSV-OLL array (Table 5). Sharks' size ranged from 138 to 300 cm TL (165.4 ± 35.36; mean ± SD) at the time of tagging, and the sex ratio was 1:1. From these 20 sharks, four were classified as NB, five as YOY, and 11 as JUV (Table 5).

Sharks detections were recorded on receivers during all months of the study period, except for the months of April and August 2015, and June-August 2016. However, individually, sharks presented a different pattern of presence and absence in the array (Figure 9). A highest number of sharks were detected during the fall and winter months (Figure 10). Only eight of the sharks were detected in multiple years, while the other twelve were detected only in one year of the study period (Figure 9).

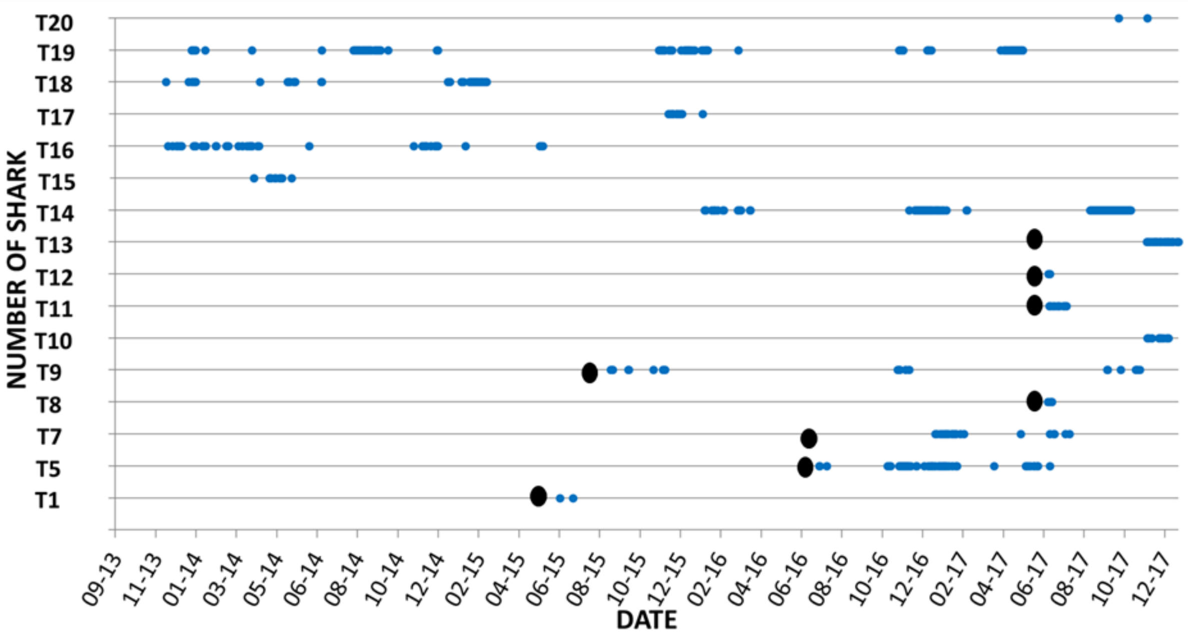

Figure 9 Time series of detections (blue circles) of immature white sharks in Ojo de Liebre lagoon and its surrounding waters from 2013 to 2017. Black circles represent the date of tagging. * represent sharks tagged at California.

Overall RI was low for all the sharks (<0.3; Table 5), but Monthly RI revealed high residency for some sharks during particular months (> 0.9; Fig. 3). For example, shark T2 was detected every year around 30 consecutive days, and shark T5 was detected 42 consecutive days in winter 2016 (Figure 9). Mean RI was higher in September (0.47), December (0.28), and January (0.20) for all the acoustic array, but in every month, some sharks were not detected (RI = 0; Figure 11). RI was higher outside the OLL than inside the lagoon (Figure 11). Higher mean RI outside the lagoon was in September, April, and May, while June and July had the lowest mean RI. Inside the lagoon, winter and early spring had higher RI (Figure 11).

White sharks were detected by all but two receivers located in the middle part of the OLL (Figure 11). All sharks showed a high percentage of detections by receivers outside OLL, except for two sharks (T12 and T13), which also had many detections in areas inside the lagoon (Figure 12). During the study period, sharks were detected from one single day up to 115 non-consecutive days. During 47 different days, there were multiple sharks (more than one) detected in a single day, with a maximum of four different sharks detected in a single day.

Table 5. White sharks tagged and detected in Vizcaino Bay. Details include sex (F, female; M, male), life stage (NB, newborn; YOY, young of the year; JUV, juvenile), total length (TL), date of tagging (DT), date of the last detection (DLD), number of days detected (DD) and residence index (RI). * represents sharks tagged at California, USA. † represents mortality. – no data.

Shark ID	Sex	Stage	TL (cm)	DT	DLD	DD	Number of receivers detected	RI
T1†	M	YOY	161	06/26/15	07/15/15	2	1	0.0667
T2†	F	JUV	182	07/12/15	-	-	-	-
T3	F	YOY	152	07/13/15	-	-	-	-
T4	F	YOY	166	07/15/16	-	-	-	-
T5	F	JUV	193	07/15/16	06/23/17	57	7	0.1133
T6†	M	NB	138	07/15/16	-	-	-	-
T7	F	JUV	190	07/16/16	07/22/17	19	6	0.0378
T8†	M	NB	142	07/31/16	-	-	-	-
T9	F	NB	148	06/20/17	06/26/17	4	2	0.0245
T10	M	YOY	152	06/20/17	11/22/17	3	1	0.0184
T11	M	YOY	153	06/20/17	07/18/17	13	2	0.0798
T12	F	NB	149	06/20/17	06/23/17	3	1	0.0184
T13	M	JUV	176	06/20/17	11/24/17	6	3	0.0368
T14*	M	JUV	156	07/26/15	10/21/17	115	3	0.2333
T15*	F	JUV	157	08/01/11	05/23/15	11	1	0.0075
T16*	F	JUV	146	06/14/12	05/31/15	41	5	0.0278
T17*	F	JUV	159	08/28/13	02/10/16	14	2	0.0095
T18*	M	JUV	145	08/16/12	03/09/15	41	4	0.0278
T19*	M	JUV	143	08/17/12	05/14/17	110	3	0.0745
T20*	UN	JUV	300	08/24/17	10/03/17	1	1	0.0102

Receiver five had the highest number of sharks detected (9), followed by receivers one (8) and two (8), both inside the lagoon (Figure 13). Receivers outside the lagoon had a higher number of detections than receivers inside OLL. The area near the mouth of the lagoon seems to be used by white sharks during more extended periods, while a lower number of detections inside the lagoon suggests that incursions are sporadic and have short-time duration.

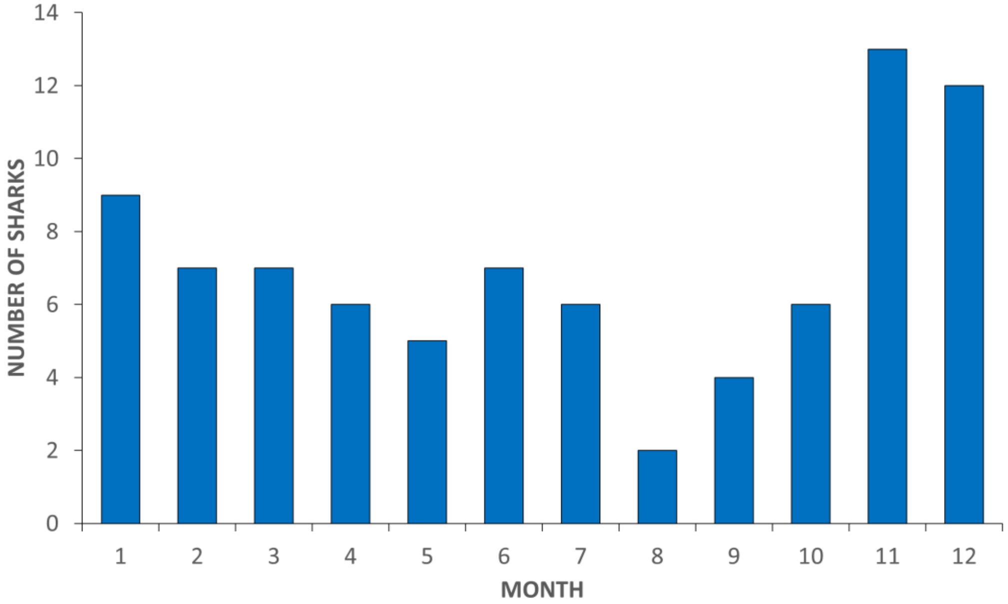

Figure 10. The cumulative number of tagged white sharks detected in Ojo de Liebre lagoon and its surrounding waters per month from 2013-2017.

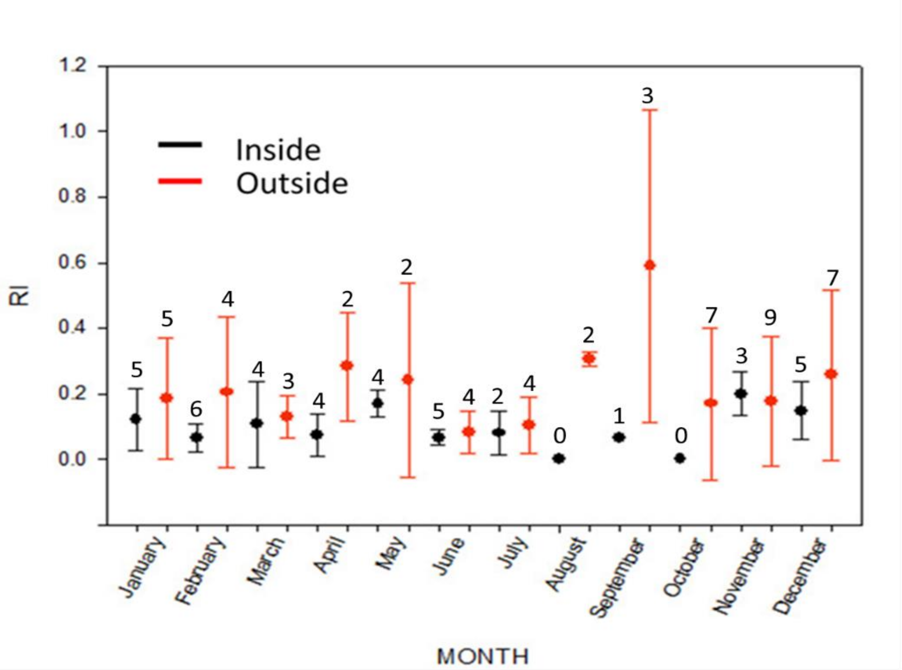

Figure 11. Mean residence index (RI) for juvenile white sharks detected inside and outside the Ojo de Liebre lagoon. The error bars represent the standard deviation in each month. Numbers above each bar represent the number of sharks detected per month.

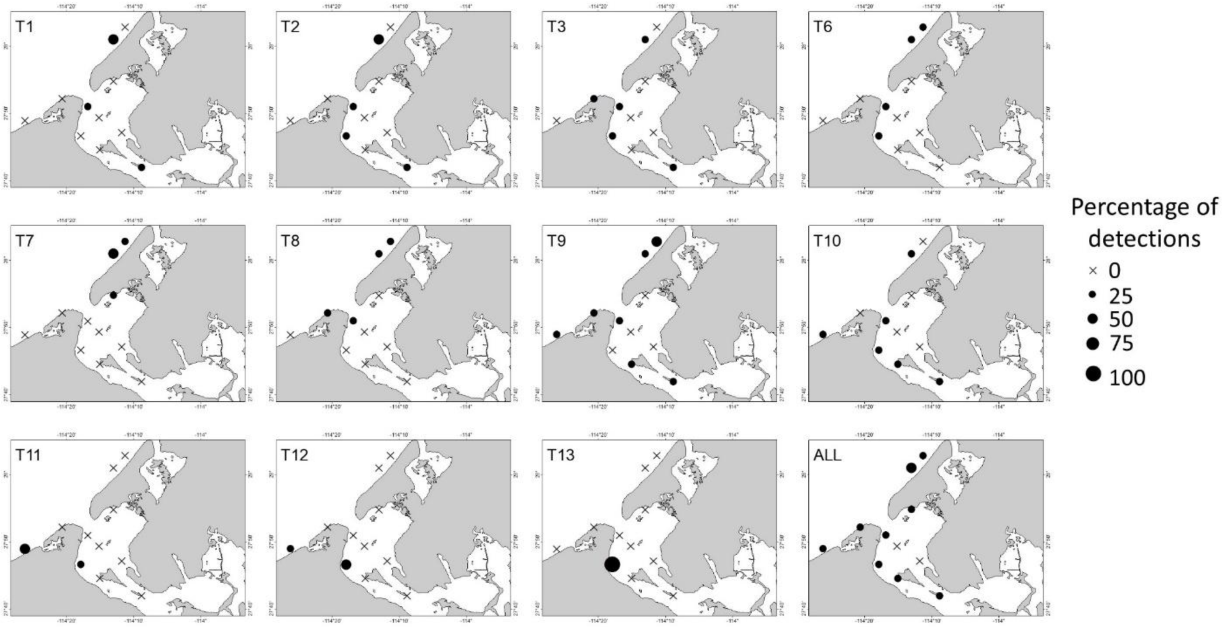

Figure 12. Percentage of detections per receiver for immature white sharks in Ojo de Liebre lagoon and its surrounding waters. Bubble size represent the proportion of overall detections for individuals detected on the array. "X" refers to the receiver location where no detections were recorded.

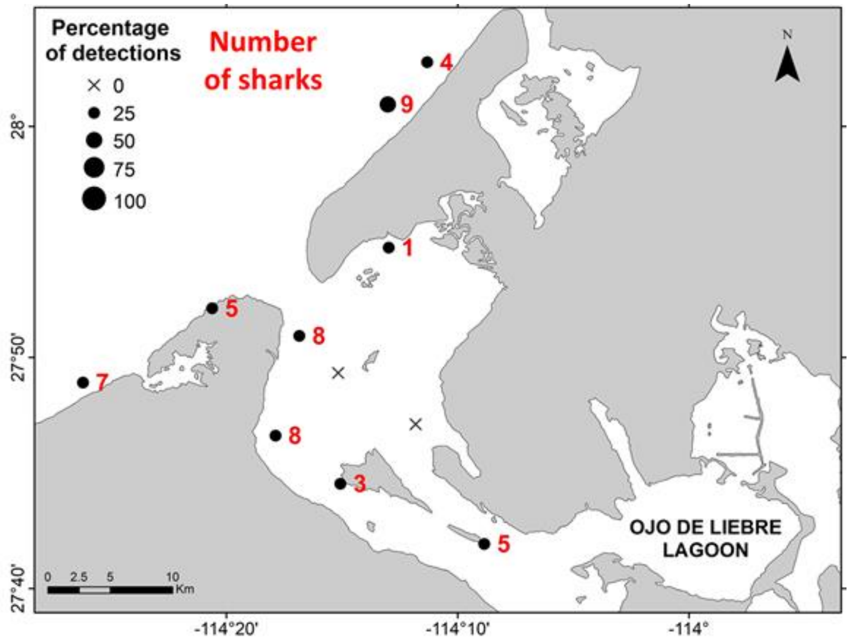

Figure 13. Percentage of detections per receiver (black dots) and number of white sharks (red numbers) detected per acoustic receiver in the Ojo de Liebre lagoon and its surrounding waters.

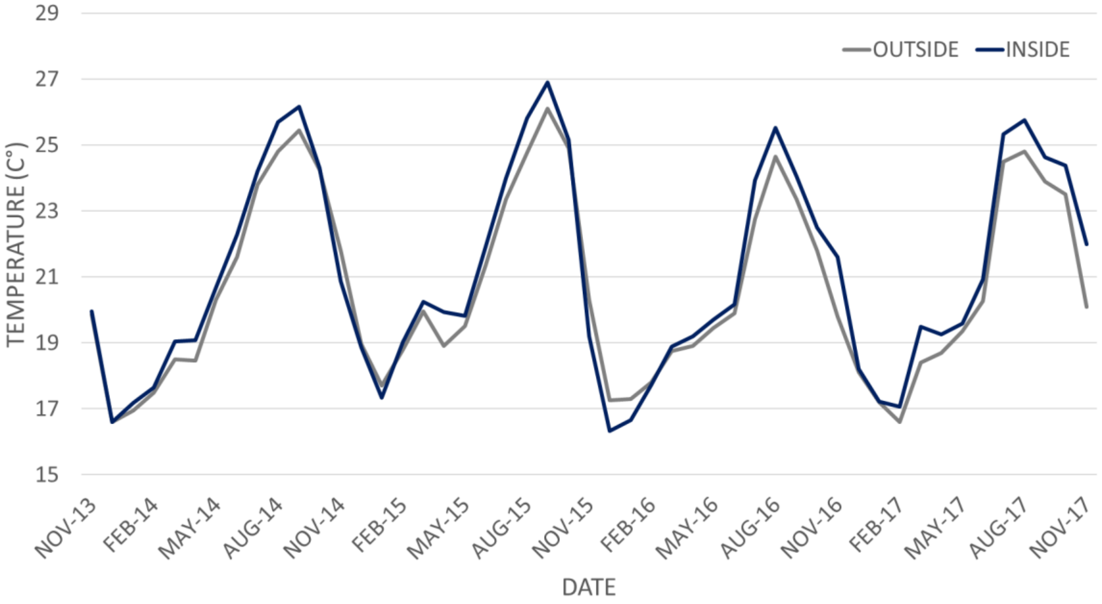

Figure 14 Average monthly surface temperatures inside and outside the Ojo de Liebre lagoon from November 2013 to November 2017.

Temperature were similar inside and outside OLL. Outside temperatures ranged from 16.6° to 26.1 °C, while inside ranged from 16.3 to 26.9 °C (Figure 14). Temperatures were higher from late spring to early fall with a maximum peak in September of each year. After that, these temperatures decreased in late fall and winter with a minimum temperature in December (Figure 14).

General Additive Model results suggested that sex (males) and origin (California) were the better predictors for the overall RI, with life stage as the less significant factor (Table 6). These results seem to be influenced by sharks tagged at California monitored for a longer time than sharks tagged at BSV. Month (September, December and January), origin (California), and sex (males) were significant predictors (*p* <0.01) of the presence of white sharks outside the lagoon, but the "best" model only includes the interaction of month and origin (Table 7). Sharks seem to be more resident outside the OLL in fall and winter months, but again, this seems to be influenced by sharks coming from California. According to GAMM, inside the OLL, life stage (Juveniles) and month (January-March) were the best predictors of the presence of sharks (RI), and temperatures were not significant (p= 0.13). Juveniles (larger than 175 cm TL) seem to use the lagoon in winter and early spring months.

Table 6. Ranking of General Additive Models of total Residence Index of white sharks explained by biological variables. AIC, Akaike Information Criterion. Only the better five models are showed.

Model	**AIC**
Sex*Origin	-68.45
Sex	-68.30
Sex*Stage	-65.80
Origin	-65.31
Stage	-63.37

Table 7. Ranking of General Additive Mixed Models of residence index of white sharks inside and outside the Ojo de Liebre Lagoon explained by independent variables. Only the better six models are showed.

Model	**AIC**
Outside OLL	
Sex + Origin * Month	-142.20
Month * Origin	-140.04
Month + Origin	-140.06
Origin + Sex * Month	-139.50
Stage + Origin * Month	-139.31
Sex + Stage * Month	-137.94
Inside OLL	
Stage + Month	-97.53
Stage + Sex * Month	-96.76
Sex * Month	-96.24
Sex + Stage	-95.84
Stage + Month	-95.59
Stage + Origin * Month	-95.41

3.4 Discussion

Our results show that immature white sharks are present in BSV during all months of the year. Their presence highlights the importance of this large bay as a primary nursery, and confirms the movements of sharks from California to Mexican waters, as previously reported (Weng et al., 2012; White et al. 2019).

Worldwide, immature white sharks are known to occupy coastal nurseries areas during several months of the year prey abundance and suitable habitat conditions that in Northeastern Pacific are related to waters with depths less than 1000 m, distances <30 km from the coastline and temperatures between 14 to 24 °C (Bradford et al., 2012; Bruce & Bradford, 2012; Harasti et al., 2017; Curtis et al., 2018; White et al., 2019). Even if previous information from satellite tags and stable isotope analysis has revealed that BSV is used by immature white sharks (Weng et al., 2007; 2012; Malpica-Cruz et al., 2013; White et al., 2019; Tamburin et al., 2020), this study is the first attempt focused in the description of the habitat use of this coastal lagoon and the areas near its inlet by the species. Sex and place of tagging were the factors that better explained the presence of immature white sharks in all the study areas, where males tagged at California resulted in the more significant effect. These results suggest that maybe there is a sex-biased use of the lagoon and the areas near the inlet, where males distribute in areas closer to the detection range of the receivers than females. Results from the GAMM modeling showed that month and origin were the factors that better explained the presence of white sharks in areas outside the OLL, with late fall and early winter months and sharks tagged at California having a more significant effect. Also, a higher number of sharks were detected during fall and winter months, probably concerning the movement of juvenile white sharks from California to Mexican waters (Weng et al., 2012; White et al., 2019). The significant effect of the sharks tagged at California in our models could be explained by the time period that sharks from both areas were monitored. Sharks from California were tagged before the acoustic array was deployed in BSV and in consequence they were monitored for more time than sharks tagged at BSV (after the deploy of the array). To explore if sharks born at BSV uses the inlet are from OLL different than sharks coming from California, the number of sharks tagged and the monitoring time at BSV should increase.

Surprisingly, the temperature was not a factor explaining the use of BSV by immature white sharks, even if this variable has been shown as a driver for the movements and distribution for several shark species (Vaudo et al., 2016; Andrzejaczek et al., 2018; Payne et al., 2018). Also, previous studies have shown that seasonal decreases in surface water temperatures in southern California may cue fall migrations of juvenile white sharks leave into Mexico waters (Weng et al., 2007; White et al., 2019). Based on its annual SST and water depth, BSV has been reported to be environmentally suitable for immature white sharks year-round, suggesting that BSV provides all the favorable conditions for these life stages compared with other nearby areas between California and BSV (White et al., 2019), and that seasonal changes of temperature do not decrease this habitat suitability. Temperature ranges inside and outside OLL were in the range that immature white sharks are known to occupy (Weng et al., 2012; White et al., 2019), so this could be an explanation to not being significant in our models. During warmer interannual events like El Niño or the Blob, waters from BSV have been reported to get warmer than usual, and the suitability for immature white sharks might change, forcing some white sharks to move to other suitable areas as happenings with other species (Cavole et al., 2016; White et al., 2019). White et al. (2019) reported that juvenile white sharks in California were found to move to areas north of Point Conception during the 2015-2016 ENSO-Blob event, to areas where neonate and YOY white sharks had previously not be observed. Some of the few months (April and August 2015, and June-August 2016) of the monitoring period where we did not get detections were during these events, suggesting that immature white sharks moved out from the acoustic array, even if their presence in the area was confirmed by the tagging of five immature white sharks during June 2016 (Table 5). This highlights the importance to understand if suitable conditions are the same for white sharks born in BSV and the ones born in California.

Our results showed that under normal conditions, white sharks enter into the OLL almost every month of the year, in some of the months only for short periods. Juvenile sharks of other species use these areas for protection from predators (Heupel et al., 2007; Knip et al., 2010). However, we found that larger white sharks (larger than 175 cm TL) enter more frequently into the lagoon, mostly during winter and early spring months. Due to the size of white sharks observed, it seems unlikely that seeking protection is the reason to enter into the lagoon. These movements could be related to taking advantage of the temporal prey availability, as reported for estuaries in Australia (Harasti et al., 2017). In the OLL, white sharks were detected mostly in the receivers located near the mouth of the lagoon, but they were also detected in receivers farther from the mouth, near islets where demersal elasmobranchs (mainly diamond stingrays and California butterfly rays) congregate and are often targeted by artisanal fishers (pers. Obs.). These species are common prey of younger white sharks (Tricas & McCosker, 1984; Santana-Morales et al., 2012; Tamburin et al., 2020; Chapter 4), suggesting that prey availability might explain better why white sharks are entering into this habitat.

Winter and spring months are when grey whales come into coastal lagoons of the Baja California peninsula, including the OLL, for breeding and calving (Urban et al., 2003; Brenner et al., 2016). Fishers have reported sightings of white sharks scavenging on dead calves of grey whales inside the OLL. A switch in diet towards feeding on marine mammals related with size has been reported for white sharks around 200 cm TL (Tricas & McCosker, 1985; Estrada et al., 2006; Carlisle et al., 2021; Hussey et al., 2012). Scavenging may be more common than reported and be an additional explanation for the presence of sharks larger than 175 cm TL inside the lagoon.

Even if immature white sharks could be present in all months of the year in the area near the mouth of the OLL, the residence index was lower, suggesting that these sharks are moving off the detection range of the acoustic receivers to other areas inside BSV but farther from the OLL inlet area or to other regions. According to reports of incidental catches and telemetry data, immature white sharks could be moving along the coast of the Baja peninsula and into the Gulf of California, so the sharks tagged in this study could be moving to any of those areas or, for sharks tagged at California, returning there (Weng et al., 2007; 2012; Santana-Morales et al., 2012; Ramírez-Amaro et al., 2013; Marquez-Farías & Lara-Mendoza, 2017; Oñate-González et al., 2017; White et al., 2019). However, for sub-adult and adult white sharks there has been reports of smaller sharks leaving an area where larger sharks come (Becerril-García et al., 2019), indicating that social components could not be discarded.

The low residence of individuals in the receiver's array could be due to two factors: movements outside the BSV area or due to the coverage area of the receivers. A low residence has been found for other migratory species like dusky sharks (Braccini et al., 2017) due to their capacity to make larger movements. In the case of these immature white sharks, it is known that they are moving between nurseries in California and Mexico (Weng et al., 2007; 2009; White et al., 2019). Stable isotope analyses (Tamburin et al., 2020; Chapter 4) and preliminary data from satellite tags have shown that immature white sharks move to offshore areas inside BSV, where they are accessing deeper depths (up to 50 m). The limitation of the coverage area from the acoustic receivers could be underestimating the presence of white sharks in BSV. Deploying more acoustic receivers throughout certain parts of the Bay was not feasible due to high seasonal shrimp trawling activity. Future efforts should be focused on the deployment of more receivers covering all the bay to account for this potential source of bias and to understand the pattern of spatial and temporal use beyond the OLL and the areas near its inlet. As well, this preliminary data from satellite tagging has shown that some sharks could move to northern areas near another coastal lagoon in the San Quintin bay area, which, like BSV, is high productivity area (Aguirre-Muñoz et al., 2001; Camacho-Ibar et al., 2003; Álvarez-Borrego, 2004). The movements of younger white sharks to San Quintin Bay and the reports of incidental catches in other coastal lagoons from the region, like San Ignacio and Bahía Magdalena (Ramírez-Amaro et al., 2013) could suggest the potential importance as nursery habitats of the coastal lagoons in the Baja peninsula for early life stages of white sharks, especially if the hypothesis of population growth in the region is correct (Lowe et al., 2012; Tinker et al., 2016).

Most of the detections came from receivers near the mouth of the OLL, an area previously reported as crucial for white sharks in the region (Guerrero-Avila et al., 2013; García-Rodríguez & Sosa-Nishizaki, 2020). These areas are also the places where there is a higher interaction with artisanal fisheries, mostly from fishers based at the fishing camp in the Ojo de Liebre lagoon (García-Rodríguez & Sosa-Nishizaki, 2020). These results suggest a higher spatial overlap between immature white sharks and artisanal fishing activities than the overlap reported for California (Lyons et al., 2013), explaining more considerable fishing mortality in Mexican waters (Benson et al., 2018). Incidental catches of immature white sharks are related with the use of bottom gillnets (Lowe et al., 2012; Santana-Morales et al., 2012; Lyons et al., 2013; Oñate-González et al., 2017), and in BSV, these incidental catches are more common when fishers are targeting high-value species, like California halibut, white seabass, and rays (García-Rodríguez & Sosa-Nishizaki, 2020). These species are common prey of juvenile white sharks (Santana-Morales et al., 2012; Chapter 4) and are caught all along the coast of BSV (García-Rodríguez & Sosa-Nishizaki, 2020) at shallow waters (less than 10 m) that are commonly used by immature white sharks (Dewar et al., 2004; Lyons et al., 2013; White et al., 2019).

Even if our results suggest a relatively high spatial overlap between fishing activities and white shark distribution, it seems than temporal overlap is shorter in time. The number of sharks detected in the array was higher during months with smaller interaction of white sharks with artisanal fisheries, indicating a smaller interaction than previously thought. These results could be, again, explained by a more extensive monitoring time of sharks tagged at California compared with white sharks tagged in Mexico but also could be due to differences in the probability of being incidentally caught due to temporal shifts of fishing gears used and ontogenetic susceptibility. Immature white sharks are commonly caught during late spring and summer in BSV when we found less residency and when the use of gillnets is higher (Santana-Morales et al., 2012; Oñate-González et al., 2017; García-Rodríguez & Sosa-Nishizaki, 2020). During the fall, some fishers switch to using traps when the lobster season stars (García-Rodríguez & Sosa-Nishizaki, 2020), so this change in the use of fishing gears could explain the lower incidental catches during the period with higher residence and number of sharks detected. In the Northeastern Pacific, it has been hypothesized that pregnant females gave birth in coastal areas of the Baja peninsula during summer when the interaction of smaller white sharks with fishing activities is higher (Domeier & Nasby-Lucas, 2013; García-Rodríguez & Sosa-Nishizaki, 2020). In this region, these smaller sharks are incidentally caught with when targeting demersal bony fishes using gillnets with a mesh size of 20-25 cm (Lyons et al., 2013; Ramírez-Amaro et al., 2013; García-Rodríguez & Sosa-Nishizaki, 2020) and most of the catches come from young of the year sharks (Lowe et al., 2012; Oñate-González et al., 2017). It is possible that smaller sharks (newborn and young of the year) present during the summer in BSV are more likely to die if they get entangled due to their size, while larger sharks (juveniles), either born in California or BSV, could be able to break through nets (Oñate-González et al., 2017; pers. obs.). White sharks could grow around 20 cm in their first year of life (Cailliet et al., 1985), so sharks born during the summer in BSV and sharks coming from California during the fall and winter could be less vulnerable to die if they got entangled in these months when there is a shift in the use of fishing gears. If this hypothesis is correct, the degree of interaction with artisanal fisheries could be smaller than previously thought with less interaction when there is a higher presence of sharks in the area. However, these sharks will still be vulnerable to be incidentally caught during their firsts four or five years of life and if shifts in fishing practices occur in the future, the vulnerability of white sharks to being incidentally caught could change, highlighting the importance of monitoring artisanal fisheries in BSV. A better understanding of the spatial use of BSV during summer could help to focus suggested management actions, like decreasing soaking time or changes in fishing gears (García-Rodríguez & Sosa Nishizaki, 2020), that helps to decrease fishing mortality.

In summary, BSV is used by all life stages of immature white sharks indistinctly of their origin, with higher presence and residence in fall and winter, highlighting the importance of BSV for sharks from both nursery areas. Future research should focus on confirming if there is sex segregation of male sharks from California using the area more constantly than sharks born at BSV, or if this is influenced for a more extended monitoring period of sharks tagged at California. The habitat of Ojo de Liebre lagoon seems to be essential for large sharks (<175 cm) in winter and early spring (indistinctly of the origin) when incursions last longer than other months. These results could help to the adjustment of existing conservation actions focused on decreasing fishing mortality. Future research should focus on the importance of other coastal lagoons and their surrounding waters along the coast of the Baja peninsula as potential nursery areas for the species, especially if the hypothesis that the population number in the NEP is increasing. Also, future studies should aim to understand how regional and global changes could drive movements of immature white sharks and, specifically, how these phenomena could affect the nursery habitat that BSV provides to this species.

Chapter 4. Trophic relationships of white sharks in Vizcaino Bay.

4.1 Introduction

Most shark species are considered top predators occupying high trophic levels (Cortés, 1999). Some of these species are highly migratory and move between coastal and pelagic habitats through ontogeny, with different life stages using distinct habitats as nurseries, or for feeding, mating, or parturition purposes (Heupel et al., 2007; Block et al., 2011; Domeier & Nasby Lucas, 2013; Carlisle et al., 2015a; Nasby-Lucas et al., 2019; Nosal et al., 2019). Habitat changes are commonly accompanied by ontogenetic switches in diet (Malpica-Cruz et al., 2013; Carlisle et al., 2015b; Estupiñan-Montaño et al., 2019; Matich et al., 2019). Characterizing the trophic relationships of sharks in each habitat used throughout their life cycle is needed for understanding their ecological role in each ecosystem.

Adult white sharks are distributed mostly in offshore areas, including oceanic islands (Klimley et al., 1992; Domeier & Nasby-Lucas, 2007; Jorgensen et al., 2010; Francis et al., 2015; Boldrocchi et al., 2017; Skomal et al., 2017; Moro et al., 2019), while juveniles occupy coastal areas as nurseries (Bruce & Bradford, 2012; Harasti et al., 2017; Curtis et al., 2018; Bruce et al., 2019). In the Northeastern Pacific, the early life stages of white sharks (newborn, YOY, and juveniles) occupy coastal areas until they become sub-adults, and can migrate between spatially separate nurseries (Dewar et al., 2004; Weng et al., 2007; 2012; Lowe et al., 2012; Oñate-González et al., 2017; White et al., 2019). These nurseries harbor high food abundance, allowing younger white sharks to grow faster, and are crucial for their juvenile survival and recruitment to adult aggregations and population growth (Heupel et al., 2007; Mollet & Calliet 2002).

The white shark is a top predator that exhibits ontogenetic changes in its feeding habits and habitat use (Estrada et al., 2006; Kim et al., 2012; Carlisle et al., 2012; French et al., 2018). Whereas adult white sharks feeding habits have been widely studied, dietary information for the early life stages is still scarce (Santana-Morales et al. 2012; Huveneers et al., 2018; Tamburin et al., 2020). Juveniles shift their diet from feeding on smaller bony fishes and elasmobranchs (mainly rays) to larger fishes as they grow. After becoming sub-adults, white sharks start to feed on marine mammals (Tricas & McCosker, 1984; Estrada et al., 2006; Hussey et al., 2012; Malpica-Cruz et al., 2013).

Vizcaino Bay (BSV) is located on the western coast of the Baja California Peninsula, Mexico. This bay has been confirmed as a natal nursery area for white sharks, and is also habitat to young sharks born in the Southern California Bight, USA, about 600 km to the north (Oñate-González et al., 2017; White et al., 2019).

Although the species is under protection since 2007 in Mexican waters (DOF, 2007; 2010; 2014), they are caught incidentally in the nearshore areas of BSV as well as within Ojo de Liebre Lagoon (OLL), a semi-enclosed hypersaline shallow estuary that is within the bay system (García-Rodríguez & Sosa-Nishizaki, 2020). These catches occur when local artisanal fishers target high-value species that are part of the white shark's diet (Santana-Morales et al., 2012, García-Rodríguez & Sosa-Nishizaki, 2020).

The potential competition between artisanal fisheries and white sharks could have an effect on the conservation of this species in this nursery area. For top predators like turtles, birds and marine mammals, it has been well documented that this competition could have negative effects on their abundance by limiting the spatial availability of prey (Huss et al., 2014; Hillborn et al., 2017; Hansson et al., 2018). For example, a switch in diet as result of prey overfishing has been reported for the spiny dogfish *Squalus acanthias* (Koen Alonso et al. 2002). Also, a high overlap between target fishery species and shark prey has been documented for the spiny dogfish (Lucifora et al., 2009). In sand tiger sharks (*Carcharias taurus*), the spatial overlap between the prey and fisheries was shown to increase their vulnerability to overfishing (Graĉan et al., 2017). Changes in prey availability as an effect of overlap with fisheries in nursery areas could decrease the benefits that these nurseries provide for early life stages of sharks, potentially changing their diets and limiting their growth.

Interspecific competition between young white sharks and sympatric shark species that inhabit BSV, like smooth hammerheads *Sphyrna zygaena* or Carcharhinids, could also occur. Previous studies report resource partitioning in communal areas to reduce interspecific competition, which could cause changes in distribution between sympatric shark species with high overlap in their diets (Bethea et al., 2004; Papastamatiou et al. 2006; Kinney et al. 2011). Hence, limitation in prey availability due to fisheries could thus increase the competition between shark species. The description of the trophic relationships between white sharks, their prey, and sympatric species that may compete for feeding resources will help to understand their ecological role in the nursery habitat provided by BSV.

Quantitative diet composition estimates are based on stomach content analysis, providing a basis for understanding a species' prey spectrum and its overall trophic ecology, including trophic level (Cortés, 1999; Bizzarro et al. 2017). Nevertheless, stomach content analysis has several constraints, since it is labor-intensive and highly invasive or lethal, with limited spatial resolution unless ambitious sampling efforts are implemented and provide only a snapshot of what a shark has eaten most recently. This approach often requires a very high sample size to quantify diet variation across a population, and can lead to a limited interpretation of their trophic ecology (Hussey et al., 2012; Munroe et al., 2018).

Bulk stable isotope analysis (SIA) of soft tissues provides information that complements that obtained through stomach content analysis by providing integrated spatio-temporal insight into trophic relationships and energy fluxes in marine ecosystems (Michener & Kauffman, 2007; Boecklen et al., 2011). Different tissues reflect the isotopic composition of prey consumed over time; tissues with higher isotope turnover rates (i. e. blood) reflecting diets faster than those with lower turnover rates (i.e., muscle) (Logan & Lutcave, 2010; Malpica-Cruz et al., 2012; Hussey et al., 2012). The rate of isotopic turnover should be considered when interpreting SIA ratios in sharks (Kim et al., 2012; Malpica-Cruz et al. 2012). δ^{13}C values provide information regarding the dominant sources of primary production, which vary between habitat types as well as between benthic and pelagic food webs. Thus, δ^{13}C values can be used to trace shark habitat shifts, particularly between coastal and oceanic ecosystems, as well as distinguishing between benthic vs. pelagic feeding (Finlay & Kendall, 2007; Munroe et al., 2019). Due to a consistent enrichment in δ^{15}N between a consumer and its assimilated diet, δ^{15}N values have been used to estimate trophic levels and characterize ontogenetic shifts in trophic level (Peterson & Fry, 1987; Post, 2002). Given prior knowledge regarding a consumer's feeding habits and an adequate characterization of the spatiotemporal scales of isotopic variability of the isotopic baseline (Phillips et al. 2014), SIA are also useful for estimating the contribution of different sources to a consumer's diet (Parnell et al. 2013). Likewise, isotopic ratios provide ecological information about individuals and communities, and can be used to characterize the isotopic niche, which is a reflective of a consumer's trophic niche and can be used to estimate the overlap in resources between different populations, life stages or species (Jackson et al. 2011, Hette-Tronquart 2019, Marshall et al. 2019).

Recently, the use of compound-specific stable isotope analysis of amino acids (CSIA-AA) has been proposed as a more robust method to understand several fish species' trophic ecology. Some AAs are not significantly enriched in ^{15}N between consumer and their foods (and are thereby termed "source AA,") while others exhibited a high and consistent enrichment (and are therefore considered "trophic AA"; Chikaraishi et al., 2009, O'Conell 2017). These analyses are advantageous because a single tissue contains both kinds of AA, allowing for the calculation of trophic position and inferring of foraging patterns without the need for an independent characterization of an isotopic baseline (Chikaraishi et al., 2010; Hoen et al., 2014; Munroe et al., 2018)

To understand the trophic ecology of the early life stages of white sharks in the BSV-OLL nursery, we used bulk SIA and CSIA-AA of shark muscle to estimate the contribution of different prey groups to the diet of juvenile white sharks, assess ontogenetic shifts in their diet, infer movements between habitats and estimate trophic level. We also infer the level of dietary overlap with sympatric shark species that also feed within the bay, evaluating the potential for competition for dietary sources with local fisheries and sympatric species. The study provides for information the development of environmentally sound management and conservation strategies in the area.

4.2 Methods

4.2.1 Sample collection

Muscle samples (1 cm^3) from the dorsal area of white sharks were collected between 2013 to 2017 either in BSV or outside of BSV (OBSV), off the northwestern coast of the Baja peninsula between Santa Rosalillita and Tijuana (Figure 15). Samples were obtained opportunistically from white sharks caught incidentally by artisanal fisheries and from individuals tagged within BSV. For all sharks sampled inside BSV, total length (TL) and sex were recorded. Based on their size, sharks were divided into three life stages: newborn (NB; less than 150 cm TL), young of the year (YOY; between 151-175 cm TL), and juveniles (JUV; larger than 175 cm TL). Although sharks sampled at OBSV were not measured because local fishers provided samples, they estimated their size > 175 cm TL and were therefore categorized as juveniles.

As mentioned before, isotopic turnover rates should be considered when interpreting SIA ratios in sharks (Kim et al., 2012; Malpica-Cruz et al. 2012). Steady state between isotopic composition from muscle tissue and diet for sharks has been estimated to be reached after several months or even years, with younger individuals reaching this equilibrium faster than older ones (Logan & Lutcave, 2010; Kim et al. 2012; Malpica-Cruz et al., 2012). For juvenile white sharks in BSV, Malpica-Cruz et al. (2013) reported that blood and muscle tissues are in isotopic equilibrium suggesting that muscle is reflecting local foraging ground. Our interpretation of the stable isotope ratios of immature white sharks sampled in BSV is based on this assumption.

Muscle tissue samples (1 cm^3) from demersal species (n=72), previously reported as prey for juvenile white sharks in BSV by Santana-Morales et al. (2012), were collected from fishing activities in BSV during summer of 2016. Individuals sampled were caught in waters near the mouth of OLL. Potential prey sampled were white seabass *Atractoscion nobilis*, California halibut *Paralichthys californicus*, California bat ray *Myliobatis californica*, California butterfly ray *Gymnura marmorata*, diamond stingray *Hypanus dipterururs,* and shovelnose guitarfish *Pseudobatos productus* (Table 10). Shovelnose guitarfish were selected because it is the most abundant demersal elasmobranch in the area.

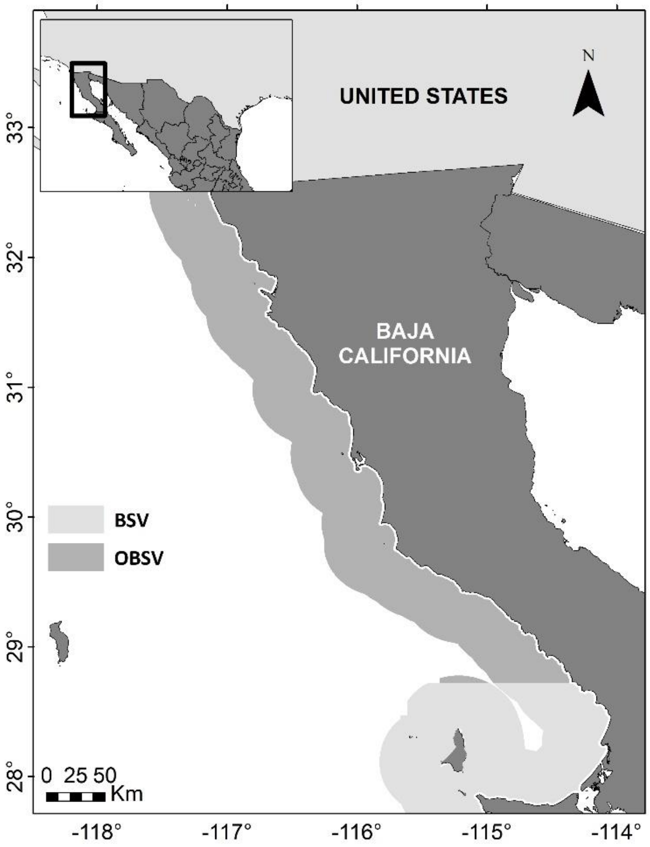

Figure 15. Areas of the Baja California peninsula where white shark muscle samples were collected. BSV = Vizcaino Bay. OBSV = Outside Vizcaino Bay.

4.2.2 Sample preparation for bulk isotope and CSIA- AA analysis

White shark samples, as well as elasmobranch prey and sympatric sharks, were lipid and urea extracted as previously recommended for bulk SIA (Li et al. 2016, Carlisle et al. 2017), following the methods of Kim & Koch (2012) and Carlisle et al. (2015). Briefly, tissue samples were soaked in petroleum ether and mixed in a vortex mixer. After letting the samples dry uncapped for eight hours, they were centrifugated for 10 min. Samples were rinsed in 10 ml of DIW and mixed in a vortex mixer. Samples were centrifugated after 30 min. Following the extraction, samples were dried in an oven at 60 °C for 24 hr. Subsequently, 0.8-1.2 mg were included in a tin capsule for shipment to the laboratory. Samples were analyzed at the Stable

Isotope Facility at the University of California Davis (SIA-UCD) using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Analytical precision for laboratory standards, bovine liver, glutamic acid, enriched alanine and nylon 6, was 0.06‰, 0.06‰, 0.06‰, and 0.05‰ for $\delta^{15}N$, respectively, and 0.06‰, 0.1‰, 0.07‰, and 0.08‰ for $\delta\ ^{13}C$, respectively.

For CSIA-AA analysis, white shark samples were directly dried in an oven for 24 h at 60°, as recommended by Hoen et al. (2014). Between 7-10 mg of dry sample was weighed and stored in pre-combusted 5 ml glass vials. Samples were analyzed at SIF-UCD with a Trace Ultra GC gas chromatography coupled to Thermo Delta V Plus through a GC IsoLink, following protocols described by Yarnes & Herszage (2017). Each sample was analyzed in triplicate.

Stable isotope values are expressed in standard delta notation (δ). For $\delta^{15}N$ values, atmospheric nitrogen was used as a standard, while the Vienna Pee Dee Belemnite (VPDB) standard was used for $\delta^{13}C$. Units are in parts per thousand (‰):

$$\delta^{15}N\ (‰) = ([R_{sample}/R_{standard}] - 1) \times 10^3 \tag{1}$$

Where R is the isotope ratio (^{15}N:^{14}N or ^{13}C:^{12}C).

Differences in mean $\delta^{15}N$ and $\delta^{13}C$ between life stages (NB vs. YOY vs. Juveniles) were estimated using one-way ANOVA with Tukey *post-hoc* test, while differences between areas (juveniles inside and outside BSV) were estimated using Kruskal-Wallis because normality was not met (tested with Shapiro-Wilk test).

4.2.3 Trophic relationships between white sharks and potential prey

To estimate the relative contribution of potential prey inside BSV to the diet of immature white sharks sampled in BSV, we categorize them into three groups depending on their habitat: *demersal*, *pelagic, and offshore* habitat species. Isotopic values of potential prey sampled in this study (see section 4.2.1) were categorized as *demersal* habitat (Table 10). For the *pelagic* and *offshore* habitats, we used the $\delta^{13}C$ and $\delta^{15}N$ values published by Tamburin et al. (2019, 2020) from potential prey of immature white sharks sampled in the BSV region (Table 10). Overall mean ± standard deviation (SD) for each habitat was used as input for mixing models.

Bayesian mixing models (Parnell et al. 2013) were used to estimate the contribution of the prey from each habitat to the diet of white sharks sampled in BSV. Analyses were performed using *simmr* package (Parnell & Inger, 2019) in R. Models were run with uninformed priors, four Markov Chain Monte Carlo (MCMC) chains, with 1000 burn-in and 10,000 iterations. We used the empirically derived trophic enrichment factors (TEF) reported for shark muscle estimated in controlled feeding experiments by Kim et al. (2012) and Malpica et al. (2012). TEF values from those studies were averaged for their use in mixing models ($\Delta\ \delta^{13}C = 1.3 \pm 0.5$ ‰; $\Delta\ \delta^{15}N = 3.0 \pm 0.9$ ‰). An abrupt increase in $\delta^{15}N$ was reported for immature white sharks larger than 170 cm in BSV (Malpica-Cruz et al., 2013), so smaller sharks (newborns and young of the year) were grouped for mixing models. Each habitat's contribution was estimated for this combined group and for juveniles. Results are reported as the percent contribution of each prey group with 95% credibility intervals.

4.2.4 Isotopic niche overlap with sympatric species

The isotopic niche was estimated as the standard ellipse area (SEAc; Jackson et al. 2011). White sharks and two other shark species found in BSV were included in the analysis: smooth hammerheads and copper sharks. Smooth hammerheads were categorized into three groups based on their size (Table 10). This categorization was designed to match the sizes of the life stages considered in this study for immature white sharks. The three groups were newborns (60-85 cm TL), small juvenile (103-147 cm TL) that have similar sizes to newborns white sharks and large juveniles (151-183 cm TL) with similar sizes to YOY white sharks. The level of isotopic niche overlap between life stages of white sharks (newborn, YOY, and juvenile caught inside and outside BSV) and between sympatric shark species was estimated. Analyses were done using the *SIBER* package in R.

4.2.5 Estimation of trophic position

Trophic position was estimated using CSIA-AA based on two equations, the one proposed by Chikaraishi et al. (2009):

$$TP = \frac{(\delta\delta^{15}N_{glu} - \delta^{15}N_{phe} - \beta)}{TEF} + 1 \tag{2}$$

Where $\delta^{15}N_{glu}$ (the canonical trophic AA) and $\delta^{15}N_{phe}$ (the canonical source AA) indicate the $\delta^{15}N$ values for glutamic acid and phenylalanine in the consumer tissues, respectively. β is the difference between the $\delta^{15}N$ values of trophic and source AAs in primary producers (3.4± 0.9‰, Chikaraishi et al. 2009), and TEF is the trophic enrichment factor. Also, we used a modification of the Hoen et al. (2014) equation that uses an integrated TEF that accounts for the differences in fractionation between grazers and carnivores, which is relevant for sharks, since there could be differences in fractionation compared to grazers due to differences in the quality or quantity of proteins in diet:

$$TP = \frac{(\delta^{15}N_{glu} - \delta^{15}N_{phe}) - \beta - TEF_{herbivore}}{TEF_{carnivore}} + 2 \tag{3}$$

Where the $TEF_{herbivore}$ is equal to 7.6‰ and the $TEF_{carnivore}$ is <7.6‰. TDF and TEF previously reported for zooplankton and fishes (Chikarashi et al., 2009) and for sharks based on controlled experiments (Hoen et al., 2014) were used (7.6 ‰ and 2.8 ‰, respectively) for TP estimations.

4.3 Results

Muscle tissue samples from 39 immature white sharks were obtained, of which 12 were from newborns, 13 from young of the year, and six from juveniles sampled inside BSV, and an additional 8 were from juveniles from areas outside BSV. Values for white sharks sampled in BSV ranged from -17.8 to -15.5‰ for $\delta^{13}C$ (-16.7 ±0.6‰ mean ± SD) and from 16.4 to 18.7‰ for $\delta^{15}N$ (17.5 ±0.6‰). Muscle samples from YOY and juveniles were slightly enriched in $\delta^{13}C$ (0.5‰ and 0.8 ‰) and $\delta^{15}N$ (0.2 ‰ and 0.8 ‰) compared with NB (Figure 16, Table 8). There were significant differences in mean $\delta^{15}N$ values between NB and YOY compared with juveniles (one-way ANOVA, p=0.02 and p=0.03) but not between NB and YOY (p=0.91). There were significant differences in mean $\delta^{13}C$ values between NB and the other life stages (p=0.01). We did not find significant differences in the mean C or N isotopic composition for juveniles caught within and outside BSV (Kruskal-Wallis, p=0.2 and p=0.7, respectively).

Muscle tissue from demersal prey showed high intraspecific variability in $\delta^{15}N$ and $\delta^{13}C$ values. The highest variability (SD) in $\delta^{15}N$ and $\delta^{13}C$ between demersal species were estimated for bat rays (2.8 ‰) and California halibut (2.2 ‰) respectively (Table 9). However, the overall variability for the *demersal* habitat was small (0.8 for both $\delta^{15}N$ and $\delta^{13}C$). White seabass and diamond stingray had higher $\delta^{15}N$ values (0.3 and 2.9 ‰ more enriched in ^{15}N) than the other demersal species (Table 9). The mean isotopic composition of the prey that were classified to *demersal* habitat were enriched in ^{13}C (0.8 ‰) compared with those from the *pelagic* habitat, but the later habitat was slightly enriched in ^{15}N (0.2 ‰). Compared worth the offshore habitat, *demersal* prey species were enriched in ^{13}C and ^{15}N (2.46 ‰ and 3.75 ‰; Table 9).

Table 8. Isotopic values for different life stages of immature white sharks collected in Vizcaino Bay and the northern part of the Baja California peninsula. OBSV: Outside Vizcaino Bay

Life stage	**n**	**Total length (cm)**	**δ^{13}C (‰)**		**δ^{15}N (‰)**	
			Mean	**SD**	**Mean**	**SD**
Newborn	12	138-150	-17.1*	0.6	17.3*	0.3
Young of the year	13	152-170	-16.6	0.7	17.4*	0.7
Juvenile	6	173-201	-16.2	0.2	18.1	0.3
Juvenile OBSV	8	176-300	-16.5	0.6	17.9	1.1

*Indicates significant differences between life stages tested with one-way ANOVA and Tukey post hoc test. Differences between juveniles inside BSV and OBSV were tested with Kruskal-Wallis test. Significance level is 0.01

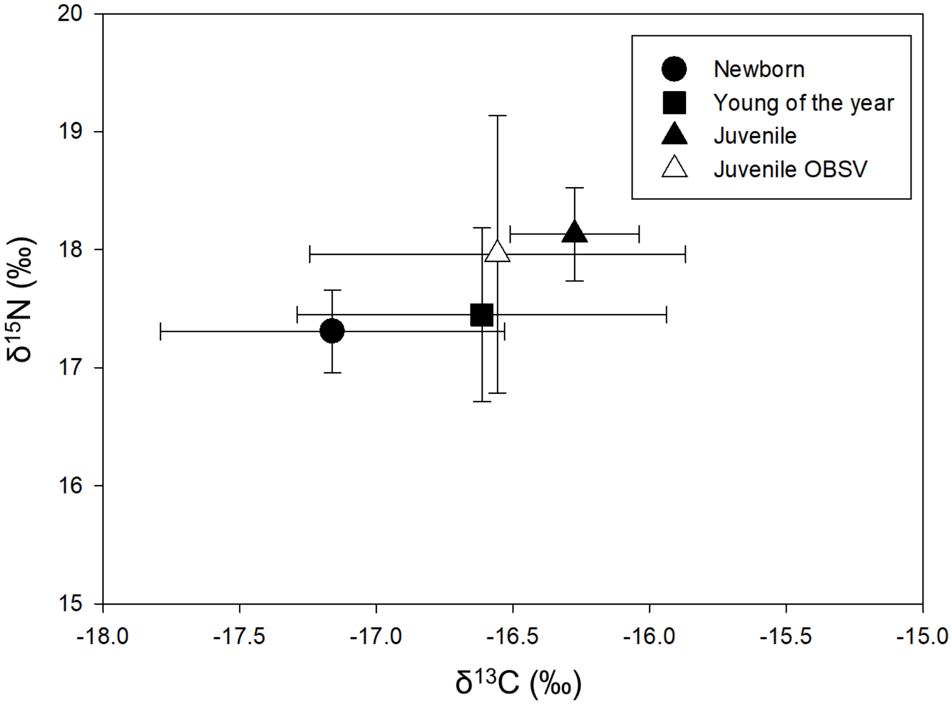

Figure 16. Mean carbon and nitrogen stable isotope ratios (±SD) measured in the muscle tissues of immature white sharks sampled in Vizcaino Bay and the northern part of the Baja California peninsula. Isotopic values are reported as a function of life stage: newborn (<150 cm TL), young of the year (between 151-170 cm TL), and juveniles (<171 cm TL). TL, total length.

Table 9. Isotopic values of potential prey of immature white sharks used in mixing models. Values are means ± one standard deviation (SD).

Habitat	Common name	Species	n	TL (cm)	$\delta^{13}C$ (SD)	$\delta^{15}N$ (SD)
Demersal	Bat ray	*Myliobatis californica*	10	56-74*	-16.4 (0.7)	14.4 (2.8)
	Butterfly ray	*Gymnura marmorata*	10	76-94 *	-15.4 (0.6)	14.7 (1.7)
	Diamond stingray	*Hypanus dipterururs*	10	66-78*	-16.2 (1.1)	16.1 (1.6)
	Shovelnose guitarfish	*Pseudobatos productus*	22	76-96	-16.6 (1.3)	15.3 (2.0)
	California halibut	*Paralichthys californicus*	10	53-78	-15.2 (2.2)	13.6 (2.1)
	White seabass	*Atractoscion nobilis*	10	49-85	-16.6 (0.6)	16.5 (1.9)
	Habitat mean				-16.8 (0.8)	15.8 (0.8)
Pelagic	Pacific mackerel*	*Scomber japonicus*			-17.8 (0.6)	15.7 (0.9)
	Corvinas*	*Cynoscion* spp.			-16.3 (0.7)	16.3 (1.0)
	Needlefish*	*Tylosurus* spp.			-18.0 (0.1)	18.3 (0.1)
	Sea robins*	*Prionotus* spp.			-18.0 (1.5)	15.5 (0.8)
	Dolphinfishes*	*Coryphaena* spp.			-18.6 (0)	13.4 (0)
	Squid*	Unid. spp.			-17.7 (1.3)	12.7 (2.5)
	Habitat mean				-17.6 (0.3)	16.0 (0.7)
Offshore	Pacific saury*	*Cololabis saira*			-19.7 (0.5)	10.7 (1.5)
	Lanternfish*	Myctophidae			-20.1 (0.5)	12.2 (0.7)
	Pacific mackerel*	*Scomber japonicus*			-18.6 (0.1)	14.6 (0.2)
	Jack mackerel*	*Trachurus symmetricus*			-19.4 (0)	12.2 (0)
	Halfbeak*	*Hyporhampus naos*			-19.2 (0.2)	8.6 (0.3)
	Pelagic triggerfish*	*Canthidermis* spp.			-20.1 (0)	11.1 (0)
	Flyingfish*	Exocoetidae			-20.1 (0)	12.4 (0)
	Humboldt squid*	*Dosidicus gigas*			-19.4 (0.2)	13.1 (0.6)
	Pelagic octopus*	*Ocythoe tuberculata*			-19.3 (0.9)	13.7 (1.9)
	Pelagic red crab*	*Pleuroncodes planipes*			-19.0 (0.9)	11.6 (0.9)
	Sardine*	*Sardinops sagax*			-19.8 (0.2)	13.6 (0.6)
	Habitat mean				-19.3 (0.7)	12.1 (1.5)

*Values taken from Tamburin et al. (2019) ** Disc width (cm). All isotopic values are in ‰.

Bayesian mixing models indicate that demersal prey species provide the higher contribution to muscle in NB/YOY (44.5%; C.I. 97.5%: 16.0-66.5%) and juveniles (47.5%; C.I. 97.5%: 9.0-81.0%) (Figure 17), followed by offshore habitat in NB/YOY (30.5%; C.I. 97.5%: 20.9-39.6%) and pelagic habitat in juveniles (37.4%; C.I. 97.5%: 6.1-75.9%).

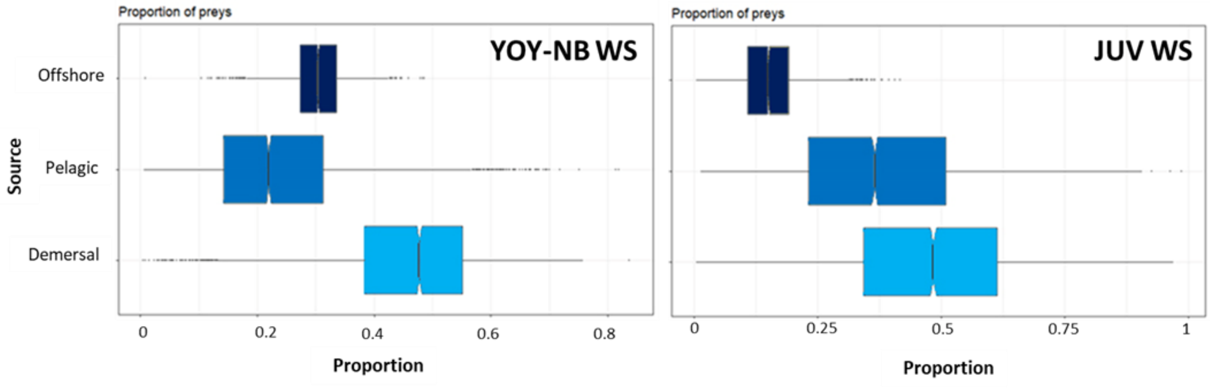

Figure 17. Contribution of prey from different habitats to the isotopic composition of the muscle tissue of immature white sharks sampled along the western coast of the Baja California peninsula. YOY= young of the year, NB = newborn, JUV = juvenile white sharks.

Isotopic niche analysis showed that juveniles OBSV had the broadest isotopic niche (SEAc =2.45) of all white shark groups, followed by BSV YOY (SEAc = 1.51), NB (SEAc = 0.65), and juveniles (SEAc= 0.38). The highest overlap between isotopic niches was between YOY and juveniles OBSV (57.4%), while juveniles sampled in BSV had the smallest overlap with the other groups (< 25%) (Figure 18).

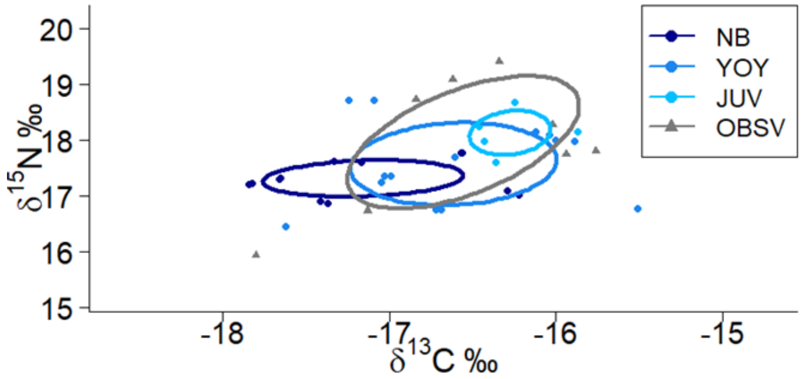

Figure 18. Standardized ellipse of isotopic niches of immature white sharks sampled along the western coast of the Baja California peninsula. NB = newborn, YOY = young of the year, JUV = juvenile collected within Vizcaino Bay, and OBSV = juveniles outside Vizcaino Bay.

Regarding sympatric shark species, in smooth hammerheads, δ^{15}N values ranged from 14.9 to 20.1 ‰ and δ^{13}C values from -14.2 to -18.0 ‰ (Table 10). Mean values of δ^{15}N from larger hammerheads were enriched compared with newborns (1.7 ‰) and small juveniles (1.5 ‰). For δ^{13}C, mean values from larger hammerhead were slightly depleted than for the other groups (1.0 ‰ and 0.4 ‰) (Figure 19, Table 10). For copper sharks, δ^{15}N values ranged from 16.5 to 20.4‰ and δ^{13}C between -17.1 to -14.4‰ (Table 10). Muscle tissue from copper sharks were enriched in δ^{13}C compared with hammerheads (1.1 ‰ to 2.1 ‰). For δ^{15}N (1.1 ‰), comparison followed the same pattern, except that large hammerheads were slightly enriched (0.6 ‰) than copper sharks.

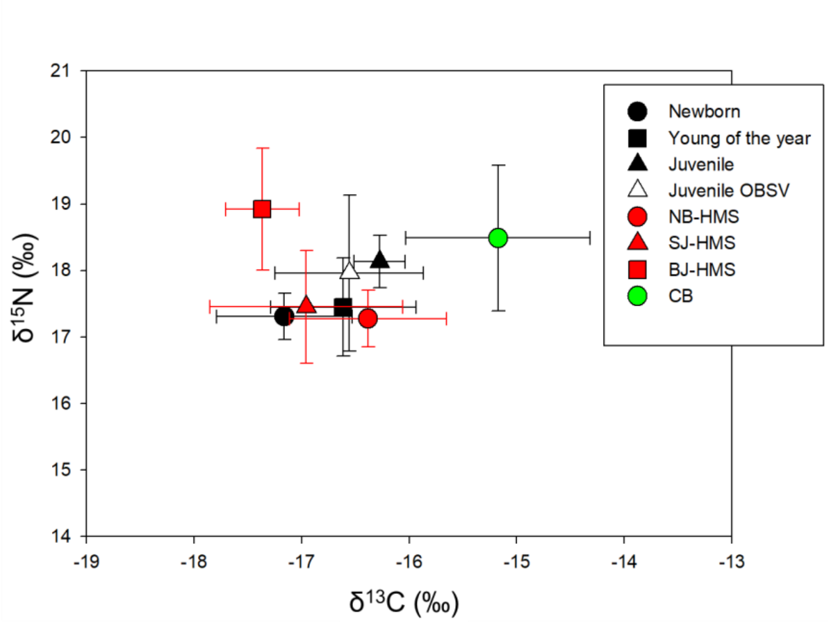

Figure 19. Mean carbon and nitrogen stable isotope ratios (±SD) measured in the muscle of immature white sharks, smooth hammerheads, dusky shark, and copper shark from Vizcaino Bay and the northern part of the Baja peninsula. NB-HMS = newborn hammerheads, SJ-HMS = small juvenile hammerheads, BJ-HMS = big juvenile hammerheads and CB = copper shark.

Table 10. Mean isotopic values for size classes of hammerheads and copper sharks on Vizcaino Bay.

Species	**n**	**Total length (cm)**	**^{13}C (‰)**		**^{15}N (‰)**	
			Mean	SD	Mean	SD
Newborn hammerhead	13	60-85	-16.3	0.7	17.2	0.4
Small juvenile hammerhead	29	103-147	-16.9	0.8	17.4	0.8
Large juvenile hammerhead	21	151-183	-17.3	0.3	18.9	0.9
Copper shark	17	102-304	-15.2	0.8	18.3	1.0

SIBER results showed that between sympatric shark species, immature white sharks had the smallest isotopic niche, while copper shark had the highest. The overlap between immature white sharks and hammerheads was higher (45.27%) than with copper shark (15.92%). A higher overlap was found when comparing life stages. The more extensive overlap was estimated between YOY and newborn hammerheads (55.17%), followed by the overlap between YOY and small juvenile hammerheads (54.69%) and the overlap between NB and newborn hammerheads (48.48%). The overlap with copper sharks was higher for YOY (27.55%) than for NB and juveniles from BSV (8.92 and 12.03%, respectively) (Figure 20).

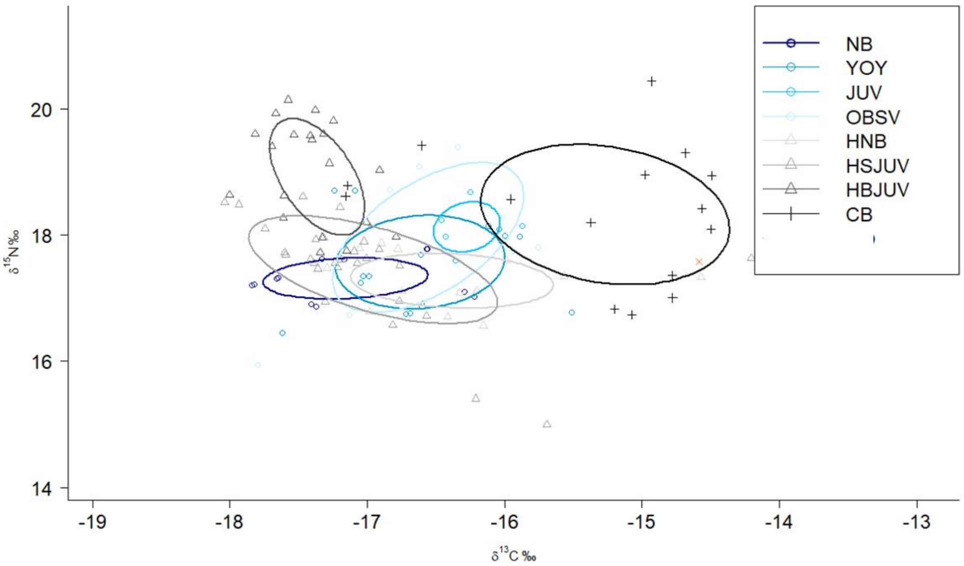

Figure 20. Isotopic niches of different life stages of different size classes of immature white sharks, smooth hammerhead sharks and copper sharks sampled in Vizcaino Bay. NB = newborn white sharks, YOY = young of the year white sharks, JUV = juvenile white sharks, OBSV = juvenile white sharks outside Vizcaino Bay, NB-HMS = newborn hammerheads, SJ-HMS = small juvenile hammerheads, BJ-HMS = big juvenile hammerheads and CB = copper sharks.

Ten sharks were sampled for CSSIA-AA of ^{15}N inside (7) and outside (3) BSV. Glutamic acid values ranged from 25.5 to 31.0‰, and phenylalanine ranged from 9.2 to 12.8‰ (Table 11). The trophic position estimated varied depending on the TDF/TEF and the equation used (Table 11).

Trophic positions were higher when the Hoen et al. (2014) equation was used (4.3 to 5.3) than with the equation of Chikaraishi et al. (2009) (2.7 to 3.0). Also, trophic position estimates were higher for sharks sampled outside BSV (3.0 to 5.3) than for sharks from inside BSV (2.7 to 4.3). Using TEF estimated for sharks and with the equation accounting for differences in fractionation between grazers and carnivores resulted in a TP of 4.34 for sharks sampled inside BSV (Table 11).

Table 11. Trophic position (TP) for immature white sharks from Vizcaino Bay and the northern part of the Baja peninsula. The trophic enrichment factors (TEF) and trophic discrimination factors (TDF) values origin is indicated. SD= Standard deviation. [1] Equation from Chikaraishi et al. (2009). [2] Equation from Hoen et al. (2014). [3] Value from Chikaraishi et al. (2009). [4] Value from Hoen et al. (2014).

Area	δ^{15}N Glx (‰)	δ^{15}N Phe (‰)	TDF/TEF	TP[1]	±SD	TP[2]	±SD
BSV	27.2 ±1.2 SD	10.8 ±1.2 SD	7.6[3]/2.8[4]	2.7	0.1	4.3	0.6
OBSV	29.6 ±2.3 SD	10.9 ±0.6 SD	7.6[3]/2.8[4]	3.0	0.2	5.3	0.8

4.4 Discussion

Differences in δ^{15}N and δ^{13}C values found between life stages of immature white sharks indicate a shift in feeding and maternal-induced processes. Adults white sharks are known to feed in offshore areas, where the baseline is depleted in ^{13}C relative to coastal and benthic habitats (Carlisle et al., 2012; Malpica et al., 2013). In the eastern Pacific, this includes oceanic islands like Guadalupe island (Jorgensen et al., 2010; Hoyos-Padilla et al., 2016). In contrast, pregnant females move to parturition grounds in coastal areas (Domeier & Nasby-Lucas, 2013; Oñate-González et al. 2015) which are enriched in ^{13}C due to the predominance of benthic production (Carlisle et al., 2012; Allen et al., 2013; Tamburin et al. 2020). Our results show that the muscle tissue of newborn sharks was depleted in ^{13}C compared with the following life stages. Given that very young white sharks are known to feed on benthic prey (Tricas & McCosker, 1984; Grainger et al., 2020), these results suggest the prevalence of maternal signature transferred to embryos during their gestation, as reported for other shark species with matrotrophic reproductive strategies (Estrada 2006, McMeans et al., 2009; Olin et al., 2011, 2018). By the time white sharks grew into the YOY stage in our study, this maternal influence seems to have disappeared by the enrichment in ^{13}C compared with newborns, with isotopic values similar to those of juveniles that have been reported to reflect exogenous feeding (Malpica-Cruz et al. 2013, Tamburin et al., 2020). In rapidly growing young sharks, exogenous feeding is quickly reflected in the isotopic composition of the tissues as size increases and the maternal isotopic composition is diluted (Malpica-Cruz et al. 2012). In immature white sharks, this change in isotopic composition that reflects active foraging has been reported to occur, for muscle tissue, at sizes around 170 cm TL (Malpica-Cruz et al. 2013).

Immature white sharks are known to primarily use coastal habitats, sometimes covering long distances (hundreds of kilometers) between nurseries (Dewar et al., 2004; Bruce and Bradford 2019, Harasti et al. 2012, Curtis et al. 2018). We did not find significant differences in the mean $\delta^{13}C$ or $\delta^{15}N$ between juvenile sharks caught inside and outside BSV. These results suggest that immature white sharks are feeding on prey with similar isotopic values along the western coast of the Baja California peninsula, as some sharks migrate from California, USA toward BSV in Mexico (Weng et al., 2007, 2012; White et al. 2019). However, a large variability in $\delta^{15}N$ was observed for sharks outside BSV. This variability is due to an enrichment in ^{15}N in larger juveniles (around 300 cm TL), that could be related with a shift in diet to feed on larger prey in coastal areas, like large bony fishes and marine mammals, as has been previously reported for the species (Carlisle et al., 2012; Hussey et al., 2012).

Changes in the estimates of prey contribution from different habitats to white shark tissues between life stages indicate shifts in feeding and habitat use. Mixing models results showed that for all life stages, most of the isotopic composition of the immature white shark muscle was attributed to demersal prey, similar to what has been reported regarding the juvenile white shark's diet based on stomach contents analysis (Tricas & McCosker 1984, Santana-Morales et al. 2012; Grainger et al., 2020) and for BSV where the most common items usually found are rays (mostly bat rays; Santana-Morales et al. 2012; pers. obs.; Chris Lowe, pers. comm.). However, the contributing of demersal prey changed between life stages.

For juvenile white sharks, the contribution of pelagic prey (37%) was larger than for newborn/YOY (25%). Previous feeding studies in juvenile white sharks report a diet based on demersal species, but also report the presence of pelagic prey like sardines, mackerel, pelagic sharks and cephalopods that become more important in bigger juveniles larger than 185 cm TL (Tricas & McCosker, 1984; Hussey et al., 2012. In BSV, also has been reported the presence of sardines and squids in stomach contents of immature white sharks (Santana-Morales et al., 2012) and preliminary tagging results show that immature white sharks move from very nearshore areas, as the Ojo de Liebre lagoon, to areas farther from the coastline inside BSV, where they might feed on pelagic species. Vizcaino Bay is an important feeding and nursery region for a large variety of pelagic and demersal species (Hernández-Rivas et al., 2000) suggesting that could sustain large prey availability for immature white sharks. The higher contribution from demersal and pelagic prey to the isotopic composition of immature white sharks confirms the importance of BSV as a nursery for this species since it provides one of the benefits from these nurseries, feeding grounds for their first life stages.

A higher contribution of prey from offshore habitats for neonates and YOY (31%) than for juveniles (14%) was also estimated, suggesting that the maternal isotopic composition may still have been detectable in some of these smaller sharks. The small contribution of this offshore prey in juveniles could imply that this life stage could actively move outside nurseries and forage in other areas along California and Baja California coasts. Even if juvenile white sharks commonly select habitats close to land (<30 km from the coast; White et al., 2019), some of these sharks could move to offshore areas as far as 1,350 km from mainland coast in the US and Mexico (Weng et al., 2012). Satellite telemetry has revealed that juvenile white sharks from California migrate to areas along the coast of Baja California and even into the Gulf of California (Weng et al., 2007; Weng et al. 2012; White et al., 2019), where offshore and pelagic prey could be an important dietary component during the migrations.

Tamburin et al. (2020) sampled muscle tissue for SIA from immature white sharks in OLL and other areas inside BSV and from potential prey from different habitats (including prey from Guadalupe Island) between 2015-2018. These authors found a higher contribution of offshore prey to the isotopic composition of muscle from neonates and YOY and they associate it to the prevalence of a maternal derived isotopic signature. They also found a higher proportion of inshore pelagic species in tissues from juvenile white sharks, proposing that these species are more important than previous studies have reported (Malpica-Cruz et al., 2013; Santana-Morales et al. 2012). Their findings are contrary to our results, where we found a higher contribution from demersal prey to the isotopic composition of immature white sharks and that are consistent to a more benthic foraging previously reported (Tricas & McCosker, 1984; Hussey et al., 2012; Grainger et al., 2020). Besides, a large portion of Tamburin et al. (2020) samples were taken inside the Ojo de Liebre lagoon during march, when juveniles (larger than 175 cm TL), either from California or BSV, enter into this habitat (Chapter 3). These juvenile white sharks could be migrating between the Southern California Bight and BSV. Unpublished data from Lowe et al. indicate that some acoustically tagged immature white sharks exhibit repeated annual migration between California and Baja California waters. These migrating sharks could be feeding on coastal pelagic species with different isotopic composition during these habitat transitions, as the high variability in the isotopic composition of sharks caught outside of BSV suggest.

In our study, all of the demersal prey samples were collected near the mouth of the Ojo de Liebre Lagoon, which is a high-intensity fishing area where most of the incidental catches of immature white sharks occurs (García-Rodríguez & Sosa-Nishizaki 2020), and where these sharks are present during all year according with acoustic telemetry data (Chapter 3). Based on information from satellite transmitters, White et al. (2019) predicted that juvenile individuals select shallow areas (>1000 m deep), close to the shore (>30 km from the coast) in water between 14 to 24° C. According to their results, BSV, including the Ojo de Liebre lagoon, is environmentally suitable year-round for immature white sharks, while other coastal areas along the west coast of the Baja California peninsula are temporarily suitable. Coastal habitats near lagoons like San Ignacio and San Quintin Bay are suitable mostly during summer and summer-fall respectively (White et al., 2019). Incidental catches of immature white sharks have been reported for San Ignacio lagoon during summer (Rochín-Alamillo, 2011) and unpublished data from a juvenile shark tagged in BSV with a satellite transmitter showed that this individual moved from BSV to areas near the San Quintin Bay where it was incidentally caught in summer. Immature white sharks seem to enter these lagoon and estuary habitats to take advantage of seasonal prey availability (Harasti et al. 2018, Chapter 3). Coastal lagoons along the Baja California peninsula and their inlet areas, presents high abundance of known prey (Daneman & de la Cruz-Agüero, 1993; De la Cruz-Agüero et al., 1994; Rosales-Casián, 1996) and seasonal environmental suitability (White et al., 2019) for immature white sharks. These conditions and the confirmed presence of white sharks incidentally caught when fishers target these prey species (Rochín-Alamillo, 2011) could suggest that coastal lagoons and their inlet areas could potentially provide benefits commonly associated with nursery areas for white sharks moving outside known nurseries in California and Mexico.

According to ecological knowledge from artisanal fishers, shovelnose guitarfishes and diamond stingray are found all year in BSV waters, while California bat rays, butterfly rays and demersal bony fishes like halibut and white seabass are found seasonally in the area (García-Rodríguez & Sosa-Nishizaki 2020). The presence of potential prey throughout the year confirms the high food availability that would in turn support the importance of this Bay for the development of this species’ early life stages.

In BSV, immature white sharks are caught mostly during summer, when some of the demersal species they feed on are targeted by the local artisanal fishery (Oñate-González et al., 2017; García-Rodríguez & Sosa-Nishizaki, 2020). The California halibut, white seabass, and ray landings represent around 30% of the total yearly landings from bony fishes in the area (CONAPESCA, 2018). Any change of fishing effort directed to these demersal species might change the white shark susceptibility to being incidentally caught. Overfishing might affect immature white shark’ feeding habits, movements, and habitat shifts. These relationships highlight the importance of monitoring potential prey and the fishing effort applied to them, and to assess their populations along with white shark monitoring.

The comparison of SEAc between life stages showed that juveniles outside BSV have a broader isotopic niche, supported by their movements between California and Baja California (Weng et al., 2007; 2012; White et al. 2019). YOY and NB likely have smaller isotopic niches because their activities are more restricted inside the BSV areas. Surprisingly, juveniles inside BSV had the narrowest isotopic niche, but this could be due to the small sample size number that is not sufficiently representative of this life stage

(Jackson et al. 2011). Many samples were obtained with the help of artisanal fisheries monitoring efforts, so the smaller sample size we obtained is mostly due to the lower susceptibility of juvenile white sharks (larger than 175 cm) to be caught incidentally in demersal bottom nets compared with newborns and YOYs (Oñate-González et al. 2017; García-Rodríguez & Sosa-Nishizaki 2020). There was partial overlap in the isotopic niche between all life stages, but the highest was between juveniles OBSV and YOY. Sharks sampled outside BSV could have been born in BSV or the Southern California Bight, but as they increase in size, they can move between nurseries and spend some months of the year in BSV, where they could feed on similar habitats or resources with similar isotopic composition than the ones smaller white sharks are feeding on.

Comparisons in isotopic niches between sympatric species showed that immature white sharks and smooth hammerheads had a 45% overlap in their isotopic niches and this overlap was higher between YOY white sharks and small juvenile hammerheads (103-147 cm), suggesting that they could be feeding on some resources with similar isotopic composition. Juvenile smooth hammerheads feed mostly on squid, small pelagic fishes like scombrids and benthic bony fishes (Smale, 1991; Ochoa, 2009), which are also prey found in the stomachs of juvenile white sharks collected in BSV (Santana-Morales et al., 2012). In contrast, there was a limited (15%) isotopic overlap with copper sharks. Based on what has been reported as their food habits in other areas, copper sharks in BSV may be feeding on many of the same pelagic species consumed by white sharks, like sardines, mackerels, skipjacks, and tunas (Smale, 1991; Santana-Morales et al., 2012). However, copper sharks are not caught all year in BSV, only in late spring and summer when it has been hypothesized that white sharks are born (Domeier & Nasby-Lucas, 2013) and when they are incidentally caught (Oñate-González et al., 2017; García-Rodríguez 6 Sosa-Nishizaki, 2020). Besides, coper sharks have a more tropical distribution than white sharks, so they may be feeding seasonally on different prey or in foraging grounds with a distinct isotopic composition. In addition, some of the copper shark we sampled were larger and spanned the adult stages, which could contribute to a broader isotopic niche. A partial overlap in the isotopic niche was reported between juvenile white sharks and juvenile makos in BSV (Tamburin et al., 2019). However, makos have been reported to feed on more pelagic prey like Pacific saury and jumbo squid off California coast (Pretti et al. 2012). This partial overlap with makos, along with the higher overlap in the smaller life stages of immature white sharks and juvenile smooth hammerheads found in this study does not necessarily mean that they are competing for resources but feeding on similar foraging grounds and preys with similar isotopic composition. When different shark species share feeding grounds, resource partitioning and spatial segregation could be a strategy to avoid competition (Bethea et al., 2004; Kinney et al., 2011). However, if prey abundance changes in the future, competition for resources with sympatric species could occur, which highlights the importance of monitoring the population trend of prey along with the white shark population and other potential competitors. This overlap with sympatric species highlights the importance of BSV as a foraging ground with high prey availability for different shark species.

As expected, trophic positions varied depending on the TDF/TEF used. Using the TDF estimated for cultured algae, zooplankton and fish (Chikaraishi et al., 2009), the TP for juvenile white shark was sub-estimated (<3). It has been reported that sharks have lower TEF than other planktivorous and carnivorous teleost due to lower discrimination because of their diets (Hoen et al., 2014). We found that using the TEF estimated for sharks along with the equation accounting for differences in discrimination between grazers and carnivores (Hoen et al., 2014), TP (4.3-5.3) were similar to those previously reported for white sharks of similar sizes, that were estimated using stomach content or bulk stable isotope analysis (Cortés, 1999; Estrada et al., 2006; Hussey et al., 2012). TP of white sharks OBSV was higher than TP from sharks in BSV. White sharks OBSV are moving between different habitats where they could be feeding on prey with higher TP. Some of the sharks analyzed where big juveniles (~300 cm TL), near the reported size, when a shift in diet occurs and start feeding on bigger prey like marine mammals. The TP estimated with the TEF from sharks was higher than any TP reported for the species, indicating that CSSIA-AA reveals that trophic relationships are more complicated than previously thought (Ishikawa, 2018). These results highlight the importance of using species-specific TDF/TEF for TP estimations and the usefulness of CSSIA-AA for estimating TP without the constraints of traditional methods (Chikaraishi et al., 2009).

Stable isotope analysis provided new information about the trophic ecology of immature white sharks in the Northeastern Pacific and new insights in how their trophic habits are related to habitat shifts through their ontogeny. Our results support the importance of BSV as a nursery and foraging ground for sharks born at BSV and California and the overlap with sympatric shark species suggest that they may be sharing resources. We found that the most important prey for white sharks are heavily targeted by BSV coastal fisheries, increasing their susceptibility to being incidentally caught in the area. However, SIA could not reveal the specific prey that white sharks are feeding in the region, so complementary methods should be used in the future to address this topic. Also, research should focus on comprehending predator-prey relationships between white sharks and their prey to understand how changes in prey abundance due overfishing could influence the early life stages of white sharks.

Chapter 5. General discussion

The results from this thesis show the importance of Vizcaino Bay and the Ojo de Liebre lagoon for the early life stages of white sharks. Vizcaino Bay offers a vast area with depths less than 100 m due to the great extension of its continental platform (DOF, 2000; Hernández-Rivas et al., 2000). Moreover, it has been shown that immature white sharks spend most of their time at depths less than 100 m (Dewar et al., 2004; Weng et al., 2007; 2012; Bruce & Bradford, 2012; Lyons et al., 2013; Curtis et al., 2014; White et al., 2019). Studies suggest that the Bay contains suitable habitat for immature white sharks, where they can spend extended periods (White et al., 2019). This was confirmed with the acoustic telemetry data from this thesis that showed that immature white sharks are present in areas associated with the Ojo de Liebre lagoon during all months of the year.

Also, in this bay, immature white sharks feed on prey that are also targeted by local artisanal fisheries. During the fishing operations, sharks are attracted to the gillnets resulting in incidental mortalities, mainly during summer months in the areas near the Ojo de Liebre lagoon inlet (García-Rodríguez and Sosa-Nishizaki, 2020). These interactions between the white shark and the fishing operations represent one of the biggest challenges for conserving this protected species in Northwestern Mexico because beside the direct interaction, a competition for resources between local fisheries and white sharks occurs. Also, the real effect of this fishing mortality on the Northeastern Pacific population should be estimated. Even if strategies like limiting the use of fishing gears in the areas and times of higher interaction and presence of white sharks in the region could help to decrease fishing mortality, other strategies with lesser effects for artisanal fishers should be explored, like decreasing soaking time to release the sharks alive. However, the effectiveness of this strategies should be evaluated in the future.

Nursery Areas Use

In Australia, juvenile white sharks move between seasonal nurseries, traveling more than 2000 km, and could move to offshore areas (Bruce and Bradford, 2012). In the Northeastern Pacific, immature white sharks also move between nurseries separated by hundreds of kilometers. Sharks tagged during their first year of live in Southern California have showed repeated migrations to BSV during several years, confirming the connectivity between these two nurseries (Weng et al., 2007; 2012; White et al., 2019). Preliminary results from acoustic tagging have shown that sharks from Mexico also go to California waters, but the degree of these movements between nurseries are not fully understood. Immature white sharks prefer coastal shallower waters, but sometimes they might go to offshore areas far from the coast (White et al., 2019). The diets of immature white sharks from BSV revealed by SIA confirmed the contribution of pelagic and offshore habitat preys. Especially for the juveniles moving between nurseries areas and into areas south from BSV (Weng et al., 2007; 2012; Marquez-Farías & Lara-Mendoza, 2017; White et al., 2019), where they could have access to a wider variety of prey.

To understand the main ecological drivers of the immature white shark movements between nurseries areas along the coast of the Baja California peninsula is essential to evaluate the effect of oceanographic changes in the region. Movements of immature white sharks to northern areas in California seems to be related with events associated with an increase in water temperatures, like El Niño and the Blob (White et al., 2019). This distribution shift affects the way juvenile sharks are using nurseries areas and, in consequence, how they interact with coastal communities. The absence of white sharks from the acoustic array at BSV-OLL during warmer months when these oceanographic events occurred suggests that abundances are lower, changing the susceptibility of being incidentally caught at BSV-OLL. The projected increase in water temperature related to climate change might impact the distribution of immature white sharks as they have been estimated for other species (McMahon & Hays, 2006; Hazen et al., 2012; Lezama et al., 2016; Báez et al., 2019). Future research should focus on describing how the distribution of immature white sharks shifts with the interannual oceanographic events to develop appropriate policies for reducing the interaction with human activities.

Furthermore, in California, fishing mortality decreased due to the establishment of federal and state fishing regulations, and an overall reduction in commercial fishing, resulting in an increase in the white sharks' population (Lowe et al., 2012). This proposed increase in population sizes, along with greater use of beaches along California, seems to be related to the increase of shark-human interactions (Moxley et al., 2019). The probability of interacting with human communities (including fishing operations at California) might increase during years when the distribution of immature white sharks is shifted to the north. Currently, fishing mortality is higher at BSV than in California's waters (Benson et al., 2018). However, the northward shifting might change this status.

Feeding Ecology

Stable isotope analyses showed that demersal prey predominate diets of immature white sharks, and their importance decreases with the size of the shark. Carbon and nitrogen ratios from smaller white sharks (newborns) suggest the prevalence of maternal influence, which is diluted out by the end of their first year. Pregnant females spend most of the gestation time in offshore waters and then move to coastal areas in California and the Baja peninsula to give birth (Domeier & Nasby-Lucas 2013; Oñate-González et al., 2015). In juveniles, the increase in the contribution of offshore and pelagic prey could be related with movements between nurseries where they could be feeding on a broader diversity of prey (Weng et al., 2007; 2012; White et al., 2019). However, the lack of significant differences in carbon and nitrogen ratios between areas (inside and outside the BSV-OLL region) suggests they are feeding in similar habitats and prey with similar isotopic composition. The higher contribution of demersal preys in the diet is supported by the results of feeding habit studies that previously reported the diet composition for white sharks with similar sizes (Tricas & McCosker, 1984; Hussey et al., 2012; Santana-Morales et al., 2012; Malpica-Cruz et al., 2013).

Furthermore, the white shark switches its diet to feed on marine mammals at sizes larger than those found inside and outside the BSV-OLL (Estrada et al., 2006; Carlisle et al., 2012; Hussey et al., 2012). The Ojo de Liebre lagoon has been recognized as an important breeding and calving area for the gray whale (*Eschrichtius robustus*) between November and March (Vargas 2006), when white sharks are present inside the lagoon, based on the telemetry results of this thesis. An undefined number of calves might die during the calving season, and fishers reports of white sharks biting dead calves could suggest that smaller white sharks could scavenge opportunistically on them.

Even if isotopic niches are not equal to trophic niches, the former gives us insights to understand the ecological role of predators (Jackson et al. 2011, Hette-Tronquart 2019, Marshall et al. 2019). A high overlap in isotopic niches was found for immature white sharks and hammerhead sharks from similar sizes. This overlap does not necessarily mean that they are competing for resources but feeding on similar foraging grounds and preys with similar isotopic composition. Vizcaino Bay also seems to be an important foraging area for smaller smooth hammerheads and could be used as a nursery area for this species. When different shark species share nursery grounds, resource partitioning could be a strategy to avoid competition (Bethea et al., 2004; Kinney et al., 2011). However, if prey abundance changes in the future, competition for resources with sympatric species could occur, which highlights the importance of monitoring the population trend of prey along with the white shark population and other potential competitors.

The trophic level estimated using CSIA-AA was similar to those estimated for juvenile white sharks in other areas (Cortés, 1999; Estrada et al., 2006; Hussey et al., 2012; 2015). This trophic level indicates that immature white sharks are the top predator in the region, suggesting the importance of this species (like other shark species) in maintaining food webs structure and ecosystem function, and taht their presence is critical to prevent cascading effects in lower trophic levels (Heithaus et al., 2008; Ferreti et al., 2010; Roff et al., 2016).

Conservation and Management Implications

Although fishing white sharks is forbidden in México (DOF, 2007; 2010; 2014), incidental catches still occur (Galván-Magaña et al., 2010; Ramírez-Amaro et al., 2013; Márquez-Farías & Lara-Mendoza, 2017), mostly in BSV (Santana-Morales et al., 2012; Oñate-González et al., 2017; García-Rodríguez & Sosa-Nishizaki, 2020). Nurseries are critical to ensure the survival of early life stages (Heupel et al., 2007; Knip et al., 2010), which for some species like white sharks could be one of the essential elements for population growth (Mollet & Cailliet, 2002). The vulnerable status of white sharks (Rigby et al., 2019) makes it necessary to understand the effect of these incidental catches of immature sharks on their populations and on the recruitment to adulthood. Since there is also a large shark cage diving tourist industry for white sharks in Mexico, fisheries related mortalities of juveniles could harm this growing non-extractive industry (Laroche et al., 2007; Cisneros-Montemayor et al., 2013; Apps et al., 2018; Becerril-García et al., 2019; Meza-Arce et al., 2020).

Recent estimations of the population size of white sharks worldwide have shown low numbers, which is expected for top predators (Dewar et al., 2013; Burgess et al., 2014; Hillary et al., 2018). For the Northeastern Pacific, population sizes have been estimated to be >3000 individuals and that currently, it is not at risk (Dewar et al., 2013; Burgess et al., 2014). However, uncertainties arise related to the fishing mortality of immature white sharks from BSV, where fishing mortality is higher than in California (Benson et al., 2018). Besides, a recent study noticed the issues related to the uncertainties in life story traits to understand population status for white sharks in the Northwest Atlantic (Bowlby & Gibson). Most of the uncertainties come from the difficulty of obtaining robust estimates of longevity, which seems to been underestimated according to recent studies ((Hamady et al., 2014; Andrews & Kerr, 2015; Natanson & Skomal, 2015; Christiansen et al., 2016). This issue has also been identified for white sharks in the Northeastern Pacific, where longevity is estimated to be >30 years and older than previous estimations (Cailliet et al., 1985; Andre & Kerr, 2015). These uncertainties highlight the importance of having the best biological information available to understand population status and the conservation and management of large sharks (Yokoi et al., 2017).

As discussed in previous chapters, according to the acoustic telemetry, stable isotope analysis, and fishers knowledge, there seems to be a high spatial overlap between artisanal fisheries and immature white sharks in the areas near the mouth of the Ojo de Liebre lagoon. However, the temporal overlap is smaller, probably due to changes in the fishing effort during the month with a higher number of white sharks present in the area. These results suggest that the probability of being incidentally caught seem to be lesser than previously thought and point to where management and conservation actions should be focused. Currently, the number of immature white sharks incidentally caught in BSV does not seem to pose a threat to the population in the Northeastern Pacific, but future studies should focus on getting better estimations of the survival probability of these early life stages. Even if, at the moment, stiffer regulations that could have a high social impact seems not to be needed, white sharks are still a vulnerable and protected species in Mexico, so actions focused on decreasing fishing mortality should be implemented. The results from this work show that due to the high post-release survival of immature white sharks, actions like releasing white sharks alive in the areas with higher interaction could be implemented to decrease this mortality with the involvement of fishing communities and without changing their fishing activities. As well, these results show the importance of monitoring the movements of white sharks between nursery areas as well as monitoring their prey to understand how trophic relationships and oceanographical changes could affect the distribution of these early life stages and their susceptibility to interact with fishing activities. Finally, the monitoring should be extended to other areas in the Baja California peninsula to evaluate the potential use of other coastal areas as nurseries (i. e. San Quintin or San Ignacio) and to identify other sources of fishing mortality.

Chapter 6. Conclusions

- Artisanal fisheries in Vizcaino Bay are multi-specific with bottom-related target species that are critical prey for immature white sharks.

- Incidental catches of immature white sharks occur in areas close to the mouth of the Ojo de Liebre lagoon, so management actions should focus there. Precisely, Las Casitas fishing camp incidental catches records of immature white sharks are the most significant in the region.

- Reducing incidental catches of immature white sharks in the region seems to be difficult given that they are incidentally caught when fishers target high-value species. However, conservation actions could focus on decreasing nets soaking time to allow the release of immature white sharks alive to decrease fishing mortality.

- All life stages of immature white sharks use the region indistinctly of their origin, confirming the connectivity between nursery areas in the Northeastern Pacific.

- The Ojo de Liebre lagoon seems to be essential habitat for white sharks with >175 cm total length, during winter and early spring (indistinctly of their origin), probably related to their prey availability. These results highlight the importance of this habitat for early life stages.

- A higher presence and residence of white sharks were identified during months with lower reports of incidental catches, suggesting a lower interaction with the local artisanal fisheries than previously thought.

- Stable isotope analysis provided new information about the trophic ecology of immature white sharks in the Northeastern Pacific and new insights in how their trophic habits are related to habitat shifts through their ontogeny in their first life stages.

- The most important prey for white sharks (demersal prey) are those that are heavily targeted by local fisheries, which increase their susceptibility to being incidentally caught in the area. The higher importance of pelagic prey for larger sharks suggest movements far from the Ojo de Liebre lagoon to areas outside Vizcaino Bay.

- The overlap in the isotopic niche with sympatric species suggests that these species feed on prey with similar isotopic composition. Also, these results indicate the potential importance of this region as a nursery for other shark species.

- The results from this thesis show the importance of Vizcaino Bay and the Ojo de Liebre lagoon as a suitable region for the early life stages of white sharks. In this region, immature white sharks can spend long periods and provides food resources for their growth. These food resources are also targeted species for local artisanal fisheries producing interaction with the sharks during summer, when smaller sharks more susceptible to die by their interaction with fisheries, are present.

- Future studies should focus on getting better estimations of the survival probability of these early life stages to understand the effect of these incidental catches in the Northeast Pacific population. As well, these results show the importance of monitoring the movements of white sharks between nursery areas as well as monitoring their prey to understand how trophic relationships and oceanographical changes could affect the distribution of these early life stages and their susceptibility to interact with fishing activities.

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Supplementary material

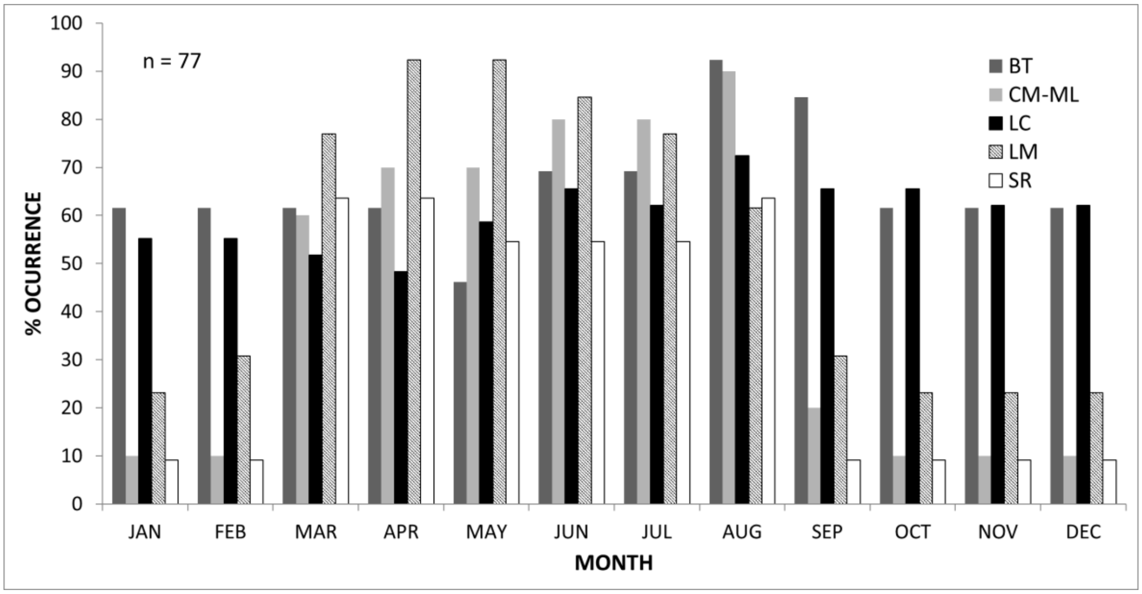

Figure 21. Use of gillnets in Vizcaino Bay by month and by fishing camp. BT: Bahía Tortugas, CM-ML: Campito-Malarrimo, LC: Las Casitas, LM: Laguna Manuela, SR: Santa Rosaliita.

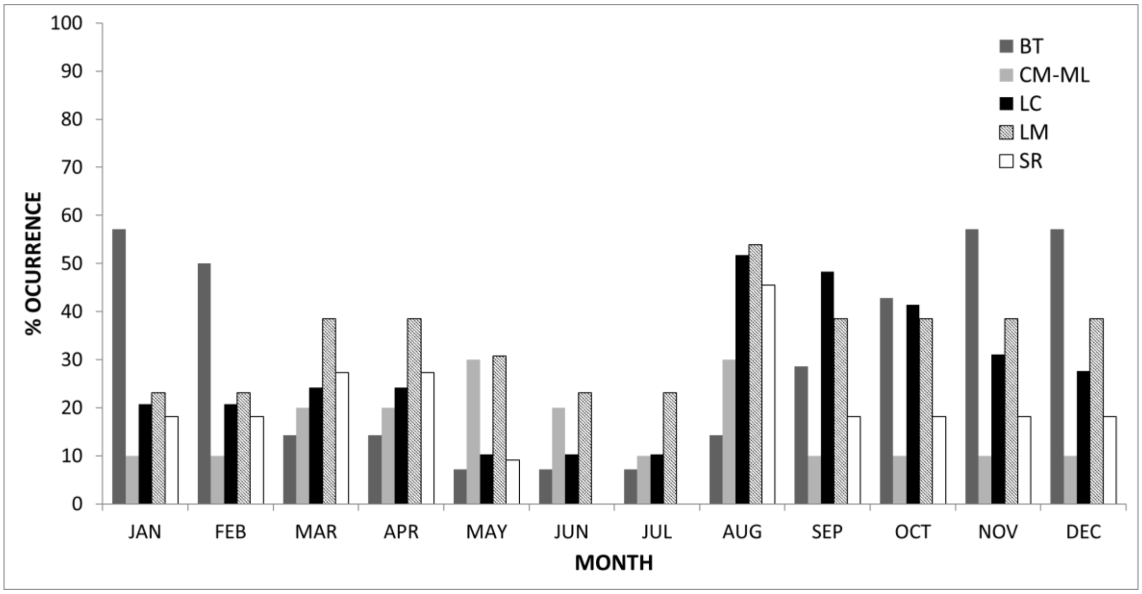

Figure 22. Use of longlines in Vizcaino Bay by month and by fishing camp. BT: Bahía Tortugas, CM-ML: Campito-Malarrimo, LC: Las Casitas, LM: Laguna Manuela, SR: Santa Rosaliita.

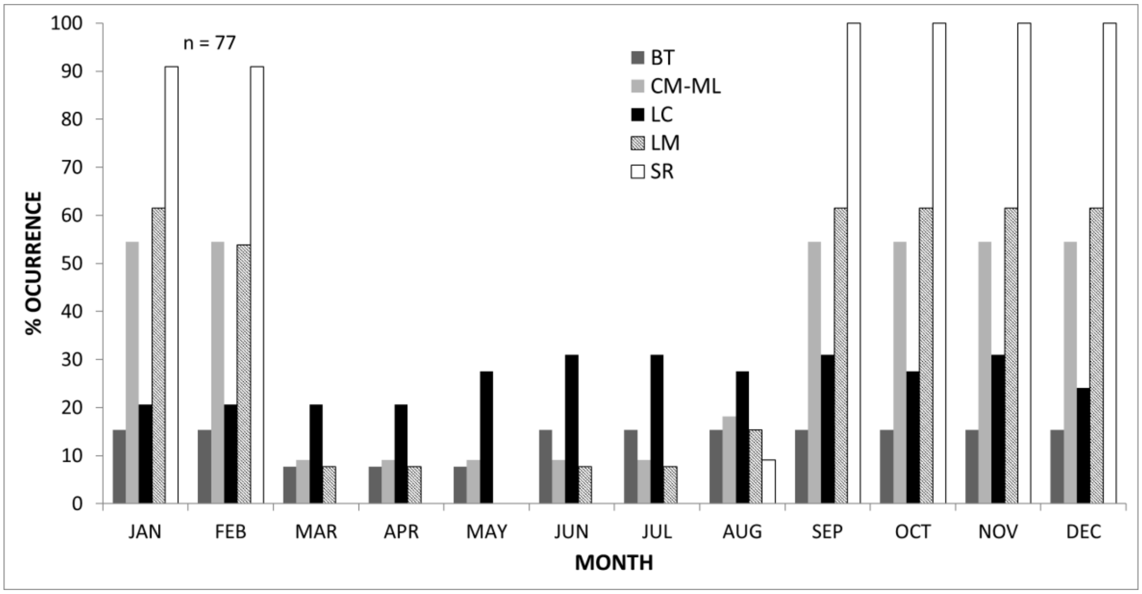

Figure 23. Use of traps in Vizcaino Bay by month and by fishing camp. BT: Bahía Tortugas, CM-ML: Campito-Malarrimo, LC: Las Casitas, LM: Laguna Manuela, SR: Santa Rosaliita.

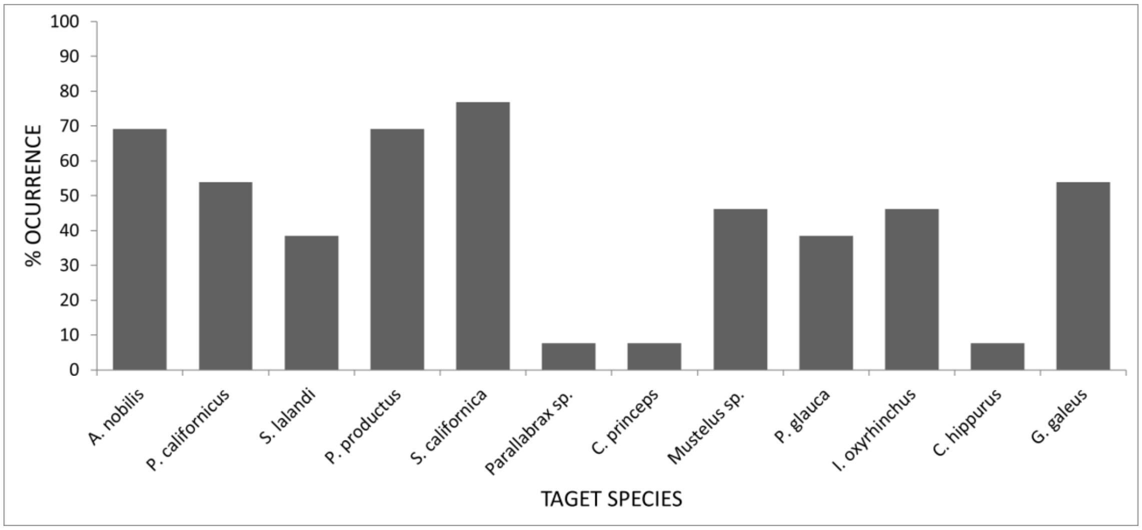

Figure 24. Target species from artisanal fisheries in the fishing camp of Bahia Tortugas

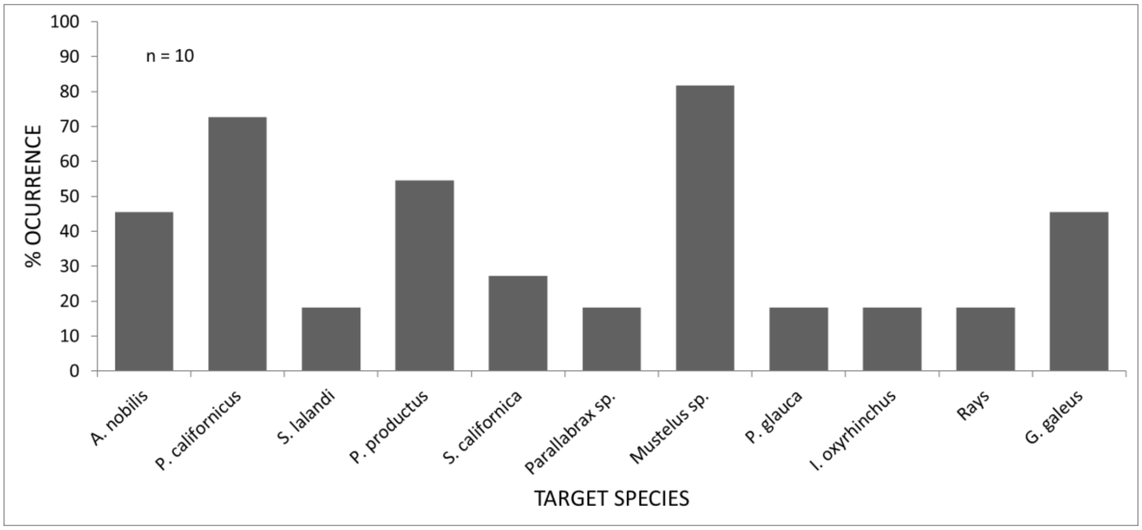

Figure 25. Target species from artisanal fisheries in the fishing camp of Campito-Malarrimo.

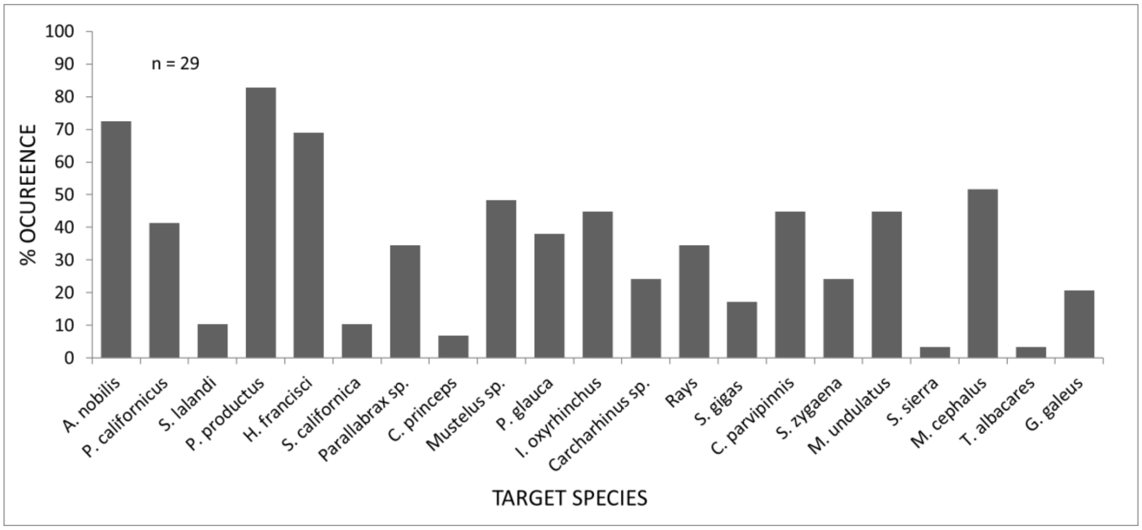

Figure 26. Target species from artisanal fisheries in the fishing camp of Las Casitas.

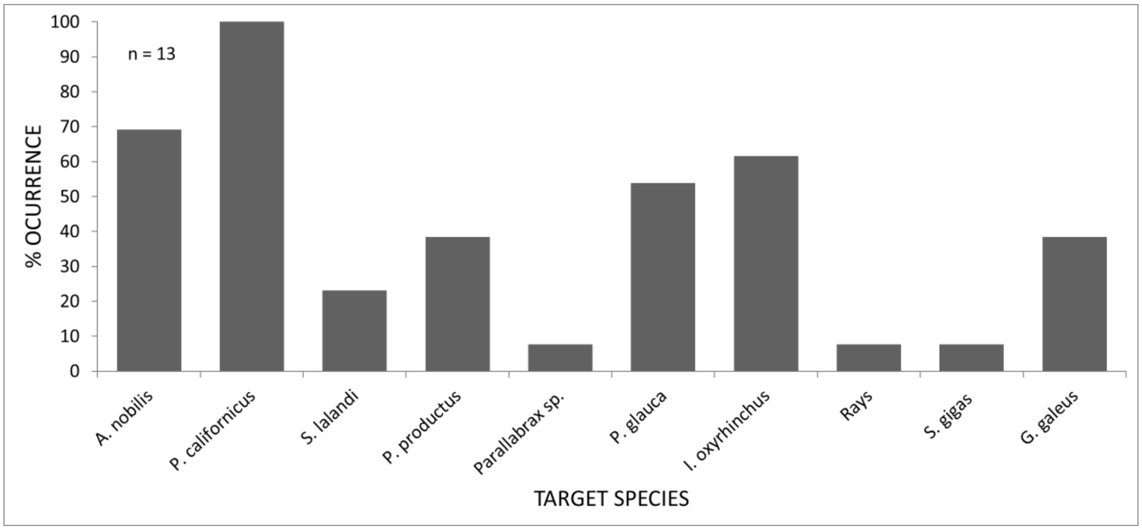

Figure 27. Target species from artisanal fisheries in the fishing camp of Laguna Manuela.

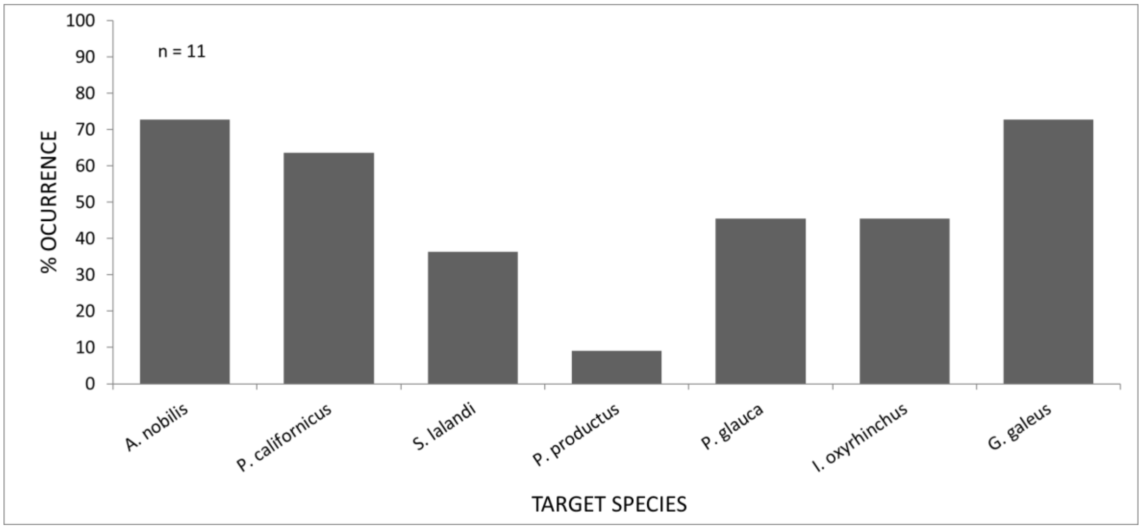

Figure 28. Target species from artisanal fisheries in the fishing camp of Santa Rosaliita.

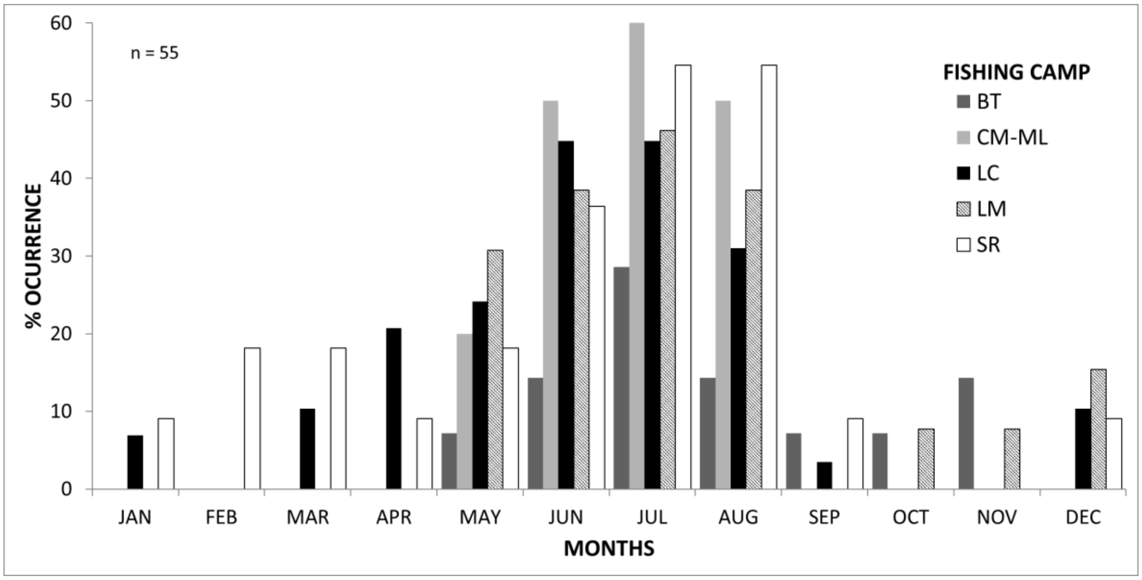

Figure 29. Incidental catches of immature white sharks by month and by fishing camp in Vizcaino Bay. BT: Bahía Tortugas, CM-ML: Campito-Malarrimo, LC: Las Casitas, LM: Laguna Manuela, SR: Santa Rosaliita.