Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California

---

Programa de Posgrado en Ciencias en Ecología Marina

Juvenile white shark (*Carcharodon carcharias*) connectivity and importance of Bahia Sebastian Vizcaino as a nursery area in the North Eastern Pacific

Tesis

para cubrir parcialmente los requisitos necesarios para obtener el grado de
Doctor en Ciencias

Presenta:

Erick Cristóbal Oñate González

Ensenada, Baja California, México
2015

Tesis defendida por

Erick Cristóbal Oñate González

y aprobada por el siguiente Comité

Dr Oscar Sosa Nishizaki

PhD. Sharon Zinah Llona Herzka

PhD. Axayácatl Rocha Olivares

PhD. Heidi Dewar

PhD. Chugey A. Sepúlveda

Autoridades

Dr. David Alberto Rivas Camargo
Coordinador del Posgrado en Ecología Marina

Dr. Jesús Favela Vara
Director de Estudios de Posgrado

Erick Cristóbal Oñate González © 2015
Queda prohibida la reproducción parcial o total de esta obra sin el debido permiso del autor

Resumen de la tesis que presenta **Erick Cristóbal Oñate González** como requisito parcial para la obtención del grado de Doctor en Ciencias en Ecología Marina.

Juvenile white shark (*Carcharodon carcharias*) connectivity and importance of Bahia Sebastian Vizcaino as a nursery area in the North Eastern Pacific

Resumen aprobado por:

Dr. Oscar Sosa Nishizaki
Director de tesis

En el Pacífico nororiental (NEP) el tiburón blanco (*Carcharodon carcharias*) tiene dos zonas de agregación de sub-adultos y adultos: en California central (CC), en E.U.A., y en Isla Guadalupe (GI), en México. Los individuos inmaduros se distribuyen en aguas costeras desde Punta Concepción en E.U.A., hasta el Golfo de California. Es una especie con protección nacional e internacional. A pesar de su amplia distribución y su estatus de protección, se desconocen aspectos importantes sobre su ecología y biología en el NEP. En la presente tesis se presentan los resultados de dos estudios enfocados en: 1) conocer las relaciones genéticas existentes entre individuos adultos e inmaduros de tiburón blanco en el NEP, y 2) entender la importancia de Bahía Sebastián Vizcaíno (BV) para la población de tiburón blanco en el NEP, a través del análisis de sus capturas incidentales. Las diferencias significativas encontradas entre haplotipos de ADNmt de hembras de tiburón blanco muestreadas en CC y GI sugieren que conforman dos subgrupos reproductivos. Adicionalmente, los individuos inmaduros de la Bahía del Sur de California (SCB) y de BV tuvieron una mayor probabilidad de tener un origen matrilineal de hembras adultas de GI; además, las diferencias significativas encontradas entre los inmaduros SCB y BV, sugieren un comportamiento reproductivo filopátrico al sitio de alumbramiento por parte de las hembras de GI. Los resultados del análisis de las capturas incidentales contrastados con los criterios para definir una zona de crianza de Heupel et al. (2007), permiten sugerir que BV es una zona de crianza importante para el tiburón blanco, ya que se registró una mayor frecuencia de individuos recién nacidos y de menos de un año de edad (YOY), durante varios meses y a través de los años muestreados (1999-2013). Estudios anteriores sugerían que la región entre Punta Concepción hasta BV era una zona de crianza para tiburón blanco. Las diferencias genéticas significativas en ADNmt entre SCB y BV, así como el cumplimiento con los criterios para denominar una zona de crianza, permiten sugerir la existencia de dos zonas de crianza en el NEP, siendo SCB y BV, con una presencia importante de recién nacidos y YOY de tiburón blanco. Estos resultados coadyuvarán en la mejoría del manejo y conservación de esta especie. En la parte final de la tesis se listan una serie de recomendaciones para futuras investigaciones.

Palabras clave: tiburón blanco, origen matrilineal, áreas de crianza para tiburones, capturas incidentales, filopatría

Abstract of the thesis presented **by Erick Cristóbal Oñate González** as a partial requirement to obtain the Master or Doctor of Science degree in Marine Ecology

Juvenile white shark (*Carcharodon carcharias*) connectivity and importance of Bahia Sebastian Vizcaino as a nursery area in the North Eastern Pacific

Abstract approved by:

Dr. Oscar Sosa Nishizaki
Thesis Director

In the North Eastern Pacific (NEP) the white shark (*Carcharodon carcharias*) has two aggregation areas for sub-adults and adults: in central California (CC), in U.S.A., and in Guadalupe Island (GI), in Mexico. Immature white sharks distribute in coastal waters from Point Conception in USA, to the Gulf of California. White shark is a species with national and international protection status; despite this, still there is a lack of some important information on the ecological and biological characteristics in NEP. The present thesis presents results of two studies focused in: 1) assess the genetic relationships between adults and immature white sharks in NEP, and 2) understand the importance of Bahia Sebastian Vizcaino (BV) for the white shark population in NEP, through the analysis of its incidental catches. Significant differences were observed among mtDNA haplotypes of female white sharks sampled, which suggest two reproductive subgroups in CC and GI, respectively. Furthermore, immature white sharks from the Southern California Bight (SCB) and BV showed a higher probability of their matrilineal origin from GI females. Significant differences in mtDNA among immature white sharks from SCB and BV suggested that adult females from GI have a reproductive philopatric behavior to breeding areas. The results of the incidental catch analysis tested against the criteria for a shark nursery area proposed by Heupel et al. (2007), suggested that BV is an important nursery area for white sharks, based on the higher frequency records of newborns and young-of-the-year (YOY), during several months, and throughout the sampled years (1999-2013). Previous studies suggested that the region between Point Conception and BV was a nursery area for white shark. Considering the significant genetic differences in mtDNA between SCB and BV, along with tested criteria, allows suggesting the existence of two white shark nursery areas in NEP, SCB and BV. These results will contribute in improving the management and conservation of this species. In the final part of the thesis a series of recommendations for future research are suggested.

Keywords: white shark, matrilineal origin, shark nursery area, incidental catch, philopatry

Dedicatory - Dedicatoria

Para el gran "Micks", el "Padrino del ahijado".
Porque creíste que este día llegaría .
Porque mucho de esto, es porque tú empezaste.
Porque siempre tendré presente el "a ver pinche gordito!!".
Porque "ASÍ ES COMPA!!!".
Porque aunque no estás, SIEMPRE estarás.

Para TI, mi recién incorporado Angelito.
Porque en poco tiempo me diste nueva vida.
Porque en poco tiempo iluminaste el mundo.
Porque en poco tiempo nos hiciste inmensamente felices.
Porque fue poco el tiempo...
SIEMPRE TE AMARÉ

Acknowledgments - Agradecimientos

Tanto tiempo se requirió para tener este escrito finalizado, que agradecer a TODOS aquellos que directa o indirectamente tuvieron algo que ver en el proceso de mi formación y desarrollo de la presente tesis, sería imposible… o al menos muy complicado. Y más, porque mi memoria no es nada buena para recordar el nombre de todos. Por lo tanto, antepongo una disculpa por aquellas personas y/o instituciones que no sean mencionadas… porque aunque no los mencione… LES AGRADEZCO ENORMEMENTE.

Agradezco a mi comité de tesis, sin el cual, definitivamente, esta tesis no habría sido posible.

Al Dr Oscar Sosa. Gracias mi Doc por todo su apoyo, por todas sus porras y por todas sus enseñanzas. Por ser mi director, pero más que nada, por ser mi amigo. Y gracias por ayudarme a llegar a la culminación de este paso… que solo es el comienzo de una vida de colaboración y crecimiento. Gracias Oscar.

A la Dra Sharon Herzka. Muchas gracias por todo tu apoyo, por tus consejos, por no desanimarte tanto conmigo y por siempre apoyarme y ayudarme a crecer. Gracias por tu cariño y siempre estar pendiente de nosotros.

Al Dr. Axayácatl Rocha. Muchas gracias Axa por el apoyo y las enseñanzas. Gracias por mostrarme una manera diferente para hacer ciencia. Gracias por permitirme aprender sobre un tema que en un principio no me llamaba la atención.

To PhD. Heidi Dewar. Thanks Heidi for all your support along all this time, for all your comments and critics on the thesis, and for your friendship.

To PhD. Chugey Sepulveda. Thank you Chugey for all your comments, your opinion and your support. Thanks for always being available to help me improve and grow.

Emphatically want to thank those institutions that friendly and selflessly supported us for sampling, without which it would not have been possible to carry out this thesis - Quiero agradecer de manera enfática a las instituciones que amable y desinteresadamente nos apoyaron para la obtención de muestras, sin las cuales, no habría sido posible llevar a cabo esta tesis:

To the Monterey Bay Aquarium, especially to John O´Sullivan, for all your support and for always rely on us to continue worling together and go forward.

To the Shark Lab from the California State University, Long Beach, especially to PhD Chris Lowe, for all your comments and support; and to Kady Lyons, for all your support, your help, your friendship and for this partnership which I hope will last for a long time.

To the Marine Conservation Science Institute (CSI), to PhD. Michael Domeier and PhD. Nicole Nasby-Lucas, for all your help, your ideas, your support, and those tagging trips where I learned so much.

A FIDEMAR, en especial al Ing Carlos Javier Godínez Padilla, por su disposición para compartir muestras con las cuales llevar a cabo los análisis de la presente tesis.

De una manera MUY ESPECIAL, quiero agradecer a aquellas comunidades pesqueras de las costas de Baja California y Baja California Sur, a todas las personas que habitan en ellas, que nos han apoyado para la obtención de datos y muestras y que a pesar de las circunstancias, siempre han sido amables y dispuestos a apoyar.

Gracias a los pescadores de Guerrero Negro, Principalmente a Edgar Zepeda y a Rodrigo, quienes siempre han estado dispuestos a ayudarnos

Gracias los pescadores y vigilantes de Laguna Manuela, un lugar que siempre llevaré en mi corazón y al que algún día regresaré. Con mucho cariño quiero mencionar a Don Chuko, un gran amigo que siempre nos recibió con una enorme sonrisa.

Gracias a los pescadores de El Barril, espcialmente a Ricardo y su familia, con quienes se generó una buena amistad por sobre las circunstancias.

Gracias a todos los pescadores de los campos pesqueros ubicados en Santa Rosaliita, Punta Cono, Punta Canoas, San Quintín, Eréndira, Ensenada, Popotla, San Felipe, San Luis Gonzaga y todos aquellos que olvide nombrar, ya que siempre estuvieron dispuestos a apoyarnos, llevarnos con ellos en sus jornadas de trabajo y conseguir muestras para nosotros. Muchas gracias

Con mucho cariño y sentimiento, quiero agradecer a TODA LA BANDA del Laboratorio de Ecología Pesquera. Se que la mejor manera de agradecerles es mencionarlos a cada uno, pero conociéndome, se que olvidaré a alguien, y por esta razón, prefiero no poner nombres, pero realmente agradezco a tod@s aquell@s que siempre me apoyaron, con los que pasamos tantas aventuras en campo, tantos cotorreos, tantas risas, tanto… Siempre los tendré en mi corazón y siempre les agradeceré. GRACIAS LAB!!!

Quiero también agradecer con mucho cariño a los integrantes del Laboratorio de Ecología Molecular, por aceptarme dentro de sus filas y siempre apoyarme con sus consejos, y su disposición a enseñarme. Igualmente no puedo mencionar a cada uno, porque olvidaré a alguien y no quiero que eso pase, pero de verdad les agradezco mucho a TODOS.

Agradezco también a TODOS mis amig@s tanto de la maestría como del doctorado, siempre me apoyaron, siempre me echaron porras, siempre me animaron, siempre disfrutaron de esta etapa conmigo y se que siempre estarán ahí. Muchas gracias!

Quiero agradecer al personal administrativo de CICESE, cuyo apoyo ha sido fundamental para el desarrollo de mi formación y de esta tesis. Gracias por su esfuerzo desde el más alto nivel hasta el más sencillo… Aunque realmente no creo que los niveles deban existir y para mí, son todos igualmente valiosos.

Agradezco al CICESE como institución por permitirme pertenecer a este centro que es de alta calidad, las facilidades para aprender nuevas tecnologías, para adquirir nuevo conocimiento y para hacer contacto con gente nacional y extranjera.

Agradezco al CONACyT por haberme otorgado la beca de sustento durante mis estudios de doctorado.

I want to thank to The Rufford Fundation for give me the “Rufford Small Grants for Nature Conservation” for the analysis of the samples and for field work.

Con mucho amor, quiero agradecer a mi familia, mis padres, mi hermana mi tiburoncina, mi abuela, mis primos, mis tíos y tías.. en fin, a todos, quienes siempre han estado ahí para apoyarme, para creer en mí, para pedir al Gran Amigo por mí y para siempre darme su amor. Gracias, sin ustedes no sería quien soy. Los amo con todo mi corazón. Arturito, gracias por cuidarme y ser mi ángel; te extraño… pero aquí estás.

Finalmente, pero (con todo respeto para todos los demás) LA MÁS IMPORTANTE… Miles de gracias a MI ESPOSA!!! Mi amor, Nancy, mi Nan, muchísimas gracias por tu amor, gracias por aceptarme y estar conmigo, gracias por ser mi esposa, gracias por animarte a emprender esta aventura llamada matrimonio y vida a mi lado. Sin ti, este logro no habría llegado, pero además, no tendría sentido. Gracias por darle sentido a mi vida. Gracias por haberme dado la mayor felicidad que un hombre puede tener, sin importar las circunstancias, siempre te amaré por haberme hecho tan feliz… Y se que seremos aún más felices. Nunca lo olvides: “Cada día te admiro más como mujer”. TE AMO MI NENA HERMOSA!!!

Y como un apartado especial, pero que no puedo dejar de mencionar, Muchas Gracias a mi Jiro; de verdad, me has acompañado en momentos alegres y difíciles, y el que siempre me recibas con tanto amor, no lo cambiaría por nada del mundo.

Table of contents

List of figures

List of tables

Chapter 1. General Introducción

1.1 Structure of the thesis

This thesis is composed of six chapters. The first chapter is composed of a general introduction to the thesis, including important information on the biology, ecology, and conservation of white shark and the study area. The second chapter is small and includes the research questions, hypothesis and objectives. The third chapter is based mainly on the article "Mitochondrial Genetic Structure and Matrilineal Origin of White Sharks, *Carcharodon carcharias*, in the North Eastern Pacific: Implications for Their Conservation," published in the Journal of Heredity (Oñate-González et al., 2015). The fourth chapter is composed of a second manuscript on the analysis of Bahia Sebastian Vizcaino as a nursery area for the white shark. The last two chapters include a general discussion (C 5) and the final discussion points from this work (C 6). Because chapters three and four are stand along chapters based on the publications, there may be some redundancy in regards to the background information.

1.2 The context of the problem

The white shark (*Carcharodon carcharias*) is broadly distributed (Figure 1) in coastal and oceanic waters of both tropical and temperate seas (Compagno et al., 2005). This species is typically found in relatively low densities in habitats that range from inshore waters to remote oceanic islands as well as offshore areas (Ebert et al., 2013). This species is more commonly observed at aggregation sites, which commonly occur proximal to pinniped colonies. Several aggregation sites have been described for white sharks, including locations in South Africa (Ferreira and Ferreira, 1996), the Mediterranean Sea, New Zealand (Fergusson, 1996), Australia (Strong et al., 1996), and in the North Eastern Pacific (NEP), at Guadalupe Island (GI), in México (Domeier and Nasby-Lucas, 2007), and the Farallon and Año Nuevo Islands in central California (CC), USA (Klimley et al., 1992; Pyle et al., 1996).

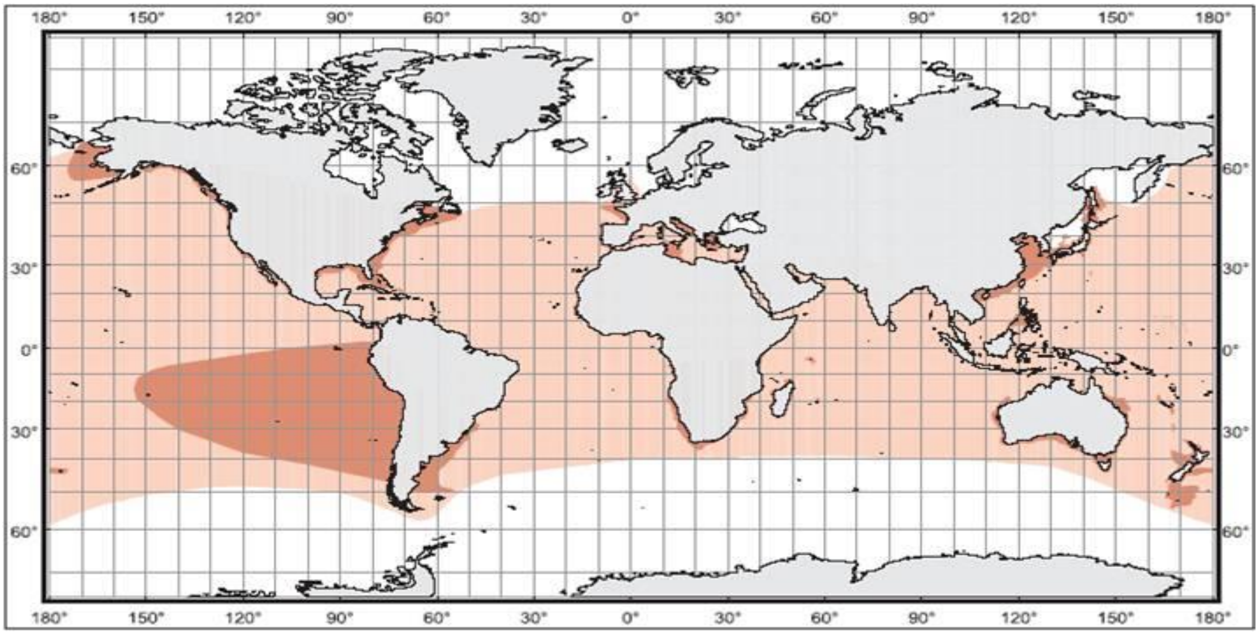

Figure 1. White shark, *Carcharodon carcharias*, world distribution (Compagno et al., 2005).

To improve management of protected species like the white shark, it is necessary to understand the relationship between the shark and its environment. Sustainable management and conservation requires an understanding of how white sharks are distributed within their habitat (Yates et al., 2015). Habitat use has been defined as “the way an animal uses the physical and biological resources in a habitat” (Krausman, 1999). Habitats include foraging areas and places to escape from predators (Torres-Rojas et al., 2014; Francis et al., 2015), nursery areas (Hueter et al., 2007; Dale et al., 2011; Hollensead et al., 2015), or other life history traits, and it is not uncommon that overlap in habitat use occurs in some areas (Pikitch et al., 2005; Dale et al., 2011).

Recent research has concentrated on the presence and use of nursery areas by young sharks. Shark nurseries are defined as areas with: a) relatively high abundance of young sharks, b) seasonality, and c) stability in use across multiple years (Heupel et al., 2007; Yates et al., 2015). In elasmobranchs habitat use has been studied using a variety of techniques including: the analyses of foraging grounds and stomach contents (Dale et al., 2011), stable isotopes analysis (Dale et al., 2011; Jaime-Rivera et al., 2013; Malpica-Cruz et al., 2013), assessing contaminant concentrations (Lyons et al., 2013a), tagging studies (Conrath and Musick, 2007) and acoustic tracking work (Kock et al., 2013).

In the NEP (Figure 2), the white shark is distributed from the Alaskan Peninsula to the Gulf of California (GC), and into the west in waters off the Hawaiian archipelago (Dewar et al., 2013). Domeier (2012) reviewed the life-history information to date, and suggested that white sharks in the NEP begin their life in the nearshore, shallow waters of the Southern California Bight (SCB) and Baja California. It is also hypothesized that the young of the year migrate to the warmer waters of coastal Baja California during their first winter. After growing, the juveniles become more tolerant of cooler waters and begin to migrate north of Point Conception. As white sharks approach maturity, it is proposed that males begin annual movements, while females undergo bi-annual migrations between offshore habitats and exclusive aggregations sites at either CC or GI, with a low number of sub-adults moving between that aggregations sites (Domeier and Nasby-Lucas, 2008). Domeier (2012) also described that males from both aggregations sites travel to a Shared Offshore Area (Domeier and Nasby-Lucas, 2008), whereas females roam in a less defined offshore habitat between Hawaii and continental waters. Moreover, Domeier (2012) hypothesized that mating may occur at aggregations sites, and after having been at sea for more than 15 months, pregnant females return to coastal regions off CC and Baja California to give birth during the parturition period between May and August.

Phylogenetic studies have shown that NEP white sharks represent a distinct population (Jorgensen et al., 2010; Tanaka et al., 2011; Oñate-González et al., 2015). However, Domeier (2012) hypothesized a complex life cycle for the white sharks of the NEP: adult white sharks are phylopatric to each aggregation site, providing the basis for hypotheses of population structure. If mating occurs only at aggregation sites, genetic differences between aggregation sites would be expected between each area. On the other hand, movement patterns suggest a high degree of demographic connectivity and subsequent genetic connectivity (Frisk et al., 2014). Genetic connectivity represents the level of genetic exchange among subpopulations, with a high degree of connectivity resulting in low genetic structure, and low connectivity could result in genetically distinct subpopulations (Frisk et al., 2014). Demographic connectivity is the exchange of individuals between geographically discrete populations or subpopulation groupings (Cowen and Sponaugle, 2009; Friedlander et al., 2009), that can occur as a result of juveniles and/or adult migration (Secor, 2015).

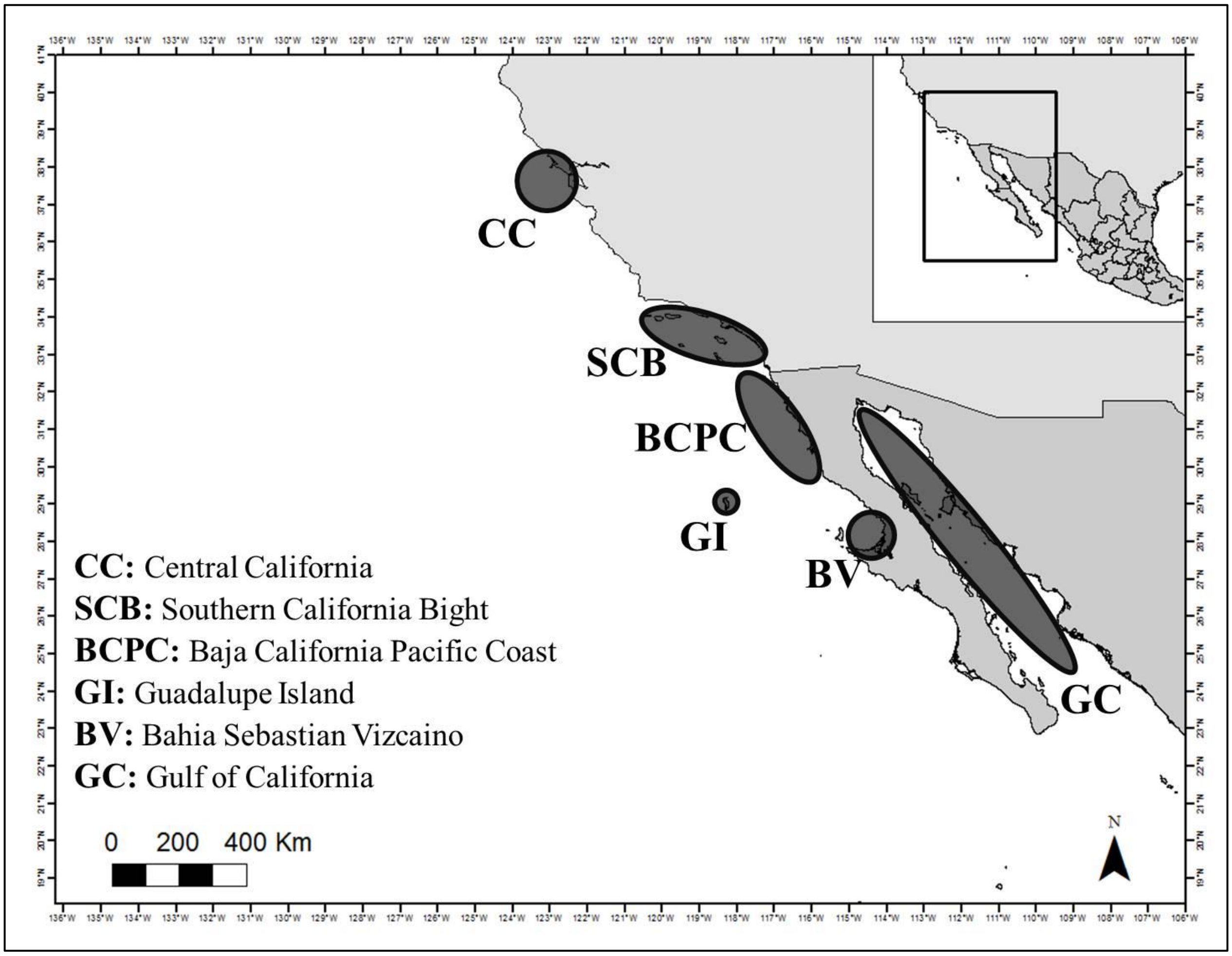

Figure 2. North Eastern Pacific (NEP) map showing the study areas: CC: Central California; SCB: Southern California Bight; BCPC: Baja California Pacific coast; GI: Guadalupe Island; BV: Bahia Sebastian Vizcaino; and GC: Gulf of California.

In order to understand the connectivity between different populations, tagging studies have been used to analyze the movements and distribution of sharks between different habitats along the NEP distribution (Chin et al., 2013; Werry et al., 2014). However, migration patterns alone are not enough to understand the connectivity between different geographic areas, therefore prompting the need for genetic assessment of connectivity among organisms from different geographic areas (Feldheim et al., 2001; Keeney et al., 2005; Gubili et al., 2014; Vignaud et al., 2014).

To improve the understanding of the ecology of the white shark in North Western Mexico, I present here a molecular genetic analysis to evaluate genetic connectivity between adults at Guadalupe Island and central California aggregations sites, and immature white sharks from coastal areas. I also present an evaluation of the Bahia

Sebastian Vizcaino region to assess its potential as a nursery area using incidental catch records.

1.3 White shark biology and ecology in the NEP

The white shark is an important apex predator that can reach a maximum size of 6.1 m (Castro, 2012). Cailliet et al. (1985) estimated that white sharks can attain up to 27 years, maturing at an age of 9-10 years. Recent estimations suggest that females might persist up to 40 years and males up to 73 years (Hamady et al., 2014). However, recent demographic analyses have assumed a conservative longevity of 30 years (Burgess et al., 2014).

The white shark has been shown to display ontogenetic differences in distribution, with adults typically associated with oceanic waters and immature individuals typically found in coastal waters. Based on size, four different life stages of white sharks have been proposed: a) Young-of-the-year (YOY) sharks, less than ≤ 1.75m TL; b) Juvenile (JWS) sharks [(> 1.75 – 3.0 m TL), those sharks larger than YOY sharks but prior to the smallest sizes commonly observed visiting pinniped colonies]; c) Sub-adult (SAS) sharks [(>3.0 to mature size), those between the size when first visiting pinniped colonies and the size on reaching maturity]; and d) Adult (AWS) sharks (> 3.6 m TL [male]; > 4.8 m TL [female]) (Cailliet et al., 1985; Francis, 1996; Pratt, 1996; Wintner and Cliff, 1999; Malcolm et al., 2001; Martin, 2005).

Reproduction in the white shark is poorly documented because of the low number of pregnant females that have been reliably examined (Bruce, 2008). White sharks are aplacental viviparous species with embryos that feed on unfertilized eggs during the gestation period (oofagy) (Compagno et al., 2005). Age of maturity is different between sexes, with females maturing later than males (Bruce, 1992; Pratt, 1996). White sharks have up to 14 pups (mainly 2-10), with a gestation period between 12 and 18 months, and parturition occurring once every two to three years. Size at birth ranges from 120 to 150 cm TL, and newborn sharks are present during the spring-summer period with a sex ratio of 1:1 (Francis, 1996; Compagno et al., 1997; Domeier, 2012).

Global white shark abundance is unknown because its wide distribution, high rate of migration, and the difficulty associated with quantifying pelagic species. There are two regional estimates on the abundance in the NEP based on photo-identification. At GI photo-identification data was used to apply a tag-and-recapture technique to quantify a local abundance of 120 organisms (51 females and 69 males) (Sosa-Nishizaki et al., 2012). In California waters, Chapple et al. (2011) also applied a tag-recapture modeling technique using photographic identification around the Farallon Islands and Tomales Point, CA. The study used a Bayesian hypergometric model to estimate a population size of 219 adult white sharks. These estimations were based on adults and sub-adults from each region, and since immature sharks and adult sharks from other regions in NEP were not included, the population estimates made to date likely underestimate the actual size of the population. Dewar et al. (2013) used the Chapple et al. (2011) and Sosa-Nishizaki et al. (2012) estimates and concluded that at least 200 adult females are need to support the observed juvenile numbers recorded from incidental catches in the SCB and Bahia Sebastian Vizcaino (BV) (Lowe et al., 2012; Santana-Morales et al., 2012). The Dewar et al. (2013) work suggested that all the life stages should be considered in the estimation of the population size of white shark in the NEP. In a recent study, Burgess et al. (2014) used a demographic Bayesian mixture model, to propose that a minimum all-life stages population size of > 2000 individuals in the California subpopulation would be required to account for the numbers and size range of individual sharks observed in the two locations of the Chapple et al. (2011) study.

Adult white sharks have been shown to display philopatry, or site fidelity, as they return each year to the same aggregation site (Klimley et al., 2002; Domeier and Nasby-Lucas, 2007) (Figure 3). In the NEP, white sharks return to GI each year after undergoing an oceanic migration to the waters off Hawaii (Domeier and Nasby-Lucas, 2007; 2008). This philopatric behavior is similar to that displayed by CC white sharks, with individuals moving offshore to oceanic waters, and up to Hawaii, and returning yearly to Farallon and Año Nuevo Islands (Klimley et al., 2002; Jorgensen et al., 2010). The philopatric behavior displayed by white sharks from both aggregation areas is suggestive of two different subpopulations, despite the recently suggested hypothesis of mating areas at aggregation areas, where male and female AWS coincide in time (Domeier, 2012).

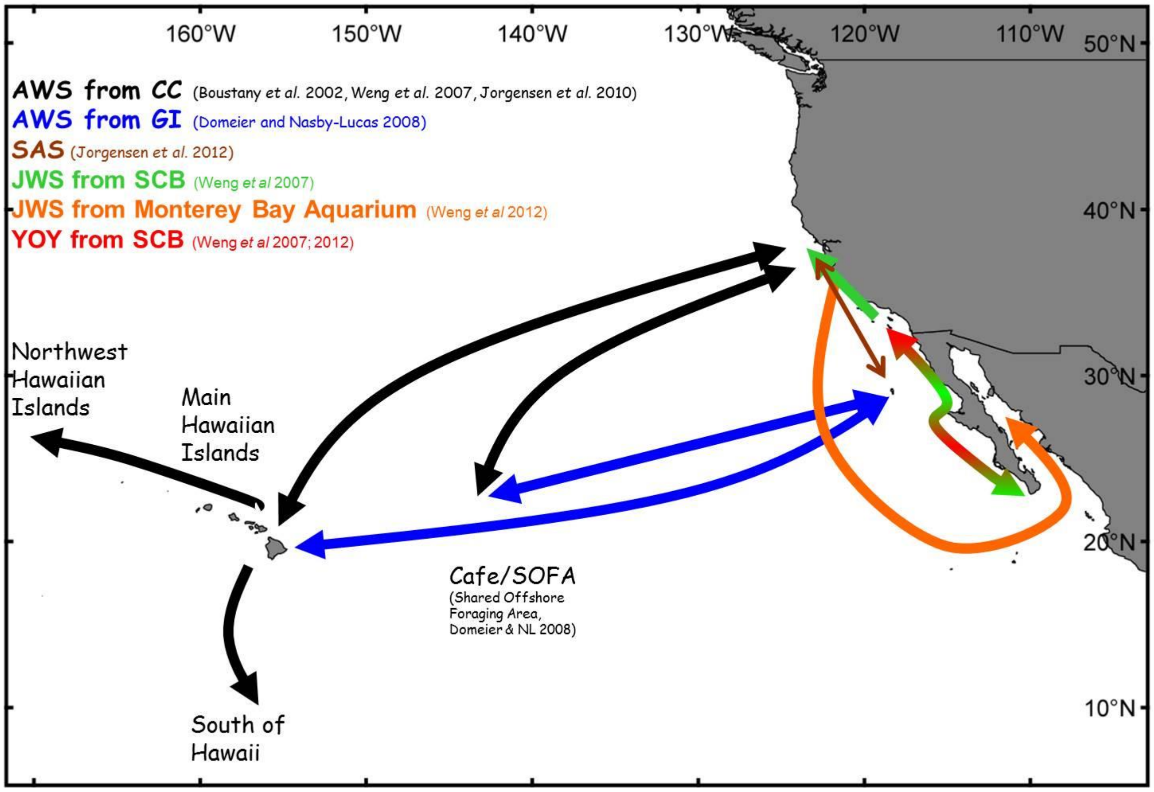

Figure 3. White shark ontogenic movements in NEP. AWS: Adult white sharks (black and blue arrows); SAS: Sub-adult white sharks (brown arrow); JWS: Juvenile white sharks (green and orange arrows); and YOY: Young-of-the-year (red arrow). (Boustany et al., 2002; Weng et al., 2007a; Weng et al., 2007b; Domeier and Nasby-Lucas, 2008; Jorgensen et al., 2010; Weng et al., 2012).

The location of white shark parturition is unknown, however, it has been suggested that pregnant females move from GI to near shore waters to pup (Domeier and Nasby-Lucas, 2013). Coastal areas like the SCB, BV and the GC, have been proposed to be parturition areas for white sharks (Domeier, 2012), although there is no evidence of females giving birth at this areas.

Immature white sharks move along the coastal areas from SCB to Mexican waters off Baja California and sometimes into the GC (Weng et al., 2007b; Weng et al., 2012). However, it remains unknown whether sharks return to the SCB after their southern migration. Based on size distribution and seasonality from catch records and reports, Klimley (1985) theorized that the SCB was a pupping and nursery ground for white sharks, because AWS were most frequently seen and caught in Central and Northern California in fall and winter months, whereas YOY were only caught south of Point Conception during summer months. The SCB is an extremely productive region that extends from Point Conception to Cabo Colonet, in Baja California, and is bounded seaward by the California Current. Given that the SCB has a diverse and rich assemblage of prey species, this region serves as a nursery ground for several shark species (Hanan et al., 1993; Holts and Bedford, 1993; Ebert, 2003; Cartamil et al., 2010), and has been proposed to be a nursery ground for the white sharks (Klimley, 1985; Weng et al., 2007b; Domeier, 2012).

Juvenile white sharks in the BV region have been shown to feed mainly along inshore-waters on benthic species like rays (*Myliobatis californica*, *Raja* spp) and crustaceans as well as small pelagics like bony fishes (*Scomber japonicus, Atractosion nobilis*) and squids (Teuthoidea) (Santana-Morales et al., 2012). As white sharks grow their prey increases in size, which includes the opportunistic preying upon marine mammals. AWS have been shown to prey upon pelagics and other elasmobranchs, however, their main diet consists of marine mammals (Klimley, 1985; Compagno et al., 2005), which include both oceanic and coastal species (Jaime-Rivera et al., 2013; Malpica-Cruz et al., 2013). With this ontogenic change in feeding habits, white sharks are an apex predator with a trophic level of 4.3 when immature and almost 5 as adults (Estrada et al., 2006).

White sharks that inhabit SCB are primarily YOY and JWS (Lowe et al., 2012). Upon reaching the juvenile size size-class, SCB sharks have been shown to migrate southward along Baja California Peninsula (Weng et al., 2012). These southward migrations make them susceptible to fishing operations that occur in waters close to shore, as white sharks are commonly caught in artisanal fisheries (Santana-Morales et al., 2012). Some of the tagged sharks from SCB have been recorded to move into BV (Weng et al., 2012), an area that seems to be important in the life cycle of NEP white sharks (Santana-Morales et al., 2012).

1.4 Bahia Sebastian Vizcaino area

The area of BV (Figure 4) is an important area for white sharks, with both YOY and JWS incidentally caught by artisanal fisheries in the region. High incidental catch rates of white sharks suggest that BV could be a nursery ground for white sharks (Santana-

Morales et al., 2012). Bahia Sebastian Vizcaino is located between Baja California and Baja California Sur along the Mexican Pacific coast and spans 35,678 km^2. BV is an area composed of marshes, coastal dunes, and three lagoons (Laguna Manuela, Laguna Guerrero Negro and Laguna Ojo de Liebre), and three islands (Natividad, Cedros and San Benito) (Hernández-Rivas et al., 2000). It is a productive region within the California Current System that is very similar in many ways to the SCB (i.e., topography, bathymetry and presence of Islands).

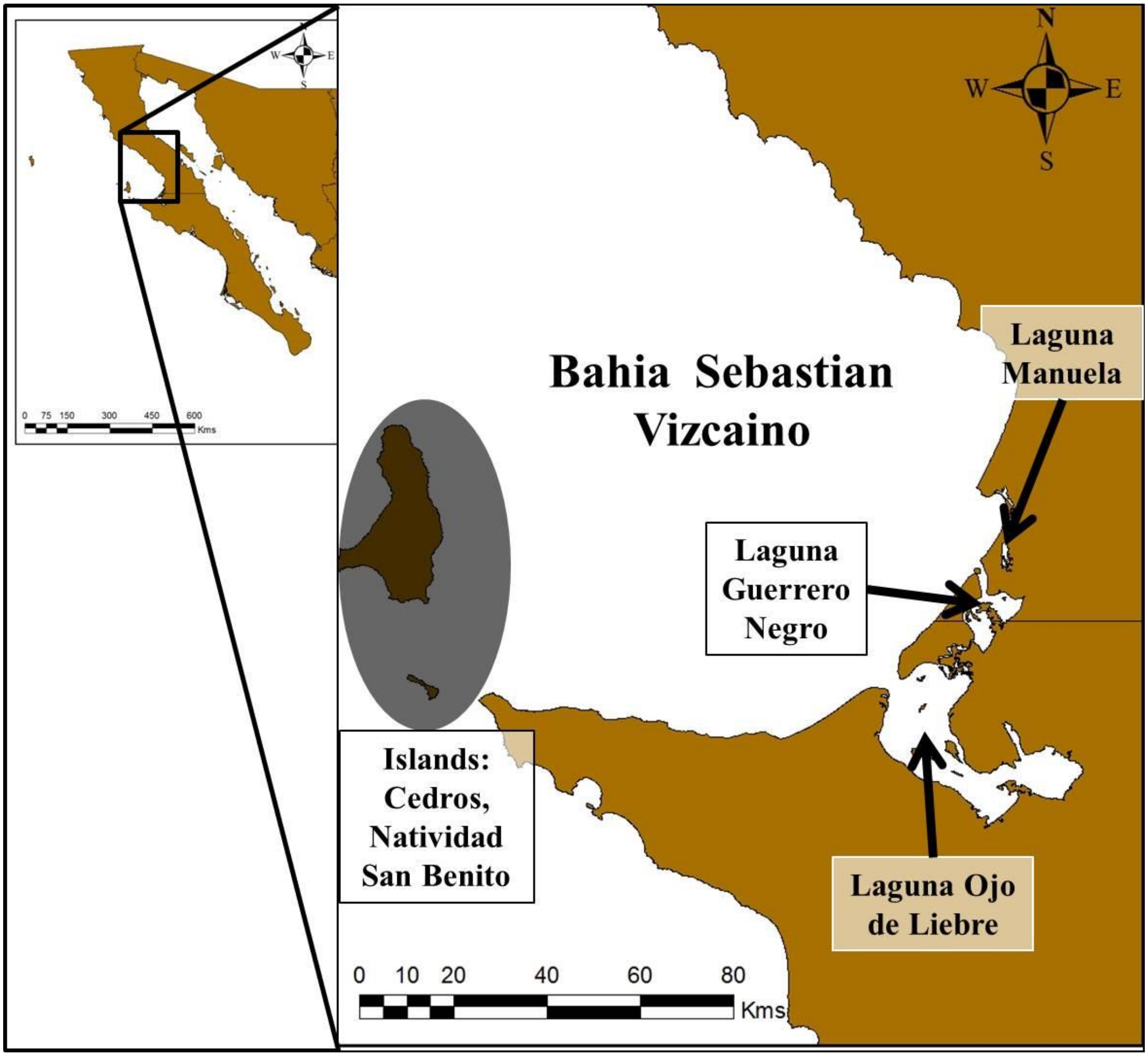

Figure 4. Bahia Sebastian Vizcaino.

The water temperature in BV is temperate from January to June increasing from July to December, and it has a variable salinity. BV is the limit of north-distribution of warmer-water species and the southern limit of temperate-water species (Hernández-Rivas et al., 2000). It is the southern limit of the Californian Province that retains warmer species from the south (Brusca and Wallerstein, 1979; Lluch-Belda et al., 2003). Some of the species that are both in high abundance and potential prey for smaller white sharks include species like shovelnose guitarfish (*Rhinobatos productus*), banded guitarfish (*Zapteryx exasperata*), and California bat ray (*Myliobatis californica*) (Cartamil et al., 2011), as well as California halibut (*Paralichthys californicus*) and white seabass, *Atractoscion nobilis* (Romo-Curiel et al., 2015).

1.5 Conservation

The white shark is recognized as a vulnerable species to overexploitation (IUCN Red list (Hilton-Taylor, 2000) and has been listed in CITES Appendix II since 2004, which bans the commerce of any body parts. In Mexico, the official record "NOM-029-PESC-2006" established the prohibition of white shark catches as well as the retention and commercialization of any body part. Similarly, this follows the regulations put forward for other species like whale shark (*Rhincodon typus*) and basking shark (*Cethorhinus maximus*) (DOF, 2007). Since 2012, a seasonal ban of sharks and rays was established during May 1st through July 31st to protect a fraction of the reproductive stock of commercial elasmobranch species (DOF, 2012). Although protection of white shark is not only the purpose of this ban, the time period of this seasonal ban likely helps with the protection of this species. More recently Mexico has established a total fishing ban for white sharks (DOF, 2014), mandating the release of any white shark incidentally caught.

Despite the national and international protection of white shark and their vulnerability to fisheries that operate in Mexican waters, there is still a lack of information on the habitat use of white sharks in Mexican waters, mainly for the immature life stages. The understanding of habitat use and the relationship between white sharks of other regions within the NEP is important for the long term sustainability of this valuable resource.

Chapter 2. General question and objectives

2.1. Research questions and hypotheses

1. Given the high degree of philopatric behavior observed among AWS of the NEP and the limited movements of adult sharks between sites, this work has focused on assessing population structure using a genetic tool set. I propose to assess how much genetic connectivity exists between the *subpopulations* from each NEP aggregation site. I tested whether genetic structure was similar between adult white sharks from the CC region and GI.

2. Based on recent movement patterns, the timing of parturition and Guadalupe Islands proximity to BV, this work has focused on assessing the genetic similarities between white sharks of BV and GI. The null hypothesis tested in this portion of my thesis was that there is no genetic difference between the white sharks of BV and GI.

3. Because BV has been shown to be an important region for juvenile white sharks, this portion of my thesis investigated the frequency of catches in ongoing fisheries to address questions related to its role as a potential nursery hot-spot. Several authors have suggested that the entire coastal area between Point Conception and BV is a nursery ground, however, I will compare catch rates of YOY among the regions and test whether BV is similar to adjacent areas.

2.2. General objectives

In this thesis I will quantify genetic similarities among white sharks from different aggregation sites within the NEP to assess connectivity between areas and test hypotheses one and two. In addition, I will also analyze catch rates and size-class composition of white sharks from BV and the entire SCB to assess whether BV is a nursery hot-spot for white sharks of this region.

Chapter 3. Genetic relationships in NEP

3.1. Introduction

The white shark occurs in temperate and subtropical regions of all major ocean basins (Compagno et al., 2005). It has been recognized as a species vulnerable to overexploitation due to its low intrinsic rate of increase or its population rebound potential (Cailliet et al., 1985; Francis, 1996; Pratt, 1996; Curtis et al., 2014). Since the mid-1990s, it has become a widely protected species (Shivji et al., 2002). White sharks were listed as vulnerable by the IUCN in 1996 (Hilton-Taylor, 2000), and included in the Appendix II of CITES. In Mexico, it has been recognized as “threatened” since 2002 (DOF, 2002), and fishing is prohibited by law (DOF, 2007; 2014). Along the U.S. Pacific coast white shark fishing is prohibited and they must be released immediately if caught, and off California they have been protected since 1995 (PFMC, 2011). In Canadian waters there is no specific protection for white sharks however, hook-and-line fisheries are not allowed to land any shark other than dogfish (COSEWIC, 2006).

Despite the global concern about white shark populations, basic facts about some aspects of their life cycle relevant for the development of conservation measures remain largely unknown. For instance, levels of genetic diversity, population connectivity and trends in abundance are poorly understood, although research is ongoing. (Blower et al., 2012; Duffy et al., 2012; Jorgensen et al., 2012; Dewar et al., 2013; Curtis et al., 2014; Gubili et al., 2015; O´Leary et al., 2015). An understanding of population structure is critical to developing conservation and management strategies.

Very few population genetic studies have been conducted on white shark, and what is known is generally consistent with known movement patterns. At an Ocean-Basin scale, there are few records of transoceanic movements of white sharks (Bonfil et al., 2005), and in the Pacific Ocean, there are no records documenting movements between or among the northwestern, northeastern and southwestern Pacific. This is consistent with the genetic differentiation found among white shark populations from Japan, Australia and California (Tanaka et al., 2011). While genetic analyses conducted in the NEP reveal global population structure, no genetic studies looking at patterns within the NEP have been conducted.

At a smaller scale, JWS tagged in eastern Australia remained in eastern nursery areas and there is no record of them moving towards western shores (Bruce and Bradford, 2012). This is consistent with the genetic differentiation found between eastern and western juveniles; a genetic structure guided by both parents as indicated by the significant differences in both mitochondrial (mtDNA) and nuclear markers between the two regions (Blower et al., 2012). No similar work has been conducted on juvenile in other regions.

In the eastern Pacific, immature white sharks are found from the SCB, in the U.S., to Baja California and the GC, in Mexico (Weng et al., 2012). Most immature sharks occur in productive near-shore waters, where, in Mexico, most artisanal fisheries operate, making them vulnerable to incidental fishing mortality (Dewar et al., 2004; Weng et al., 2007b; Lowe et al., 2012; Santana-Morales et al., 2012). Based on catch, sightings, and electronic tagging data there are ontogenetic shifts in distribution (Klimley, 1985; Bruce et al., 2005; Bruce et al., 2006; Bruce, 2008; Domeier and Nasby-Lucas, 2008; Domeier, 2012; Jorgensen et al., 2012). As sub-adults their distribution is similar to that of adults and includes both coastal and oceanic waters from Alaska to the GC and out to Hawaii (Martin, 2004; Domeier and Nasby-Lucas, 2008; Galván-Magaña et al., 2010; Jorgensen et al., 2012; Weng and Honebrink, 2013). YOY and JWS white sharks occur primarily in nearshore waters from Point Conception to the GC (Klimley, 1985; Dewar et al., 2004; Weng et al., 2007b; Galván-Magaña et al., 2010; Weng et al., 2012; Dewar et al., 2013). Within that broader range, two hypothetical nursery hot-spots have been suggested: the SCB, in California (Weng et al., 2007b), and BV, in Baja California (Santana-Morales et al., 2012).

In the NEP, AWS aggregate in two primary areas: GI, in Mexico (Domeier and Nasby-Lucas, 2008), and in the shelf waters and coastal Islands off CC, in the U.S. (Boustany et al., 2002; Anderson and Pyle, 2003; Weng et al., 2007a; Jorgensen et al., 2010). AWS from both areas make long-distance seasonal migrations into oceanic waters. Males tend to move to a region in the subtropical eastern Pacific called SOFA -Shared

Offshore Oceanic Area-, whereas females may visit this area but have a broader off-shore distribution including the waters around the Hawaiian Islands (Boustany et al., 2002; Weng et al., 2007a; Domeier and Nasby-Lucas, 2008).

A comparison of the spatial and temporal distributions of males and females indicates specific differences in the timing and duration of migrations and time spent at aggregation sites. Adult male white sharks arrive first to GI around May-August and females arrive after August. Both sexes leave GI and migrate to oceanic waters in December-March; the reason of these large-scale migrations is unknown (Domeier and Nasby-Lucas, 2008). At the SOFA, males are initially distributed in a concentrated core-area whereas females move mainly in the periphery with limited overlap with the males (Domeier and Nasby-Lucas, 2012). This lack of overlap makes mating in the SOFA improbable (Domeier and Nasby-Lucas, 2012; Jorgensen et al., 2012). Both sexes show philopatry to GI, where they return yearly (males) or approximately every other year (females). It is assumed that the different return periodicity of females is related to reproduction; females are thought to pup every two to three years (Domeier, 2012). The tracks from a small number of female sharks show visitation to the coastal nursery area after more than a year at sea at the time of year when pupping occurs providing additional support for this hypothesis.

AWS from CC show a comparable behavior. They have the same sex-biased distribution, after leaving CC they migrate to the SOFA and/or the waters around Hawaii, and are philopatric to CC (Jorgensen et al., 2012). The timing, distribution and migration of CC sharks to oceanic waters are similar to those from Guadalupe (Weng et al., 2007a). Photo ID and acoustic tagging studies indicate that, as off GI, females return every 2-3 years. Unfortunately there are no tracks of greater than 12 months for any females from CC and consequently no data available on their movements to nursery areas when pupping is thought to be occurring (Anderson and Pyle, 2003).

Although philopatric behavior of white sharks to aggregation sites in NEP is the common pattern, there are some white sharks that move between CC and GI. The first white shark recorded moving between aggregation areas was a sub-adult female, which was acoustically tagged at CC and detected on GI receivers (Jorgensen et al., 2012). Dewar et al. (2013) mentioned a female white shark satellite tagged at GI that moved into offshore waters and then came back to coastal areas close to Point Conception, as well as two other sharks acoustically tagged at either GI or CC that were later detected in the other aggregation area. With regards to population structure in the NEP, it is not known whether mature sharks moving between the sites are mating or not. If they are mating even a small number of immigrants would impact genetic results.

The limited information on the long-term movements patterns for female leaves important gaps in our understanding of population dynamics in the NEP. Is there connectivity between aggregation sites? How are aggregation sites connected to coastal nursery areas? If there is strong philopatry to breeding aggregations, where are females from the two sites pupping and is their philopatry to nursery areas?. These questions are relevant because they would provide important insight into population dynamics with regards to reproductive behaviors and provide the means to trace their offspring to these areas. This information would increase our understanding of how AWS make use of coastal regions in California and Baja California as nursery areas and the relative contribution of adults from the different aggregations sites to recruitment. Genetic analyses are a powerful tool to address these questions.

This study used two genetic approaches. First, matrilineally inherited mitochondrial DNA (mtDNA) was analysed to examine the agreement between known movements and those inferred from genetic analyses and to determine if the matrilineal origin of young white sharks can be traced to one or both aggregation sites. Nuclear DNA was used to examine the bi-parentally inherited genetic patterns among immature white sharks from different regions and between immature and adult white sharks from GI. This will shed light on the genetic patterns and reproductive dynamics of white shark in the NEP and on their relative use of coastal nursery areas in California and Baja California. A better understanding of these biological aspects can have major implications for its management and conservation.

3.2. Material and Methods

3.2.1. Tissue samples and DNA extraction

White sharks genetic samples were collected from SCB; Baja California Pacific Coast (BCPC), BV, the Gulf of California (GC), and GI. Muscle or skin samples consisted of biopsies of free-ranging sharks, necropsies from incidental catches and dry heads from fishing dumps. All samples were kept frozen or preserved in 96% ethanol prior to genetic analyses. DNA was extracted using standard proteinase K digestion, purified using standard salting-out extraction protocols with LiCl, followed by organic extraction and subsequent ethanol precipitation (Aljanabi and Martinez, 1997).

3.2.2. Amplification and data analyses of mtDNA control region

The mtDNA control region of white sharks was amplified with primers Pro-L2 and PheCacaH2 (Pardini et al., 2001) in 25μl reactions containing 0.18 mM dNTPs, 1X PCR buffer (Tris HCl 10mM, KCl 50 mM and $MgCl_2$ 1.5 mM), 0.4 μM of each primer, 1 U of *Taq* DNAPol and 20 ng of genomic DNA. Thermal cycling included an initial denaturation of 5 min at 94°C, 35 cycles of 15 s at 94°C, 120 s at 63 °C and 45 s to 72 °C, and a final step of 5 min at 72 °C (Sandoval-Castillo et al., 2004). PCR products were enzymatically cleaned (exoSAP-IT, Affymetrix, Santa Clara, CA) before directly sequencing both DNA strands with an ABI 3130xl Genetic Analyzer. Base calling was verified with the program Codon Code Aligner v.1.6.3 and DNA sequences were aligned using MEGA v.5.10 (Kumar et al., 2004). The identification of distinct haplotypes and their frequencies was carried out using DNASP v4.0 (Rozas et al., 2003). Sequences produced in this study were from SCB, BCPC, BV, GI, GC and CC (Genbank accession: KM014766-KM014781), and were analyzed with additional (n=59) published sequences from CC (Genbank accession: GU002302–GU002321, (Jorgensen et al., 2010) (Table 1).

A neighbor-joining (NJ) tree was constructed using MEGA v.5 (Tamura et al., 2011) to analyze worldwide mitochondrial lineages including all mtDNA sequences available to from NEP, Northwestern Atlantic, South Africa, Australia and New Zealand (Genebank accession: AY026196–AY026224; (Pardini et al., 2001), and Mediterranean Sea (Genebank accession: HQ540294–HQ540298; (Gubili et al., 2011).

Genetic diversity was estimated as haplotype (*h*) and nucleotide (*π*) diversities for mtDNA sequences as implemented in Arlequin v.3.5.1.2 (Excoffier et al., 2005). Patterns of genetic differentiation was tested using Analyses of Molecular Variance (AMOVA) implemented in Arlequin v.3.5.1.2 with a matrix of inter-haplotype distances based on a model on nucleotide evolution obtained with MODELTEST v3.7 (Posada and Crandall, 1998) and PAUP* v4.0b10 (Swofford, 2002).

3.2.3. Matrilineal origin

Given the contrasting sex-ratios of the GI (f:m=1.4) and CC (f:m=3.8) adult samples, the genetic differentiation (F_{st}) between sexes at each location was estimated using Arlequin v3.5.1.2. In addition, the influence of the contrasting sex-ratios on the patterns of mitochondrial genetic structure was assessed using a resampling approach in which female and male control region haplotypes from GI and CC were randomly resampled with replacement to simulate 50 random samples possessing a close to even [f:m = 1:1.6 for CC similar to GI (Sosa-Nishizaki et al., 2012) or biased f:m = 1:3.8 for GI similar to CC (Dewar et al., 2013)] sex-ratio. I computed pairwise F_{st} between samples of equivalent sex ratios (simulated biased GI or even CC with observed biased CC or even GI) as implemented in Arlequin v3.5.1.2.

In order to assess the parental origin of immature shite sharks, their haplotype frequencies were used to calculate the most probable geographic origin of matrilineal haplotypes. This was defined as the probability of randomly sampling a non-private (i.e., shared) mtDNA haplotype from an adult aggregation site (GI or CC) times the probability of sampling a shared haplotype with the adult aggregation area from the immature coastal sample (SCB, BCPC, BV or GC). Given that haplotypes may also be shared between adult aggregation areas, I computed and added the probabilities independently for non-shared and shared haplotypes between adult aggregation areas (Equation 1).

$$P_O = (I_U * O_{unshared}) + (I_S * O_{shared}) \qquad \text{(Eq 1)}$$

where: P_o is defined as the probability of matrilineal origin to adult aggregation area O (GI or CC), I_u is the frequency among the immature white sharks sample of haplotypes shared with area O but unshared between adult aggregation areas, and $O_{unshared}$ is the frequency of haplotypes in area O unshared with the other aggregation area. I_s and O_{shared} refer to equivalent frequencies but of shared haplotypes between aggregation areas.

3.2.4. Amplification and data analyses of nuclear DNA

The nuclear DNA was amplified using five microsatellite loci: Ccar1, Ccar3.1, Ccar9, Ccar13 and Ccar19 that were previously used to estimate white shark genetic structure (Pardini et al., 2000). Multiplex amplifications were performed in two ways: one consisted in a total volume of 10µl PCR reaction of 0.3µM fluorescent FAM-labeled M13 primer, according to (Schuelke, 2000), 0.3µM reverse primer (for each locus – Ccar3.1 and Ccar13), 0.075µM forward primer (with M13 extension, for each loci – Ccar3.1 and Ccar13), 1X PCR buffer (10mM Tris HCl, 50mM KCl and 1.5mM $MgCl^2$), 0.2mM dNTPs, 5X BSA, 0.5 U Kapa *Taq* DNA polymerase and 15ng of genomic DNA. The second consisted in a total volume of 10µl PCR reaction of 0.3µM fluorescently-labeled forward primers (for each locus: Ccar1-VIC-, Car9-PET- and Ccar19-NEB-), 0.3µM reverse primer, 1X PCR buffer (10mM Tris HCl, 50mM KCl and 1.5mM $MgCl^2$), 0.2mM dNTPs, 0.5 U Kapa *Taq* DNA polymerase and 15ng of genomic DNA. Touchdown PCR profile consisted of 94°C for 5min, followed by 28 cycles of 94°C for 20s, 65°C down until 55°C (-1°C each cycle) for 20s, and 72°C for 30s; finally 8 cycles of 94°C for 30s, 53°C for 45s and 72°C for 45s, with an extended at 72°C for 10min.

For each individual, loci were amplified in two multiplex reactions and products were subsequently pooled for electrophoretic separation and detection in an automated genetic analyzer 3130xl (Applied Biosystems). The presence and size of amplicons were scored from electropherograms using GeneMarker ver1.7 (Softgenetics ®). Null alleles and large allele dropout were assessed in MICRO-CHECKER (Van Oosterhout et al., 2004).

In order to assess departures from Hardy-Weinberg expectations (HWE) and linkage disequilibrium among loci, GENEPOP v 4.0 (Rousset, 2008) was used. To evaluate the genetic diversity, I estimated the expected (*He*) and observed (*Ho*) heterozygosities, allelic richness (*AR*) and F_{IS} using FSTAT 2.9.3 (Goudet, 2001). The degree of genetic differentiation was estimated at a global scale and between pairs of samples using Wright's F_{ST} using Arlequin v3.5.1.2 (Excoffier et al., 2005). When needed, significance was adjusted for multiple testing with sequential Bonferroni correction (Rice, 1989).

The population subdivision was tested using a Bayesian model-based clustering analysis in STRUCTURE 2.3.4 (Pritchard et al., 2000) using the admixture model, no prior information about population of origin, 10 000 iterations of burn-in, and 1 000 000 samples from the posterior distribution to estimate the likelihood of *K*-clusters given the data. It was assessed a $K = 1–5$ and averaged the log-likelihood based on four iterations of the MCMC chain. The most likely value for *K* based on STRUCTURE was determined with *ΔK (Evanno et al., 2005)* as implemented in STRUCTURE HARVESTER (Earl and vonHoldt, 2012). CLUMPP 1.1.2 (Jakobsson and Rosenberg, 2007) was used to minimize the variance across all the iterations of the selected *K* value and DISTRUCT (Rosenberg, 2004) to plot the graph of individual membership coefficients to inferred clusters. The statistical power of microsatellites was analyzed with POWSIM (Ryman and Palm, 2006).

3.3. Results

Tissue samples from 127 white sharks were collected from 2005 to 2012. Those from SCB, BCPC, and BV were from YOY and juvenile specimens (22 females, 12 males and 39 unknown); those from the GC were for juvenile to adult life-stages (2 females, 1 male and 4 unknown), whereas those from GI were mostly from adults (13 females, 21 males and 11 unknown) and both tissue samples from CC were from adults (2 males). In total, we analyze 186 mtDNA sequences (1099 pb) of white shark from NEP, included the 59 sequences from the Jorgensen et al. (2010) study.

3.3.1. Genetic diversity

Combining our results with those of Jorgensen, I identified 32 mtDNA haplotypes (see Supplementary Material online). BV and CC presented the highest number of different haplotypes, and the latter the highest number of private haplotypes (Table 1). In general, all localities had high values of haplotype diversity, BCPC and SCB showed the highest values (*h* = 0.83 and 0.80 respectively).

Table 1. Genetic diversity of mtDNA sequences (1099 bp) of white sharks in North Eastern Pacific. Sample size (*n*), number of haplotypes (*A*), private haplotypes (*pA*), haplotype diversity (*h* ± SD), and nucleotide diversity (*π* (%) ± SD).

Region	*N*	*A*	Ontogenetic stage	*pA*	*h*	*π* (%)
Central California *	61	18	Adult	16	0.77 +/- 0.04	0.13 +/- 0.09
Southern California Bight	25	7	Immature	3	0.80 +/- 0.05	0.36 +/- 0.21
BC Pacific Coast	9	5	Immature	0	0.83 +/- 0.10	0.11 +/- 0.08
Guadalupe Island	45	7	Both	1	0.73 +/- 0.04	0.16 +/- 0.11
Bahia Sebastian Vizcaino	39	11	Immature	5	0.78 +/- 0.05	0.11 +/- 0.08
Gulf of California	7	4	Both	1	0.71 +/- 0.18	0.10 +/- 0.08
TOTAL and Average	186	36			0.77	0.0018

* Data from Genbank (59): accession numbers GU002302–GU002321 (Jorgensen et al., 2010), and 2 from tissue samples.

3.3.2. Phylogeography and genetic structure

The neighbor joining tree using all available mitochondrial haplotypes shows that the NEP forms a monophyletic group separate from all other regions (Figure 5). There was a significant mtDNA genetic structure among all NEP samples (Φ_{st} = 0.351; $p < 0.001$). This differentiation was driven mainly by the CC samples, which were significantly different from all other samples (Table 2).

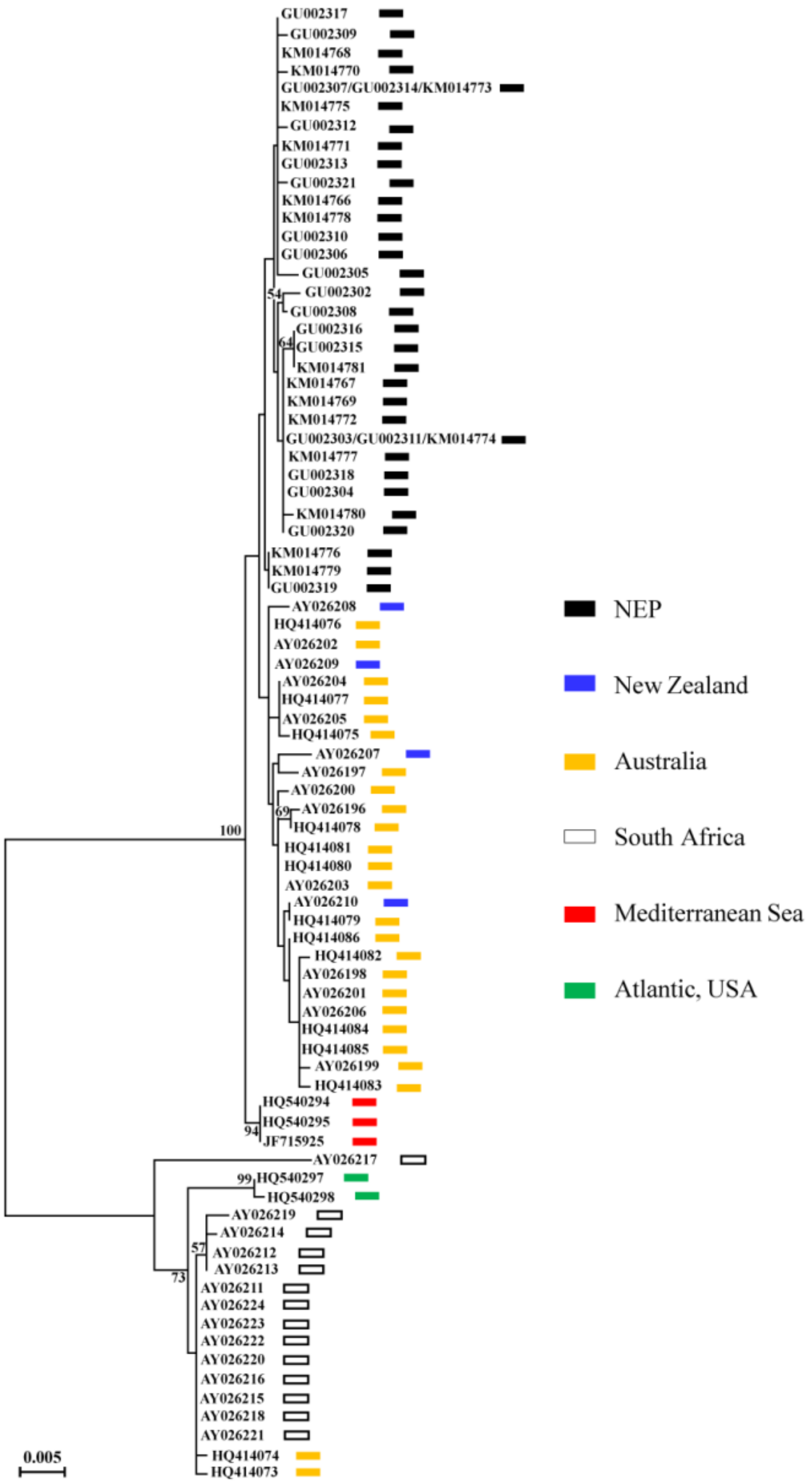

Figure 5. Neighbor-joining tree of available mitochondrial control region sequences from white sharks from North Eastern Pacific (NEP) (present study and Jorgensen et al. (2010)-black squares), New-Zealand [(Pardini et al., 2001)-blue squares], Australia [(Blower et al., 2012; Pardini et al., 2001)-orange squares], Mediterranean Sea [(Gubili et al., 2011)-red squares], and Atlantic, USA [(Gubili et al., 2011)-green squares] and South Africa [(Pardini et al., 2001)-white squares]. Numbers represent non-parametric bootstrap values.

Table 2. White shark´s Φ_{st} pairwise comparisons between sampled regions. Pairwise Φ_{st} below diagonal; significance above diagonal.

	CC	SCB	BCPC	GI	BV	GC
CC (n=61)	---	***	***	***	***	***
SCB (n=25)	0.39	---	*	ns	***	ns
BCPC (n=9)	0.19	0.11	---	ns	ns	ns
GI (n=45)	0.38	0.04	0.11	---	ns	ns
BV (n=39)	0.40	0.10	0.10	0.01	---	ns
GC (n=7)	0.45	0.04	0.09	0.07	0.07	---

ns: non significant; *: $p < 0.05$, ***: $p < 0.001$. Localities: Central California (CC), Southern California Bight (SCB), Baja California Pacific coast (BCPC), Guadalupe Island (GI), Bahia Sebastian Vizcaino (BV) and Gulf of California (GC).

In a comparison of the males and female AWS from GI and CC, 50% of the haplotypes were shared between males and females in GI, but in CC only 13% were shared and most of unshared haplotypes were present in males. There were no significant genetic differences between sexes at GI or CC; however, the F_{ST} and *p*-values were different in each location (Table 3). At CC the F_{ST} was essentially zero with a high p value (F_{ST} = -0.012, $p = 0.51$) whereas at GI it was larger and closer to being significant ($F_{ST} = 0.044$, $p = 0.08$). On the other hand, comparisons between sites of males and females were different and highly significant (Table 3). The same was true for both simulated and observed data sets with both equivalent and biased sex ratios producing highly significant F_{ST} values between CC and GI (biased sex ratio $0.35 < F_{ST} < 0.46$; unbiased sex ratio $0.34 < F_{ST} < 0.39$).

Table 3. Pairwise comparison between male and female white sharks from Guadalupe Island (GI) and Central California (CC). Pairwise F_{st} below diagonal; significance above diagonal.

	GI-Females	GI-Males	CC-Females	CC-Males
GI-Females (n=14)	---	ns	***	***
GI-Males (n=19)	0.04	---	***	***
CC-Females (n=9)	0.42	0.32	---	ns
CC-Males (n=34)	0.41	0.39	-0.01	---

ns: non significant; ***: $p < 0.001$

Immature white sharks from some of the nearshore areas were significantly different. SCB was significantly different from both BCPC and BV (Φ_{st} = 0.10 and 0.11, respectively; both $p < 0.05$; Table 2). The most frequent SCB haplotype was rare in BV and absent in BCPC (Figure 6).

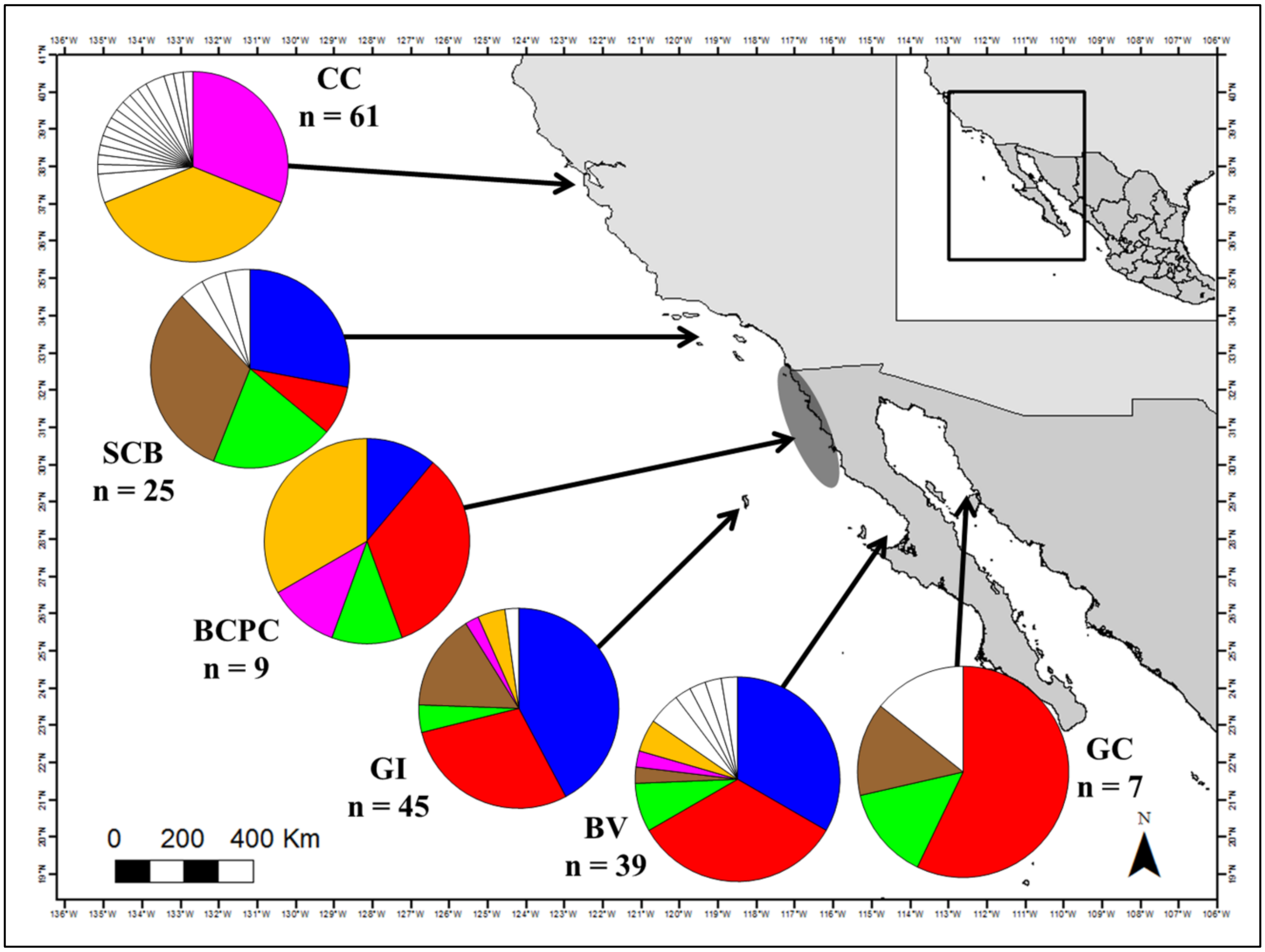

Figure 6. Mitochondrial variation in haplotype frequencies from white shark samples from the North Eastern Pacific. Each filled slice represents a shared haplotype whereas white haplotypes are private. Studied areas are: central California (CC), Southern California Bight (SCB), Baja California Pacific coast (BCPC), Guadalupe Island (GI), Bahia Sebastian Vizcaino (BV) and the Gulf of California (GC).

3.3.3. Matrilineal origin of immature sharks

The matrilineal origin analysis (Table 4) showed that immature white sharks from all regions were more likely to be related to females from GI than from CC (Table 4) with some variation in the probabilities of relatedness among sites.

Table 4. Matrilineal origin probabilities (P_O) of immature white sharks based on mtDNA haplotype frequencies from adult aggregation areas (CC and GI).

Immatures	CC	GI
SCB	0.00	0.80
BCPC	0.31	0.54
BV	0.05	0.71
GC	0.00	0.78

Central California (CC), Southern California Bight (SCB), Baja California Pacific coast (BCPC), Bahia Sebastian Vizcaino (BV), Guadalupe Island (GI), Gulf of California (GC).

3.3.4. Nuclear genetic diversity

The level of polymorphism of microsatellite loci was low for the 91 multilocus genotypes obtained, with an average of 5.6 alleles per locus. All localities had low observed heterozygosis with GC presenting the highest (*Ho*: 0.633; Table 5). Deviations from HWE were detected in all loci except in Ccar 19 (Table 5), and we found linkage disequilibrium only between Ccar 1 and Ccar 3.1 across all samples.

Table 5. Genetic diversity of microsatellite loci. Number of alleles (*A*), expected heterozygosity (*He*), observed heterozygosity (*Ho*), and significance of Hardy-Weinberg equilibrium test (*p H-W*): in bold those in disequilibrium after Bonferroni correction.

		Microsatellite loci					
Area	**Parameter**	**Ccar 1**	**Ccar 3.1**	**Ccar 9**	**Ccar 13**	**Ccar 19**	**All**
SCB (n=21)	*A*	4	4	6	4	3	4.2
	He	0.541	0.617	0.810	0.742	0.411	0.624
	Ho	0.400	0.278	0.556	0.688	0.421	0.468
	H-W	0.017	**0.002**	**0.000**	0.303	1.000	**0.000**
BCPC (n=8)	*A*	3	2	2	4	3	2.8
	He	0.633	0.600	0.667	0.643	0.433	0.595
	Ho	0.875	0.333	0.000	0.500	0.500	0.442
	H-W	0.754	1.000	0.200	0.052	0.421	0.324
GI (n=30)	*A*	5	3	2	5	3	3.6
	He	0.630	0.660	0.429	0.772	0.541	0.606
	Ho	0.407	0.333	0.000	0.583	0.536	0.372
	H-W	**0.000**	**0.000**	**0.000**	0.018	0.912	**0.000**
BV (n=26)	*A*	4	4	3	5	3	3.8
	He	0.649	0.634	0.800	0.574	0.358	0.603
	Ho	0.385	0.133	0.000	0.286	0.280	0.217
	H-W	**0.002**	**0.000**	**0.000**	**0.000**	0.335	**0.000**
GC (n=6)	*A*	3	2	4	2	3	2.8
	He	0.621	0.600	0.800	1.000	0.682	0.741
	Ho	0.500	0.333	0.667	1.000	0.667	0.633
	H-W	1.000	0.143	0.600	1.000	0.636	0.830
Overall	*A*	5	5	9	6	3	
	He	0.620	0.661	0.803	0.743	0.483	
	Ho	0.513	0.282	0.244	0.611	0.481	
	H-W	**0.000**	**0.000**	**0.000**	**0.0004**	0.891	

3.3.5. Nuclear DNA genetic structure

Microsatellite analyses revealed no significant genetic differences among sampled localities (F_{ST} = 0.018; p<0.16 – Figure 7). POWSIM simulations indicated a low statistical power of the microsatellite data. A much larger sample size (n > 500) is needed to detect a significant differentiation of an expected F_{ST} 250 between 0.001 and 0.01 with the current levels of variation in these five nuclear loci. On the other hand, plots of Evanno ΔK from STRUCTURE HARVESTER did indicate the existence of two clusters (Figure 8a). The average probability of membership of individual sharks to each genetic cluster (Figure 8b) reveals that all localities comprise a mixture of organisms from both clusters and of mixed origin. These results corroborate the lack of genetic structure in the sampled area.

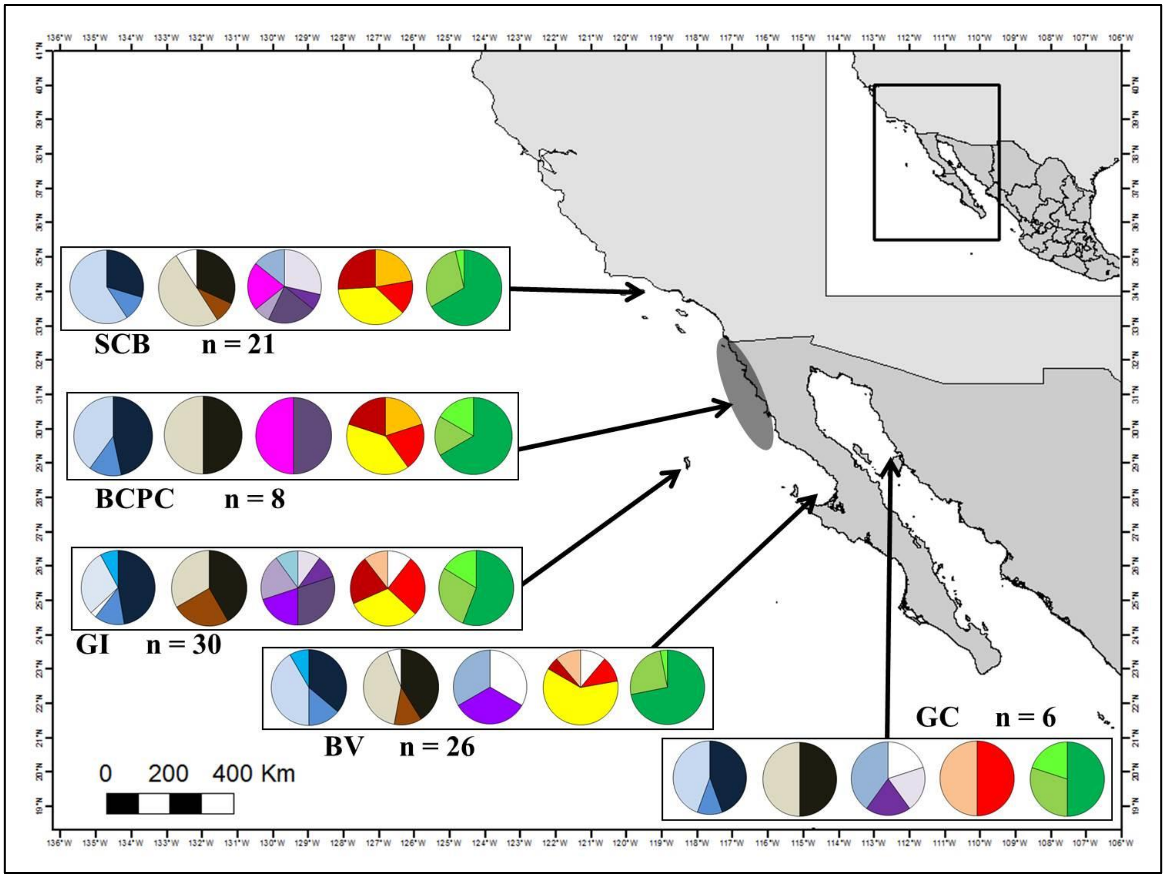

Figure 7. Gene variation in white shark samples from the North Eastern Pacific. nDNA allele frequencies; each circle represent a color-coded microsatellite locus, colored slices represent shared alleles and white slices private alleles. Studied areas are: Southern California Bight (SCB), Baja California Pacific coast (BCPC), Guadalupe Island (GI), Bahía Sebastian Vizcaino (BV) and the Gulf of California (GC).

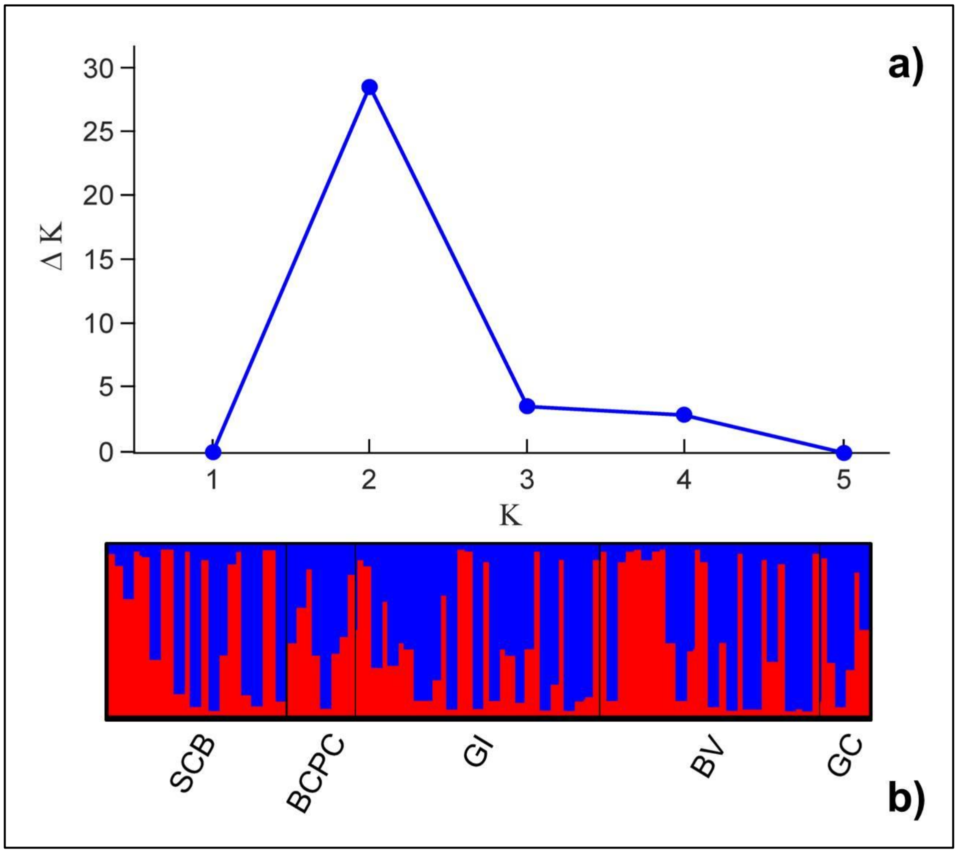

Figure 8. Genetic structure of white shark obtained with STRUCTURE using allele frequencies from microsatellite DNA. a) Plot of Evanno *ΔK* analyzing up to 5 clusters (*K*); b) Bar plot of estimated probability of membership of individual white sharks to two clusters (blue and red) ordered by location: BCPC-Baja California Pacific coast, SCB-Southern California Bight, GC-Gulf of California, GI-Guadalupe Island and BV-Bahia Sebastian Vizcaino.

3.4. Discussion

This represents the most comprehensive study of white shark genetics in the NEP. The previous study examined only the basin-scale relationship among sharks at CC and other locations around the Pacific and Indian Ocean. In addition to expanding this work to include GI, I used matrilineally inherited molecular markers (mtDNA) to address connectivity among aggregations site and nursery areas. This is also the first study in the NEP using nuclear DNA. For the nuclear DNA, results should be interpreted with caution given the small sample size and number of microsatellites, and the lack of samples from CC.

MtDNA allows for examination of maternally inherited patterns. Results of this research show significant differences between the aggregation sites suggesting female philopatry to two different breeding areas. In addition, efforts to link these females to nursery areas suggest that the majority of immature sharks sampled in this study had mothers originating at GI. My results highlight the complexity of the genetic patterns of white sharks in the NEP. Additional studies are needed to fully resolve these patterns.

3.4.1. NEP white sharks represent an independent population

The phylogenetic results, which expand the scope of previous studies in the NEP, confirm that white sharks from this region form a monophyletic mtDNA clade distinct from others in major distribution areas in the Pacific and Indian Oceans. Jorgensen et al. (2010) first established that white sharks from CC share an independent mtDNA lineage more closely related to those in Australia/New Zealand. White sharks from Japan represent an additional monophyletic sister to clade to sharks from the NEP and New Zealand/Australia (Tanaka et al., 2011). Our extended results support that NEP white sharks represent a separate distinct population from other populations in the world. These findings are important regarding the evaluation of the stability and persistence of population, as they suggested there is no recruitment of white sharks from other regions that would add to local populations. Thus, management and conservation efforts should be made at the scale of the NEP.

3.4.2. Patterns of genetic variation in mitochondrial DNA suggest female philopatry to nursery areas

There were significant differences in mtDNA among sampled localities in the NEP. The mtDNA sequences revealed matrilineal genetic differentiation between white sharks from CC and those from SCB and Mexican waters, and among immature sharks from some of the coastal localities. Given that mtDNA is maternally inherited, this differentiation could be affected by the different sex-ratios observed in samples from the adult aggregation areas, where GI has a female:male ratio of 1.6 (Sosa-Nishizaki et al., 2012) and CC of 3.6 (Jorgensen et al., 2010; Dewar et al., 2013). Even though there was no statistically significant differentiation between sexes in both adult aggregation sites, as estimated by F_{ST}, the degree to which sexes were genetically undistinguishable and the distribution patterns of shared and unshared haplotypes between sexes differed between CC and GI. This could have affected genetic structure in the face of significant sex-ratio bias in one of the localities. However, our simulation results equating sex-ratios between these samples (either as biased or unbiased) show that the significant differentiation between CC and GI is unaffected by the presence or absence of sex ratio bias. Differentiation at local scales was also found in Australia, where genetic differentiation of immature white sharks between eastern and western coasts agrees with a lack of movements between these areas (Blower et al., 2012) and a level of philopatry to the different nursery areas.

Overall, the significant differences in mtDNA between immature white sharks from SCB and BV, as well as the lack of mtDNA genetic differences between these areas with GI, suggest that adult female white sharks from GI may display philopatric behavior to distinct coastal parturition areas (SCB and BV). In a study comparing Australia/New Zealand with South Africa, Pardini et al. (2001) found mitochondrial genetic differentiation between both populations, but nuclear DNA revealed no significant differentiation. The difference between maternal and paternal markers suggests male-mediated gene flow in white sharks from Australia/New Zealand and South Africa. While data from CC are missing the results collected to date suggest a similar pattern. However, more long-term tracks of females from both CC and GI, larger sampling efforts looking at temporal patterns in mtDNA over time, as well as expanded analyses of nuclear DNA are needed to understand the reproductive genetic patterns between sexes. Efforts are currently being directed toward that goal.

3.4.3. Patterns of genetic variation in nuclear loci suggest a male-mediated gene flow

The lack of genetic differentiation observed at microsatellite loci showed high levels of connectivity among sampled localities. Unlike the matrilineal mtDNA, homogeneity at nuclear loci among sampled locations suggests a male mediated gene flow between GI and coastal areas. While females may be philopatric to nursery areas, the results of nuclear DNA suggest that males from GI mate with females from GI, regardless of their later preference for parturition areas. High levels of male mediated gene flow have been found by Pardini et al. (2001) using these same genetic markers among white sharks from South Africa and Australia/New Zealand. The patterns and levels of variation reported by Pardini et al. (2001) are comparable to those found in this study. Nevertheless, the statistical power analysis revealed a low power afforded by the low variability of these microsatellite loci, which suggests that they could be overestimating the degree of genetic connectivity by an inflated Type II error. On the other hand, an independent model-based Bayesian clustering analysis (STRUCTURE) does support the lack of genetic differentiation among sampled localities, given the very similar contribution of the two inferred genetic clusters to each of the sampled locations. However, addition samples throughout the NEP, including CC, and an increase the number and quality of nuclear loci are needed.

3.4.4. Congruence between movements and genetic heterogeneity

Mitochondrial sequences revealed significant differences in MtDNA between white sharks from both adult aggregation areas (GI and CC). This is consistent with the vast majority of the tracking data showing that sharks from both regions display philopatric behavior, returning to their respective aggregation sites after migrating to oceanic areas (Weng et al., 2007b; Domeier and Nasby-Lucas, 2008). While there is some limited movement between aggregation sites, it may be that these sharks are not breeding when they are away from their primary aggregation site. One limitation of these analyses is the very small number of females sampled at CC and the lack of long-term tracks.

Tagging studies have been conducted on both adults at aggregation sites and immature sharks in coastal areas. Electronic tags demonstrate the links between females at GI and nursery areas (Jorgensen et al., 2012; Domeier and Nasby-Lucas, 2013). Adult females from GI move to BV, GC and back to GI (Domeier and Nasby-Lucas, 2013). This is consistent with the lack of genetic differentiation between GI and any of the sampling sites. The lack of long-term tracks for CC females makes inferences about the match between movements and genetic patterns impossible.

Tagging studies can also provide insight into the genetic patterns seen in coastal areas. Some sampled immature white sharks show matrilineal (mtDNA) genetic differentiation between areas; SCB was different from BV. This pattern is consistent with female philopatry to specific areas with females returning to the same location to pup. This is suggested in the few long-term tracks that capture more than one reproductive cycle. Across most coastal regions, there are no significant genetic differences. This is consistent with the electronic tags showing movements of immature white sharks from SCB to BV and into GC suggesting mixing across the nursery area (Weng et al., 2007b; Weng et al., 2012). The fact that some regions are different and others are not may be linked to ontogenetic differences in movement patterns and the lack of an even distribution of genetic samples across immature age classes. Most YOY from SCB remain in that nursery during early growth and start increasing their range of movements (mostly southward) after close to one year of life (Weng et al., 2007b; Weng et al., 2012). To better understand the dynamics of pupping and movements within the larger nursery area, extending from Point Conception to GC, additional genetic samples are needed at each study area and electronic tagging studies should be expanded across age classes. Also, based on genetic differences between historical and contemporary samples (Gubili et al., 2015), it will also be important to examine patterns over time.

3.4.5. Matrilineal origin of immature sharks

The majority of immature white sharks sampled in coastal localities possessed a higher probability of having a mitochondrial lineage to females from GI. Although SCB is geographically closer to CC, sharks from SCB are more likely born from GI mothers as are white sharks from BV. This is consistent with tagging data showing females from GI visiting both the SCB and BV in the spring when pupping occur. Unfortunately there is limited genetic information on females from CC and no tracks long enough to capture visits to nursery areas when they would be expected to be pupping. Consequently the potential links to CC and any nursery area are not known.

3.4.6. Conservation implications

Genetic differences in mtDNA between SCB and BV in consistent with females showing philopatry to a specific area for pupping. Given these differences, management efforts aimed at protecting sharks in both BV and SCB will be needed to conserve genetic diversity. Conservation in both locations would benefit from more information on the overlap between habitat use and fisheries activities. Options for management include no-take zone or seasons. Additional information that will be important to any management plan includes a better understanding on the overall use of the juvenile habitat that extends from Point Conception into GC, and how this varies across age classes. Finally, a better understanding of the recruitment of juveniles to the adult and sub-adult aggregation sites is needed.

Another conservation measure that would reduce fisheries mortality is to require the release of immature white sharks that are still alive during artisanal fishing operations. As reported by (Santana-Morales et al., 2012), incidental catch of white sharks occurs along the west coast of Baja California. The Mexican government established a threatened status for the species (DOF, 2002), and more recently has established a total fishing ban for white sharks in Mexican waters (DOF, 2014). The new requlations promote the live release of any incidentally caught white sharks. The reduced fishing mortality should increase recruitment into the adult population especially if set durations are shorter than 24 h.

Finally, future genetic studies are needed to fill a number of data gaps. The sample sizes from all locations should in increased as well as the number of loci to make results more robust. A very large data gap exists due to the lack of nuclear DNA analyses from CC. Without this, the degree of reproductive isolation between the aggregation sites cannot be determined. At this point only half of the picture has been examined, what the females are doing. A relatively new technique that has great promise, especially for small populations, is parentage analysis that would allow young to be assigned to specific parent individuals. Over time this could provide incredible insight into philopatry to pupping and aggregation sites, reproductive behaviors and recruitment to aggregation sites from coastal nursery areas Genetic analyses should be a part of any long-term monitoring and conservation plan.

Chapter 4. Bahia Sebastian Vizcaino as a Shark Nursery Area

4.1. Introduction

Near-shore habitats are highly productive and have a relatively high abundance and diversity of fish and invertebrates (Knip et al., 2010). Many of these systems have been recognized to support the production of large abundances of juvenile fishes, many of which utilize different habitats as adults (Dahlgren et al., 2006). Springer (1967) suggested that in several pelagic shark species the young are born in nearshore nursery areas during the spring/summer, where they remain until reaching the size of sexual maturity. Upon maturation it is proposed that the sharks before migrate offshore, join adult populations and remain segregated from the young except when they move inshore to give birth and possibly mate in spring/summer (Knip et al., 2010).

In order to be successful, the management and conservation of shark populations is dependent upon successful juvenile recruitment. For several species, juvenile survivorship is dependent upon the use of a suitable nursery area (Yates et al., 2012; Ward-Paige et al., 2015). Such suitable habitat is likely dependent on several characteristics including temperature, salinity and depth as well as bottom type and anthropogenic activity (Morrissey and Gruber, 1993; Heupel et al., 2006; Heithaus et al., 2007; Heupel and Simpfendorfer, 2008; Knip et al., 2010; Ward-Paige et al., 2015). Identifying these nursery areas and documenting this critical habitat is an essential step for conservation and sustainable long term management (Heithaus, 2007).

In the past, potential nursery areas were identified simply on the basis of the presence or absence of specific life stages. Castro (1993) proposed that, for viviparous sharks, nursery areas could be inferred based on the presence of gravid females, neonates and small juveniles. However, not all species have defined nursery areas, as some species have been shown to spend all life stages in the same area (Knip et al., 2010) while others are much more transient. Hence the mere presence of gravid females or immature sharks in an area does not always indicate its function as a nursery area (Castro, 1993; Heupel et al., 2007). Bass (1978) suggested that immature sharks might require two distinct types of nursery areas depending on their size and life stage: A primary nursery area, which is an area where young sharks are born and spend the first part of their lives, and a secondary nursery area that is inhabited by the slightly older but not yet mature individuals. Recently, Heupel et al. (2007) argued that the definition of nursery types proposed by Bass (1978) was ambiguous and the areas were difficult to define. Further, given the distribution and movements patterns of some sharks, primary and secondary nurseries can overlap, as newborn individuals that are born in a given area (primary) can move to another region and then subsequently return (secondary nursery). For this reason, Heupel et al. (2007) proposed the elimination of the terms "primary” and “secondary" and the use of the term "nursery area" to collectively represent these critical habitats. Heupel et al. (2007) also proposed the following three criteria for identifying a shark nursery area for newborns and young-of-the-year sharks: 1) The area must have a higher relative abundance of neonates and young juveniles compared to other areas, 2) young sharks must have a tendency to remain or return to the area for extended periods, and 3) the area is used by young sharks across years. Based on the Heupel et al. (2007) hypothesis, all three criteria must be met for a particular area to be considered a nursery habitat.

The white shark is an apex predator which size at birth is between 120 to 150 cm total length (TL) (Francis, 1996), and which grows to a maximum length of 610 cm TL (Castro, 2012). Four different life stages have been proposed based on size: a) young-of-the-year (YOY) sharks that are less than ≤ 1.75 m TL; b) juvenile (JWS) sharks (> 1.75 m – 3.0 m TL), which are larger than YOY sharks but smaller than the sizes commonly observed visiting and feeding on pinniped colonies; c) sub-adult sharks (SAS) sharks (>3.0 to mature size), those between the size first visiting pinniped colonies and the size of maturity; and d) adult (AWS) sharks (> 3.6 m TL [male]; > 4.8 m TL [female]), which includes sharks that have reached sexual maturity (Cailliet et al., 1985; Francis, 1996; Pratt, 1996; Wintner and Cliff, 1999; Malcolm et al., 2001; Martin et al., 2005). White sharks are mainly found in tropical and temperate oceans with relatively low population densities (Compagno et al., 2005) and their distribution varies based on their size. While AWS aggregate around islands that typically harbor pinniped colonies and oceanic waters, newborn and juvenile white sharks are primarily distributed close to shore (Weng et al., 2007b; Domeier, 2012; Ebert et al., 2013).

In the NEP, juvenile age-classes primarily inhabit nearshore waters off California and Baja California peninsula (Cailliet et al., 1985; Klimley, 1985; Malcolm et al., 2001; Weng et al., 2007b; Santana-Morales et al., 2012). Based on electronic tagging studies, it has been shown that some immature white sharks move along the coastal areas from SCB to Mexican waters off Baja California and sometimes into the GC (Weng et al., 2007b; Galván-Magaña et al., 2010; Weng et al., 2012). Based on mitochondrial DNA analyses, it has been suggested that there are differences between the SCB and BV white sharks, however, no differences were found between the SCB and GC (Oñate-González et al., 2015). However, given the short duration of the tagging studies to date, we do not fully understand if sharks return to SCB after their southern migration. Further, given the low number of samples in the Oñate-González et al. (2015) study and the lack of nuclear DNA data, connectivity between SCB and adjacent areas is not well understood.

Based on size distribution and seasonality from catch records and reports, Klimley (1985) proposed that the SCB was a parturition and nursery area for white sharks in the NEP. He also report that AWS were most frequently seen and caught in central and northern California during the fall and winter months, and YOY were only caught south of Point Conception during summer months. Recently, the NEP white shark nursery area was expanded based on the presence of immature white sharks in nearshore waters between Point Conception, California, and BV in Baja California (Weng et al., 2007b; Domeier, 2012). However, this proposed extension of the white shark nursery grounds, and whether or not the nursery habitat is indeed continuous, has not been tested against the three criteria proposed by Heupel et al. (2007).

Internationally the white shark is recognized as a species vulnerable to overexploitation [IUCN Red list (Hilton-Taylor, 2000)], and has been included in Appendix II of the CITES since 2004. This inclusion was intended to regulate the trade of products derived from its body parts, including fins, jaws and teeth, and to ensure that such trade does not contribute further to its population decline (García-Nuñez, 2008). In Mexico, the white shark is rated as a “threatened species” by the Mexican official regulations “NOM-059-SEMARNAT-2001” (DOF, 2002; 2010), and “NOM-029-PESC-2006”. The later establishes the prohibition of intentional catch, retention and commercialization of any body part of this species and includes protection for other vulnerable species like the whale shark (*Rhincodon typus*) and basking shark (*Cethorhinus maximus*) (DOF, 2007). Since 2012, in Mexico, a shark and ray seasonal closure was established during May 1st through July 31st to protect a fraction of the reproductive stock of commercially important elasmobranch species (DOF, 2012). Although the protection of the white sharks is not the purpose of this regulation, the timing of this closure does help in the protection of this species since it coincides with time of year in which the young are found close to shore (Santana-Morales et al., 2012). Since February of 2014, a complete fishing ban for white sharks was established in Mexican waters (DOF, 2014), which emphasizes the release of incidentally caught white sharks.

Despite the protective measures that have been implemented worldwide, the incidental catch of this species still occurs in Mexico as well as other countries (Lowe et al., 2012; Santana-Morales et al., 2012). This continued pressure supports the need to assess population status, fishery interaction rates and identify critical habitats, such as nursery areas. Artisanal and industrial fisheries on the west coast of Baja California target coastal and pelagic elasmobranchs, bony fishes and invertebrates using a variety of fishing gears such as bottom-set gillnets, surface longlines, traps, pelagic nets, purse seines and hand lines (Sosa-Nishizaki et al., 2008; Cartamil et al., 2011). The artisanal operations are performed mainly along the inshore waters and on the continental shelf, while the industrial fisheries operate mainly offshore from 30 to 200 nm from the coast (Escobedo-Olvera, 2009; Cartamil et al., 2011; García-Rodríguez, 2012).

Santana-Morales et al. (2012) documented the incidental catch of 111 white sharks along the Pacific coast of Baja California between 1999 and 2010. Eighty-three of them (74.7% of the total) were caught by artisanal bottom-gillnets. The size of the sharks ranged from 123 to 274 cm TL, with most of the catch (79.8%) consisting of YOY (≤175 cm TL) and the remainder being juveniles. Analysis of the white shark catch data suggests that the continental shelf is an important habitat for YOY and JWS, and because 66 of their YOY were caught in BV, Santana-Morales et al. (2012) suggested that the bay could serve as an important nursery area. However, this has not been tested using a conceptual framework such as the one proposed by Heupel et al. (2007).

In this chapter, I analyzed the historical (1999-2010) data from Santana-Morales et al. (2012) and more recent (2011-2013) immature white shark data on incidental capture and sighting records from the western coast of northern Baja California peninsula to test if the area proposed by Santana-Morales et al. (2012) is a white shark nursery area. I gathered artisanal fishery-dependent catch data, which has resulted in the largest white shark data set compiled for the NEP. I primarily focused on the Bahia Sebastian Vizcaino region because of the Santana-Morales et al. (2012) work that reported a high incidence of white sharks occurrence in the fisheries within the bay and proposed this region to be an important nursery area for the white shark. I present an analysis of the size composition of incidentally caught white sharks which has allowed me to segregate catch by life history stages and describe seasonal catch trends. I also present data on incidental white shark catch rates compared to total catch per month of different fish species caught in the bottom gillnet fishery to understand the seasonal use trends of BV. The total monthly catch of fish species caught by bottom gillnets is also presented to evaluate whether there is a correlation with target type and to better understand white shark catch rates during fishing operations directed towards a specific species. I also compared the white shark incidental catch records with the nursery criteria proposed by Heupel et al. (2007). This study provides information that will lead to improved conservation and management of the white shark in Mexican waters and offers an improved baseline for future study on population dynamics within the region.

4.2. Methodology

4.2.1. Study Area

The Pacific waters off the Baja California peninsula are under the influence of the southern portion of the California Current System. At Punta Eugenia, the California Current meets a warmer current from the south, creating a complex region (Dawson et al., 2006). Durazo et al. (2010) described the oceanographic characteristics of the areas off Punta Eugenia, located close to the center of the peninsula. North of Punta Eugenia, they described an oceanographic province influenced by subarctic waters most of the year, while to the south, they described a province that is influenced by tropical and subtropical surface waters that are observed during summer and fall (Durazo et al., 2010). Punta Eugenia also represents the southern limit of the distribution of many fish taxa common to the San Diegan Biogeographical Province, and the northern limit of distribution of many fish taxa common to the tropical Panamic Province (Horn et al., 2006).

The Pacific coast of Baja California is characterized by long stretches of sandy coastline occasionally fragmented by rocky outcroppings (Dawson et al., 2006). The northern portion of the western coast of the Baja California peninsula (Tijuana to Punta Baja) is characterized by a narrow continental shelf, extending only five to twenty km offshore. The continental shelf widens toward the south, reaching its greatest width close to the central part of the peninsula within BV, spanning up to 140 km (Cartamil et al., 2011).

Bahia Sebastian Vizcaino is a large embayment (35,678 km^2) with Punta Eugenia making up its southernmost point (Cartamil et al., 2011). The bathymetry in the bay has an average depth of 75 m with a maximum up to 100 m in the central part and 200 m in the northeast outer part of the bay. The most prevalent sediment material in northeast region of BV consists of coarse grains, and abundant and very fine sand and mud in the central western portion of the bay (Amador-Buenrostro et al., 1995; Navarro-Palacios and Mancilla-Peraza, 2008). Off the bay, the predominant winds blow from the northwest generating a large region that is influenced by intense coastal upwelling (Hernández-Rivas et al., 2000). An anticyclonic gyre in the region makes the water flow into the bay (Álvarez-Borrego and Granados-Guzmán, 1992) generating a productive and enriched ecosystem. Like the Southern California Bight (Dailey et al., 1993; Allen et al., 2007), it is one of the most productive areas in the California Current System due the presence of anticyclonic gyres, mixing processes, the presence of islands, coastal topography, and the regional wind patterns (Mancilla-Peraza et al., 1993; Amador-Buenrostro et al., 1995). The bay is characterized by high primary productivity, which is concentrated and retained within the bay and supports higher relative abundances of consumers compared to the northern region of Baja California (Lluch-Belda, 2000).

Laguna Ojo de Liebre (LOL) is the main coastal lagoon located within BV (Figure 4). LOL has an area of 366 km^2 and it is located between 27°35’ and 27°55’N and 113°50’ and Il4°2O’W. Variations in temperature and salinity are present primarily attributed to the tidal movements as well as the evaporative process, with salinity reaching up to 47 in the internal parts of the lagoon (De la Cruz-Agüero et al., 1996). Predominant currents do not surpass 2.3 knots, but they can be very turbulent, with a tidal range between 1.20 and 2.7 m. LOL is isolated somewhat from the major oceanic processes of BV due to the limited connection with BV. However, the anticyclonic circulation within BV and large tidal exchange (up to 2.7m) within LOL helps the flow of nutrient rich water into the lagoon (Álvarez-Borrego and Granados-Guzmán, 1992). LOL has a length of ~40 km and a width of ~6 km with a maximum depth reaching 25-30 m (Gutiérrez-de Velazco, 2000).

4.2.2. Fisheries landings in the western coast of Baja California

In order to describe the importance of the fisheries off the western coast of Baja California, I analyzed the landings by species (in tons) reported by fishermen at local offices of the National Commission for Fisheries and Aquaculture (CONAPESCA, in Spanish). I used the records from the offices located in Ensenada (ENS), San Quintin (SQU), El Rosario (ERO), Isla de Cedros (ICD) and Jesus Maria (JM) in the state of Baja California and the office of Guerrero Negro (GN) in Baja California Sur (Fig. 9) (CONAPESCA, 2014). Cartamil et al. (2011) reported that of the 55% of the 44 artisanal fishing camps that they described along the Pacific coast of the Baja California peninsula, teleosts and/or elasmobranchs were the primary target of the fishing operations, but in 95% of the fishing camps one of these fisheries were the secondary target of their operations. In this study, I only report landings for some teleost species and excluded large and small pelagic teleost landings (e.g. swordfish, Pacific sardine, and mackerel) that are not caught by the artisanal bottom gillnet fishery (see below). Landings for elasmobranchs are also included. The official landing statistics only reports landings based on common or group names (species complex), and I used the same nomenclature in this thesis to avoid reclassifying taxa in the absence of a study directed toward identifying their species composition. In some cases, fishermen report their catch using different common names for the same species and the actual fishery registration form does not distinguish between different species clearly; landings were pooled for these instances. Also, in the case of the flounder group (lenguados), cazon (small sharks) and smooth-hounds (tripa), each should be considered as a species complex.

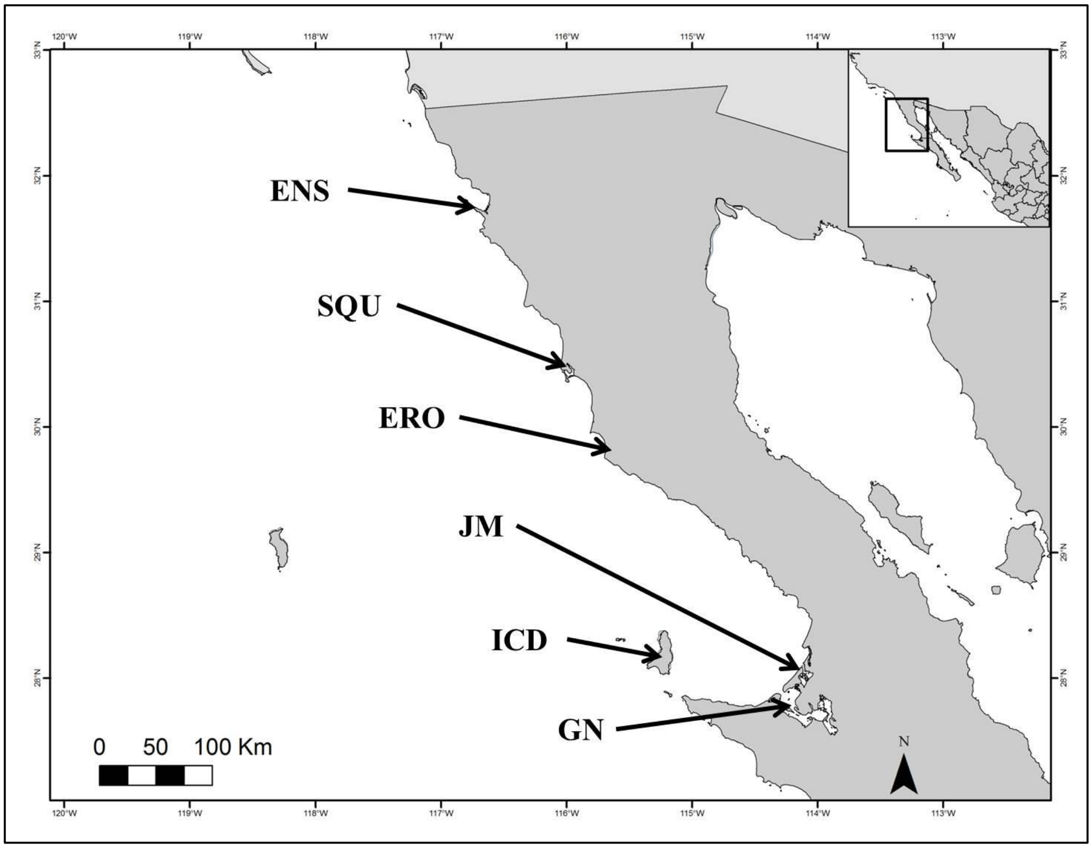

Figure 9. Fishing offices where landings records come from: ENS (Ensenada), SQU (San Quintin), ERO (El Rosario), ICD (Isla Cedros), JM (Jesus Maria) and GN (Guerrero Negro).

4.2.3. White shark incidental catch data sources

White shark catch records were obtained from two main sources. For the period from 1999 to 2010, I used the Santana-Morales et al. (2012) database, which included the incidental catch records of sharks landed along the different artisanal fishing camps found along the west coast of Baja California (Fig. 10) as well as the commercial drift-gillnet fishing vessels based out of Ensenada. For the period from May of 2011 to December of 2012, surveys of artisanal-fishing operations were conducted at specific camps (Ensenada, San Martin-San Quintin, Santa Rosaliita, Laguna Manuela and Las Casitas, Fig. 10) and logbook data from the same camps were analyzed. In 2013 effort diminished, because we did not have access to logbook data and the surveys were only performed in April, May, September and November. These camps were selected because they have been shown to conduct most of their fishing operations using bottom gillnets and the known susceptibility of white sharks to this gear type (Cartamil et al., 2011). However, sampling effort was concentrated mainly on the fishing camps located within BV (Santa Rosaiilita, Laguna Manuela and Las Casitas), to compare the white shark incidental catches with landings (see below). Monthly sampling visits lasting two to three days per camp were carried out. Each white shark was identified, and when a whole organism was available, total length was measured to the nearest cm, and individuals were sexed by trained field technicians. To maximize the number of sampled white sharks, the person in charge of landings was trained to identify and measure each individual; 50% of all white shark records were obtained using these sampling techniques.

4.2.4. Incidental catch analysis

In order to characterize temporal and size-based catch patterns, white sharks were divided into three categories: Newborns-NWS (<150 cm TL), YOY (150–175 cm TL) and JWS (175–300 cm TL). The study area was segregated based on whether the camps were located to the north of Bahia Sebastian Vizcaino (NBV; Popotla to Pta Canoas, Figure 10) or within BV, and the size frequency distribution of white sharks caught in those two regions was compared using a Kruskal-Wallis one-way analysis of variance test. The seasonality of the catch-records was qualitatively compared across years.

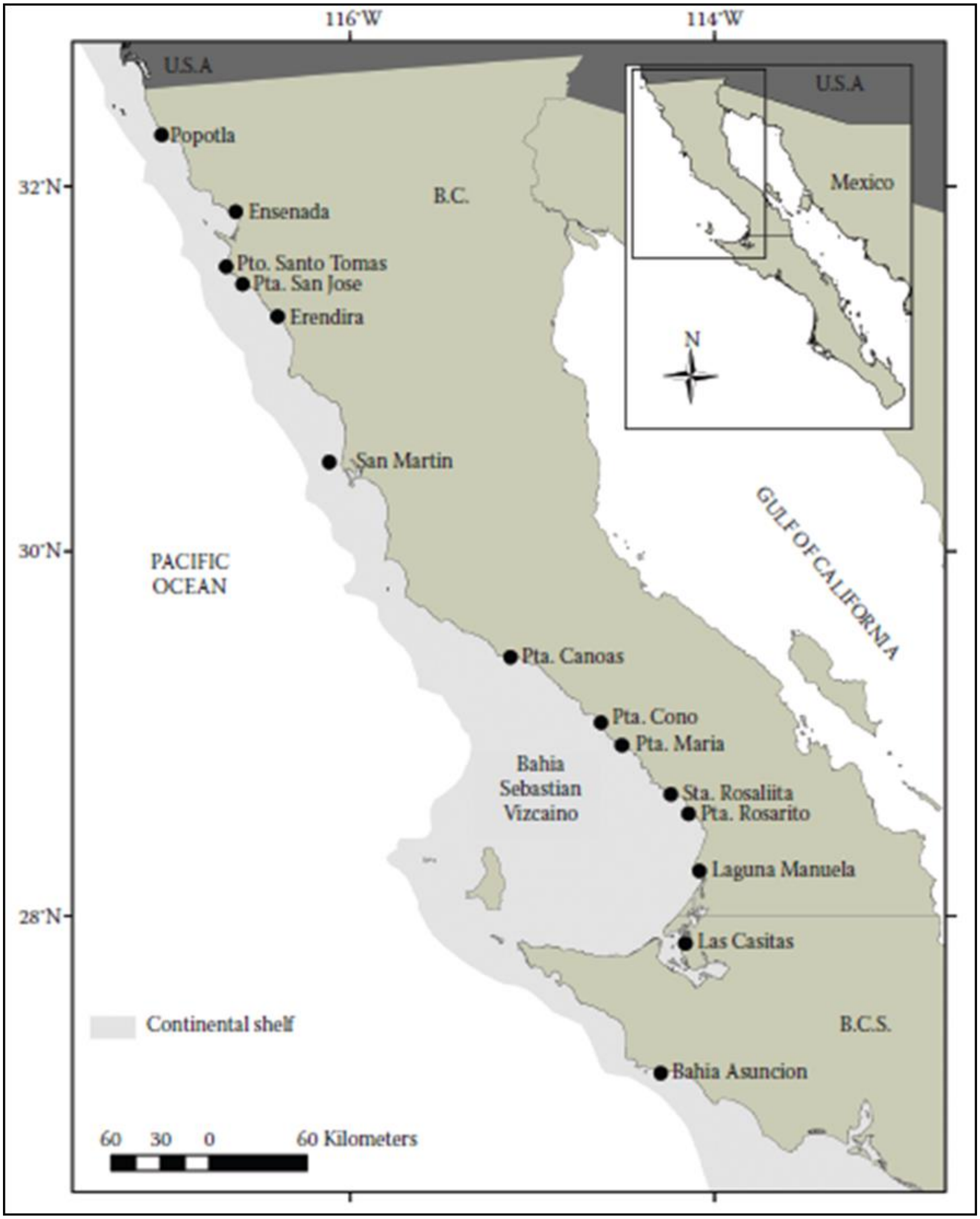

Figure 10. Location of the fishing camps with white shark records on the Pacific coast of Baja California, [taken from Santana-Morales et al. (2012)].

4.2.5. Relationship between white shark incidental catches and fishery landings of selected demersal species

Although incidental catch records suggest BV to be an important area for white sharks in NEP (Santana-Morales et al., 2012); an estimation of white shark relative abundance using a catch per unit effort (CPUE) index was not possible due to the lack of fishing effort data for the operations within BV. Instead, I analyzed the number of white sharks caught incidentally with respect to the tonnage of fish landed and reported to the CONAPESCA official offices based within BV (*i.e*. Jesus Maria and Guerrero Negro). Because Santana-Morales et al. (2012) reported that around 75% of the incidental catches analyzed were caught by bottom gillnets, I selected only landings of demersal species that were recorded and caught by this fishing gear type. The selected demersal species (SDS) were: Flounders, Bat rays, Diamond stingray, Shovelnose guitarfish, Angel shark, Cazon and Smooth-hounds.

4.2.6. Bahia Sebastian Vizcaino as nursery area

To evaluate whether there was evidence to support Heupel et al. (2007)´s three main criteria for considering BV a nursery area, I examined whether 1) YOY were present in higher density in BV compared to NBV, 2) if there was a monthly seasonality of incidental catches along the west coast of Baja California, and in particularly within BV, and 3) whether catch records across years could determine consistency between years.

4.3. Results

4.3.1. Fisheries landings along the western coast of Baja California

During the period of 2008 to 2013 a yearly mean of 2,077 tons of fish were landed and registered in the six official offices of CONAPESCA (Table 6). This weight only considers the 30 fish groups that are mainly caught in the artisanal fisheries of the region. Landings from Ensenada represent 70% of the total catch (Table 6), and sharks were the most important group of fish species recorded (78%, Fig. 11). For these records of the Ensenada office, I was not able to distinguish among the vessel size and type of fishery (i.e., artisanal vs industrial), so the 1,460 tons might largely be from the industrial fisheries (Sosa-Nishizaki et al., 2008). However, for the rest of the CONAPESCA offices, landings correspond to artisanal fisheries only. The office at Jesus Maria was the second in importance in terms of the total catch, with a yearly mean of 295 tons (14% of the total average annual catch). The Jesus Maria and Guerrero Negro annual landings were 432 tons (21%), which represents the collective landings for BV. Based on a similar species composition with Jesus Maria and Guerrero Negro fishing offices, it is likely that Isla de Cedros landings might also come from fishing activities within BV (Table 6), however, landings recorded in the CONPESCA office for this island were excluded from the BV dataset to avoid the inclusion of catches from outside the bay.

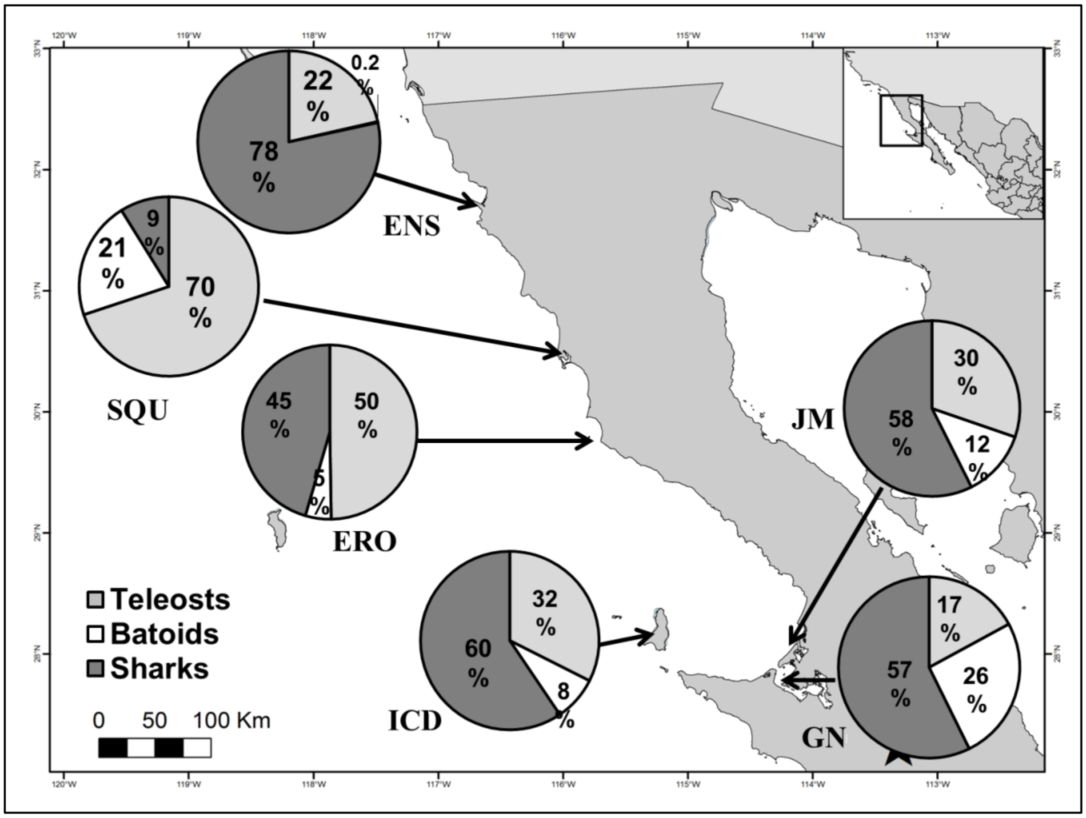

Figure 11. Percentage of reported landings (tons) from Northern Baja California: ENS (Ensenada), SQU (San Quintin), ERO (El Rosario), ICD (Isla Cedros), JM (Jesus Maria) and GN (Guerrero Negro). Species are grouped as teleosts (light grey slices), batoids (white slices) and sharks (dark gray slices).

Table 6. Total landings (tons) of species and multispecies groups reported at official fishing office (CONAPESCA, 2014) from 2008–2013 in northern Baja California. ENS-Ensenada, SQU-San Quintin, ERO-El Rosario, ICD- Isla Cedros, JM-Jesus Maria, GN-Guerrero Negro.

Common name	ENS	SQU	ERO	ICD	JM	GN
Stripped bonito[a]	242.41	2.30	1.09	0	0.15	0.55
White seabass[a]	12.21	4.89	8.72	5.84	20.23	11.46
Yellowtail[a]	33.70	1.22	4.23	16.20	22.76	5.74
Flounders[a]	20.46	12.71	27.39	1.18	46.76	5.60
Teleosts	**308.78**	**21.11**	**41.43**	**23.22**	**89.90**	**23.35**
Bat eagle ray	0.25	3.26	0.01	2.60	0.22	0.37
Diamond stingray[a]	2.08	0.53	2.50	0.71	7.84	4.96
Shovelnose guitarfish[a]	0.11	2.63	1.49	2.50	28.49	29.70
Batoids	**2.44**	**6.41**	**3.99**	**5.81**	**36.54**	**35.03**
Angel shark	0.06	0.13	0.53	20.07	3.43	1.25
Cazon[a]	0.26	0.18	0.10	0.05	7.84	8.42
Scalloped hammerhead shark	0.87	0	0	0	0.05	1.17
Nurse shark[a]	0.01	0	1.13	1.47	0.17	0.05
Sharks[a]	481.22	1.08	25.52	18.24	78.82	29.55
Silky shark*	0.34	0	0	0	0	0
Blacknose shark	0.05	0	0	0	0	0
Blue shark	659.07	1.22	10.39	2.33	70.21	30.22
Bigeye thresher shark	0.02	0	0	0	0	0
Spinous shark[a]	0.36	0	0	0.14	0	0
Hammerheads[a]	0.23	0	0	0	0	0
Mako shark	0.35	0	0.01	0	2.72	2.83
Mayo**	1.71	0.05	0	0.17	4.43	0.31
Pacific sharpnose shark[a]	0.00	0	0	0.07	0	0
Blacktip shark[a]	0.00	0	0	0	0.03	0.05
Silky shark*	0.47	0	0	0	0	3.71
Soupfin shark[a]	0.00	0	0.02	0	0.90	0.61
Thresher shark	2.40	0.06	0.29	0	0.13	0
Tiger shark***	0.58	0	0	0	0	0
Blacktip shark[a]	0.52	0	0	0	0	0
Smooth-hounds[a]	0.00	0	0	0	0.05	0.09
Tiger shark	0.04	0	0	0.01	0	0.12
Sharks	**1,148.55**	**2.72**	**37.98**	**42.55**	**168.78**	**78.37**
TOTAL	**1,459.78**	**30.25**	**83.40**	**71.58**	**295.22**	**136.76**

*	Species recorded with different common names, but may represent the same species
**	It is likely mako shark (*Isurus oxyrhinchus*), but the database lists it as “Mayo”.
***	It is likely the leopard shark (*Triakis semifasciata*).
[a] Multispecies group

Figure 11 shows the percentage of the total landings that correspond to teleosts, batoids, and sharks for each official office. In San Quintin and El Rosario teleosts are the most important part of the catch (70% and 50% of total, respectively), while landings in the southern offices were dominated by sharks and batoids (JM 58% and 12%, respectively, and at GN 57% and 26%, respectively; Fig. 11).

4.3.2. White shark incidental catches

I compiled a total of 390 white shark incidental catch records that occurred along the western coast of Baja California from 1999 to 2013. Records between 1999 and 2005 were sporadic with no more of 6 white sharks recorded for any one year (Fig. 12). Records increased during 2006 due to the carcass discard site surveys and the reports by Santana-Morales et al. (2012); only six white sharks were actually incidentally caught and reported that year. From 2007 to 2010 the number of incidental white sharks registered fluctuated between 10 and 25 sharks per year. For 2011 and 2012, the white shark-specific surveys resulted in 167 white sharks recorded in 2011 and 93 in 2012, whereas in 2013 only 7 records were obtained (Fig. 12).

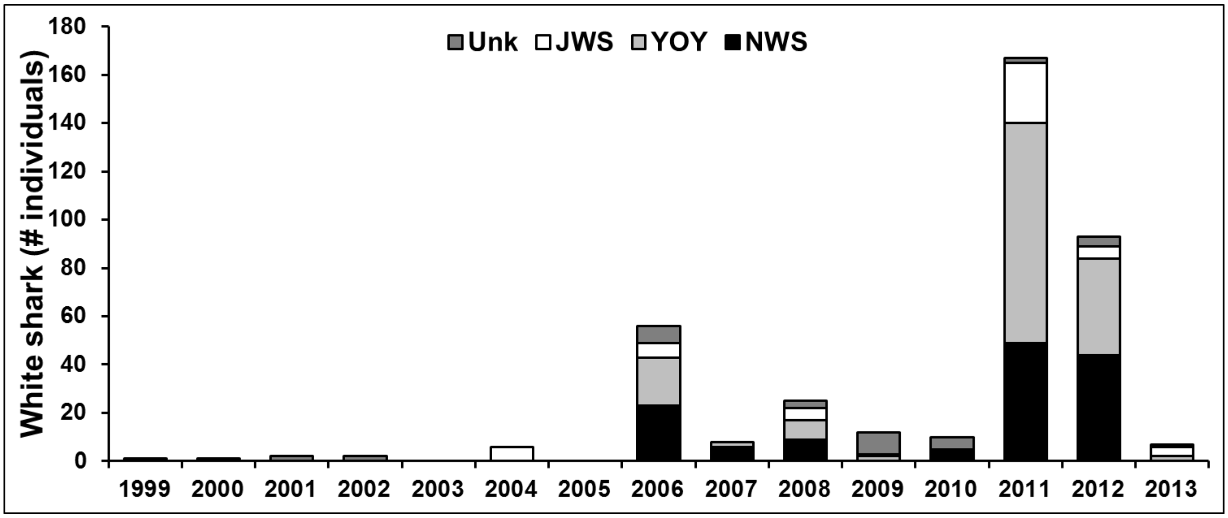

Figure 12. All incidental white shark catch records. NWS: Newborn white sharks (black); YOY: Young-of-the-year (light grey); JWS: Juvenile white sharks (white); and Unk: Unknown (dark gray).

Of the 390 white sharks recorded, total length was measured in 91.8% of cases. White shark size ranged from 118 to 300 cm of total length (TL), and the size-frequency distribution presented two peaks: one for the 135 to 140 cm TL size class, and a second encompassing the 170-175 size interval (Fig. 13). Based on their size, 135 sharks were categorized as NWS, 166 as YOY, and 52 as JWS (Fig 12).

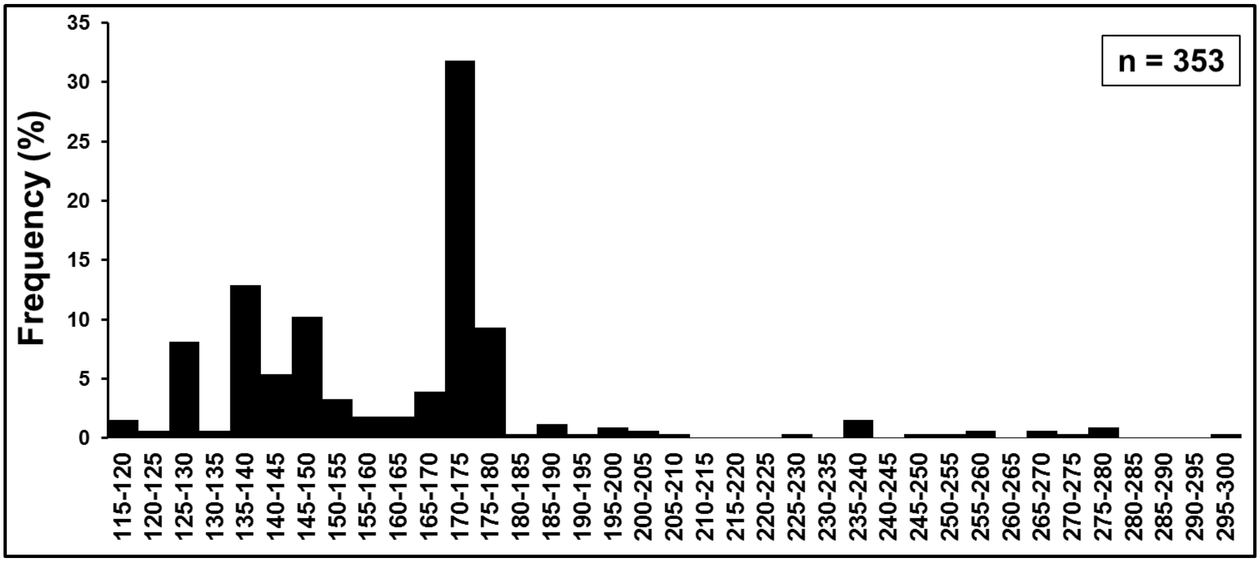

Figure 13. Size-based frequency histogram of white sharks recorded as incidental catches along the western coast of Baja California from 2004 to 2013.

Of the 353 sharks that were measured, 94% were caught at BV and landed in the fishing camps south of Pta. Canoas, and the other 6% of the sharks were landed at Pta. Canoas or to the north (Figure 10) and hence outside of BV. Of the 20 white sharks caught at NBV, 75% were juveniles, 10% YOY and 15% newborn (Fig. 14). When comparing the proportions of sharks of different sizes caught at NBV and BV, there were significant differences driven mainly by JWS from both regions (p < 0.0001), but NWS and YOY were also significantly different between regions (p < 0.05 and p < 0.001, respectively). At BV, YOY were the most abundant of all size-classes in the incidental catch records, followed by NWS, while JWS were the less abundant (Fig 14).

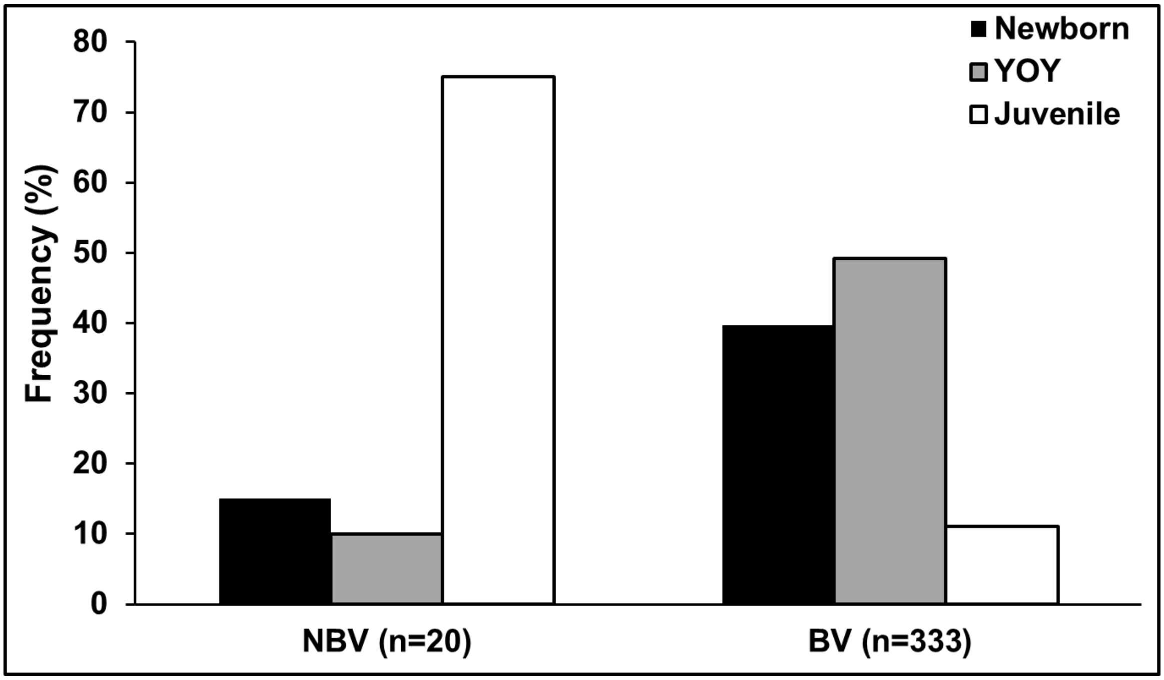

Figure 14. Frequency histogram of the different size classes of white sharks recorded as incidental catch in the regions of north of Bahia Sebastian Vizcaino (NBV) and within Bahia Sebastian Vizcaino (BV) from 2004 to 2013.

From the 333 white sharks sampled within BV, 40% were categorized as NWS, 49% as YOY, and 11% as JWS (Fig. 14). Sharks belonging to the three size groups were caught during most of the months of the year. The highest numbers of the three size categories were recorded between May and September; as 92% of the 132 newborns recorded were caught during these months (Fig. 16). Newborn white sharks with total lengths < 135 cm were mainly caught during June and July.

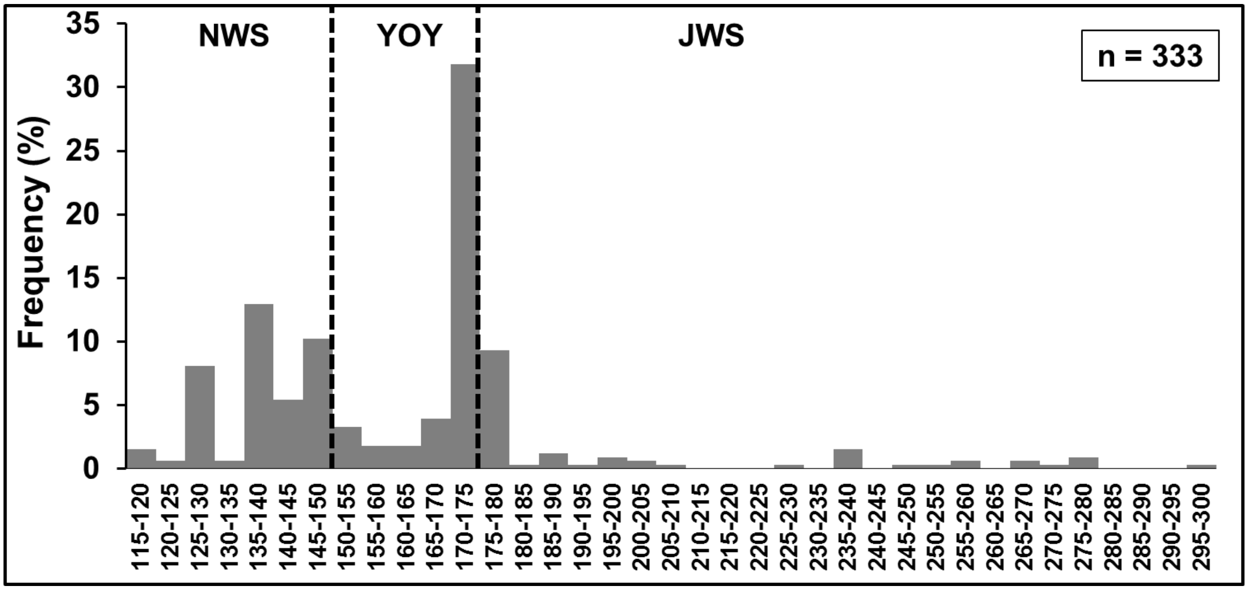

Figure 15. Size-based frequency histogram of white sharks recorded as incidental catch in Bahia Sebastian Vizcaino, at the fishing camps of Sta. Rosaliita, Laguna Manuela and Guerrero Negro from 2004 to 2013.

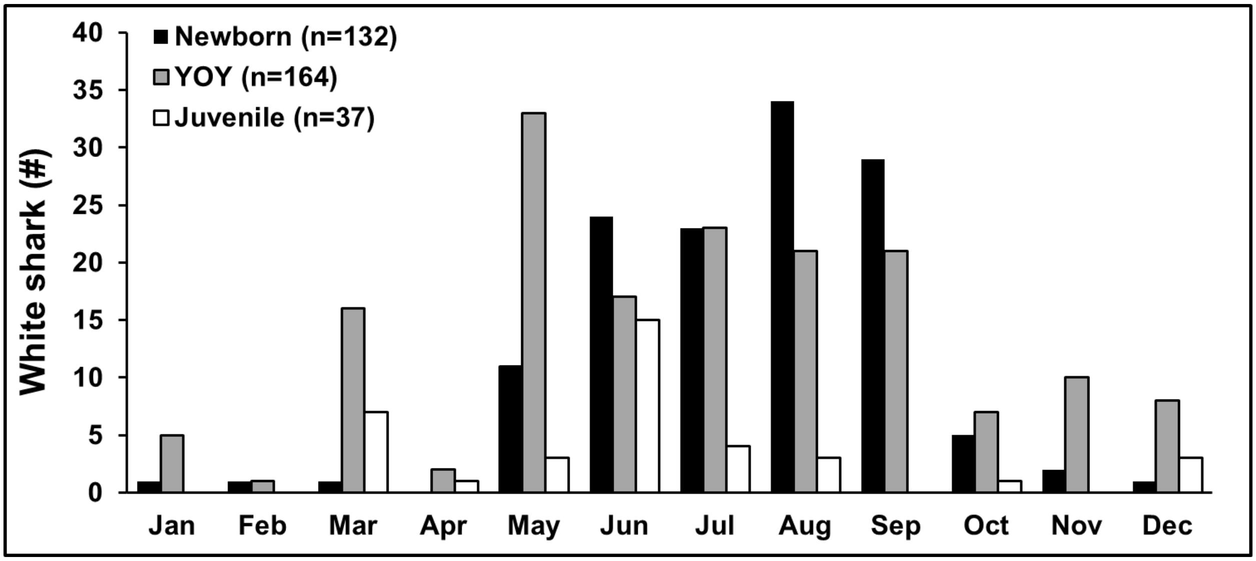

Figure 16. Size-based histogram of the numbers of white sharks caught incidentally in Bahia Sebastian Vizcaino from 2004-2013 Newborn (< 150 cm TL); YOY (150-175 cm TL); Juvenile (175-300 cm TL).

Within BV, YOY white sharks were incidentally caught mainly between May and September (Fig 17a), and of these, the YOY white sharks of 170 to 175 cm TL were the size group most frequently recorded (n=106; Fig. 17b), representing 32% of the total sample of sharks caught inside the bay. These YOY were caught during most the months of the year, except March and April, and the highest percentages of the incidental catch was observed between May and September (Fig. 17). All but one of these sharks were recorded during the surveys conducted in 2011 and 2013.

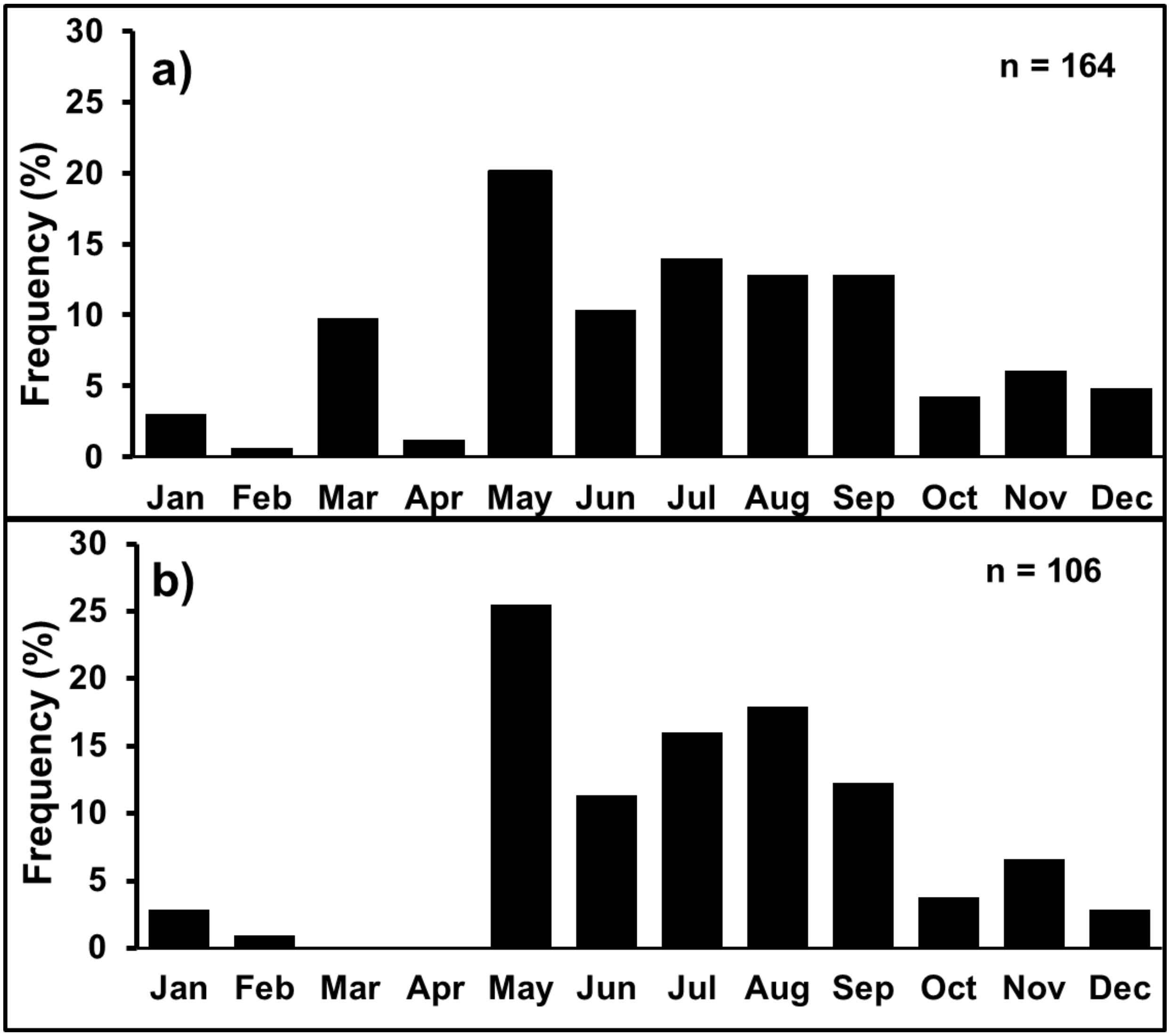

Figure 17. Frequency histogram in a monthly basis of a) all YOY white sharks, and b) 170-175 cm TL YOY white sharks recorded as incidental catch in Bahia Vizcaino from 2008 (1 organism) and 2011-2012 (n=105).

4.3.3. Relationship of the white shark incidental catch with selected demersal species (SDS) fishery landings

Table 7 shows the yearly landings of the SDS fisheries for the period of 2008 to 2013. The largest landings are composed of shovelnose guitarfish, with an average catch of 116 tons per year, followed by the flounders with mean landings of 103 tons per year.

Table 7. Total landings (tons) of selected demersal species (SDS) reported in the CONAPESCA fishing offices of Jesus Maria and Guerrero Negro in the Bahia Sebastian Vizcaino region from 2008–2013 (CONAPESCA, 2014).

	2008	**2009**	**2010**	**2011**	**2012**	**2013**	**Total**
Teleosts (Flounder group)	123.8	127.71	87.7	78.0	75.3	124.7	**617.1**
Bat eagle ray	0.8	1.0	0.2	0.9	1.3	2.8	**7.1**
Diamond stingray	18.9	25.5	19.6	24.5	24.6	36.9	**150.0**
Shovelnose guitarfish	104.5	139.2	123.9	104.2	109.0	117.5	**698.3**
Batoids	**124.2**	**165.8**	**143.6**	**129.7**	**134.9**	**157.2**	**855.4**
Angel shark	36.8	17.2	48.3	34.9	24.0	34.0	**195.1**
Cazon	11.3	7.0	12.6	4.8	11.2	8.4	**55.3**
Smooth-hounds	0	0	0	0	1.0	0.6	**1.6**
Sharks	**48.1**	**24.1**	**60.9**	**39.7**	**36.1**	**43.0**	**251.9**
TOTAL	**296.1**	**317.6**	**292.2**	**247.3**	**246.4**	**324.8**	**1,724.5**

The monthly variation of landings for the flounders, batoids and all sharks revealed that most flounder landings took place between February and August, with a peak in April, May or July depending on the year. Monthly catches ranged between 17 to 40 tons (Figure 18). Batoids were mainly landed during April through October between 2008 and 2011. During 2012 and 2013 this pattern changed to two peak periods during the year. In 2012 landings peaked in May (23 tons) and in August (57 tons), and in 2013 in April (40 tons) and August (76 tons), and there were no landings reported in May and June (Fig. 18). Shark landings did not show a consisting temporal pattern; in some years landings peaked in June and July, while in other years in April and November. However, during 2012 and 2013 shark landings showed two distinct high landings periods: March and April and August to October, reaching levels of around 10 tons landed per month. This change in landing pattern might be also related to the initiation of the fishing ban in 2012.

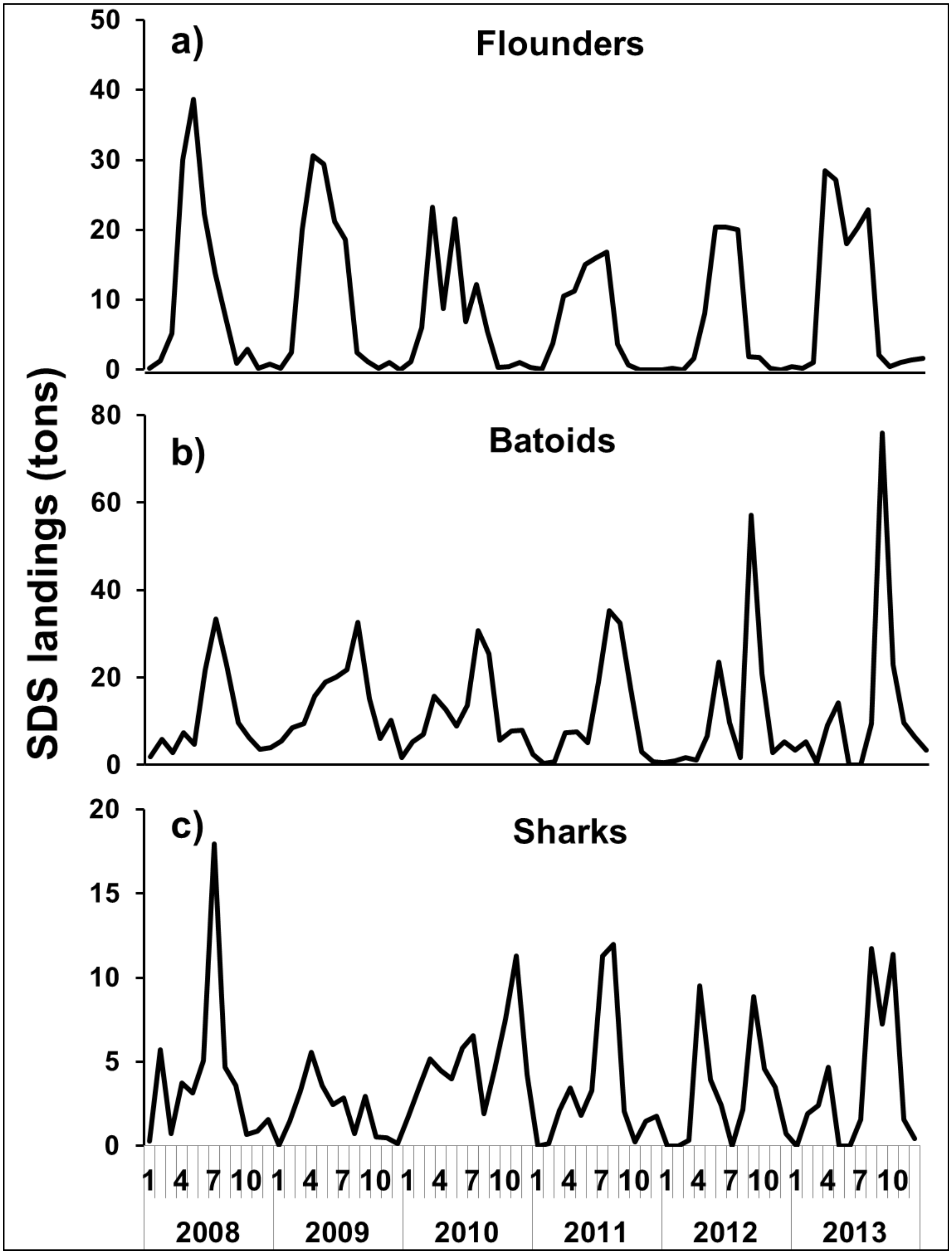

Figure 18. Monthly total landings of selected demersal species (SDS), a) flounders, b) batoids and c) sharks reported at the fishing offices of Jesus Maria and Guerrero Negro from 2008 to 2013.

If we consider the monthly pattern of landing values of flounders, batoids and sharks together (Fig. 18), it suggests that during all months of the year there are artisanal fishing operations using bottom gillnets in the bay. In order to evaluate the monthly changes of incidental white shark catches in greater detail, I examined the landings for the period in which the incidental catches were quantified with the most effort (May 2011 to May 2012). SDS landings were pooled by month to produce a single series of landings (Fig. 19 a), and compared with the white shark incidental catches in number of sharks (Fig. 19 b). Both catch series have a significant correlation ($r^2=0.86$; $p < 0.0001$) and both peaked during July 2011 and May 2012. SDS landings were high between May and September and very low during the rest of the year.

White shark incidental catches during May 2011 to May 2012 in BV peaked in July, when 38 sharks were caught (Fig. 19 b). Incidental catches decreased to an average of 12 sharks caught per month between September and November. No sharks were recorded as caught in March 2012, and incidental catches increased once again in May 2012 with a catch of 29 individuals (Fig. 19 b). Comparison of SDS and white shark catches indicates both trends follow the same pattern, implying that in months with large SDS landings there is a higher incidental catch of white sharks (Fig 19 a and b).

The proportion of incidental white shark catches was standardized to the SDS landings (Fig. 19c), which suggests that about one shark was landed for every ton landed. During the period between October 2011 and February 2012 more than one and up to five sharks were caught per landed ton of SDS (Fig. 19 c). These data suggest that during the autumn and winter months, sharks may be more susceptible to capture in the bottom gill net fishery or possibly that they are more abundant in the area.

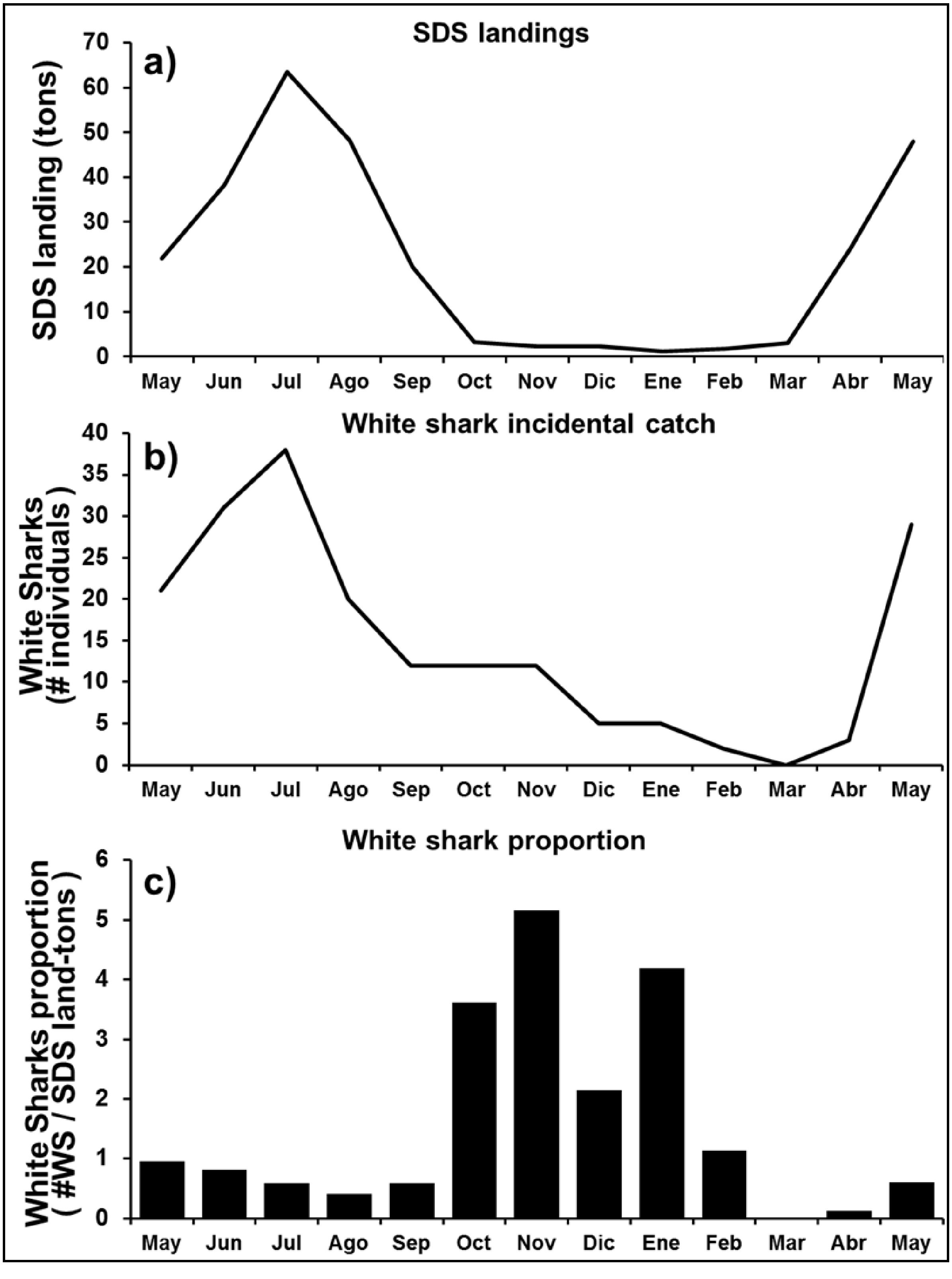

Figure 19. Monthly basis graphs of a) Selected Demersal Species -SDS- landings, b) white shark incidental catch, and c) white shark proportion (# white sharks / SDS landings) from Jesus Maria and Guerrero Negro between May 2011 and May 2012. Note that graphs are at different scales.

4.3.4. Bahia Sebastian Vizcaino as a nursery area

Heupel et al. (2007) provided the following three basic criteria for identifying shark nursery areas for newborns and YOY sharks: 1) the area must have a higher relative abundance of neonates and young juveniles compared with other areas, 2) sharks will have a tendency to remain in the area or return for extended periods, and 3) the area must be consistently used by white sharks across years. Below I compared my data with Heupel et al. (2007) criteria:

1) There were significant differences in the catches between NBV and BV, with a relatively low catch of newborn and YOY sharks outside of BV (5 at NBV vs. 296 at BV) (Fig. 14). The NBV area had a higher proportion of juveniles (75%), while the BV area had a higher abundance of newborns and YOY (89%). These data suggest that BV meets the first criterion.

2) Although NWS and YOY were caught during most of the months, most of the catches occurred between May and September, when 92% of the newborns and 70% of the YOY were recorded (Fig. 16). Both life stages were caught throughout the year (Figure 12). These results support the second criterion.

3) Finally, NWS and YOY white shark were incidentally caught within BV between 1999 and 2013, which supports the third criterion.

In summary, the data are consistent with Heupel et al. (2007) criteria, and BV can therefore be considered as a white shark nursery area. Furthermore, given the high abundance of juveniles captured within BV, these data suggest that BV may be an important hotspot within the larger nursery area.

4.4. Discussion

In this chapter I present a compilation of white shark incidental catches off the western coast of the state of Baja California. These data represent an update of previous compilations and the most complete data set to date. The results suggest that NWS and

YOY could be present at BV every year and in higher frequencies from May to September, while juvenile white sharks are caught in lower frequency. All three criteria proposed by Heupel et al. (2007) were supported, suggesting BV provides critical nursery habitat for white sharks. Further, given the high incidence of capture within BV, the data from this work suggest that BV may be a nursery hot-spot that is deserving of special management consideration.

4.4.1 White shark incidental catches

Springer (1967) presented a model to explain the spatial use of a hypothetical shark population. He suggested that young sharks are born in nearshore nursery areas during spring/summer, where they remain until reaching sexual maturity when they join the adult population further offshore. In this study, immature white sharks, mainly NWS and YOY, were recorded as incidentally caught during the late spring and summer months of the years sampled. Newborns were recorded in high numbers during June and July. Hence, white shark populations in BV seem to fit Springer’s (1967) description well.

Although generating estimates of the relative abundance of immature white sharks at BV was not possible, the SDS landings reflected the yearly pattern of the use of bottom gillnets in BV. Further, this work was also able to document that the bottom gillnet is the fishing gear that leads to the highest white shark incidental catches (Santana-Morales et al., 2012). Cartamil et al. (2011) reported that trap fisheries targeting spiny lobster (*Panulirus interruptus*) were the dominant activity in some fishing camps of BV during the legal season (September 15 to February 15). Hence, the decrease in SDS landings is most likely representative of this gear switch. During the summer months, when the largest landings of the SDS are observed, the largest records of incidental white shark catches are also recorded with approximately one or slightly fewer white sharks taken per ton of landed product. In contrast, during the autumn and winter months, even though the SDS landings decreased substantially, the proportion of incidental catches increased to around 4 sharks per ton of SDS product landed. These results may be in response to several factors including possible changes in relative white shark abundance in the bay, changes in bottom set gillnet dynamics or possibly the grouping or aggregation of resources during certain times of the year. However, to fully understand the white shark resource within BV, annual monitoring of white shark movements, catch rates and SDS fishery dynamics are necessary. Further, understanding incidental catch rates within BV and how they can be further reduced requires catch specific information and habitat characteristics (e.g., temperature, type of bottom, depth). When coupled with movement studies, it may be that certain areas can be identified as potential conservation zones in which fishing activities with specific gear types (i.e., bottom set nets) can be reduced.

The immature white shark size composition caught within BV showed two modes: one at the 135 to 140 cm TL size interval, and a larger one at the 170-175 size interval. The larger grouping represents the largest of the YOY grouping, because sharks bigger than 175 are considered as juveniles. The high percentage of relatively large YOY caught within BV could be related to the selectivity of the fishing bottom gillnets used in the area or possibly due to a higher abundance of this size-class within the BV region. As previously documented, larger YOY tagged within the SCB have been shown to make rapid and direct movements from the SCB to the BV region (Weng et al., 2007b).

Cartamil et al. (2011) found that in BV demersal teleosts and coastal elasmobranchs (mainly batoids and small sharks) were targeted using bottom-set gillnets deployed on the continental shelf. These nets are made of monofilament and have lengths of 100–500 m, heights of up to 5.5 m, and a stretch-mesh sizes of 6–12 cm. Multiple gillnets, either strung together or set in various locations, are often deployed for a 24 h (h) period before retrieval. The maximum number of gillnets in use simultaneously by one vessel was eight.

Usually gillnets are highly selective and used principally for those species captured mainly by gilling (i.e., captured behind the gill-cover) or by wedging (being held by a mesh around their maximum body girth) (Fonseca et al., 2005). Selectivity curves for a certain mesh size are typically dome shaped, and retention is supposed to increase with size up to a length of maximum catch and decrease thereafter. Consequently the range of sizes of a target species can typically be controlled by the careful choice of the mesh size (He and Pol, 2010). However, given the size frequency of white sharks recorded in this study (Fig. 15), it is probably that the target/mesh size dynamic does not hold true for juvenile white sharks. However, for the larger sizes (>175 cm), it may be that white sharks are able to penetrate the net and break free. Support for this comes from local fishermen that commented on the presence of large holes in their nets, which they proposed were from sharks escaping capture (García-Rodríguez, *pers. comm.*). Thus, it is possible that larger white sharks could be interacting with bottom gillnets, but they are not being caught because they have the size and strength enough to cut the nets and avoid being incidentally caught.

The high frequency of white sharks caught within the 170-175 cm TL size class could also be due to a higher abundance of that size-class within the bay. Southward movements of juvenile white shark from SCB to the BV area have been reported from satellite tagged individuals (Weng et al., 2007b; Weng et al., 2012). However, the one shark reported by Weng et al. (2007b) that reached BV was a 156 cm TL YOY tagged in early September 2003 within the SCB. This shark arrived in BV during late September and mid October of the same year. Three of the white sharks that were tagged by Weng et al. (2012) moved from the SCB to the south, with one shark (176 cm TL) entering into the GC in mid June 2008. Another shark (187 cm TL) tagged in January 2007 moved along the shore proximal to the waters of BV. The third shark (166 cm TL) tagged in November 2009 moved to the BV proximal to the mouth of LOL and was incidentally caught in February 2010. All these three white sharks were ~170-175 cm TL when first captured providing evidence that this size class has a tendency to migrate to the waters of BV. Another potential explanation for the prevalence of this size-class may be the size measurements taken in the field, as processed sharks or released individuals are often measured boatside and subject to several forms of estimation. Collectively, this region, its fisheries and the white shark resource would benefit tremendously from a comprehensive monitoring program that could better track habitat use and the anthropogenic activities of BV.

Even though BV is a large area (35,678 km^2), the fishermen are largely based in fishing camps along the southern portion of the bay (Laguna Manuela and Las Casitas), and they mainly operate their nets in waters close to the mouth of LOL or inside the lagoon (Fig. 20) (Guerrero-Ávila et al., 2013). This fishing ground produces the largest amount of flounder and batoid catch for the western coast of Baja California (Table 6 and 7). In the case of the flounder grouping, the primary species captured is the California halibut (*Paralichthys californicus*), which ranges from central California to northern Baja California (Allen, 1988). Juvenile California halibut use coastal lagoons, bays, and estuaries as nurseries (López-Rasgado and Herzka, 2009), and LOL has been described as an important habitat for this lucrative resource of BV (De la Cruz-Agüero et al., 1996).

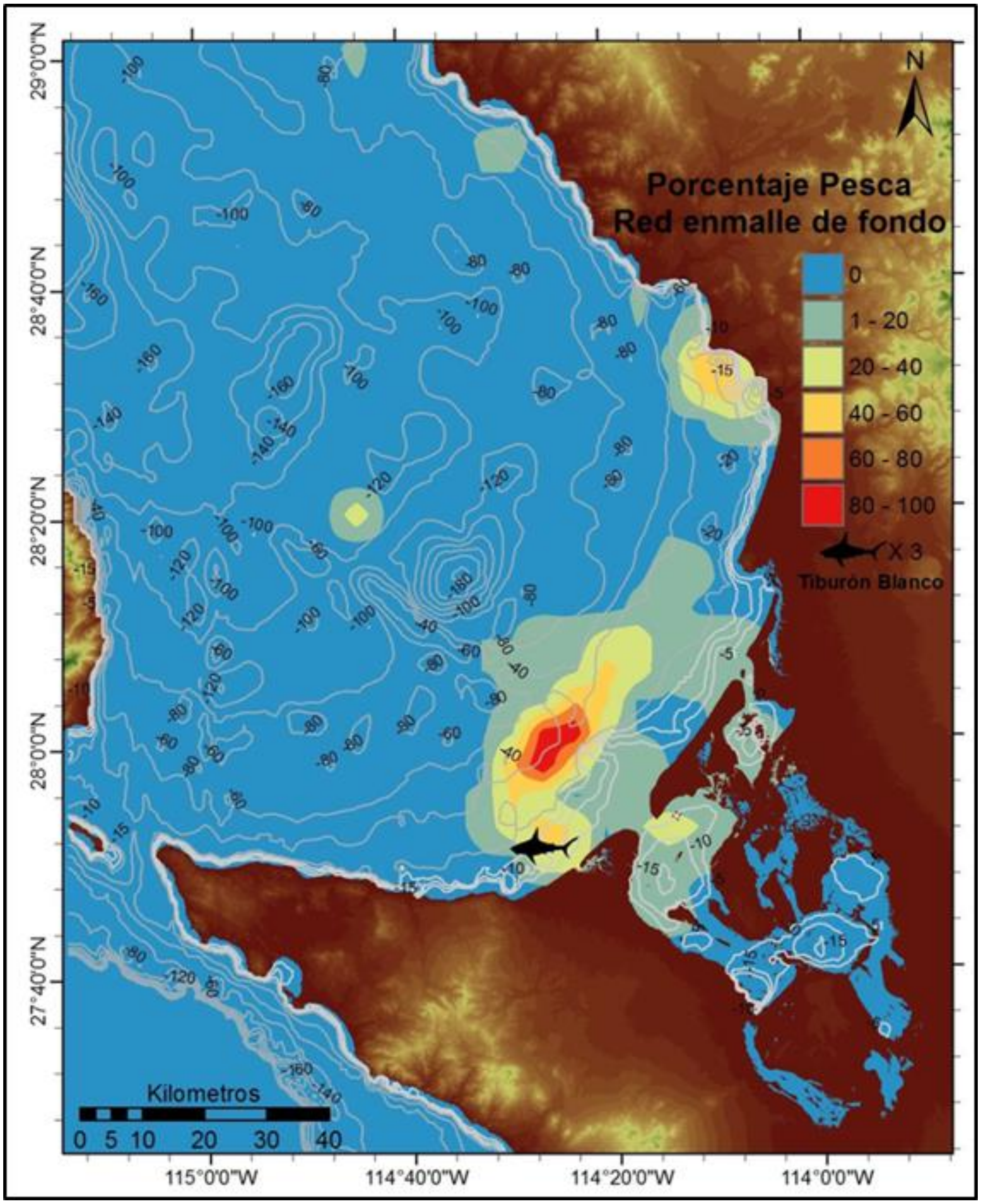

Figure 20. Map of the bottomset gillnet fishing area in Bahia Sebastian Vizcaino including the area where three white sharks were recorded (Taken from Guerrero-Ávila et al., 2013).

4.4.2. Bahia Sebastian Vizcaino as a nursery area

Bahia Sebastian Vizcaino has been proposed as a nursery area for white sharks (Santana-Morales et al., 2012) based on the high frequency of incidentally caught white sharks recorded. Collectively, this chapter of my thesis focused on assessing whether BV met the criteria proposed by Heupel et al. (2007) for shark nursery areas. Further, this work was performed to highlight the importance of this region and better document BV as a regional "hotspot" for juvenile white sharks of the NEP.

The first criteria of Heupel et al. (2007) stipulated that a shark nursery area should exhibit the presence of immature sharks in greater abundances than in other areas. My results showed that BV had the highest incidental catch rate of NWS and YOY sharks compared to any location along the northern Baja Peninsula. The high frequency of small juveniles within the BV region parallels that of the SCB, an embayment that has also been proposed to be a nursery area (Lowe et al., 2012). Given that several sharks have been documented to move between the SCB and the BV region, it is aparent that this entire area is important to the juvenile white shark resource (Weng et al., 2012). The high frequency of YOY in SCB and BV suggests that these areas may be regional "hot-spots" of high abundance. Such hotspots may be critically important areas for focusing conservation efforts. Additional data focused on identifying parturition areas and regional movement patterns are needed to assess if these two hot-spots are in fact sites of heightened importance or whether the locations can change over time with oceanic conditions. It may also be that the SCB and BV are locations that provide optimal foraging for NWS and YOY and thus serve as aggregation areas that also have a high amount of fishing pressure. Although these hypotheses need to be further tested, the data from this thesis suggests that both BV and SCB are important areas to focus white shark conservation efforts.

NWS and YOY white sharks were incidentally caught mostly between May and September. This period coincides with the season when adult females (supposedly pregnant) were shown to move from GI to the near-shore waters, close to BV. From these data it has been suggested that the parturition area for GI sharks is close to shore (Domeier and Nasby-Lucas, 2013); however there are no additional evidence to support this hypothesis. Given the amount of speculation surrounding parturation areas, future tagging of pregnant females from GI as well as reproductive studies on white sharks in Mexican waters are needed. Nonetheless, the high frequency of newborn and YOY white sharks recorded as incidental catch within BV suggests the idea that this area is an important location for the early life stages of white sharks in the NEP.

The seasonality of incidental catch records of NWS have been documented over the past 14 years (1999–2013) within the BV region. In addition, the carcasses recorded by Santana-Morales et al. (2012) correspond to organisms that were incidentally caught and the remains discarded at proximal to the fishing camps. The high heat and low humidity of the desert quickly desiccates these remains and preserves them in a state resembling mummification (Cartamil et al., 2011), which could mean that they were incidentally caught over a longer period. All the records, those from 1999–2010 (Santana-Morales et al., 2012) and those from 2011–2013 (collected during this study), showed a tendency toward an increase in the incidental catches during the summer months, which coincides with the movements of supposedly pregnant females from GI to BV (Domeier and Nasby-Lucas, 2013).

Nursery areas should provide enough food and protection against predators (Beck et al., 2001). The waters of BV, have been characterized as an area with a permanent surface enrichment with abundance of primary producers that result in a higher relative abundance of consumers (Lluch-Belda, 2000) which could be the main prey for white sharks. White sharks change their diet during ontogeny (Tricas and McCosker, 1984). Immature white sharks in BV feed on benthic species such as rays (*Myliobatis californica*, *Raja* spp) and crustaceans, as well as small pelagics such as bony fishes (*Scomber japonicus*, *Atractosion nobilis*) and squids (Teuthoidea) (Santana-Morales et al., 2012). As they grow, their prey becomes larger, and common prey include pelagic bony fishes (*Thunnus spp.*), squid (*Dosidicus gigas*), and elasmobranchs. Immature white sharks also feed opportunistically on dead marine mammals. The main prey species for immature white sharks (mostly newborns and YOY) are benthic species, which in BV are an important component of the fisheries (Cartamil et al., 2011; Santana-Morales et al., 2012). In this study, I was able to report on the landings of some species that are mainly caught in the bottom gillnet fisheries (Table 7), and have also been reported as prey for white sharks in BV (Santana-Morales et al., 2012). Most of these species are fished close to shore by the artisanal fisheries of BV (Guerrero-Ávila et al., 2013). Because of the high incidence of capture of white sharks proximal to the mouth of LOL (Guerrero-Ávila et al., 2013), it may be that this species preys upon the same assemblage that is targeted by fishers of the region.

Juveniles were caught mainly during the winter months, when grey whales (*Eschrichtius robustus*) migrate to and from the region for wintering and parturition (Rice et al., 1981). Because white sharks have been shown to feed on whale carcasses (Curtis et al., 2006; Fallows et al., 2013), the juveniles could also be capitalizing on carcasses that are common within the region. It also may be that these larger individuals are preying on other food sources that are more prevalent during the winter season. Also, support for our findings is also available from tagging data which has shown JWS to move into the region from the SCB during the winter months (Weng et al., 2007b; Weng et al., 2012). Although fewer sharks were observed in the NBV region, their presence supports the hypothesis that the region from BV to Point Conception is an important nursery area for several age classes of juvenile white sharks.

The parturition areas of white sharks in the NEP are unknown, but previous movement studies of supposedly pregnant adult females suggest they move to nearshore waters for parturition (Domeier, 2012). In the NEP, sub-adult and adult white sharks aggregate at GI from July to March. They have been documented to depart on an offshore migration with the females leaving GI later in the year than the males, and some of these females returning every other year (Domeier and Nasby-Lucas, 2008). Recently, it was discovered that four supposed pregnant females observed around GI had moved towards coastal habitat during the summer months, and were observed close to BV and the GC (Domeier and Nasby-Lucas, 2013). These movements coincide with increase in the incidental catches of immature white shark reported in this study, suggesting that BV and GC may be important parturition areas for GI white sharks; however, as stated previously, more research on the movements of pregnant females is needed.

Some habitats in eastern Australia have been proposed as nursery areas for white sharks (Bruce and Bradford, 2012). There are two main regions that were reported, the Cornet Inlet and the Port Stephen estuarine system (Bruce and Bradford, 2012). Cornet Inlet is a similar to BV in that is an estuarine habitat with some lagoons within the area and that it is a productive area that supports species that are main prey for immature white sharks, like stingrays (*Dasyatis brevicaudata*), perch (*Johnius belangerii*), flathead (*Platycephalus endrachtensis*) (Barton et al., 2012). The Port Stephen estuarine system is similar to BV in that it is extremely productive system (Oke and Middleton, 2001) with an abundance of fish species like Australian salmon (*Arripis trutta*), Australasian snapper (*Pagrus auratus*), mulloway (*Argyrosomus hololepidotus*), striped mullet (*Mugil cephalus*), and gummy shark (*Mustelus antarcticus*), as well as various other elasmobranchs (e.g., Eagle Rays *Myliobatis australis*), all of which are common prey for JWS (Bruce and Bradford, 2012). These areas have been proposed as a white shark nursery areas based on satellite tracking studies (Bruce and Bradford, 2012), and authors suggest that the high frequencies of NWS and YOY recorded in both areas met the Heupel et al. (2007) criteria, similar to what my results led me to suggest for BV area. They also recognize a migration corridor between both areas, which may be similar to the results reported in this study. However, adequate sampling of the areas between the SCB and BV are necessary to determine if in fact this area a corridor, as it is possible that the sharks may be using the entire stretch for foraging.

Another region proposed as a white shark nursery area was the waters less than 50 m deep on the broad continental shelf in the New York Bight area (Casey and Pratt, 1985). This is based on the occurrence of small and intermediate sized organisms (< 200 cm TL) and the presence of several species of prey. However, despite recent study on the importance of this region to juvenile white sharks, (Curtis et al., 2014), to date there have been no attempts to test the region following the Heupel et al. (2007) hypothesis. Another proposed white shark nursery area is the Sicilian Channel in the Mediterranean Sea. This location was proposed due to the presence of neonates and pregnant females (Fergusson, 1996; Kabasakal and Özgür-Gedíkoglu, 2008); however, this area has also not been tested following the (Heupel et al., 2007) criteria.

All the proposed white shark nursery areas, (i.e. SCB, Cornet Inlet, Port Stephen, New York Bight, and the Sicilian Chanel) are similar in having a large continental shelf and the presence of several species that could be potential prey for newborn and YOY white sharks. This trait links all of these proposed nursery areas to the waters of BV, and suggests that foraging success may be the most important factor in identifying suitable white shark nursery habitat.

4.4.3. Management implications

The year-round presence of white sharks in BV, as demonstrated in this work, supports the need for increased conservation efforts within this region. Fishing activities are not consistent throughout the year, with changes in target species and gear type that may result in varying white shark catch rates. Despite changing targets, bottom set gillnets are used throughout the year targeting batoids to flounders and small shark species ("cazón") (Cartamil et al., 2011). Despite the year round pressure, NWS and YOY sharks were mainly incidentally caught in summer months. Since 2012, an elasmobranch fishing closure was established from May to July (DOF, 2012), and although the protection of white sharks is not the purpose of this regulation, the timing of this ban does help in the protection of the white shark since it coincides with time of year in which the immature white sharks are found close to shore. The temporal change in the catch patterns reported in this work (Fig 18) likely reflects the beginning of the May 1 to July 31 fisheries closure. However, these data indicate that during 2012 the ban was not effective until July, and for 2013 it was effective only during May and June. These results suggest the need to strengthen surveillance in the implementation of the proposed closure, as it is during the months covering the ban season when the highest catch of white shark has been recorded. Thus, the application of this management measure in a more effective way will contribute to the survival and decrease of the incidental catch of this species.

My results suggest a high fishing pressure on the immature white shark population within Mexican waters, which could in turn affect the health of the white shark population in NEP. Mollet and Cailliet (2002) assessed the importance of immature stages in several species by comparing different demographic models, *i.e.,* life history tables, Leslie matrices and stage-based matrix. They concluded that stage-based models explain better the population trends in a slow growing species like the white shark. These models emphasize the survival and abundance newborns, juveniles and adults. Mollet and Cailliet (2002) suggested that survival and abundance of immature white sharks are important components of population growth rate estimations.

The survival rate is negatively related to the total mortality rate, which is the sum of the natural mortality and the mortality induced by fishing (King, 1995). Thus, with high levels of fishing mortality, the survival of a population will be negatively affected. Therefore, understanding fishing pressure and catch rates within the region are critical for long term management success. In the SCB, Lowe et al. (2012) reported incidental catches of white sharks between 1936 and 2009, and in a rough estimation from 1981-2009, when "changes in catch patterns, adjusted for changes in fishing activity and pressure" occurred (Lowe et al., 2012). These authors reported an incidental catch of 12 white sharks per year during this period, while my estimation for the west coast of Baja California had a rough estimation of 25 individuals caught per year from 1999-2013. When I analyzed the incidental catch records between May 2011 and May 2012, a rough estimation of 175 white sharks per year was obtained. This period was before the implementation of the seasonal closure on shark fishing by the Mexican government in 2012 (DOF, 2012). To evaluate the effect of this seasonal closure, the records from June to December 2012 were assessed and estimated approximately 91 white sharks incidentally caught per year, which translated into a decrease of 52% in the incidental catch after the closure. These results coupled with the landings records (Fig.17), suggest a positive effect of the shark seasonal closure for the immature white shark population. Given the limited information of population size and dynamics, these results may have a significant impact on the larger white shark population of the NEP.

Understanding the use patterns of a nursery area is important for management and conservation of the white shark resource of the NEP. Although the Mexican government has established the white shark as a threatened species (DOF, 2002), and more recently initiated a fishing ban for this species in Mexican waters (DOF, 2014), emphasizing that white sharks must be released when captured. The mandated release of live sharks may provide an additional means to reduce fishing mortality, especially within BV. Given the high survivorship of post release net captured sharks in the SCB, it may be that other fishery protocols, such as soak time can be visited to reduce incidental mortality even further. When coupled with existing conservation measures (i.e, seasonal closures) already in place, it may be that minimal changes in the fishery can make a significant contribution towards conserving the juvenile white shark resource of the NEP.

Chapter 5. General Discussion

In the two main chapters of this thesis I present results that yield insight into the genetic connectivity of white sharks in the NEP, mainly in the Mexican part of its distribution, and that show the BV is likely a particularly important part of the nursery area for NWS and YOY white sharks. The immature sharks found in BV seem to have a matrilineal origin mainly from females that aggregate at Guadalupe Island. Both results suggest potential options for the conservation and management of white sharks in the North Eastern Pacific, especially in Mexican water, since incidental catch of this species still occurs, and the abundance and population trends of immature white sharks is poorly understood.

5.1. Nursery areas and its connectivity to adult aggregations sites

The genetic differences in mtDNA found between white sharks from the adult aggregations areas at GI and CC, and the genetic differences in mtDNA, but no differences in nuclear DNA between immature sharks sampled in areas of the NEP (SCB and BV), highlights the complexity of the white shark population in NEP. Based on the mtDNA analysis, there appears to be female mediated gene flow, with females showing philopatry to a breeding aggregation. These results are not indication of two different populations. Without nuclear DNA from CC it was not possible to evaluate the bi-parental gene flux between aggregation areas. Similar differences in mtDNA between regions were found in white sharks from Australia (Blower et al., 2012), where samples from the east coast were significantly different from the southwest coast, which led to the authors to suggest a female reproductive philopatry. Such reproductive philopatry has been documented in other shark species (Hueter et al., 2005), including a high mobile but coastally orientated species such as sandbar shark *Carcharhinus plumbeus* (Heist et al., 1995) and the bull shark *C. leucas* (Tillett et al., 2012). However, more studies on the reproductive behavior of female white sharks in NEP and genetic studies increasing the number of females sampled are needed to rigorously test this hypothesis.

The mitochondrial results suggest philopatry of females from GI to pupping areas but, at at this point, do not reveal the connection between CC and nursery areas. The mitochondrial results show significant genetic differences between adults at CC and immature sharks from all the sampled coastal areas (SCB, BCPC, BV and GC), but no genetic differences in mtDNA were found between GI and immature white sharks from those coastal areas. One problem with this analyses is the very small samples size for female sharks in CC. Further, the immature sharks sampled within SCB were genetically different in the matrilineally inherited mtDNA from those sampled in BV, suggesting that their mothers could be from different reproductive subgroups or have a specific preference for different pupping areas. Similar significant differences in mtDNA between immature white sharks off the eastern and western coasts have been found in Australian waters (Blower et al., 2012) although these regions are much farther apart than in the NEP. Based on their genetic results and tagging studies (Bruce and Bradford, 2012), Blower et al. (2012) suggest that females show a site fidelity, returning to the same coastal regions to give birth, and that juveniles sampled remained in the natal areas. In the NEP, a white shark nursery hotspots have been proposed at SCB and BV based on the high frequency in catch records of YOY (Klimley, 1985; Lowe et al., 2012). Differences in mtDNA between SCB and BV suggest philopatric reproductive behavior where females return to same parturition area. What are needed is broader tagging studies to examine movements within the larger nursery area from the SCB to BV and even into GC to determine the relative importance of the two hotspots across age classes. Additional genetic studies to examine the stability of the pattern over time and the potential input of females from CC will also be important to test this hypothesis.

The results of nuclear analyses provide some insight into patterns of gene flow, even without the inclusion of samples from CC. Male white sharks could be mediating the gene flow in the NEP population. Male white shark from both aggregation areas in NEP (CC and GI) migrate to the same oceanic area and up to Hawaii, but they show a philopatric behavior in returning to the same aggregation area in a yearly basis where it is presumed that breeding is occurring (Weng et al., 2007a; Domeier and Nasby-Lucas, 2008; 2012; Jorgensen et al., 2012). The results of the analysis with bi-parentally inherited microsatellite markers suggest a genetic relationship between white sharks from GI and immature white sharks from all sampled coastal areas. Unlike the mtDNA results, there are no genetic differences in nuclear DNA between immature white sharks sampled in SCB and BV. These results suggest that males from GI mate with females from GI, regardless of their preference for parturition areas, leading to the homogeneity found in the nuclear DNA in young sharks across coastal sampled locations. Pardini et al. (2001) suggested a similar male-mediated gene flux by AWS in Australia/New Zealand and South Africa based on genetic homogeneity found in the by-parental inherited nuclear DNA. Contrastingly, Blower et al. (2012) found significant genetic differences in nuclear DNA between eastern and southwestern Australia and they suggested that adult males might exhibit some degree of reproductive philopatry; however, because the Bonferroni correction show no significant differences, authors highlight the need of more nuclear loci (they used 6 microsatellite loci) and other genetic markers. Although my nuclear DNA results suggest a male-mediated gene flux similar to Pardini et al. (2001), the number and quality of nuclear loci must be increased (O´Leary et al., 2013; O´Leary et al., 2015). In addition, to fully understand male and female mediated gene-flow samples from CC must be included. In addition a parentage analysis would dramatically increase the knowledge of the genetic relationships of white sharks between aggregation sites and the coastal nursery area.

In the NEP, the potential for two independent nursery areas for white sharks is suggested by the mtDNA differences between SCB and BV, together with the analysis of incidental catch records of white sharks tested against the Heupel et al. (2007) criteria. First, the SCB has been proposed as a nursery ground based on the presence of immature sharks (Klimley, 1985; Lowe et al., 2012). This concept was then expanded to include the region between Point Conception and BV based on the presence and movements of YOY and JWS (Weng et al., 2007b; Domeier, 2012; Weng et al., 2012). The results of this study supports Santana-Morales et al. (2012)´s suggestion that BV is also an important hotspot nursery area for white sharks in NEP. The seasonality and high frequency of incidental catches of NWS and YOY in the area support the proposing that BV could be an important and distinct nursery habitat. Based on tagging data there is movement between these hotspots (Weng et al., 2007b; Weng et al., 2012). This pattern of movement and habitat use is similar to the findings on juvenile white sharks from Australia (Bruce and Bradford, 2012). These researchers concluded that juveniles were using two small areas (called as “primary residency areas (nursery areas)”) at a higher frequency, but that sharks were using all the western region of Australia as a large corridor between nurseries (Bruce and Bradford, 2012).

Although some YOY and JWS from SCB move southward to the proposed BV white shark nursery hotspot (Weng et al., 2007b; Weng et al., 2012), to fully examine connectivity between regions it is necessary to conduct tagging studies for white sharks in BV. This will compliment current efforts to understand the timing of movements of the early life-stages of the white sharks in the west coast of Baja California. Heupel et al. (2015) used acoustic arrays to study the movements of bull sharks in Australia, and found that approximately half of 75 bull sharks moved from temperate to tropical reef regions. The study region of Heupel et al. (2015) comprised two state jurisdictions of eastern Australia (Queensland and New South Wales) with different management regimes for bull shark, highlighting the need to understand their movements. Understanding the distribution and movement of white sharks will improve the management of the immature white sharks in the NEP in both US and Mexican coastal waters. Chapman et al. (2015) mentioned that seasonal residency and site fidelity shark species render them vulnerable to spatially concentrated fishing when that fishing affects them during their residency periods. The impact of localized overfishing can be even broader when parturition or nursery sites are targeted. This can not only reduce the pool of returning adult females and newborns but also the local abundance of individuals at older life stages over time if juveniles typically reside in or return to their natal sites, as was suggested for lemon shark *Negaprion brevirostris*, in the Bahamas (Chapman et al., 2009). Effective management of species with movement patterns similar to white sharks requires a considerable information on movements in relation to the spatiotemporal distribution of fishing and other threats (Chapman et al., 2015).

5.2. Importance of Bahia Vizcaino for white sharks population

Based on Myers (2002), recruitment could be defined as the number of sharks that reach certain age or class. Clearly, juvenile and sub-adults white sharks are important in the recruitment to adult aggregation areas in the NEP population; however, the processes and rate of recruitment of juvenile white sharks from nursery areas to sub-adult and adult habitats are poorly understood (Kanive et al., 2015).

The genetic relationship between immature white sharks from BV and sub-adults and adults from GI as well as the high frequency of NWS and YOY incidentally caught reported in BV, suggest that some white sharks are born near BV, spent their first life-stage around the area. Unfortunately without nuclear DNA from CC, how coastal regions are linked to adult aggregation sites it not clear. Yates et al. (2012) suggested that delimitation of a nursery areas has ecological and management implications, so it is important to understand how these areas may affect recruitment. In the general shark population model proposed by Springer (1967), young are born in nearshore nursery areas in spring/summer, where they growth until reaching the size of maturity and then they leave to offshore waters to the adult population. This model is different to the model proposed for coastal shark populations (Knip et al., 2010), where all the life stages remain in nearshore environments. Clearly, the model for white sharks is different and more complicated. It is critical to develop a population model for NEP white sharks, where we don’t understand either the dynamics of movements within the nursery area and between nursery hotspots or the recruitment from coastal nursery regions to sub-adult and adult habitat.

The global abundance of white sharks is unknown because it’s wide distribution and the difficulty in assessing populations of large highly migratory species for which there is little to no fisheries data. There were two local estimates of the abundance in NEP based on photo-identification. In CC, Chapple et al. (2011) used Photo ID and tag-recapture analyses for individuals aggregating off the Farallon Islands and Tomales Point (central California). They estimated a central California population of 219 adult and sub-adult white sharks and suggested that this number comprised approximately half the total abundance in the NEP. At GI, photo-identification data was similarly used to estimate a local population size of 120 sharks (Sosa-Nishizaki et al., 2012), and authors mentioned that together with results on central California (Chapple et al., 2011), the population estimates suggest a total of 349 sub-adult and adult white sharks visiting these two aggregation sites. Neither of these estimates included immature white sharks from coastal areas nor adult sharks from other regions in NEP. For these, and a number of other reasons (Dewar et al., 2013; Burgess et al., 2014), this is an underestimate of the total population size of white sharks in the NEP.

Table 8. White shark population estimates in the North Eastern Pacific (NEP).

Source	Region	# individuals	Scale	Life stages	Details
Chapple et al., 2011	Central California, USA	219	Local	Adults and sub-adults	Bayesian Mark/Recapture algorithm. Photo-Identification
Sosa-Nishizaki et al., 2012	Guadalupe Island, Mexico	120	Local	Adults and sub-adults	Mark/Recapture with CJS and JS. Photo-Identification
Dewar et al., 2013	North Eastern Pacific	~ 3,000 (> 200 mature females)	Regional	All	PVA of SEDM using Chapple et al., 2011 and Sosa-Nishizaki et al., 2012
Burgess et al., 2014	Central California, USA	2,418	Local	All	Demographics using Jorgensen et al., 2010 and Chapple et al., 2011

Estimates presented average or most probable number; CJS indicates a Cormack-Jolly-Seber for superpopulation size estimate used; JS indicates a Jolly-Seber based open population mark/recapture model was used; PVA indicates a Population Viability Analysis used; SEDM indicates a Structured Expert Decision Making method to make decisions used.

Dewar et al. (2013) use the data from Chapple et al. (2011) and Sosa-Nishizaki et al. (2012) to estimate a total population of ~ 3,000 white sharks including males and females across size classes and a mature female abundance level of > 200 (Table 8). In a recent study, Burgess et al. (2014) applied a demographic model using the data from Jorgensen et al. (2010) and Chapple et al. (2011) to estimate a minimum population size of ~2000 individuals across life stages. Burgess et al. (2014) mentioned that their estimation is similar and comparable to the estimation of ~3,000 individuals made by Dewar et al. (2013) using all dataset available for NEP. Based on their estimations, Dewar et al. (2013) and Burgess et al. (2014) suggest that the population is at least stable, with data suggesting that the population size is increasing. Both studies highlighted the importance of survival in immature sharks for the stability and growth of the population.

My results suggest high fishing pressure on the immature white sharks in Mexican Pacific waters, which could negatively impact the white shark population in NEP. Mollet and Cailliet (2002) assessed the importance of immature stages in several species using stage-based models to explain the population trends in species like white sharks. These models emphasize the use of the survival and abundance of newborns, juveniles and adults, suggesting that survival and abundance of immature white sharks are relevant for population growth rate estimations. Consequently, there is a need to evaluate the fishing pressure on the white shark population in nursery habitats especially in SCB and BV. A rough estimate of the incidental catches rates of white sharks in BV, suggest a positive effect of the shark fishing ban imposed by federal government (DOF, 2012). This could, in turn, have a positive impact on the survival and abundance of the population of white sharks in the NEP. However, more data is needed on fishing mortality and population dynamics over time to fully assess the population status of white sharks in the NEP.

5.3. Conservation needs for white sharks

In order to help ensure the long-term stability the white shark population in the NEP, the release of immature white sharks from artisanal fisheries should be promoted. As reported by Santana-Morales et al. (2012), incidental catches of white sharks occurs along the west coast of Baja California. Their near-shore distribution makes them susceptible to being incidentally caught. The Mexican government established a threatened status for white sharks in 2002 (DOF, 2002) and more recently established a total fishing ban for white sharks in Mexican waters (DOF, 2014), emphasizing the practice of release the incidentally caught white sharks. Based on studies on post-release survival of juveniles (Lyons et al., 2013b), the vast majority of white sharks can survive if released after being in a net for up to 24 hr. The release of live sharks will reduce fishing mortality rates of juveniles and YOY without requiring a total fishing ban.

Other protective measured are also in place on white sharks across life-history phases. In Mexico, GI has been protected since 2005 (DOF, 2005), which has led to conservation measures on sub-adult and adult white shark and increased interest in their biology and ecology. Regarding the immature white sharks life stages, the Mexican government implemented a Conservation Program of Threatend Species (PROCER, in

Spanish – Programa de Conservación de Especies en Riesgo), leading to monitoring programs on the incidental catch of this species, as well as social programs to raise awareness with fishermen (Guerrero-Ávila et al., 2013).

The results of the present thesis suggest the need for a coordinated management strategy between the U.S. and Mexico given the overlap in habitat use across life history stages. To implement coordinated management plan additional information would be helpful. It will be important to 1) understand the rates of exchange between the nursery hotspots in the U.S. and Mexico; 2) to map high-use areas used and then manage fishing effort and/or soaks times to reduce fishing mortality and 3) to determine the patterns of recruitment between the coastal regions and sub-adult and adult aggregation sites.

5.4. Final remarks

Klimley (1985) used the data on size distribution and seasonality from catch records and reports to describe the habitat use of white sharks in the NEP across life history stages. He theorized that SCB was a pupping and nursery ground for white sharks in the summer months given the occurrence of YOY. For adults, he concluded that their primary habitat was Central and Northern California. Recently, the nursery area has been extended to Bahia Vizcaino in Baja California (Weng et al., 2007b; Domeier, 2012). The results of this thesis led to suggest the existence of two nursery hot-spots, i.e. nursery areas, SCB and BV, important potential sites for concentrating management and conservation efforts.

Additional research needs include 1) determining pupping locations of females from CC, 2) tagging YOY and juveniles from BV to determine the relative importance of different regions and the connectivity between regions, 3) increasing the sample size and number of loci in genetic studies and including samples from CC in the analyses of nuclear DNA, 4) implement trophic studies to understand the habitat use of white shark in BV, and 5) enhance studies on sub-adult movements, distribution and genetic relationships to understand the recruitment patterns in the NEP white shark population.

Chapter 6. General Conclusions

My first hypothesis focused on assessing genetic similarity in the white shark population of the NEP. Based on the mtDNA findings, this work suggests genetic differences between adults from the central California region and Guadalupe Island. The results from this work suggest that there may be two genetically distinct reproductive subgroups of white sharks within the study region. Adult and sub-adult white sharks from central California differed genetically from all age classes observed from Guadalupe Island as well as coastal waters between Point Conception and the Gulf of California. Future work needed to confirm these findings should focus on increasing the number of females sampled from central California, nuclear DNA analyses and the inclusion of samples from all NEP regions to assess bi-parental genetic relationships.

The second hypothesis was that immature white sharks from Bahia Sebastian Vizcaino are genetically similar to adults from Guadalupe Island. Based on the mtDNA results, there is a high probability of a matrilineal origin of most of the immature white sharks sampled in coastal waters from adult white sharks from Guadalupe Island. These results further suggest the need to understand habitat use in Bahia Sebastian Vizcaino and other coastal habitats. It is needed to increase samples from all coastal areas, and it is also needed parentage analysis using mitochondrial and nuclear DNA markers to fully understand the relationship between adults and immature white sharks in NEP.

The immature white sharks from Bahia Sebastian Vizcaino and Southern California Bight were found to have no genetic differences in mtDNA with sharks from Guadalupe Island. However, there were differences between the immature shark areas that were sampled, suggesting that adult females from Guadalupe Island give birth to sharks found in both the SCB and BV. Future work focused on movement patterns of adults and juveniles is needed to better understand the reproductive dynamics of white sharks in the NEP.

The third hypothesis was that Bahia Sebastian Vizcaino is an important nursery area or “hot-spot” for juvenile white sharks in the NEP. In Mexico, Bahia Sebastian Vizcaino has been shown to be an important habitat for newborn and young-of-the-year white sharks. Incidental catch data from this study and previous work suggests that YOY and newborn sharks are more frequently caught in this region than anywhere else in the northern region of Baja California. These findings were found to fully support the criteria put forth by Heupel et al. (2007) for defining shark nursery areas and confirms previous hypotheses on the importance of Bahia Sebastian Vizcaino for YOY and newborn white sharks. Additional study that focuses on assessing newborn presence in other areas along Baja California that receive less fishing pressure are needed to determine how important BV is relative to adjacent areas. This work has also identified the need to investigate fishing gear dynamics (i.e., nets size, depth fished, soak time) within the BV region. I am confident that gear development and field observation hold the keys to reducing incidental catch mortality within this nursery hot-spot of the NEP.

References

Aljanabi, S. M., Martinez, I. (1997). Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic acids research*, *25* (22), 4692-4693. doi:10.1093/nar/25.22.4692.

Álvarez-Borrego, S., Granados-Guzmán, A. (1992). Variación espacio-temporal de temperatura en un hábitat de invierno de la ballena gris: Laguna Ojo de Liebre. *Ciencias Marinas*, *18* (1), 151-165.

Allen, L. G. (1988). Recruitment, distribution, and feeding habits of young-of-the-year California halibut (*Paralichthys californicus*) in the vicinity of Alamitos Bay-Long Beach Harbor, California, 1983-1985. *Bulletin of the Southern California Academy of Science*, *87* (1), 19-30.

Allen, M. J., Mikel, T., Cadien, D., Kalman, J. E., Jarvis, E. T., Schiff, K. C., Diehl, D. W., Moore, S. L., Walther, S., Deets, G., Cash, C., Watts, S., Pondella II, D. J., Raco-Rands, V., Thomas, C., Gartman, R., Sabin, L., Power, W., Groce, A. K., Armstrong, J. L., (2007). Southern California Bight 2003 regional monitoring program: IV. Demersal fishes and megabenthic invertebrates. Southern California Coastal Water Research, Costa Mesa, CA. pp. 365.

Amador-Buenrostro, A., Argote-Espinosa, M. L., Mancilla-Peraza, M., Figueroa-Rodríguez, M. (1995). Variaciones de periodo corto de la circulación anticiclónica en Bahía Sebastián VIzcaíno, BC. *Ciencias Marinas*, *21* (2), 201-223.

Anderson, S. D., Pyle, P. (2003). A temporal, sex-specific occurrence pattern among white sharks at the South Farallon Islands, California. *California Fish and Game*, *89* (2), 96-101.

Barton, J., Pope, A., Howe, S., (2012). Marine natural values study. Vol 2: Marine Protected Areas of the Victorian Embayments Bioregion, Part 2 Western Bay & Corner Inlet Parks Victoria Technical Series, Parks Victoria, Melbourne. pp. 126.

Bass, A. J., (1978). Problems in studies of sharks in the Southwest Indian Ocean. in: Hodgson, E.S. Mathewson, R.F. (Eds.), *Sensory biology of sharks, skates and rays*. Office of Naval Research, Department of the Navy, Arlington, VA, pp. 545-594.

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F., Weinstein, M. P. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience*, *51* (8), 633-641. doi:10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2.

Blower, D. C., Pandolfi, J. M., Bruce, B. D., Gomez-Cabrera, M., Ovenden, J. R. (2012). Population genetics of Australian white sharks reveals fine-scale spatial structure, transoceanic dispersal events and low effective population sizes. *Marine Ecology Progress Series*, *455* 229-244. doi:10.3354/meps09659.

Bonfil, R., Meyer, M., Scholl, M. C., Johnson, R., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D., Paterson, M. (2005). Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science*, *310* (5745), 100-103. doi:10.1126/science.1114898.

Boustany, A. M., Davis, S. F., Pyle, P., Anderson, S. D., Le Boeuf, B. J., Block, B. A. (2002). Satellite tagging. Expanded niche for white sharks. *Nature*, *415* (6867), 35-36. doi:10.1038/415035b.

Bruce, B. D. (1992). Preliminary observations on the biology of the white shark, *Carcharodon carcharias*, in South Australian waters. *Aust J Mar Fresh Res*, *43* (1), 1-11.

Bruce, B. D., (2008). The biology and ecology of the white shark, *Carcharodon carcharias*. in: Camhi, M.D., Pikitch, E.K. Babcock, E.A. (Eds.), *Sharks of the open ocean. Biology, fisheries and conservation*. Blackwell Publishing, Oxford, U.K., pp. 69-81.

Bruce, B. D., Bradford, R. W., (2012). Habitat use and spatial dynamics of juvenile white sharks, *Carcharodon carcharias*, in Eastern Australia. in: Domeier, M.L. (Ed.), *Global perspectives on the biology and life history of White Shark*. CRC Press, New York, USA, pp. 225-254.

Bruce, B. D., Stevens, J. D., Bradford, R. W., (2005). Site fidelity, residence times & home range patterns of white sharks around pinniped colonies. in: Trust, N.H., (Ed). CSIRO Marine and Atmospheric, Australia. pp. 45.

Bruce, B. D., Stevens, J. D., Malcolm, H. (2006). Movements and swimming behaviour of white sharks (Carcharodon carcharias) in Australian waters. *Marine biology*, *150* (2), 161-172. doi:10.1007/s00227-006-0325-1.

Brusca, R. C., Wallerstein, B. (1979). Zoogeographic patterns of idoteid isopods in the Northeast Pacific, with a review of shallow water zoogeography for the region. *Bulletin of the Biological Society of Washington*, *3* 67-105.

Burgess, G. H., Bruce, B. D., Cailliet, G. M., Goldman, K. J., Grubbs, R. D., Lowe, C. G., MacNeil, M. A., Mollet, H. F., Weng, K. C., O'Sullivan, J. B. (2014). A re-evaluation of the size of the white shark (*Carcharodon carcharias*) population off California, USA. *PloS one*, *9* (6), e98078. doi:10.1371/journal.pone.0098078.

Cailliet, G. M., Natanson, L. J., Weldon, B. A., Ebert, D. A. (1985). Preliminary studies on the age and growth of the white shark *Carcharodon carcharias*, using vertebral bands. *Southern California Academy of Sciences Memoirs*, *9* 46-60.

Cartamil, D., Santana-Morales, O., Escobedo-Olvera, M., Kacev, D., Castillo-Geniz, L., Graham, J. B., Rubin, R. D., Sosa-Nishizaki, O. (2011). The artisanal elasmobranch fishery of the Pacific coast of Baja California, Mexico. *Fisheries Research*, *108* (2-3), 393-403. doi:10.1016/j.fishres.2011.01.020.

Cartamil, D. P., Wegner, N. C., Kacev, D., Ben-aderet, N., Kohin, S., Graham, J. B. (2010). Movement patterns and nursery habitat of juvenile thresher sharks *Alopias vulpinus* in the Southern California Bight. *Marine Ecology Progress Series*, *404* 249-258. doi:10.3354/meps08495.

Casey, J. G., Pratt, H. L., Jr. (1985). Distribution of the white shark, *Carcharodon carcharias*, in the western North Atlantic. *Southern California Academy of Sciences Memoirs*, *9* 2-14.

Castro, J. (1993). The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environmental Biology of Fishes*, *38* (1-3), 37-48. doi:10.1007/BF00842902.

Castro, J. I., (2012). A summary of observations on the maximum size attained by the white shark, *Carcharodon carcharias*. in: Domeier, M.L. (Ed.), *Global perspectives on the biology and life history of White Shark*. CRC Press, New York, USA, pp. 85-90.

Compagno, L. J. V., Dando, M., Fowler, S., (2005). Sharks of the World. Princeton University Press, New Jersey.

Compagno, L. J. V., Marks, M. A., Fergusson, I. K. (1997). Threatened fishes of the world: *Carcharodon carcharias* (Linnaeus, 1758) (Lamnidae). *Environmental Biology of Fishes*, *50* (1), 61-62. doi:10.1023/A:1007308406137.

CONAPESCA. (2014). *Consulta específica por especie*. Access on June 2014, from http://www.conapesca.sagarpa.gob.mx/wb/cona/consulta_especifica_por_produccion

Conrath, C. L., Musick, J. A. (2007). Investigations into depth and temperature habitat utilization and overwintering grounds of juvenile sandbar sharks, *Carcharhinus plumbeus*: the importance of near shore North Carolina waters. *Environmental Biology of Fishes*, *82* (2), 123-131. doi:10.1007/s10641-007-9263-0.

COSEWIC, (2006). COSEWIC assessment and status report on the White Shark *Carcharodon carcharias* (Atlantic and Pacific populations) in Canada. Ottawa. pp. vii + 31.

Cowen, R. K., Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, *1* (1), 443-466. doi:10.1146/annurev.marine.010908.163757.

Curtis, T. H., Kelly, J. T., Menard, K. L., Laroche, R. K., Jones, R. E., Klimley, A. P. (2006). Observations on the behavior of white sharks scavenging from a whale carcass at Point Reyes, California. *California Fish and Game*, *92* (3), 113-124.

Curtis, T. H., McCandless, C. T., Carlson, J. K., Skomal, G. B., Kohler, N. E., Natanson, L. J., Burgess, G. H., Hoey, J. J., Pratt, H. L., Jr. (2014). Seasonal distribution and historic trends in abundance of white sharks, *Carcharodon carcharias*, in the western North Atlantic Ocean. *PloS one*, *9* (6), e99240. doi:10.1371/journal.pone.0099240.

Chapman, D. D., Babcock, E. A., Gruber, S. H., Dibattista, J. D., Franks, B. R., Kessel, S. A., Guttridge, T., Pikitch, E. K., Feldheim, K. A. (2009). Long-term natal site-fidelity by immature lemon sharks (Negaprion brevirostris) at a subtropical island. *Molecular ecology*, *18* (16), 3500-3507. doi:10.1111/j.1365-294X.2009.04289.x.

Chapman, D. D., Feldheim, K. A., Papastamatiou, Y. P., Hueter, R. E. (2015). There and Back Again: A Review of Residency and Return Migrations in Sharks, with Implications for Population Structure and Management. *Annual Review of Marine Science*, *7* (1), 547-570. doi:doi:10.1146/annurev-marine-010814-015730.

Chapple, T. K., Jorgensen, S. J., Anderson, S. D., Kanive, P. E., Klimley, A. P., Botsford, L. W., Block, B. A. (2011). A first estimate of white shark, *Carcharodon carcharias*, abundance off Central California. *Biology letters*, *7* (4), 581-583. doi:10.1098/rsbl.2011.0124.

Chin, A., Heupel, M. R., Simpfendorfer, C. A., Tobin, A. J. (2013). Ontogenetic movements of juvenile blacktip reef sharks: evidence of dispersal and connectivity between coastal habitats and coral reefs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *23* (3), 468-474. doi:10.1002/aqc.2349.

Dahlgren, C. P., Kellison, G. T., Adams, A. J., Gillanders, B. M., Kendall, M. S., Layman, C. A., Ley, J. A., Nagelkerken, I., Serafy, J. E. (2006). Marine nurseries and effective juvenile habitats: concepts and applications. *Marine Ecology Progress Series*, *312* 291-295. doi:10.3354/meps312291.

Dailey, M. D., Anderson, J. W., Reish, D. J., Gorsline, D. S., (1993). The Southern California Bight: background and setting. in: Dailey, M.D., Reis, D.J. Anderson, J.W. (Eds.), *Ecology of the Southern California Bight: A synthesis and interpretation*. University of California Press, Berkeley, CA, USA, pp. 1-18.

Dale, J. J., Wallsgrove, N. J., Popp, B. N., Holland, K. N. (2011). Nursery habitat use and foraging ecology of the brown stingray *Dasyatis lata* determined from stomach contents, bulk and amino acid stable isotopes. *Marine Ecology Progress Series*, *433* 221-236. doi:10.3354/meps09171.

Dawson, M. N., Waples, R. S., Bernardi, G., (2006). Phylogeography. in: Allen, L.G., Pondella II, D.J. Horn, M.H. (Eds.), *The ecology of marine fishes. California and adjacent waters*. University of California Press, California, Usa, pp. 26-54.

De la Cruz-Agüero, J., Arellano-Matínez, M., Cota-Gómez, V. M. (1996). Lista sistemática de los peces marinos de las lagunas Ojo de Liebre y Guerrero Negro, BCS y BC, México. *Ciencias Marinas*, *22* (1), 111-128.

Dewar, H., Domeier, M., Nasby-Lucas, N. (2004). Insights into young of the year white shark, *Carcharodon carcharias*, behavior in the Southern California Bight. *Environmental Biology of Fishes*, *70* (2), 133-143. doi:10.1023/B:Ebfi.0000029343.54027.6a.

Dewar, H., Eguchi, T., Hyde, J., Kinzey, D., Kohin, S., Moore, J., Taylor, B. L., Vetter, R., (2013). Status review of the Northeastern Pacific population of white sharks (*Carcharodon carcharias*) under the Endangered Species Act. National Oceanic and Atmospheric Administration, La Jolla, California. pp. 153.

DOF, (2002). NORMA Oficial Mexicana NOM-059-ECOL-2001, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo in: SEMARNAT, (Ed). Diario Oficial de la Federación, México. pp. 1-85.

DOF, (2005). DECRETO por el que se declara área natural protegida, con la categoría de reserva de la biosfera, la zona marina y terrestre que incluye a la Isla Guadalupe, de jurisdicción federal, así como a las demás superficies emergidas que se encuentran dentro de la misma, localizada en el Océano Pacífico, frente a la costa de la Península de Baja California, con una superficie total de 476,971-20-15.79 hectáreas. in: SEMARNAT, (Ed). Diario Oficial de la Federación, México. pp. 9-15.

DOF, (2007). NORMA Oficial Mexicana NOM-029-PESC-2006, Pesca responsable de tiburones y rayas. Especificaciones para su aprovechamiento. in: SAGARPA, (Ed). Diario Oficial de la Federación, México. pp. 59-101.

DOF, (2010). NORMA Oficial Mexicana NOM-059-SEMARNAT-2010, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. in: SEMARNAT, (Ed). Diario Oficial de la Federación, México. pp. 75.

DOF, (2012). ACUERDO por el que se modifica el Aviso por el que se da a conocer el establecimiento de épocas y zonas de veda para la pesca de diferentes especies de la fauna acuática en aguas de jurisdicción federal de los Estados Unidos Mexicanos, publicado el 16 de marzo de 1994 para establecer los periodos de veda de pulpo en el Sistema Arrecifal Veracruzano, jaiba en Sonora y Sinaloa, tiburones y rayas en el Océano Pacífico y tiburones en el Golfo de México. in: SAGARPA, (Ed). Diario Oficial de la Federación, México. pp. 27.

DOF, (2014). ACUERDO por el que se establece veda permanente para la pesca de tiburón blanco (*Carcharodon carcharias*) en aguas de jurisdicción federal de los Estados Unidos Mexicanos. in: SAGARPA, (Ed). Diario Oficial de la Federación, México. pp. 1-3.

Domeier, M. L., (2012). A new life-history hypothesis for white sharks, *Carcharodon carcharias*, in the Northeastern Pacific. in: Domeier, M.L. (Ed.), *Global perspectives on the biology and life history of White Shark*. CRC Press, New York, USA, pp. 199-224.

Domeier, M. L., Nasby-Lucas, N. (2007). Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico). *Marine biology*, *150* (5), 977-984. doi:10.1007/s00227-006-0380-7.

Domeier, M. L., Nasby-Lucas, N. (2008). Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Marine Ecology Progress Series*, *370* 221-237. doi:10.3354/meps07628.

Domeier, M. L., Nasby-Lucas, N., (2012). Sex-Specific Migration Patterns and Sexual Segregation of Adult White Sharks, *Carcharodon carcharias*, in the Northeastern Pacific. in: Domeier, M.L. (Ed.), *Global perspectives on the biology and life history of White Shark*. CRC Press, New York, USA, pp. 133-146.

Domeier, M. L., Nasby-Lucas, N. (2013). Two-year migration of adult female white sharks (*Carcharodon carcharias*) reveals widely separated nursery areas and conservation concerns. *Animal Biotelemetry*, *1* (1), 2. doi:10.1186/2050-3385-1-2.

Duffy, C. A. J., Francis, M. P., Manning, M. J., Bonfil, R., (2012). Regional Population Connectivity, Oceanic Habitat, and Return Migration Revealed by Satellite Tagging of White Sharks, *Carcharodon carcharias*, at New Zealand Aggregation Sites. in: Domeier, M.L. (Ed.), *Global perspectives on the biology and life history of White Shark*. CRC Press, New York, USA, pp. 301-318.

Durazo, R., Ramírez-Manguilar, A. M., Miranda, L. E., Soto-Mardones, L. A., (2010). Climatología de variables hidrográficas. in: Gaxiola-Castro, G. Durazo, R. (Eds.), *Dinámica del ecosistema pelágico frente a Baja California. 1997-2007*. SEMARNAT, INE-SEMARNAT, CICESE, UABC, Baja California, México, pp. 25-57.

Earl, D., vonHoldt, B. (2012). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, *4* (2), 359-361. doi:10.1007/s12686-011-9548-7.

Ebert, D. A., (2003). Sharks, rays and chimaeras of California. University of California Press, Berkeley, CA.

Ebert, D. A., Fowler, S., Compagno, L. J. V., (2013). Sharks of the World. A fully illustrated guide. Wild Nature Press, Plymouth.

Escobedo-Olvera, M. Á., (2009). Análisis biológico pesquero de la pesquería con red agallera de deriva en la península de Baja California durante el período 1999-2008. Ecologia Marina. CICESE, Ensenada, BC, México. pp. 159.

Estrada, J. A., Rice, A. N., Natanson, L. J., Skomal, G. B. (2006). Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. *Ecology*, *87* (4), 829-834. doi:10.1890/0012-9658(2006)87[829:Uoiaov]2.0.Co;2.

Excoffier, L., Laval, G., Schneider, S. (2005). Arlequin (version 3.0): An integrated software package for population genetics data analysis. *Evol Bioinform*, *1* 47-50.

Fallows, C., Gallagher, A. J., Hammerschlag, N. (2013). White sharks (Carcharodon carcharias) scavenging on whales and its potential role in further shaping the ecology of an apex predator. *PloS one*, *8* (4), e60797. doi:10.1371/journal.pone.0060797.

Feldheim, K. A., Gruber, S. H., Ashley, M. V. (2001). Population genetic structure of the lemon shark (*Negaprion brevirostris*) in the western Atlantic: DNA microsatellite variation. *Molecular ecology*, *10* (2), 295-303.

Fergusson, I. K., (1996). Distribution and autoecology of the white shark in the eastern north Atlantic Ocean and in the Mediterranean Sea. in: Klimley, A.P. Ainley, D.G. (Eds.), *Great white sharks: The biology of Carcharodon carcharias*. Academic Press, Inc., San Diego, pp. 321-345.

Ferreira, C. A., Ferreira, T. P., (1996). Population dynamics of white sharks in South Africa. in: Klimley, A.P. Ainley, D.G. (Eds.), *Great white sharks: the biology of Carcharodon carcharias*. Academic Press, San Diego, pp. 381-391.

Fonseca, P., Martins, R., Campos, A., Sobral, P. (2005). Gill-net selectivity off the Portuguese western coast. *Fisheries Research*, *73* (3), 323-339. doi:10.1016/j.fishres.2005.01.015.

Francis, M. P., (1996). Observations on a pregnant white shark with a review of reproductive biology. in: Klimley, A.P. Ainley, D.G. (Eds.), *Great white sharks: the biology of Carcharodon carcharias*. Academic Press, San Diego, pp. 157-172.

Francis, M. P., Duffy, C., Lyon, W. (2015). Spatial and temporal habitat use by white sharks (*Carcharodon carcharias*) at an aggregation site in southern New Zealand. *Marine and Freshwater Research* -. doi:10.1071/MF14186.

Friedlander, A., Kobayashi, D., Bowen, B., Meyers, C., Papastamatiou, Y., DeMartini, E., Parrish, F., Treml, E., Currin, C., Hilting, A., Weiss, J., Kelley, C., O'Conner, R., Parke, M., Clark, R., Toonen, R., Wedding, L., (2009). Connectivity and integrated ecosystem studies. in: Friedlander, A., Keller, K., Wedding, L., Clarke, A. Monaco, M. (Eds.), *A Marine Biogeographic Assessment of the Northwestern Hawaiian Islands: Connectivity and Integrated Ecosystem Studies*. CCMA, Silver Spring, MD, pp. 291 - 330.

Frisk, M. G., Jordaan, A., Miller, T. J. (2014). Moving beyond the current paradigm in marine population connectivity: are adults the missing link? *Fish and Fisheries*, *15* (2), 242-254. doi:10.1111/faf.12014.

Galván-Magaña, F., Hoyos-Padilla, E. M., Navarro-Serment, C. J., Márquez-Farías, F. (2010). Records of white shark, *Carcharodon carcharias*, in the Gulf of California, Mexico. *Marine Biodiversity Records*, *3*. doi:10.1017/s1755267210000977.

García-Rodríguez, E., (2012). Análisis de la pesquería del tiburón azul en la costa oeste de Baja California con inferencias en el estado de la población. Ecología Marina. CICESE, Ensenada, BC, México. pp. 71.

Goudet, J., (2001). FSTAT, a program to estimate and test gene diversities and fixation indices Recuperado de: http://www2.unil.ch/popgen/softwares/fstat.htm.

Gubili, C., Bilgin, R., Kalkan, E., Karhan, S. U., Jones, C. S., Sims, D. W., Kabasakal, H., Martin, A. P., Noble, L. R. (2011). Antipodean white sharks on a Mediterranean walkabout? Historical dispersal leads to genetic discontinuity and an endangered anomalous population. *Proceedings Biological sciences / The Royal Society*, *278* (1712), 1679-1686. doi:10.1098/rspb.2010.1856.

Gubili, C., Robinson, C. E. C., Cliff, G., Wintner, S. P., de Sabata, E., De Innocentiis, S., Canese, S., Sims, D. W., Martin, A. P., Noble, L. R., Jones, C. S. (2015). DNA from historical and trophy samples provides insights into white shark population origins and genetic diversity. *Endangered Species Research*, *27* (3), 233-241. doi:10.3354/esr00665.

Gubili, C., Sims, D. W., Verissimo, A., Domenici, P., Ellis, J., Grigoriou, P., Johnson, A. F., McHugh, M., Neat, F., Satta, A., Scarcella, G., Serra-Pereira, B., Soldo, A., Genner, M. J., Griffiths, A. M. (2014). A tale of two seas: contrasting patterns of population structure in the small-spotted catshark across Europe. *Royal Society Open Science*, *1* (3), 140175-140175. doi:10.1098/rsos.140175.

Guerrero-Ávila, C., González-Romero, S., Gracia-Ruiz, J. J., Ayala-Martínez, J. J., Alarcón-Farfán, S., (2013). Caracterización de las zonas de mayor captura incidental de juveniles y recién nacidos de tiburón blanco (*Carcharodon carcharias*) en la Bahía Sebastián Vizcaíno por la pesca comercial: Implementación de un programa piloto de marcaje y recaptura. in: Protegidas, C.N.d.Á.N., (Ed). Terra Peninsular, Ensenada, BC, México. pp. 56.

Gutiérrez-de Velazco, G., (2000). Análisis de la Circulación y las condiciones físicas de la Laguna Ojo de Liebre, B.C.S. con relación a la mortandad de tortuga marinas durante Diciembre de 1997. CICESE, La Paz, BCS. pp. 45.

Hamady, L. L., Natanson, L. J., Skomal, G. B., Thorrold, S. R. (2014). Vertebral bomb radiocarbon suggests extreme longevity in white sharks. *PloS one*, *9* (1), e84006. doi:10.1371/journal.pone.0084006.

Hanan, D. A., Holts, D. B., Coan, A. L. J. (1993). The California drift gill net fishery for sharks and swordfish, 1981–82 through 1990–91. *Fish Bulletin*, *175* 95.

He, P., Pol, M., (2010). Fish behavior near gillnets: Capture process and influencing factors. in: He, P. (Ed.), *Behavior of marine fishes: capture processes and conservation challenges*. Willey-Blackwell, Ames, Iowa, pp. 183-204.

Heist, E. J., Graves, J. E., Musick, J. A. (1995). Population genetics of the sandbar shark (Carcharhinus plumbeus) in the gulf of Mexico and mid-Atlantic Bight. *Copeia* (3), 555-562.

Heithaus, M. R., (2007). Nursery areas as essential shark habitat: A theoretical perspective. in: McCandless, C.T., Kohler, N.E. Pratt, H.L.J. (Eds.), *Shark nursery* *grounds of the Gulf of Mexico and the East coast waters of the United States*. American Fisheries Society, Bethesda, Maryland, pp. 3-13.

Heithaus, M. R., Burkholder, D., Hueter, R. E., Heithaus, L. I., Pratt, J. H. L., Carrier, J. C. (2007). Spatial and temporal variation in shark communities of the lower Florida Keys and evidence for historical population declines. *Canadian Journal of Fisheries and Aquatic Sciences*, *64* (10), 1302-1313. doi:10.1139/f07-098.

Hernández-Rivas, M. E., Jiménez-Rosenberg, S. P., Funes-Rodríguez, R., Saldierna-Martínez, R. J., (2000). El Centro de Actividad Biológica de la Bahía de Sebastián Vizcaíno, una primera aproximación. in: Lluch-Belda, S.E., Lluch-Cota, J. Ponce, G., (Eds). BACs: Centros de Actividad Biológica del Pacífico Mexicano. CICIMAR y CONACyT, La Paz, BCS, México. pp. 65-85.

Heupel, M., Simpfendorfer, C., Espinoza, M., Smoothey, A., Tobin, A., Peddemors, V. (2015). Conservation challenges of sharks with continental scale migrations. *Frontiers in Marine Science*, *2*. doi:10.3389/fmars.2015.00012.

Heupel, M. R., Carlson, J. K., Simpfendorfer, C. A. (2007). Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series*, *337* 287-297. doi:10.3354/meps337287.

Heupel, M. R., Simpfendorfer, C. A. (2008). Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. *Aquatic Biology*, *1* 277-289. doi:10.3354/ab00030.

Heupel, M. R., Simpfendorfer, C. A., Collins, A. B., Tyminski, J. P. (2006). Residency and movement patterns of bonnethead sharks, Sphyrna tiburo, in a large Florida estuary. *Environmental Biology of Fishes*, *76* (1), 47-67. doi:10.1007/s10641-006-9007-6.

Hilton-Taylor, C. (2000). *IUCN Red list of threatened species*. Access on 2013, from http://www.iucnredlist.org/details/3855/0

Holts, D. B., Bedford, D. W. (1993). Horizontal and vertical movements of the shortfin mako shark, *Isurus oxyrinchus*, in the Southern California Bight. *Aust J Mar Fresh Res*, *44* 901-909.

Hollensead, L. D., Grubbs, R. D., Carlson, J. K., Bethea, D. M. (2015). Analysis of fine-scale daily movement patterns of juvenile *Pristis pectinata* within a nursery habitat. *Aquatic Conservation: Marine and Freshwater Ecosystems*. doi:10.1002/aqc.2556.

Horn, M. H., Allen, L. G., Lea, R. N., (2006). Biogeography. in: Allen, L.G., Pondella II, D.J. Horn, M.H. (Eds.), *The ecology of marine fishes. California and adjacent waters*. University of California Press, California, USA, pp. 3-25.

Hueter, R. E., Castillo–Géniz, J. L., Márquez–Farías, J. F., Tyminski, J. P., (2007). The use of Laguna Yalahau, Quintana Roo, Mexico as a primary nursery for the blacktip shark (*Carcharhinus limbatus)*. in: McCandless, C.T., Kohler, N.E. Pratt, H.L., Jr. (Eds.), *Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States*. American Fisheries Society, US, pp. 345-364.

Hueter, R. E., Heupel, M. R., Heist, E. J., Keeney, D. B. (2005). Evidence of Philopatry in Sharks and Implications for the Management of Shark Fisheries. *Journal of Northwest Atlantic Fishery Science*, *37* 239-247. doi:10.2960/J.v35.m493.

Jaime-Rivera, M., Caraveo-Patiño, J., Hoyos-Padilla, E. M., Galván-Magaña, F. (2013). Feeding and migration habits of white shark *Carcharodon carcharias* (Lamniformes: Lamnidae) from Isla Guadalupe inferred by analysis of stable isotopes δ15N and δ13C. *International Journal of Tropical Biology*, *62* (2), 637-647.

Jakobsson, M., Rosenberg, N. A. (2007). CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, *23* (14), 1801-1806. doi:10.1093/bioinformatics/btm233.

Jorgensen, S. J., Chapple, T. K., Anderson, S. D., Hoyos, M., Reeb, C., Block, B. A., (2012). Connectivity among white shark coastal aggregation areas in the Northeastern Pacific. in: Domeier, M.L. (Ed.), *Global perspectives on the biology and life history of White Shark*. CRC Press, New York, USA, pp. 159-167.

Jorgensen, S. J., Reeb, C. A., Chapple, T. K., Anderson, S., Perle, C., Van Sommeran, S. R., Fritz-Cope, C., Brown, A. C., Klimley, A. P., Block, B. A. (2010). Philopatry and migration of Pacific white sharks. *Proceedings Biological sciences / The Royal Society*, *277* (1682), 679-688. doi:10.1098/rspb.2009.1155.

Kabasakal, H., Özgür-Gedíkoglu, S. (2008). Two new-born great white sharks, *Carcharodon carcharias* (Linnaeus, 1758) (Lamniformes; Lamnidae) from Turkish waters of the north Aegean Sea. *Acta Adriatica*, *49* (2), 125-135.

Kanive, P. E., Rotella, J. J., Jorgensen, S. J., Chapple, T. K., Anderson, S. D., Klimley, A. P., Block, B. A. (2015). Estimating apparent survival of sub-adult and adult white sharks (Carcharodon carcharias) in central California using mark-recapture methods. *Frontiers in Marine Science*, *2*. doi:10.3389/fmars.2015.00019.

Keeney, D. B., Heupel, M. R., Hueter, R. E., Heist, E. J. (2005). Microsatellite and mitochondrial DNA analyses of the genetic structure of blacktip shark (*Carcharhinus limbatus*) nurseries in the northwestern Atlantic, Gulf of Mexico, and Caribbean Sea. *Molecular ecology*, *14* (7), 1911-1923. doi:10.1111/j.1365-294X.2005.02549.x.

King, M., (1995). Fisheries biology, assessment and management. Fishing News Book, Blackwell Science Ltd, UK, USA and Australia.

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

Klimley, A. P., Anderson, S. D., Pyle, P., Henderson, R. P. (1992). Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia* (3), 680-690.

Klimley, A. P., Beavers, S. C., Curtis, T. H., Jorgensen, S. J. (2002). Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. *Environmental Biology of Fishes*, *63* (2), 117-135.

Knip, D. M., Heupel, M. R., Simpfendorfer, C. A. (2010). Sharks in nearshore environments: models, importance, and consequences. *Marine Ecology Progress Series*, *402* 1-11. doi:10.3354/meps08498.

Kock, A., O'Riain, M. J., Mauff, K., Meyer, M., Kotze, D., Griffiths, C. (2013). Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PloS one*, *8* (1), e55048. doi:10.1371/journal.pone.0055048.

Krausman, P., (1999). Some basic principles of habitat use. in: Launchbaugh, K., Sanders, K. Mosley, J., (Eds). Grazing behavior of livestock and wildlife. University of Idaho, Moscow, USA. pp. 89-90.

Kumar, S., Tamura, K., Nei, M. (2004). MEGA3: Integrated software for molecular evolutionary genetics analysis and sequence alignment. *Brief Bioinform*, *5* (2), 150-163.

López-Rasgado, F. J., Herzka, S. Z. (2009). Assessment of habitat quality for juvenile California halibut (*Paralichthys californicus*) in a seasonally arid estuary. *Fish B-Noaa*, *107* 343-358.

Lowe, C. G., Blasius, M. E., Jarvis, E. T., Masori, T. J., Goodmanlowe, G. D., O'Sullivan, J. B., (2012). Historic fishery interactions with white sharks in the Southern California Bight. in: Domeier, M.L. (Ed.), *Global perspectives on the biology and life history of White Shark*. CRC Press, New York, USA, pp. 169-186.

Lyons, K., Carlisle, A., Preti, A., Mull, C., Blasius, M., O'Sullivan, J., Winkler, C., Lowe, C. G. (2013a). Effects of trophic ecology and habitat use on maternal transfer of contaminants in four species of young of the year lamniform sharks. *Marine environmental research*, *90* 27-38. doi:10.1016/j.marenvres.2013.05.009.

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

Lluch-Belda, D., (2000). Centros de Actividad Biológica en la costa occidental de Baja California. in: Lluch-Belda, S.E., Lluch-Cota, J. Ponce, G. (Eds.), *Centros de Actividad Biológica del Pacífico Mexicano*. CIBNOR, CICIMAR y CONACyT, La Paz, BCS, pp. 49-64.

Lluch-Belda, D., Lluch-Cota, D. B., Lluch-Cota, S. E. (2003). Baja California's Biological Transition Zones: Refuges for the California sardine. *Journal of Oceanography*, *59* (4), 503-513. doi:10.1023/A:1025596717470.

Malcolm, H., Bruce, B. D., Stevens, J. D., (2001). A review of the biology and status of white sharks in Australian waters. CSIRO Marine Research, Hobart. pp. 113.

Malpica-Cruz, L., Herzka, S. Z., Sosa-Nishizaki, O., Escobedo-Olvera, M. A. (2013). Tissue-specific stable isotope ratios of shortfin mako (*Isurus oxyrinchus*) and white (*Carcharodon carcharias*) sharks as indicators of size-based differences in foraging habitat and trophic level. *Fisheries Oceanography*, *22* (6), 429-445. doi:10.1111/fog.12034.

Mancilla-Peraza, M., Palacios-Hernández, E., López-Castillo, G. (1993). Variabilidad hidrográfica de Bahía Vizcaíno, Baja California, México. *Ciencias Marinas*, *19* (3), 265-284.

Martin, R. A. (2004). Northerly distribution of White Sharks, *Carcharodon carcharias*, in the Eastern Pacific and relation to ENSO events. *Marine Fisheries Review*, *66* (1), 16-28.

Martin, R. A., (2005). Predatory behaviour of white sharks at a Cape fur seal colony in South Africa. JMBA Global Marine Environment, South Africa. pp. 2.

Martin, R. A., Hammerschlag, N., Collier, R. S., Fallows, C. (2005). Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J Mar Biol Assoc Uk*, *85* (5), 1121-1135. doi:10.1017/S002531540501218x.

Mollet, H. F., Cailliet, G. M. (2002). Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. *Marine and Freshwater Research*, *53* (2), 503-516. doi:10.1071/Mf01083.

Morrissey, J. F., Gruber, S. H. (1993). Home range of juvenile lemon sharks, *Negaprion brevirostris*. *Copeia*, *1993* (2), 425-434. doi:10.2307/1447141.

Myers, R. A., (2002). Recruitment: Understanding density-dependence in fish populations. in: Hart, P.J.B. Reynolds, J.D. (Eds.), *Handbook of fish biology and fisheries*. Blackwell Publishing Ltd, pp. 123-148.

Navarro-Palacios, R. A., Mancilla-Peraza, M. (2008). Sedimentología de la Bahía Sebastián Vizcaíno, Baja California, México. *CICIMAR Oceánides*, *23* (1,2), 79-82.

O´Leary, S. J., Feldheim, K. A., Chapman, D. D. (2013). Novel microsatellite loci for white, Carcharodon carcharias and sandtiger sharks, Carcharias taurus (order Lamniformes). *Conservation Genetics Resources*, *5* (3), 627-629. doi:10.1007/s12686-013-9866-z.

O´Leary, S. J., Feldheim, K. A., Fields, A. T., Natanson, L. J., Wintner, S., Hussey, N., Shivji, M. S., Chapman, D. D. (2015). Genetic Diversity of White Sharks, Carcharodon carcharias, in the Northwest Atlantic and Southern Africa. *Journal of Heredity*. doi:10.1093/jhered/esv001.

Oke, P. R., Middleton, J. H. (2001). Nutrient enrichment off Port Stephens: the role of the East Australian Current. *Continental Shelf Research*, *21* (6–7), 587-606. doi:10.1016/S0278-4343(00)00127-8.

Oñate-González, E. C., Rocha-Olivares, A., Saavedra-Sotelo, N. C., Sosa-Nishizaki, O. (2015). Mitochondrial genetic structure and matrilineal origin of white sharks, *Carcharodon carcharias*, in the Northeastern Pacific: Implications for their conservation. *Journal of Heredity*, *106* (4), 347-354. doi:10.1093/jhered/esv034.

Pardini, A. T., Jones, C. S., Noble, L. R., Kreiser, B., Malcolm, H., Bruce, B. D., Stevens, J. D., Cliff, G., Scholl, M. C., Francis, M., Duffy, C. A. J., Martin, A. P. (2001). Sex-biased dispersal of great white sharks. *Nature*, *412* 139-140. doi:10.1038/35084125.

Pardini, A. T., Jones, C. S., Scholl, M. C., Noble, L. R. (2000). Isolation and characterization of dinucleotide microsatellite loci in the Great White Shark, *Carcharodon carcharias*. *Molecular ecology*, *9* (8), 1176-1178. doi:10.1046/j.1365-294x.2000.00954-4.x.

PFMC, (2011). Fishery Management Plan for U.S. west coast fisheries for Highly Migratory Species. As amended through amendment 2. Pacific Fishery Management Council, Portland, OR. pp. 106.

Pikitch, E. K., Chapman, D. D., Babcock, E. A., Shivji, M. S. (2005). Habitat use and demographic population structure of Elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). *Marine Ecology Progress Series*, *302* 187-197.

Posada, D., Crandall, K. A. (1998). MODELTEST: Testing the model of DNA substitution. *Bioinformatics Applications Note*, *14* (9), 817-818. doi:10.1093/bioinformatics/14.9.817.

Pratt, H. L., (1996). Reproduction in the male white shark. in: Klimley, A.P. Ainley, D.G. (Eds.), *Great white sharks: the biology of Carcharodon carcharias*. Academic Press, San Diego, pp. 131-138.

Pritchard, J. K., Stephens, M., Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155* (2), 945-959.

Pyle, P., Anderson, S. D., Klimley, A. P., Henderson, R. P., (1996). Environmental factors affecting the occurrence and behavior of white sharks at the Farallon Islands, California. in: Klimley, A.P. Ainley, D.G. (Eds.), *Great white sharks: The biology of Carcharodon carcharias*. Academic Press, San Diego, pp. 281-291.

Rice, D. W., Wolman, A. A., Withrow, D. E., Fleischer, L. A. (1981). Gray whales on the winter grunds in Baja California. *Reports of the International Whaling Commission*, *31* 477-489.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution; international journal of organic evolution*, *43* 223-225. doi:10.2307/2409177.

Romo-Curiel, A. E., Herzka, S. Z., Sosa-Nishizaki, O., Sepulveda, C. A., Aalbers, S. A. (2015). Otolith-based growth estimates and insights into population structure of white seabass, *Atractoscion nobilis*, off the Pacific coast of North America. *Fisheries Research*, *161* (0), 374-383. doi:10.1016/j.fishres.2014.09.004.

Rosenberg, N. A. (2004). distruct: a program for the graphical display of population structure. *Molecular Ecology Notes*, *4* (1), 137-138. doi:10.1046/j.1471-8286.2003.00566.x.

Rousset, F. (2008). genepop’007: a complete re-implementation of the genepop software for Windows and Linux. *Molecular ecology resources*, *8* (1), 103-106. doi:10.1111/j.1471-8286.2007.01931.x.

Rozas, J., Sanchez-DelBarrio, J. C., Messeguer, X., Rozas, R. (2003). DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics*, *19* (18), 2496-2497. doi:10.1093/bioinformatics/btg359.

Ryman, N., Palm, S. (2006). POWSIM: a computer program for assessing statistical power when testing for genetic differentiation. *Molecular Ecology Notes*, *6* (3), 600-602. doi:10.1111/j.1471-8286.2006.01378.x.

Sandoval-Castillo, J., Rocha-Olivares, A., Villavicencio-Garayzar, C., Balart, E. (2004). Cryptic isolation of Gulf of California shovelnose guitarfish evidenced by mitochondrial DNA. *Marine biology*, *145* (5), 983-988. doi:10.1007/s00227-004-1378-7.

Santana-Morales, O., Sosa-Nishizaki, O., Escobedo-Olvera, M. A., Oñate-González, E. C., O'Sullivan, J. B., Cartamil, D., (2012). Incidental catch and ecological observations of juvenile white sharks, *Carcharodon carcharias*, in western Baja California, Mexico. Conservation implications. in: Domeier, M.L. (Ed.), *Global perspectives on the biology and life history of the White Shark*. CCRC Press, New Yor, USA, pp. 187-198.

Schuelke, M. (2000). An economic method for the fluorescent labeling of PCR fragments. *Nat Biotech*, *18* (2), 233-234.

Secor, D. H., (2015). Migration ecology of marine fishes. Johns Hopkins Univeristy Press, Baltimore, USA.

Shivji, M., Clarke, S., Pank, M., Natanson, L., Kohler, N., Stanhope, M. (2002). Genetic identification of pelagic shark body parts for conservation and trade monitoring. *Conservation Biology*, *16* (4), 1036-1047.

Sosa-Nishizaki, O., Márquez-Farías, J. F., Villavicencio–Garayzar, C. J., (2008). Case study: Pelagic shark fisheries along the west coast of Mexico. in: Camhi, M.D., Pikitch, E.K. Babcock, E.A. (Eds.), *Sharks of the open ocean. Biology, fisheries and conservation*. Blackwell Publishing, UK, pp. 276-287.

Sosa-Nishizaki, O., Morales-Bojórquez, E., Nasby-Lucas, N., Oñate-González, E. C., Domeier, M. L., (2012). Problems with photo identification as a method of estimating abundance of white sharks, *Carcharodon carcharias.* An example from Guadalupe Island, Mexico. in: Domeier, M.L. (Ed.), *Global perspectives on the biology and life history of White Shark*. CRC Press, New York, USA, pp. 393-404.

Springer, S., (1967). Social organization of shark populations. in: Gilbert, P.W., Mathewson, R.F. Rall, D.P. (Eds.), *Sharks, skates, and rays*. Johns Hopkins Press, Baltimor, Maryland, pp. 149-174.

Strong, W. R. J., Bruce, B. D., Nelson, D. R., Murphy, R. D., (1996). Population dynamics of the white sharks in Spence Gulf, South Australia. in: Klimley, A.P. Ainley, D.G. (Eds.), *Great white sharks: The biology of Carcharodon carcharias*. Academic Press, Inc., San Diego, pp. 401-414.

Swofford, D. L., (2002). PAUP*: Phylogenetic Analysis Using Parsimony (* and other methods). Sinauer, Sunderland, Massachussetts.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., Kumar, S. (2011). MEGA5: Molecular Evolutionary Genetics Analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol Biol Evol*, *28* (10), 2731-2739. doi:10.1093/molbev/msr121.

Tanaka, S., Kitamura, T., Mochizuki, T., Kofuji, K. (2011). Age, growth and genetic status of the white shark (*Carcharodon carcharias*) from Kashima-nada, Japan. *Marine and Freshwater Research*, *62* (6), 548-556. doi:10.1071/Mf10130.

Tillett, B. J., Meekan, M. G., Field, I. C., Thorburn, D. C., Ovenden, J. R. (2012). Evidence for reproductive philopatry in the bull shark Carcharhinus leucas. *Journal of fish biology*, *80* (6), 2140-2158. doi:10.1111/j.1095-8649.2012.03228.x.

Torres-Rojas, Y. E., Páez-Osuna, F., Hernández-Herrera, A., Galván-Magaña, F., Aguiñiga-García, S., Villalobos-Ortíz, H., Sampson, L. (2014). Feeding grounds of juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in the south-eastern Gulf of California. *Hydrobiologia*, *726* (1), 81-94. doi:10.1007/s10750-013-1753-9.

Tricas, T. C., McCosker, J. E. (1984). Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proceedings of the California Academy of Sciences*, *43* 221-238.

Van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M., Shipley, P. (2004). micro-checker: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, *4* (3), 535-538. doi:10.1111/j.1471-8286.2004.00684.x.

Vignaud, T. M., Maynard, J. A., Leblois, R., Meekan, M. G., Vazquez-Juarez, R., Ramirez-Macias, D., Pierce, S. J., Rowat, D., Berumen, M. L., Beeravolu, C., Baksay, S., Planes, S. (2014). Genetic structure of populations of whale sharks among ocean basins and evidence for their historic rise and recent decline. *Molecular ecology*, *23* (10), 2590-2601. doi:10.1111/mec.12754.

Ward-Paige, C. A., Britten, G. L., Bethea, D. M., Carlson, J. K. (2015). Characterizing and predicting essential habitat features for juvenile coastal sharks. *Marine Ecology*, *36* (3), 419-431. doi:10.1111/maec.12151.

Weng, K., Honebrink, R. (2013). Occurrence of White Sharks (Carcharodon carcharias) in Hawaiian Waters. *Journal of Marine Biology*, *2013* 1-7. doi:10.1155/2013/598745.

Weng, K. C., Boustany, A. M., Pyle, P., Anderson, S. D., Brown, A., Block, B. A. (2007a). Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine biology*, *152* (4), 877-894. doi:10.1007/s00227-007-0739-4.

Weng, K. C., O'Sullivan, J. B., Lowe, C. G., Winkler, C. E., Blasius, M. E., Loke-Smith, K. A., Sippel, T. J., Ezcurra, J. M., (2012). Back to the wild. Release of juvenile white sharks from the Monterey Bay Aquarium. in: Domeier, M.L. (Ed.), *Global perspectives on the biology and life history of White Shark*. CRC Press, New York, USA, pp. 419-446.

Weng, K. C., O'Sullivan, J. B., Lowe, C. G., Winkler, C. E., Dewar, H., Block, B. A. (2007b). Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Marine Ecology Progress Series*, *338* 211-224. doi:10.3354/Meps338211.

Werry, J. M., Planes, S., Berumen, M. L., Lee, K. A., Braun, C. D., Clua, E. (2014). Reef-fidelity and migration of tiger sharks, *Galeocerdo cuvier*, across the Coral Sea. *PloS one*, *9* (1), e83249. doi:10.1371/journal.pone.0083249.

Wintner, S. P., Cliff, G. (1999). Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa. *Fish B-Noaa*, *97* (1), 153-169.

Yates, P. M., Heupel, M. R., Tobin, A. J., Moore, S. K., Simpfendorfer, C. A. (2015). Diversity in immature-shark communities along a tropical coastline. *Marine and Freshwater Research*, *66* (5), 399-410. doi:10.1071/MF14033.

Yates, P. M., Heupel, M. R., Tobin, A. J., Simpfendorfer, C. A. (2012). Diversity in young shark habitats provides the potential for portfolio effects. *Marine Ecology Progress Series*, *458* 269-281. doi:10.3354/meps09759.