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DISTRIBUTION PATTERNS OF SHARKS IN THE REVILLAGIGEDO ARCHIPELAGO AND THEIR CONNECTIVITY IN THE EASTERN TROPICAL PACIFIC

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PRESENTA

FRIDA LARA LIZARDI

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"DISTRIBUTION PATTERNS OF SHARKS IN THE REVILLAGIGEDO ARCHIPELAGO AND THEIR CONNECTIVITY IN THE EASTERN TROPICAL PACIFIC"

Presentada por el alumno:

LARA	**LIZARDI**	**FRIDA**
Apellido paterno	materno	nombre(s)

Con registro: **B 1 4 0 0 8 2**

Aspirante de:

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M en C. FRIDA LARA LIZARDI

Nombre y firma del alumno

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III. GLOSSARY

Population. The set of individuals of a wild species that share the same habitat. It is considered the basic unit of management of the species.

Habitat. The specific site in a physical environment, occupied by an organism, by a population, by a species or by communities of species in a given time.

Ecosystem. The basic functional unit of interaction of organisms live among themselves and of these with the environment, in a specific space and time.

Biodiversity. reflects the variability among living organisms. These diverse organisms interact with one another and with the various plants and animals in the ecosystem forming a complex web of biological activity.

Marine Protected Areas. The zones of the national territory and those over which the Nation exercises its sovereignty and jurisdiction, where the original environments have not been significantly altered by the activity of the human being or that need to be preserved, to maintain or recover the biodiversity and the functionality of the ecosystems subject to the regime foreseen in this Law.

Conservation. The protection, management and maintenance of ecosystems, habitats, species and populations of wildlife and their genetic diversity, so as to safeguard the natural conditions for their long-term permanence. This includes the set of policies and measures to maintain the conditions that propitiate the evolution and continuity of ecosystems and natural habitats, as well as the viable populations of species in their natural environments and the components of biodiversity outside their natural habitats.

Biological corridors. Defined geographical spaces that provide connectivity between other priority areas for conservation, landscapes, ecosystems and habitats, natural or modified, and that contribute to the maintenance of biological diversity and ecological and evolutionary processes.

Highly migratory species. Those that move latitudinally, longitudinally or altitudinally periodically as part of their biological cycle.

Population study. The one that is carried out in order to know its demographic parameters; such as size and density, the proportion of sexes and ages, and the birth, death and growth rates during a given period as well as the addition of any other relevant information.

Environmental management. One that is performed on vegetation, soil and other elements or physiographic characteristics in defined areas with specific goals of conservation, maintenance, improvement or restoration.

Management plan. The operational technical document of the management units for the sustainable use of biodiversity, the units of intensive wildlife management and the premises or facilities that manage wildlife specimens subject to approval by the secretariat. The secretariat describes and schedules management activities and establishes goals and indicators of success.

Priority regions. Areas with a high biodiversity value and ecosystem services in the land, marine and aquatic epicontinental environments of the Nation identified and delimited with different analytical tools. The participation of experts and other relevant actors considering different scales and diverse criteria of biological type, of ecological representativeness, the degree of threat to the maintenance of biodiversity and ecosystem services as well as the opportunities for their management.

Ecosystem services. The benefits of social interest that derive from ecosystems and the wildlife that inhabits them such as climate regulation, conservation of hydrological cycles, nitrogen fixation, soil formation, carbon capture, the erosion control, the pollination of plants, the biological control of pests or the degradation of organic waste.

Region. A sub global geographical area, such as a continent, country, state, or province.

Regional population. The portion of the global population within the area being studied which may comprise one or more subpopulations.

Subpopulations. Geographically or otherwise distinct groups in the (global) population between which there is little demographic or genetic exchange (typically one successful migrant individual or gamete per year or less; IUCN 2001, 2012); a subpopulation may or may not be restricted to a region.

Buffer zones. Zones of reduced human impact surrounding core no-take protected areas enhance the conservation value of core no-take areas.

Ecological spatial connectivity. Refers to the physical and biological processes connecting areas in the marine environment in ways that support wildlife and ecosystem. Population connectivity and migration are the main focus. They rely on dispersal and migration estimates for key taxa as well as distances between refuges with relevant habitats.

IV. ABSTRACT

Determining shark distribution patterns and species habitat use is important to assessing the risk of exposure to fishing, habitat degradation and climate change. In Chapter I, the habitat associations were defined by using Baited Remote Underwater Video Stations (BRUVS) deployed along the Revillagigedo Archipelago over a four year period. Eight species of sharks from three families were recorded. Whitetip (*Trianenodon obesus*), silky (*Carcharhinus falciformis*), silvertip (*C. albimarginatus*) and galapagos sharks (*C. galapagensis*) were the most abundant shark species. A Principal Component Analysis showed that differences between pelagic/benthic BRUVS, current exposure and substrates produced the primary split separating shark assemblages. Describing how the behavior and spatial ecology of shark species change across habitats is important for effective management. In Chapter II, the residency and movement patterns of *C. falciformis* and *C. galapagensis* in the Revillagigedo Archipelago were examined using an array of 12 acoustic receivers covering the four islands across 235km to monitor shark movements. Twenty-three *C. falciformis* and twenty-one *C. galapagensis* were monitored from 2008 to 2016. Most sharks were detected on a single island; however, some individuals moved between the islands (over 40 times). Although *C. falciformis* were present year-round. Juvenile sharks had higher residency to their tagging site than adult sharks. Long-term monitoring data revealed that *C. falciformis* and *C. galapagensis* exhibited high residency to their tagging site. Long-distance movements of sharks within and between marine protected areas (MPA) create strong challenges for resource managers in multiple jurisdictions. In Chapter III, evidence of the occurrence of *Nasolamia velox* at the Revillagigedo Archipelago, Mexico, was provided using acoustic telemetry and videos taken from 2014 to 2016 recording movements from a coastal location, Cabo Pulmo National Park to Revillagigedo Archipelago, by one single individual. Mantas, silky and tiger sharks have been also move from Revillagigedo to the Gulf. This supports the idea of the potential connectivity of sharks between the Gulf of California and the Revillagigedo Archipelago. Moreover, shark movements between the MPAs of the Eastern Tropical

Pacific (Revillagigedo, Cocos, Malpelo and Galapagos), have been studied for years. However, little is known about which areas support connectivity between these sites and the existence of marine corridors or “swimways”. In Chapter IV, the detailed examination of the spatial ecology and behavior of *C. falciformis* and *C. galapagensis* in the Eastern Tropical Pacific is described. Network analysis (NA) was used to determine the most connected sites that link these MPAs. An extensive MigraMar ultrasonic telemetry dataset was used to assess how sharks use MPAs as stepping-stones during their migrations across the ETP. The frequency of movements was compared with the distance travelled by each species. Networks and their metrics were estimated for each species. *C. falciformis* produced more inter-connected networks with migrating distances as far as 2,200 km; whereas galapagos sharks showed a maximum distribution range of 3,300 km, from Socorro, Revillagigedo to Darwin Island, Galapagos. Although long-distance distribution was not common, 9.5% were inter-insular and less than 1% was across MPAs, our results highlight the need for cooperation between national jurisdictions to ensure sharks receive sufficient protection. Furthermore, the results demonstrate that acoustic monitoring can serve as a useful platform for designing more effective MPA networks for pelagic predators displaying a range of movement patterns.

V.

VI. RESUMEN

La determinación de los patrones de distribución y el uso del hábitat de los tiburones es importante para evaluar el riesgo de exposición a la pesca, la degradación del hábitat y el cambio climático. En el Capítulo I, las asociaciones a los hábitats se definieron mediante el uso de estaciones de video con carnada (BRUVS) desplegadas a lo largo del Archipiélago de Revillagigedo durante un período de 4 años. Se registraron ocho especies de tiburones de tres familias. Las especies de tiburones más abundantes fueron: el tiburón punta blanca (*Trianenodon obesus*), piloto (*Carcharhinus falciformis*), punta plateada (*C. albimarginatus*) y galápagos (*C. galapagensis*). De acuerdo con el análisis de componentes principales se observaron las diferencias entre los BRUVS pelágicos/ bentónicos, la exposición a la corriente y el tipo de sustrato produjeron las diferencias en la distribución de los tiburones. La abundancia relativa de tiburones fue significativamente mayor en los hábitats bentónicos que en los pelágicos. En el Capítulo II, los patrones de residencia y movimiento de *C. falciformis* y *C. galapagensis* en el Archipiélago de Revillagigedo son descritos, utilizando un conjunto de 12 receptores acústicos que cubren las cuatro islas a lo largo de 235km para estudiar los movimientos de los tiburones. Veintitrés *C. falciformis* y veintiún *C. galapagensis* fueron monitoreados desde 2008 hasta 2016. La mayoría de los tiburones se detectaron en una sola isla; sin embargo, algunos individuos se movieron entre las islas (más de 40 veces). Aunque *C. falciformis* estuvo presente durante todo el año, los tiburones juveniles tenían una mayor residencia que los adultos. Los datos de monitoreo a largo plazo revelaron que ambas especies exhibieron una alta residencia en el sitio de marcaje, lo que indica que los hábitats protegidos dentro del Parque Nacional del Archipiélago de Revillagigedo son primordiales para los tiburones. Los movimientos de tiburones de larga distancia dentro y entre las AMP crean grandes desafíos para los administradores de recursos

en múltiples jurisdicciones. En el Capítulo III, se muestran evidencias de la ocurrencia del tiburón pico blanco *Nasolamia velox* en el Archipiélago de Revillagigedo, usando telemetría acústica y videos tomados de 2014 a 2016, registrando movimientos desde una ubicación costera, el Parque Nacional Cabo Pulmo, al Archipiélago de Revillagigedo por un solo individuo, apoyando la idea de la conectividad potencial de los tiburones entre el Golfo de California y el Archipiélago de Revillagigedo. Además, se registran los movimientos ocasionales de otras especies como: tiburón tigre (*Galeocerdo cuvier*), tiburón piloto (*C. falciformis*), y la Manta gigante (*Mobula bistrostris*). En el Capítulo IV, los movimientos de los tiburones entre las reservas marinas del Pacífico Tropical Oriental (Revillagigedo, Clipperton, Cocos, Malpelo y Galápagos) han sido estudiados durante años, sin embargo, se sabe poco sobre qué áreas de conectividad entre estos sitios y la existencia de corredores marinos o "vías de navegación". Este es el primer examen detallado de la ecología espacial y el comportamiento de *C. falciformis* y *C. galapagensis* en el Pacífico Tropical Oriental. Mediante el análisis de red (NA) determinamos los sitios más conectados que vinculan estas reservas. Se utilizó un extenso conjunto de datos de telemetría ultrasónica de la red de MigraMar para evaluar cómo los tiburones utilizan las AMP como puntos de paso durante sus migraciones. La frecuencia de los movimientos se comparó con la distancia recorrida por cada especie. Las redes y sus métricas se estimaron para cada especie. *C. falciformis* produjo más redes interconectadas con distancias de migración de hasta 2.200km. *C. galapagensis* mostro un rango de distribución máximo de 3,300km (desde Socorro hasta la isla de Darwin, Galápagos). Aunque la dispersión a larga distancia no era común (el 9,5% era interinsular y menos del 1% en AMP), sin embargo, nuestros resultados ponen de manifiesto la necesidad de cooperación entre las jurisdicciones para garantizar que los tiburones reciban un manejo suficiente. Además, los resultados demuestran que la monitorización acústica puede servir como una plataforma útil para el diseño de redes MPA más efectivas para depredadores pelágicos que muestran una gama de patrones de movimiento.

1. INTRODUCTION

Sharks, rays and stakes are classified as Elasmobranchs. They are considered one of the most ancestral and successful vertebrates (Brazeau and Friedman, 2015). According to the fossil evidence they are a group present from the Devonian, possibly from the Silurian, and later diversified during Triassic in a wider range of environments presenting morphological and ecological differences (Grogan *et al.*, 2012).

From the eight orders 56% of all shark species are classified as Carcharhiniformes. These include 8 families, 48 genera and more than 196 species. Due to technological innovation in recent years the number of species of Elasmobranchs described has risen from 554 to 1221 species (Naylor *et al.,* 2012), and it is considered that the number of species will increase..

The Carcharhinidae family is one of the most important. The members of this family are predominantly tropical inhabiting a range of ecosystems (FAO, 1997). They are all predators and most of the species are found within continental shelves and oceanic slopes (Pelkey *et al.*, 2007). Their life cycle, as other elasmobranchs is commonly characterized by slow growth, late maturation and low fecundity which increases their susceptibility to the effects of overfishing (FAO, 1997).

Unlike large oceanic teleosts sharks lack pelagic larvae. Juveniles are laid in demersal egg cases or born live. Dispersal is accomplished exclusively by juvenile and adult stages. Sharks do not exhibit parental care, but many species use shallow, coastal nurseries that are geographically distinct from adult feeding areas (Springer 1967; Lund 1990). This habitat partitioning may indicate philopatry which would explain the unexpected degree of population structure found in sharks, including some widely distributed, highly vagile species. Even if they are not loyal to specific nurseries, reproduction in many species is strongly affiliated with sheltered, coastal habitats (Compagno, 2005).

According to FAO fisheries statistics 720,000 t of sharks were landed in 2009; an independent estimate, based on the global shark fin trade alone estimated 1.7

million tons or 38 million sharks (Clarke *et al.*, 2006). Given, not all captured sharks are destined for shark fin markets and the occurrence of illegal, unregulated and unreported shark catches. The differences between official and unofficial data highlights the poor regulation of shark fisheries. The lack of knowledge on fishing statistics itself hinders management actions (Baum and Worm, 2009).

However, sustainable alternatives are gaining more importance. Economic benefits from shark watching are particularly important in some places (Gallagher and Hammerschlag, 2011). For example, individual sharks in French Polynesia were estimated to have an ecotourism value of c. USD 1,200 per kg, and species length–weight relationships compared with a landed value to local fishers of 1.5 USD per kg for shark meat. The sum of expenditures at sites with available information is USD 215 million per year which is more than the total landed value of sharks. Shark watching generates USD 314 million, almost half the current value of global shark fisheries, and supports 10,000 jobs (Cisneros-Montemayor *et al.,* 2013).

Sharks play an important role as top predators in the structure and functioning of marine communities (Ferretti *et al.*, 2010; Spaet *et al.*, 2016). They can influence, directly or indirectly, the behavior, distribution and abundance of other species through competition (Papastamatiou *et al.*, 2009), and predation (Heithaus *et al.,* 2008; Mourier *et al.,* 2013). Decline of top predators tend to produce changes down the food chain, the lack of predatory control (Dulvy *et al.,* 2000; Heithaus *et al.,* 2008; Ferretti *et al.,* 2010), or reductions in biodiversity and ecosystem health (Ruppert *et al.,* 2013; Heithaus *et al.,* 2014). If shark populations are affected by the loss and degradation of near shore habitat and fishing, their ecosystem benefits could not be recovered (Myers and Baum, 2007; Worm *et al.*, 2013; Papastamatiou *et al.,* 2015; Ward-Paige, 2017).

Recent global evaluations of elasmobranchs estimated that one-quarter of all the species are threatened according to International Union for Conservation of Nature Red List criteria mainly due to illegal and/or unsustainable fishing practices (Dulvy *et al.,* 2014). Endangered species such as scalloped hammerhead (*Sphyrna lewini*) are nearly extinct (90% of the original population has declined) in some regions. Landing reports show that other species such as the silky (*Carcharhinus falciformis*) are getting caught before they reach sexual maturity (FAO, 2012).

A better understanding of how shark species use specific habitats and how life history traits predictably change in response to local environmental and ecological context is critical to defining their role in the ecosystem. It is also critical to developing effective management approaches that ensure their long-term conservation (Heupel and Simpfendorfer, 2007). For instance, Heupel and Simpfendorfer (2008), determined that tolerances of lower salinities by juvenile sharks may contribute to niche separation from adults as documented for bull (*Carcharhinus leucas*) and bonnethead sharks (*Sphyrna tiburo*). White *et al.* (2015), showed that whitetip reef sharks have a preference for relatively turbid water which may relate to their nocturnal feeding strategy and adaptation to low light conditions. For grey reef sharks (*Carcharhinus amblyrhychos*), in addition to temperature (Speed *et al.*, 2012; Vianna *et al.,* 2013), low turbidity also correlates to higher occurrence in specific sites. These conditions may improve the shark ability to detect prey or predators; however, the nature of this relationship remains poorly understood.

2. BACKGROUND

Some studies have been focused on the degrees of habitat association comparing the connectivity of different shark species using acoustic telemetry and complementary techniques:

Papastamatiou *et al.* (2006) showed that competition and predation are important in structuring the distribution of gray reef (*Carcharhinus amblyrhynchos*), sandbar (*Carcharhinus plumbeus*), tiger (*Galeorcerdo cuvier*) and galapagos sharks (*Carcharhinus galapagensis*) in the Hawaiian Islands. Dietary overlap was high between gray reef and sandbar sharks and between sandbar and galapagos sharks. The data supported the hypothesis that interspecific competition influences the distribution of carcharhinid sharks throughout the Hawaiian Archipelago.

Meyer *et al.* (2010) showed that tiger sharks may use cognitive maps to navigate between distant foraging areas. Galapagos sharks were more resident around oceanic islands. Both galapagos and tiger sharks primarily used the mixed layer (<100 m depth) and made occasional deeper dives through the thermocline down to 680 m. Their results showed reef-associated sharks utilize a wide variety of habitats ranging from shallow atoll lagoons to deep reefs and open ocean. Their results may provide important trophic links between these habitats.

Espinoza *et al.* (2015) used acoustic monitoring and network analysis to improve the understanding of the spatial ecology and functional connectivity of reef-associated species providing a useful approach for reef-based conservation planning. *C. amblyrhynchos* and *C. albimarginatus* were detected most days at or near their tagging reef. Despite both species moving similar distances (<50 km), a large portion of the population of *C. albimarginatus* (71%) was detected on multiple reefs and moved more frequently between reefs and management zones than *C. amblyrhynchos*. *C. leucas* was detected less than 20% of the time within the tagging array. 42% of the population undertook long-range migrations to other arrays in the GBR. Networks derived for *C. leucas* were larger and more complex than those for *C. amblyrhynchos* and *C. albimarginatus*.

Espinoza *et al.* (2016) described the spatial ecology and behavior of silvertip sharks (*C. albimarginatus*) on coral reefs. Silvertip sharks remained resident at coral reef habitats over long periods. However, our results also suggest this species may have more complex movement patterns and use larger areas of the Great Barrier Reef than common reef shark species.

In the Eastern Tropical Pacific, studies that have been ongoing for decades focused mainly on the schooling sharks like the scalloped hammerhead shark (*Sphyrna lewini*):

One of the first studies that described the distribution patterns of the hammerheads (*Sphyrna lewini*) associated to the seamounts was done by Dr. Klimley *et al.* (1984). They found that sharks disperse and return to the seamount in a rhythmical fashion where there is a social system of the scalloped hammerhead sharks. The refuging behavior reflects a common strategy of these predators to minimize activity when not foraging by remaining at a single central location in their home range.

Klimley *et al.* (1987) also defined that there is sexual segregation in the same species*.* They found that female scalloped hammerhead sharks move offshore at a smaller size than do males to form schools composed primarily of intermediate size female sharks. This movement results in smaller females feeding more on pelagic prey than do males and with greater predatory success. It is contended that this change in habitat causes females to grow more rapidly to reproductive size. It is suggested that female segregation increases fitness resulting in more rapid growth for the former sex.

Hammerhead swimming movements are highly oriented as Klimley *et al.* (1993) described. The hammerheads swam at night with repeated vertical excursions ranging from 100 to 450 m deep; out of view of either the sea surface or the sea floor. The shark was attracted to and move back and forth along ridges and valleys; features in the relief of magnetic field intensities occurring over a geographical area.

The aggregations of scalloped hammerhead sharks and other pelagic species are present in very specific areas where currents bring nutrients and higher abundance of potential prey. Hearn *et al.* (2010) described the “hot spots” in the southeastern corner of Wolf Island in the Galapagos Marine Reserve.

Ketchum *et al.* (2014) showed that currents, season, and individual behavior mainly drive inter-island movements of hammerheads at small (SBF) and medium (MDT) scales. Hammerheads remained more days at the northern islands during part of the warm season (December–February), compared to the cool season (July -September). However, fewer individuals were present during the cooler season. Movement modes were diel island excursions (24-h cycles), in the northern Galapagos and inter-island in the GMR and ETP at different scales.

Hammerheads show preference for the up-current habitat where the thermocline produces a large amount of available food. Ketchum *et al.* (2014b) studied vertical and horizontal movements and determined habitat and environmental preferences of scalloped hammerhead sharks (*Sphyrna lewini*). They provided evidence that hammerheads: (1.) are highly selective of location; (i.e., habitat on up-current side of island) and depth (i.e., top of the thermocline) while refuging where they may carry out essential activities such as cleaning and thermoregulation; and (2.) perform exploratory vertical movements by diving the width of the mixed layer and occasionally diving below the thermocline while moving offshore; most likely for foraging.

Bessudo *et al.* (2011) showed that there is connectivity of *Sphyrna lewini* between Malpelo, Cocos and the Galapagos Islands. The most common depth at which the sharks swam coincided with the thermocline. They also found that hammerheads spent significantly more time on the up-current side of the island.

Hoyos-Padilla *et al.* (2014) documented for the first time the ontogenetic migration of a juvenile scalloped hammerhead shark in the Gulf of California. This female shark carried out part of her biological cycle in both coastal and offshore areas of the central and southwestern Gulf of California suggesting maximization of foraging opportunities and continued growth.

Particularly about silky (*C. falciformis*) and galapagos sharks (*C. galapagensis*), there are some studies conducted in the region:

Hoyos *et al.* (2011) studied the reproductive biology of *C. falciformis* in the Eastern Pacific Ocean to support fishery or management. In the gravid females examined, the average number of embryos per female were five with a range of 2-9 embryos. The total length ranged between 88 and 316 cm TL and 116 males, ranging between 142 and 260 cm TL. The sex ratio of females to males was 1: 0.6. Female maturation occurred at about 180 cm TL while males matured at about 182 cm TL.

Cabrera-Chávez Costa (2010) established the trophic niche of the silky shark to determine the ecological role of this predator in the ecosystem close to Baja California. According to the Levin Index (Bi), the trophic niche breadth in silky sharks is low (Bi = <0.6). This means that silky sharks are specialist predators because they mainly consume three prey types: pelagic red crab (*Pleuroncodes planipes*), chub mackerel, and jumbo squid (*Dosigiscus gigas*).

Wetherbee *et al.* (1996) studied the galapagos shark (*C. galapagensis*) in Hawaii. They found that males appear to reach maturity between 205 and 239 cm TL and females between 215 and 245 cm TL. Litter size ranged from 4 to 16 pups with an average of 8.7. In Hawaiian waters, galapagos sharks are born at just over 80 cm TL. Mating and parturition occur early in the year and gestation is estimated to be about 12 months. Stomach contents consisted mainly of teleosts and benthic prey. Ontogenetic changes in diet occurred as sharks increased in size. Sharks consumed a smaller proportion of teleosts and more elasmobranchs when their size was increasing. Dietary diversity also increased with increasing size of shark.

Pazmiño *et al.* (2017) examined the stock structure and connectivity of the galapagos shark in the ETP using mitochondrial markers. They found clear evidence of at least two (east Pacific and central-west Pacific), and possibly four (west 372 Pacific, Mexico, Galapagos Islands and Hawaii), galapagos shark populations in the Pacific. Reliance on shelf habitats for crucial aspects of their ecology may ultimately explain the population structure seen in this potentially wide-ranging shark. Results based on outlier SNPs support the biogeographic provinces defined by Glynn and Ault (2000), which separate mainland Ecuador, Costa Rica, the Galapagos Archipelago and Cocos Island (Equatorial province) from mainland Mexico and the Revillagigedo Archipelago (Northern province) based on reef building coral species.

Pazmiño et al. (submitted) showed that there are areas where *C. galapagensis* and *C. obscurus* co-occur across the Pacific Ocean and with nuclear genome-wide markers they showed hybridization between the two species. Four hydrid individuals (~1%) were detected bi-directional between *C. galapagensis* and *C. obscurus* in the Gulf of California along the east Pacific coast. The presence hybrid at Clipperton Atoll and Galápagos Islands suggests movement of female Galapagos sharks (potentially hybrid mothers) from the primary area of contact (Gulf of California or Revillagigedo) towards the Galápagos Islands using Clipperton Atoll as a stepping-stone.

The Revillagigedo Archipelago exploration

The first documented description of the Revillagigedo was in 1533, when the Spanish explorer Hernando de Grijalva discovered Isla Socorro while trying to navigate to southeast Asia. Toward the end of the 18th century, all four islands had been discovered but were still largely ignored as they were not found on any trade routes. It is believed that for short periods the islands were inhabited by traders, explorers and pirates though only on a temporary basis to refill their supplies from the islands' minimal natural resources. By the 19th Century the island group was of interest for scientific research due to its degree of intactness which was then quickly degraded in places by the island group's first settlers in the 1870's. Non-native grazers such as sheep were released on the islands. Research in various scientific fields continued in the archipelago throughout the 20th Century. By 1957, the archipelago’s strategic importance was recognized when the Mexican Navy established a permanent military base on Isla Socorro. Since then activities have been more controlled within the archipelago. No settlements of civil populations or indigenous groups currently live on the islands.

1533: The Spanish explorer Hernando de Grijalva discovers Isla Socorro while trying to find a route to southeast Asia and names it Isla Tomas.

1542: Isla San Benedicto first discovered and originally named ‘Los Inocentes’.

1569: Roca Partida Islet first discovered.

1608: Isla Tomas is renamed by Martin Yanez de Armida to Isla Socorro in honor of his wife.

1779: Isla Clarion is discovered.

1793: James Colnett, a British explorer, is captured on Isla Socorro after visiting the Galapagos. He is released by the new Spanish viceroy in Mexico City, III Count of Revillagigedo. James Colnett names the island group after him, creating the prevailing name to this day.

1869: The Mexican Government grants a lease for a group of Australians and Canadians to start raising cattle and sheep on Isla Socorro but the failed project was quickly abandoned.

1874: The first topographic survey of Revillagigedo was completed by an expedition led by the U.S.A.

1957: The Secretariat of the Mexican Navy establishes a permanent military base on Isla Socorro.

1994: A scientific research network specialized on the property is organized which still convenes regularly for conferences.

1994: The Archipelago de Revillagigedo is designated as a national Biosphere Reserve.

2016: The property is inscribed as a World Heritage site under natural criteria.

2017: Revillagigedo changed its designation to National Park, the most restricted form for the Mexican law to protect natural resources (Bezaury-Creel, 2005), and expanded the reserve to 148,000km^2.

3. JUSTIFICATION

The Revillagigedo Archipelago is a protected area since 1994, characterized by high diversity and abundance of elasmobranchs and other pelagic species of ecological and commercial importance (Ricker, 1959). The International Union for the Conservation of Natural Resources included the Revillagigedo Archipelago in the Global Strategy for Conservation as a priority area within the biogeographic provinces of the terrestrial environment for protection through some category of MPA.

In addition, the International Council for the Preservation of Birds (ICBP) considers it an Endemic Bird Area of primary importance (Brattstrom, 1990). In 2016, the Revillagigedo Reserve was declared a World Heritage Site by UNESCO (United Nations Educational, Scientific and Cultural Organization, IUCN) (Ruiz *et al.,* 2017).

There are 121 fish (including elasmobranchs) species: 73.5% are typical of the Eastern Tropical Pacific, 23.1% are known in both coasts of the Pacific, 16.5% are cosmopolitan and 9% are endemic (Castro-Aguirre and Balart, 2002). According to observations done since 2008 (Hoyos *et al., unpublished*), shark communities in the Revillagigedo Archipelago are highly complex due to their distribution, variation in abundance and different patterns of behavior according to gender and size. Therefore, to carry out efficient management strategies requires constant planning that leads to the protection of the community.

The National Fisheries Charter of Mexico (2012) has estimated 16 species of sharks in the Revillagigedo Archipelago: *Galeocerdo cuvier, Alopias pelagicus, Alopias superciliosus, Alopias vulpinus, Carcharhinus albimarginatus, Carcharhinus falciformis, Carcharhinus limbatus, Carcharhinus longimanus, Carcharhinus plumbeus, Echinorhinus cookei, Isurus oxyrinchus, Nasolamia velox, Negraprion brevirostris, Prionace glauca, Sphyrna lewini, Sphyrna zygaena* and *Rhicodon typus.*

At present there is no published study that has determined the carrying capacity or effect of the fishing operation within the reserve despite the fact that commercial activities such as the exploitation of sharks by fishermen from Baja

California Sur, Sinaloa, and Sonora have been recorded. In addition, between 70 and 80 tourist boats visit the area for diving and sport fishing (CONANP, 2017).

Sport and commercial fishing are activities where there is no adequete control. Despite the fact that the service providers, authorized by SAGARPA, report the quantities of fish extracted cannot be validated as there is no surveillance on board these vessels that verifies the data reported by the permit holders. In addition, the cost of monitoring is very high as the area of protection is wide. Difficulties related to the remoteness of the reserve are also very important. The reserves is located in the Pacific Ocean, 720 km west of Manzanillo, Colima and 386 km south of Cabo San Lucas, Baja California Sur.

Shark fisheries have been found to be highly complex and vary according to geographic location and environmental conditions. For example, differences in the fisheries of Baja California and Baja California Sur are remarkable. In Baja California the volume of fishing is 80% of sharks. In Baja California Sur the fisheries are composed mainly of smaller or juvenile species, 1.5 m TL, such as *Alopias vulpinus, A. supercilious, Isurus oxyrinchus* and *Shpyrna zygaena* (Holts *et al.*, 1998).

Currently, shark fishing volumes in Mexico are among the 10 highest in the world (CONAPESCA, 2010). However, there is little information on the current state of the fishery, the data is not precise because all fisheries are grouped into five groups: shark (more than 1.5 m TL), cazon (less than 1.5 m total length), “angelitos” (Angel sharks of the genus *Squatina*), mantarays and guitars (SAGARPA, 2009). For this reason, the effects of fisheries on each species are unknown and current data are considered to underestimate actual fishery volumes (Santana-Morales *et al.,* 2012).

The East Equatorial Pacific Corridor is formed by the Galapagos Islands, Cocos, Malpelo and Revillagigedo. This group of islands are an important example for conservation since it is composed of oceanic islands, which due to oceanic bathymetry and current patterns, provide suitable habitats for pelagic biodiversity and in particular for large predators such as sharks (Worm *et al.,* 2003). Most of these MPAs have been designated around oceanic islands to protect marine coastal and pelagic species such as sharks. The ETP is renowned for its high ecological value, providing habitat for endangered species, and also for its inherent cultural value. Four of the five MPAs have been designated as UNESCO World Natural Heritage Sites. UNESCO first recognized Cocos Island National Park in 1997, then the Galapagos Marine Reserve in 2001, Coiba National Park in 2005, Malpelo Flora and Fauna Sanctuary in 2006 and Revillagigedo Archipelago in 2016 (Ruiz *et al.*, 2017).

In this corridor, governments in different countries have responded to the need to create marine reserves to protect assemblages of pelagic and large predator species by prohibiting commercial fishing in priority areas for conservation (Hearn *et al.,* 2010). Despite the well-known importance, marine reserves are threatened by the following human activities: poorly regulated legal and illegal fishing, overexploitation of coastal and oceanic marine resources, inadequately regulated tourism growth, pollution from commercial vessels (marine transport), habitat loss and degradation, and the introduction of exotic species (Bigue *et al.,* 2010).

Current literature shows that inter-island movements of sharks in the ETP are not uncommon. The knowledge of movement pathways in an area may help inform management plans to maintain or restore connectivity. Incorporating this information can improve the design and functionality of Marine Protected Areas (MPAs) and help define the functional role of a wide range of predators in marine ecosystems (Espinoza *et al.,* 2015). Functional and physical links between different habitats, defined here as connectivity are fundamental to maintain the biodiversity and resilience of an ecosystem (Jacoby *et al.,* 2012).

The movements in and out of marine protected areas imply that these species are vulnerable to domestic fisheries within Exclusive Economic Zones (EEZs) and multinational fisheries on the high seas (Ketchum *et al.,* 2014; Stevens, 2000). There is evidence that suggest that sharks may use islands as ‘stepping stones’ for long distance oceanic dispersal (Hearn *et al.,* 2010; Ketchum *et al.,* 2014).

It has been recognized, that to carry out management plans, it is necessary to increase information on these species especially in areas with high vulnerability. For this reason, population size (or stock), natural mortality, migratory rates and reduction in fishing mortality need to be considered for stock management (Baum and Worm, 2009; Gallagher *et al.*, 2012; Simpfendorfer and Tobin, 2015).

4. RESEARCH HYPOTHESIS

Based on the previous literature and the preliminary observations whether there are differences in the distribution patterns of sharks in the Revillagigedo Archipelago in time and space, or not. These differences are dependent to biological and environmental variables. Furthermore, based on the shark movements, there is a physical connectivity of the Revillagigedo Archipelago and the ETP, including the Gulf of California.

5. OBJECTIVES

5.1. General objective

The main objective of this project is to determine the distribution patterns of sharks in the Revillagigedo Archipelago and its connectivity with respect to other insular areas of the Tropical Eastern Pacific.

5.2 Specific objectives

1. To determine the distribution patterns and habitat use of sharks in the Revillagigedo Archipelago.

2. Describe which environmental variables (current exposure, depth and sea surface temperature) are related to the distribution patterns of the Revillagigedo Archipelago sharks.

3. Estimate residency indices and temporal distribution of galapagos and silky sharks in the reserve.

4. Establish the spatial and temporal patterns of intra- and inter-island connectivity of the Revillagigedo Archipelago with respect to other marine areas of the Tropical Eastern Pacific, including the Gulf of California.

5. Determine critical management areas for sharks in the Revillagigedo Archipelago as well as the swim ways that should be taken into account in future zoning proposals.

6. CHAPTER 1. HABITAT USE AND DISTRIBUTION PATTERNS OF SHARKS IN THE REVILLAGIGEDO ARCHIPELAGO

Figure 1. Setting the baited cameras (BRUVS) in the west of San Benedicto Island, Revillagigedo Archipelago. Photo by : Carlos Aguilera.

6.1. INTRODUCTION

The knowledge of the biological, geographic and environmental drivers responsible for distribution patterns, diversity, movement and habitat use of sharks can help inform managers about effective management approaches to maintain healthy populations. This information on when/why/how long sharks spend in specific habitats may also help define their role in the ecosystem (Espinoza, 2015). Sharks, for instance, tend to aggregate at specific sites or central locations near islands and seamounts which they use for foraging, reproduction, thermoregulation and refuging known as biological hotspots (Hearn *et al.*, 2010, Espinoza *et al.,* 2015). Incorporating this information can improve the design and functionality of Marine Protected Areas (MPAs) and help define the functional role of a wide range of predators (Espinoza *et al.,* 2015).

Traditional methods used for estimating shark abundances, such as, visual censes or fishing dependent techniques (Dale *et al.*, 2011), only provide a snap-shot of a decreasing trend in abundance (Robbins, 2007). Uncertainty about their status has raised global concern (Dulvy *et al.,* 2014). BRUVS (Baited Underwater Video Stations), have become the standard tool for monitoring large bodied, potentially cautious reef fish, including sharks (Harvey *et al.*, 2007; Meekan *et al.*, 2006). They are non-invasive, repeatable and allow the accurate collection of data on the relative abundance and distribution of the marine faunal community (Harvey *et al.*, 2007), particularly for motile fauna (Figure 1).

The use of bait with the BRUV system serves to attract motile predators to the camera unit. However, while bait increases the abundance of generalist carnivores in the area immediately surrounding the BRUV system, it does not influence the abundance or distribution of herbivorous fish (Harvey *et al.,* 2007). The use of video stereo allows greater accuracy and allows differences in length, biomass and body condition which are not detectable by visual censes (Harvey *et al.*, 2012; Dorman *et* *al.*, 2012). The estimation error of the stereo-video is between 1-2% of the actual length (Harvey *et al.*, 2011).

The number of videos in a study depends on the complexity, extent and variation of the research area (Santana-Garcon *et al.,* 2014). Moreover, the combination of BRUVS with complementary techniques, such as telemetry, photo identification and visual censuses produces accurate and adequate results to study the diversity of marine species such as reef fish and top predators (Bond *et al.,* 2012).

According to previous studies, juvenile sharks typically segregate from adults in what are often termed nursery areas, a strategy that is presumed to enhance survival by providing shelter from predation and abundant prey (Heupel *et al.,* 2010). Environmental factors such as salinity (Heupel and Simpfendorfer, 2007), temperature (Galaiduk *et al.*, 2007), turbidity (Chirocentridae *et al.*, 2006), dissolved oxygen (Worm, 2005) and proximity to tidal inlets (Lea *et al.*, 2016), are also important determinants of habitat use but may be moderated by species-specific physiological requirements (Martin, 2007).

Due the lack of information about the distribution patterns of sharks in the Revillagigedo Archipelago, BRUVS were used to describe the differences between habitats, islands and the presence of sharks. This is the first time that this technique has been used in the northern Eastern Tropical Pacific. Results of this technique are a baseline for the region and they could be used for more effective management strategies.

6.2. MATERIALS AND METHODS

6.2.1. Study area

The Revillagigedo Archipelago is located between N 17° 39’19” and N 20° 0’31”; and W 110° 4’41” and W 115° 28’17”, 400 km south of Baja California, Mexico (Figure 2). It consists of four volcanic oceanic islands: Roca Partida, San Benedicto, Clarion and Socorro. These islands are all formed from volcanoes rising from the Clarion Fracture Zone, a submarine fracture zone defined by numerous transform faults that traverse the northern part of the Eastern Pacific rise in the floor of the Pacific Ocean. The islands are located on southern tip of the north westward moving Pacific plate just west of the junction between the East Pacific Rise, the Middle America Trench and the Pacific, Rivera and Cocos plates. It is thought that the islands range from early Pliocene to late Pleistocene in age (Brattstrom, 1990).

As for the oceanographic characteristics, the Revillagigedo Archipelago is influenced by the California current, the Norecuatorial current and the Coastal current of Costa Rica. In addition, the bodies of water present are characterized by the surface influence of the California current and the surface mass of the Norecuatorial current which has a predominantly semidiurnal mixed tide and a high swell. Socorro Island is in the zone of transition where the masses of superficial and sub superficial water converge by cyclonic and anticyclonic rotating movements and where the northern and southern hemispheres converge. In the vicinity of the eastern coast of the Mexican Pacific Ocean, these turns are constituted by the California current and the Pacific North-Equatorial Countercurrent (Brattstrom, 1990; Figure 3).

The archipelago is impacted on average by 3 tropical cyclones per year, typically between May and November (https://coast.noaa.gov/hurricanes/). The tropical cyclones can have episodic effects on oceanographic conditions in the form of increased wind and wave energy, and cool SST anomalies (Carrigan and Puotinen, 2011). Cooling effects of up to 6 °C have been recorded in their wake, caused by the upwelling and mixing of cold subsurface waters (Price *et al.*, 2008).

The magnitude of each cooling impact is likely to be related to the proximity and strength of each storm and the duration it’s in the zone of influence of the island (Carrigan and Puotinen, 2011).

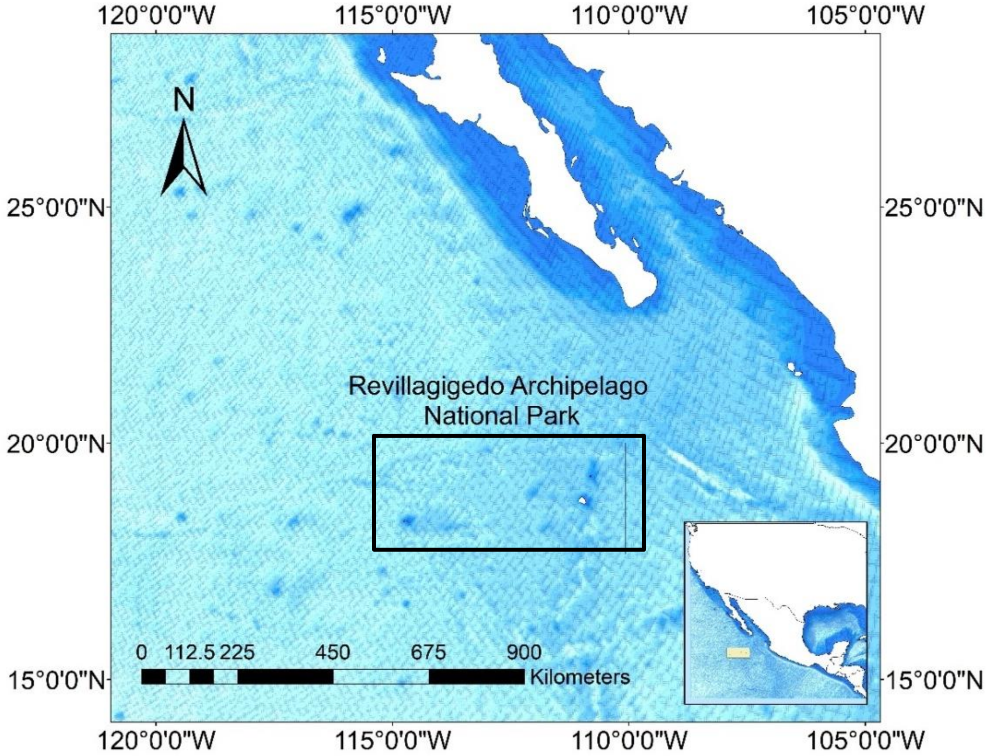


Figure 2. Map showing the location of the Revillagigedo Archipelago National Park. The new polygon shows the no take zone of 14.8 million hectares.

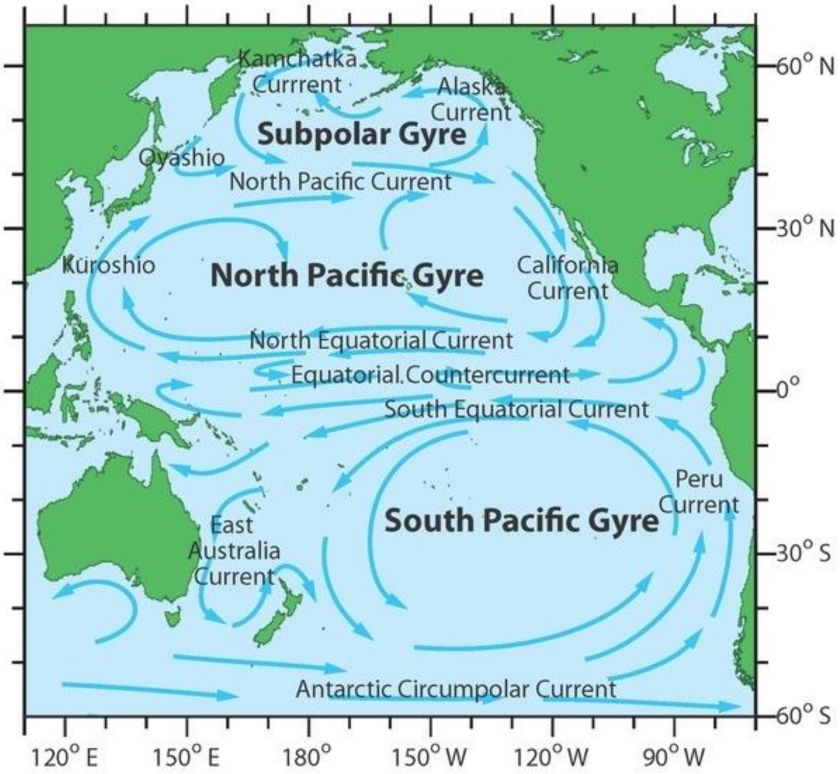


Figure 3. Map of the main oceanic currents that bring and regulate oceanographic conditions in the Revillagigedo Archipelago and the Eastern Tropical Pacific. (Taken from NOAA).

Ocean depths around the islands are variable. San Benedicto, Socorro and Clarion have some shallow bays and shelf areas (<50m), before a gradual descent to deeper waters. Roca Partida and the east side of San Benedicto have steep sides which rapidly reach hundred meters in depth. At 10-12 km from the islands ocean depths increase abruptly to around 3400 m (Gonzalez, 1993; Figure 4).

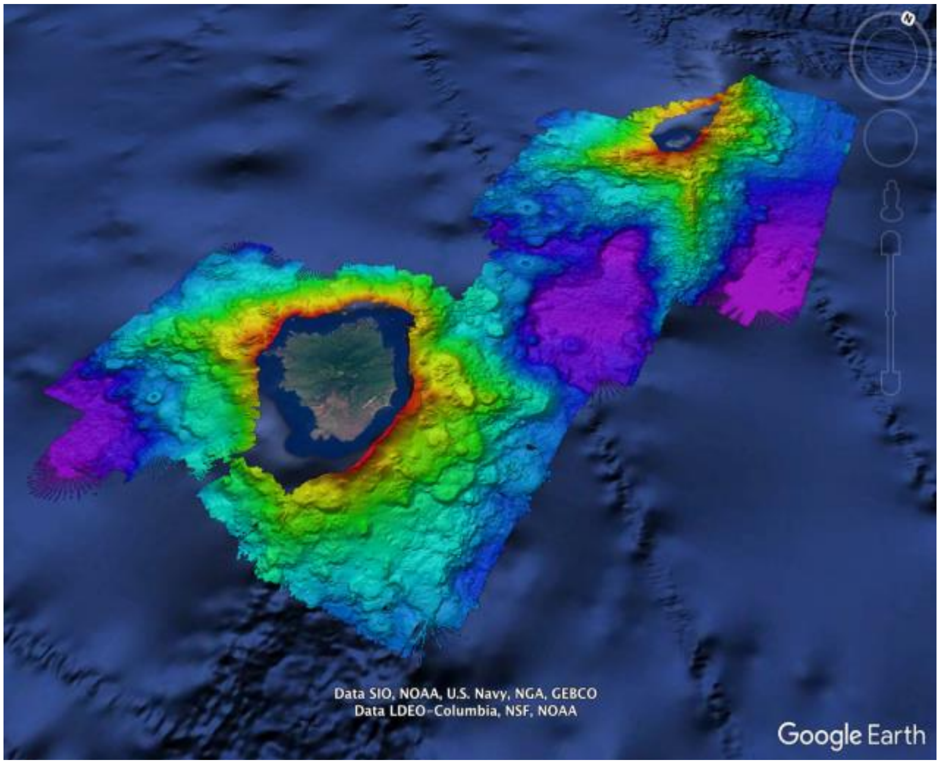


Figure 4. Image of the high definition bathymetry of Socorro and San Benedicto Island in Revillagigedo Archipelago (taken from MV/ Nautilus Exploration, 2017).

The average sea temperature surrounding the islands fluctuates between 28° C and 29° C during the summer. While in winter the average surface temperature of the adjacent seas ranges between 22° C and 25° C. Around the islands, temperatures are cooler 22° C and 23° C. The average sea temperature and salinity are 23.5° C and 34.265 ppm, respectively. Some natural phenomena occur periodically affecting oceanographic conditions such as eruptions, El Niño, tropical storms and hurricanes, (Carter, 2017).

Socorro is the largest island measuring 15 km by 15 km. It is the most topographically diverse island with a volcanic peak of 1130 m and numerous basaltic flows which descend to the sea, (Brattstrom, 1990; Figure 5).

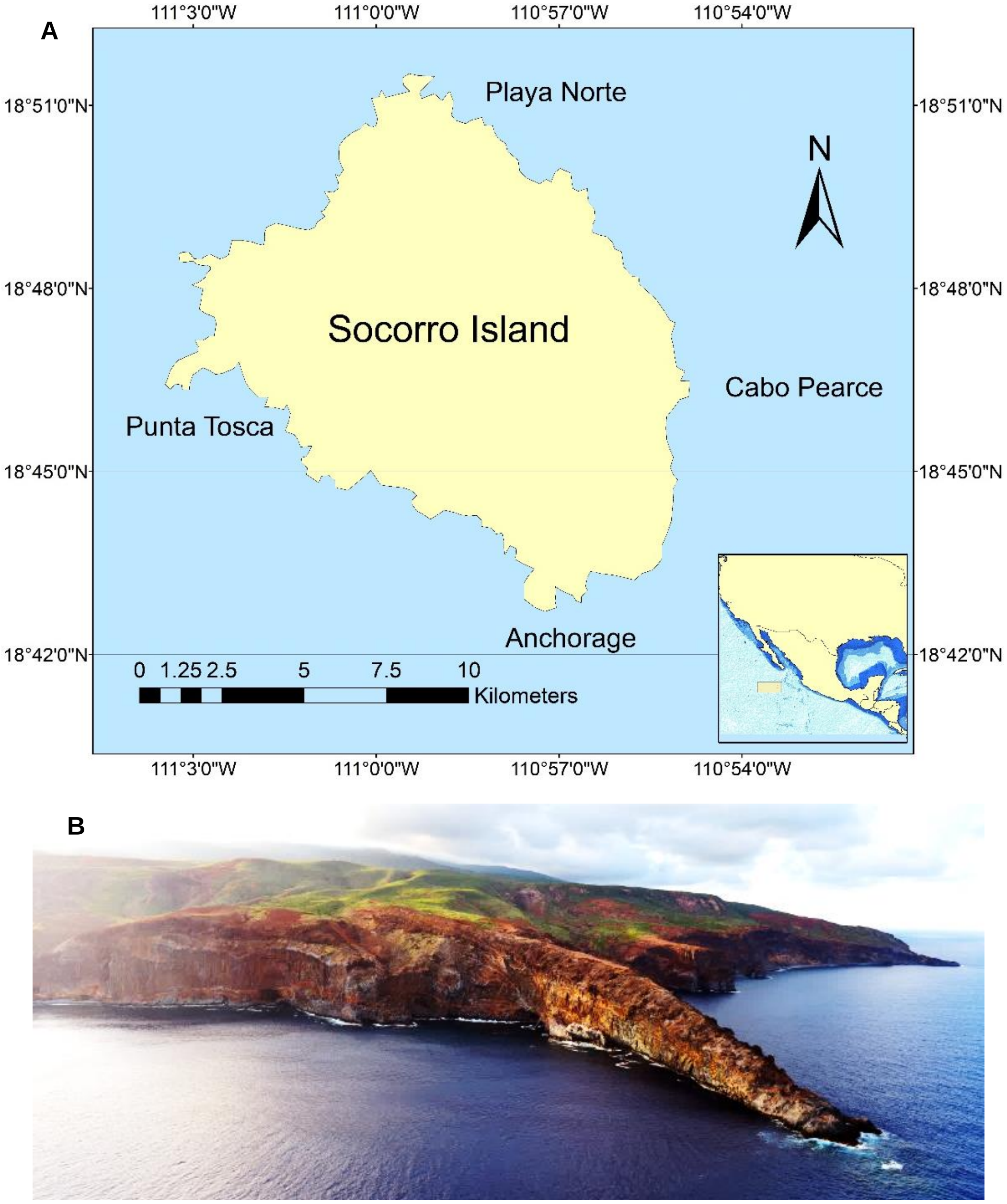


Figure 5. A) Map of the Socorro Island, Revillagigedo Archipelago and B) an aerial view of Cabo Pearce. Photo taken by Leonardo Gonzalez (2018).

San Benedicto is thought to be the youngest island in the archipelago; it is 6.4 km long and 3.2 km wide. In 1952, a new volcano named Bárcena was formed. The eruption of Barcena had an index of explosiveness of ~90%, 5 the highest recorded index of any known oceanic volcano in the eastern Pacific Ocean. It formed a pyroclastic cone 335 m above sea level and a lava delta reaching 800 m out to sea, denuding the island of flora and fauna (Rodríguez-Estrella *et al.,* 1996; Figure 6).

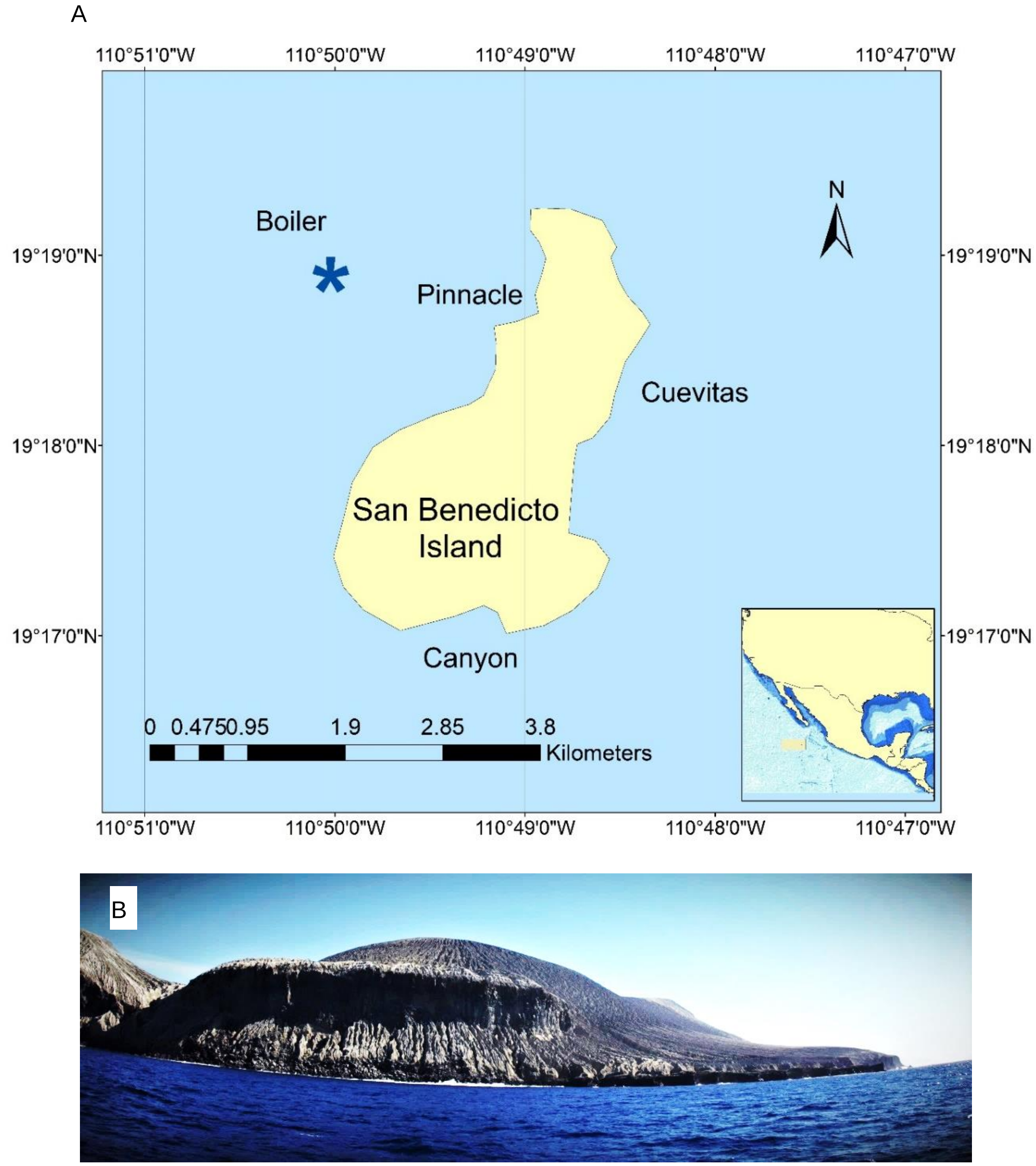


Figure 6. San Benedicto Island, Revillagigedo Archipelago: A) Map of island (and sites of the study) and B) an image of the Bársena volcano. Photo by Frida Lara (2018).

Roca Partida is an islet, measuring just 93 m long and 8 m wide. It is the crest of a submarine stratovolcano and has steep sides, rising to two peaks 25 m and 34 m in height (Rodríguez-Estrella *et al.,* 1996; Figure 7).

Figure 7.Image of Roca Partida Island, Revillagigedo Archipelago. Photo by Frida Lara (2018).

Clarion is 6.4 km wide and 9.7 km long. There are three prominent peaks on Clarion, the highest being 305 m high. It is the western most island and the oldest (likely early Pliocene; Rodríguez-Estrella *et al.,* 1996; Figure 8).

Figure 8. Image of the landscape characteristic of Clarion Island, Revillagigedo Archipelago. Photo by: Frida Lara (2018).

The Roca Partida, Socorro and San Benedicto islands are related to the transitional zone of the Mountains of the Mathematicians which constitute the volcanic submarine arc near the southeast zone of the oceanic bed, constituted by the Pacific Ridge, where they present processes of separation of the tectonic blocks in transverse direction (Rodríguez-Estrella *et al.,* 1996).

6.2.2. Species of interest

The galapagos shark (*C. galapagensis*) and the silky shark (*C. falciformis*), are two of the most common shark species that inhabit the insular platform that surrounds the Mexican Pacific coast. *C. galapagensis* has a wide distribution from very distant islands to coastal sites in the Pacific, Atlantic and Indian Oceans (Wetherbee *et al.*, 1996). *C. falciformis* is essentially pelagic and is most often found near the edge of continental and insular shelves. Both species are found from surface waters at depths of more than 500 m with some records of segregation by size (Compagno, 2005).

The silky shark, *C. falciformis*, is among the three most important sharks in the world trade in shark fins; between half a million and a million and a half individuals being traded annually. For many years the two species have been part of the main fisheries in Mexico and it is believed that they have been severely over exploited. Evaluations of the relative abundance of *C. falciformis* in the tropical central Pacific estimate a decrease in abundance of ~ 90% and in biomass> 90% (IUCN, 2012). Both species are globally classified as Near Threatened in the IUCN Red List. Due to its low recovery potential local recruitment (juveniles born annually), and local reductions may occur (Compagno, 2001).

The silvertip shark, *C. albimarginatus*, is a slow-growing shark with a maximum recorded total length (TL) of 300 cm. Males and females reach maturity between 160–180 and 160–200 cm TL (Last and Stevens, 2009). Although widely distributed throughout the tropical Indian and Pacific Oceans, populations appear fragmented with minimal dispersion (Compagno, 2001). The silvertip shark inhabits coastal and offshore waters and individuals are most commonly observed near coral reefs and nearshore reef slopes from the intertidal zone to depths of 600–800 m. Juveniles inhabit shallow nearshore waters such as lagoons. In contrast, adults occupy a larger range of habitats, (Dulvy *et al.*, 2014; Last and Stevens, 2009). Few studies have examined the horizontal movements of silvertip sharks. At Osprey Reef, Australia, silvertips demonstrated both year-round residency to this isolated seamount and unidirectional migrations briefly being detected on neighboring reefs (~14 km away) (Dulvy *et al.*, 2014).

In Revillagigedo, Muntaner (2017), determined differences in the movement patterns of adults and juvenile *C. albimarginatus*. Adults were mainly present in Roca Partida and Canyon performing frequent inter-island movement. Whereas, juvenile sharks remain in the shallow areas of Punta Tosca and Canyon for a couple of years until their growth probably finding refuge from other large predators.

The blacktip shark, *Carcharhinus limbatus* (Muller and Henle, 1841), is a cosmopolitan species found throughout tropical and subtropical waters (Heagney *et al.*, 2007). The blacktip shark is a fast-moving species that is often seen at the surface often leaping out of the water. It is commonly caught by commercial longline and gillnet fishing techniques. It is the most important commercial shark species in the southeastern United States after the sandbar shark (*Carcharhinus plumbeus*), and one of the most sought after by consumers. Two geographically distinct maternal lineages (western Atlantic, Gulf of Mexico, and Caribbean Sea clades, and eastern Atlantic, Indian, and Pacific Ocean clades) were identified and shallow population structure was detected throughout their geographic ranges. The historical dispersal of this widespread, coastal species may have been interrupted by the rise of the Isthmus of Panama. Genetic structure within the eastern Indo-Pacific supports maternal philopatry throughout this area (Keeney and Heist, 2006). Large juvenile aggregations have been observed in the Gulf of California (Cabo Pulmo and San Jose Island), reaching almost 300 individuals close to the shoreline (Pelagios Kakunjá, 2017). High association to reefs and mangroves make them vulnerable to habitat destruction and human development (Compagno *et al.,*2005). Very little is known about the spatial ecology in the Eastern Tropical Pacific.

The whitetip reef shark, *Triaenodon obesus* (Ruppell, 1837), is associated to reef habitats. These medium-sized (c. 1.8 m total length), sharks remain motionless in caves, resting for hours during the day, and emerging at night to feed on benthic prey amongst reef holes and crevices (Randall and Museum, 2004). The few studies of their movements indicate small daily home ranges of 1 km ^{2}, with maximum dispersal distances of 9–24 km over several years (Whitney *et al.*, 2012). Although usually not directly targeted by commercial fisheries, *T. obesus* populations may be highly vulnerable to recreational fishing, with populations along the Great Barrier Reef declining at 7% every year (Robbins, 2007). Despite the apparent lack of movement, *T. obesus* is the most broadly distributed reef shark, recorded in the Red Sea and Western Indian Ocean, throughout the tropical Indo-Pacific, and into the Central and Eastern Pacific Oceans, including some of the most isolated island groups in the world (Compagno, 2002). Paradoxically, this species exhibits a level of site-fidelity comparable to that of many coral reef teleosts (bony fishes), but has a distribution spanning nearly 70% of the Earth's circumference (Robbins, 2007; Figure 9).

The scalloped hammerhead shark (*Sphyrna lewini*) is circumglobally distributed in tropical waters (Compagno 1984). This species, and perhaps all hammerhead sharks (Sphyrnidae), have geomagnetic orientation and navigation abilities, possibly enhanced by their unique laterally expanded head (Klimley, 1993; Klimley *et al.*, 2001; Figure 9). Seasonal aggregations of scalloped hammerheads at seamounts (Nelson *et al.,* 2016) and the predictable appearance of adults in nursery grounds (Klimley, 1993; Hazin *et al.*, 2001) suggest a capacity for philopatry. Recent genetic evidence indicates that the nominal *S. lewini* may actually comprise two species, and there are currently seven described species within the genus Sphyrna. In contrast, *S. lewini*, *S. mokarran* and *S. zygaena* are larger, ocean-going, and more widely distributed. The global distribution of the larger hammerhead sharks implies some level of trans-oceanic dispersal. *Sphyrna lewini* is abundant along continental margins and around mid-oceanic islands in tropical waters (Compagno, 1984; Compagno, 2001), but it may not be a truly oceanic species.

The tiger shark (*Galeocerdo cuvier*) is a large (up to 5.5 m total length, TL) apex predator found in tropical and warm-temperate waters worldwide (Compagno, 1984). *G. cuvier* occur in a wide variety of marine habitats, including those associated with continental shelves, oceanic islands and atolls, and also range extensively into open-ocean (Compagno, 2001; Kohler and Turner, 2001). Tiger sharks are opportunistic predators that consume a diverse array of taxa, including teleosts, elasmobranchs, mollusks, crustaceans, reptiles, mammals and birds and exhibit a clear ontogenetic shift in diet, with both prey diversity and size increasing with tiger shark size (Kohler and Turner, 2001, Figure 9).

Figure 9. Shark species of interested in Revillagigedo Archipelago: whitetip (*T. obesus*), silvertip (*C. albimarginatus*), silky (*C. falciformis*), galapagos (*C. galapagensis*), blacktip (*C. limbatus*), tiger (*G. cuvier*), scalloped hammerhead (*S. lewini*), dusky (*C. obscurus*) and whitenose shark (*N. velox*). (Photos by Andy Murch, Rodrigo Friscione and Carmen Pasos).

6.2.3. Fieldwork

BRUVS were deployed at depths of 12 to 45 m (mean 20.15 ± 6.2 SD; 43.5 ± 11.3 m; Appendix 1) and set approximately 350-400 m apart. All the stations were deployed during day-times (mean 10:30 AM). Aluminum frames for stereo and mono-BRUVS were used (the stereo BRUVS consisted in a frame with two cameras). The GOPRO 3+ with 1080 pixels with 60 frames/ second, automatic mode was selected to provide at 90 min of filming. Two types of BRUVS were deployed, the benthic ones were set 1 m from the bottom, whereas the pelagic cameras were placed in the column of the water 10 meters below the surface (Figure 10).

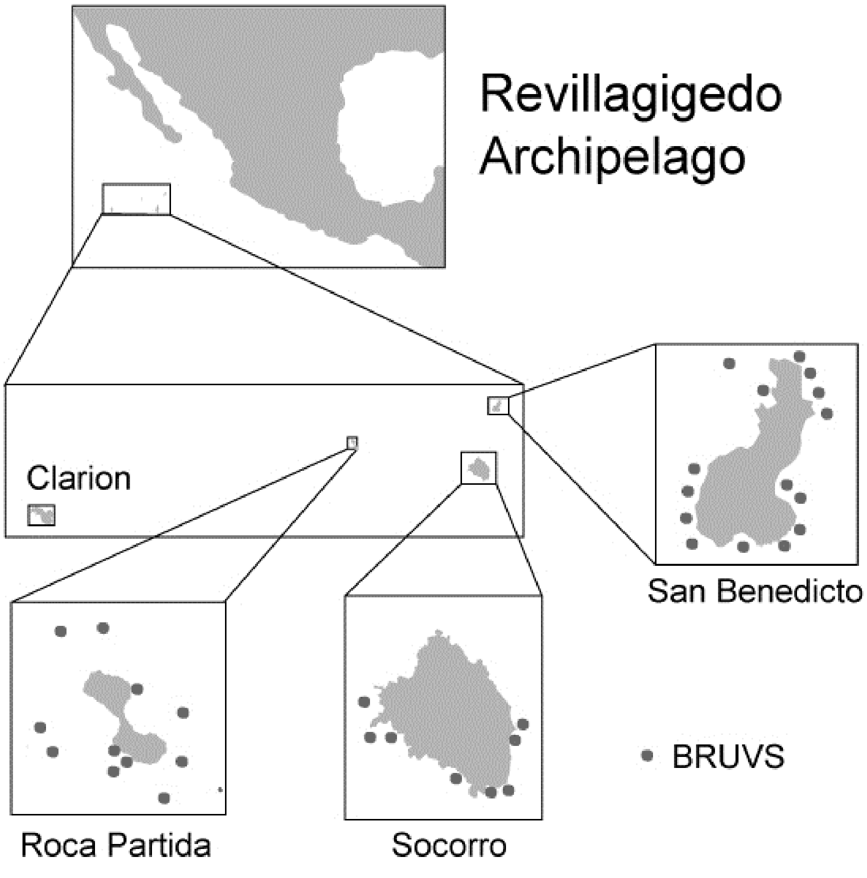


Figure 10. Map of the study sites showing the sampling sites of BRUVS (gray dots), needed to monitor habitat use and distribution patterns of sharks in the Revillagigedo Archipelago.

Detachable bait arms (100 mm plastic conduit), had a 10 cm x 2 in diameter pipe containing 0.300 kg of crushed oily fishes (yellow fin tuna, *Thunnus albacares*, lisa *Mugil cephalus*, sierra *Scomberomorus sierra*, black jack, *Caranx lugubris*), as bait. BRUVS were deployed either with 8 mm polypropylene ropes and polystyrene surface floats bearing a marker flag or placed in an underwater buoy where the receivers were attached, (Cappo *et al.*, 2001). Previous studies demonstrated that distances of 100 m and 450 m, (Cappo *et al.,* 2004; Dorman *et al.*, 2012), between simultaneously deployed BRUV systems was adequate to ensure independence indicating that a distance of 1 km between BRUV systems is sufficiently large to be considered independent (Figure 11).

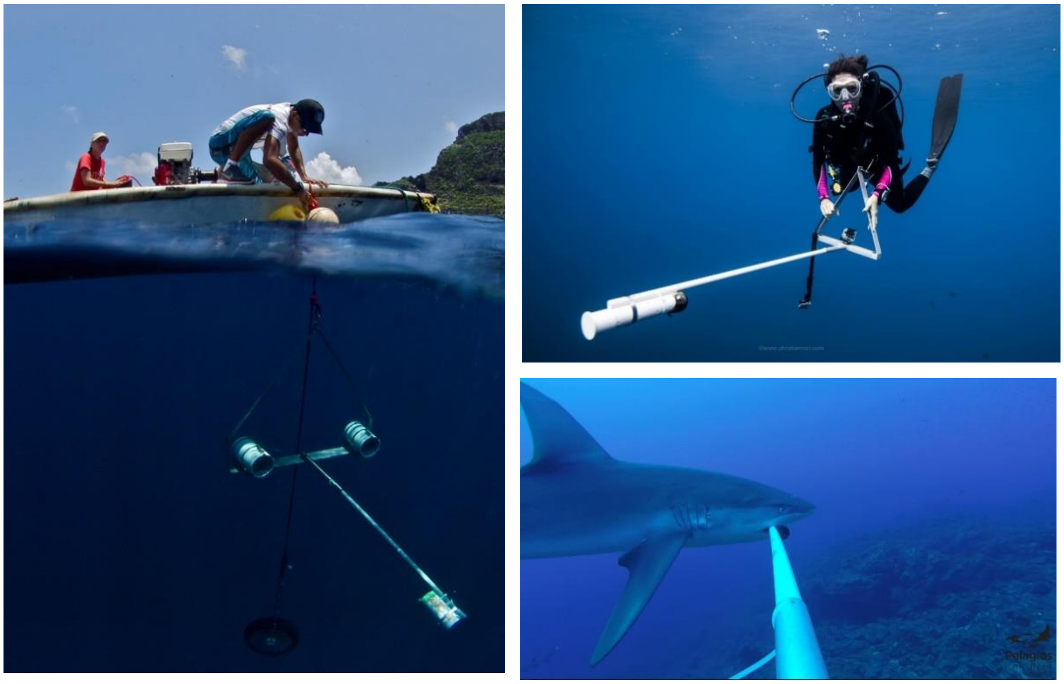


Figure 11. Design of stereo-BRUVS (left), Mono-Bruvs (top right) and an example of the frames for the analysis (bottom right).

Habitat and *associated species classification*

The date/time, location (latitude/longitude), depth (m), soak time (hrs.), current (3 categories), type of BRUVS (benthic/ pelagic) and substrate were recorded for each BRUVS.

Benthic habitat characterization was then determined analyzing the footage. For each image, two independent observers qualitatively estimated the percent cover of six major benthic groups: 1) plants/macro algae; 2) soft coral; 3) hard coral; 4) other filter-feeders (e.g. sponges, clams); 5) bare sand/mud; and 6) encrusting algae/rubble. A qualitative index (1-4; low to high). was used to assess the degree of topographic complexity of the seafloor for each image.

In order to compare differences between each site, general groups were used to classify the species recorded in the videos. The general groups were the following: cleaner fishes, dolphins, groupers, mantas, pelagic fishes, reef fishes, sharks and turtles. Relative abundance and richness (number of species), were determined by each group.

6.2.4. Data analysis

The maximum number of individuals from each shark species observed together at any one time on the whole tape was recorded as maximum abundance or MaxN (Cappo *et al.,* 2004). Estimates of MaxN are considered a conservative representation of fish abundance particularly when fish density is high (Cappo *et al.,* 2004, 2007). Replicate MaxN of each shark species were summed across sites. To standardize the sampling effort, the total hours of video (soak time), were summed for each site. Relative abundance was defined as the total MaxN of each species per site divided by the effort (MaxN hrs-1). The use of MaxN is a preferred metric of counting fish on BRUVS since it considers counts of the same individual. Species were identified to the lowest taxonomic level possible by analyzing the collection of reference images. Unidentified species. (<5% of all records). were pooled at the genus level. Shark species were classified as juveniles and adults based on length measurement analysis of video tape readings.

To ensure that there were no significant differences in the structure of assemblages between sites, and that sites were directly comparable, we constructed a similarity matrix using the Bray-Curtis similarity coefficient. A principal component analysis (PCA) was performed by constraining the BRUVS scores to display only the variation among BRUVS that could be explained by the percent cover of major habitat types, the current, and the type of substrate (Joliffe, 2002). All the tests were performed in R 3.4.4 using the library vegan (Oksanen *et al.*, 2010). A non-metric multidimensional scale (nMDS) ordination plot of relative abundance estimates (MaxN) was examined to identify patterns in predatory fish assemblages between surveyed sites and an ordered one-way analysis of similarities (ANOSIM) was used to test for differences in assemblage structure between sites. Tests were also performed in R 3.4.4 using the library vegan (Oksanen *et al.*, 2010). Non parametric Kruskal wallis and Dunn post-hoc tests were calculated to compare predator diversity (species richness) across sites since the principles of normality and homoscedasticity were not accomplished.

6.3. RESULTS

In total, 74 unique species of fishes were recorded from 7 distinct families: sharks (Carcharhinidae, Sphyrnidae), trevallies (Carangidae), snappers (Lutjanidae), groupers (Serranidae), emperors (Lethrinidae), and eels (Muraenidae). All nive species of sharks tiger (*Galeocerdo cuvier)*, whitetip reef (*Triaenodon obesus*), galapagos (*C. galapagensis*), silky (*C. falciformis*), silvertip (*C. albimarginatus)*, blacktip (*C. limbatus*), dusky (*C. obscurus*) and scalloped hammerhead (*S. lewini*) (Figure 12) were present in 100 of the 112 surveys. Despite whale sharks (*Rhincodon typus*) was never recorded in the BRUVS, several sightings have proven their presence in the archipelago.

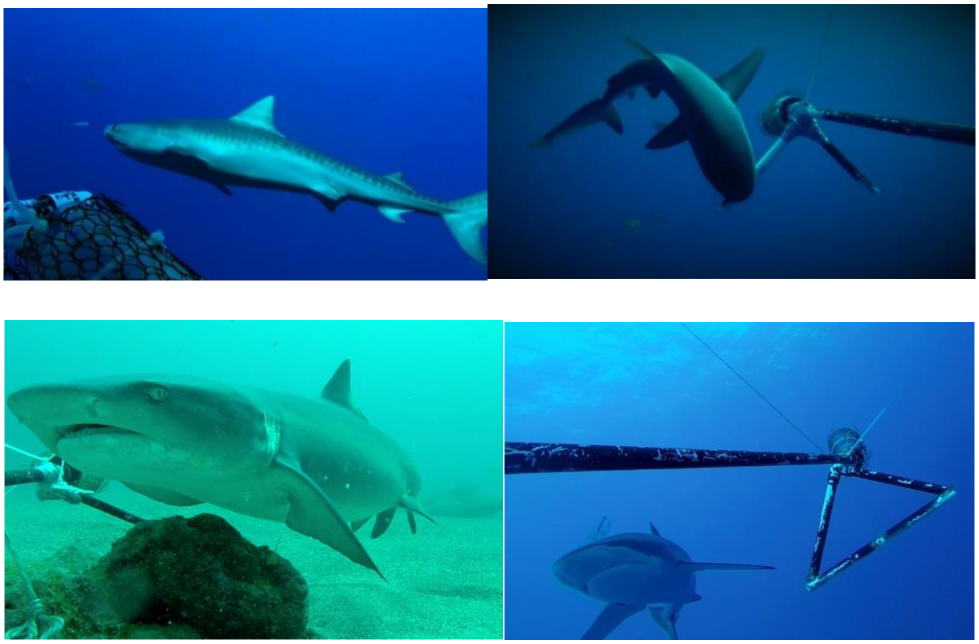


Figure 12. Sharks recorded in baited remote underwater video stations along the Revillagigedo Archipelago: tiger (*Galeocerdo cuvier*), galapagos (*C. galapagesis*), white tip (*Triaenodon obesus*) and silky shark (*C. falciformis*), images in that order. By Frida Lara and Pelagios Kakunjá.

Associated species: defining differences between the islands

According to previous observations, each island and site present characteristic fish assemblages, from very pelagic to more reef associated species. To define the differences between these environments, we compare the relative abundance of the fishes (Appendix 1). We found that three islands sampled present a large abundance of *Trachurus symmetricus*, *Paranthias colonus, Caranx lugubris* and *Xanthichthys mento*. These were the most common reef fish species present in the Revillagigedo Archipelago.

In San Benedicto and Roca Partida, the Pacific Creol fish, *P. colonus* was the most abundant. Whereas, in Socorro, the most abundant was the Pacific jack mackerel, *T. symmetricus*. The presence of the yellow fin tuna, *Thunnus albacares* was recorded in the three island (Figure 13).

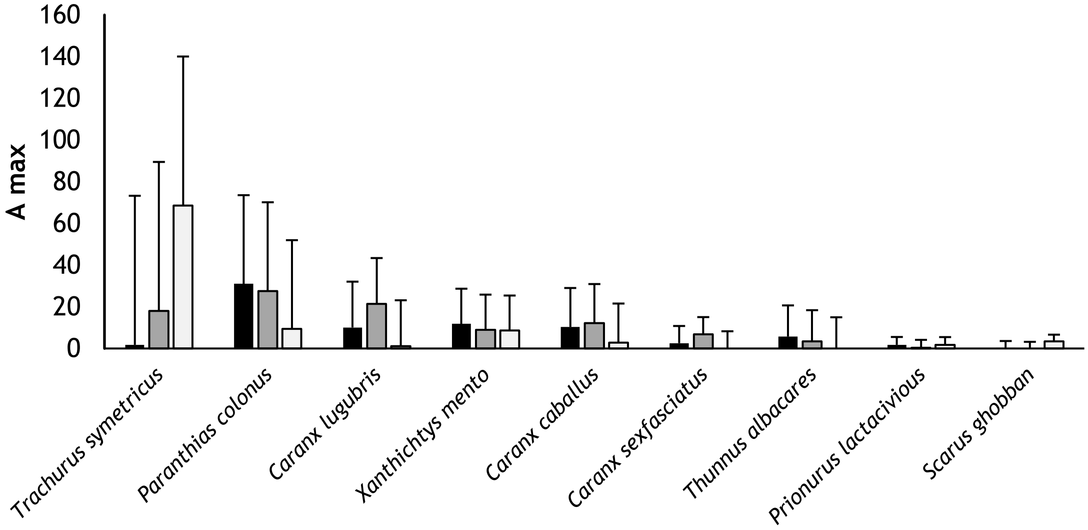


Figure 13. Average relative abundance (MaxN) of fish assemblages in Revillagigedo recorded by the BRUVS: Black bars refer to San Benedicto; Gray, Roca Partida and White, Socorro.

Roca Partida, Canyon and Boiler presented the highest abundance of pelagic species, such as: tunas (*Thunnus albacares*), wahoos (*Acanthocybium solandri*) and jacks (*Caranx lugubris, C. sexfasciatus*), etc. Socorro Island presented more abundance of reef associated fishes, such as: parrot fishes (*Scarus rubroviolaceus*). High abundances of cleaner fishes like the endemic Clarion angel fish, *Holacanthus clarionensis* and the butterfly fishes (*Johnr*and*allia nigrirostris*) could be indicators of cleaning stations (Table 1).

To determine the differences between the fish assemblages recorded in each site, the species were classified in 8 groups. The group "Pelagics" (i.e. jacks, tunas, wahoos) presented the highest relative abundance in Roca Partida and Cabo Pearce (Average MaxN 3.5 and 14.2, respectively). Whereas, in the Canyon cleaner fishes and reef fishes were the most relative abundant (Average MaxN: 5.52; 7.17).

Table 1. Average number of relative abundance (MaxN) of the general groups recorded by BRUVS in the Revillagigedo Archipelago.

Site **Group**	**Boiler**	**Cabo Pearce**	**Canyon**	**Braulia**	**Roca Partida**	**Total**
Cleaner fishes	1	5	5.2		1.33	3.14
Dolphins			1.5			1.5
Groupers	2	1.33	1.2	1	1	1.23
Mantas	1	1	1.17		2	1.22
Pelagics		3.75	4.48	3	14.29	5.97
Reef fishes	1	2.55	7.17	2	3.29	3.58
Sharks	1.05	2.5	2	2	2.46	1.95
Turtles			1			1

In terms of number of species by each functional group, reef fishes were the most diverse, compose by 17 species, followed by pelagics and sharks. The highest richness was found at the Canyon, with 35 species, then Roca Partida with 28 (Table 2, Species list by group in Appendix II).

Table 2. Number of species (richness) divided by the general groups recorded by BRUVS in each site of the Revillagigedo Archipelago.

Groups Site	Boiler	Cabo Pearce	Canyon	Braulia	Roca Partida
Cleaner fishes	1	1	1		1
Dolphins			1		
Groupers	1	3	3	1	1
Mantas	1	1	1		1
Pelagics		2	6	1	4
Reef fishes	6	8	14	11	17
Sharks	6	4	8	1	4
Turtles			1		
Total no. species	15	19	35	14	28

Differences were also observed with ANOSIM (Similitude Analysis, Appendix 1b), where the pelagic BRUVS had a high percentage of dissimilarity according with the fish assemblages (r= 0.322, p< 0.001).

Shark richness and *relative abundance*

The shark species, relative abundance, % of adults and the ranges of depth were determined by each site. Despite silvertip sharks showed the highest relative abundance, with a maximum of 12 sharks in a single frame, silky sharks and whitetip reef sharks were more often recorded in the different sites around the islands. Other species, like hammerhead sharks, were mostly recorded in just one site, the Canyon of San Benedicto (Table 3).

Table 3. Summary of shark sightings, abundance (MaxN; % MaxN) and the proportion of adults recorded on baited remote underwater video stations.

Family	Species	No. sighting	MaxN	% MaxN	Adults(%)	Depth
Carcharhinidae	*C. albimarginatus*	**53**	10	30%	9%	15- 31m
	C. falciformis	**91**	6	18%	43%	10-29m
	C. galapagensis	70	6	18%	13%	18-33m
	C. obscurus	1	1	3%	100%	25m
	C. limbatus	2	1	3%	100%	25m
	G. cuvier	3	2	6%	50%	12-25m
	T. obesus	90	5	15%	90%	18-33m
	N. velox	1	1	3%	1%	22m
Sphyrnidae	*S. lewini*	11	2	6%	100%	15- 25m

Distribution and shark species richness was examined at 112 BRUVS. Although most BRUVS were deployed at inter-reef habitats dominated by rocky reefs. Overall, sharks were common, occurring in 85% of the BRUVS. *C.falciformis* (44%) and *T. obesus* (22%) were observed in the most surveys, followed by *C. albimarginatus* and *C. galapagensis* (12 and 12%, respectively; Figure 14).

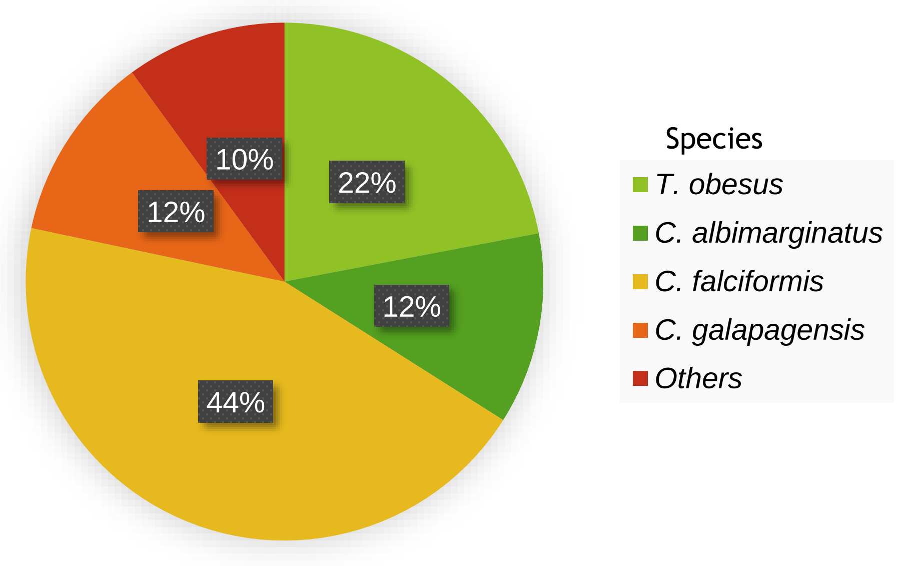


Figure 14. Shark species composition recorded using BRUVS in Revillagigedo Archipelago.

Sharks were sighted at all the stations and the number of sightings per BRUVS varied between 1 and 12 sharks (mean ± SD: 2.07±3.09). Species richness varied between 0 and 3.52 (mean ± SD: 1.84 ± 1.12), with most BRUVS where sharks were sighted recording one or two species (40.4%, 36.2%, respectively). Sharks were sighted at 65 sites, and the number of sightings per site varied between 1 and 18 sharks per site (mean ±SD: 2.07 ± 3.01).

According the shark richness, based on the type of BRUVS (benthic or pelagic), significant differences were found (KW X^2 = 6.0809, df = 1, p <0.01), where the benthic (mean ±SD: 2.5 ± 1.5055) had a higher richness than pelagic BRUVS (mean ±SD: 1.45 ± 0.68) (Figure 15).

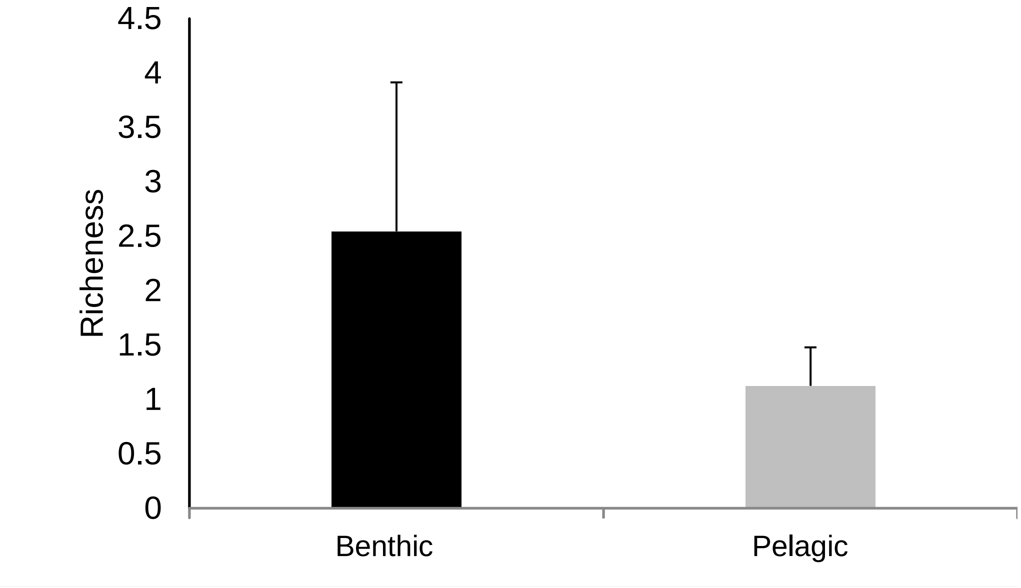


Figure 15. Average shark richness (number of shark species) according to the types of BRUVS deployed in the Revillagigedo Archipelago (t test t = 2.6159, df = 24.265, p-value = 0.01508).

In a comparison of the average shark richness per island, it is observed that Roca Partida (X = 2.2, DE = 1.4491) has the highest richness, followed by San Benedicto (X = 2.1, DE = 1,304) and Socorro (X = 1.5, DE = 0.5) (Figure 16). However, comparisons between sites and islands, differences were not significant (KW sites: x^2=10.913, df = 13, p= 0.6181; KW islands x^2=1.285, df = 2, p= 0.526).

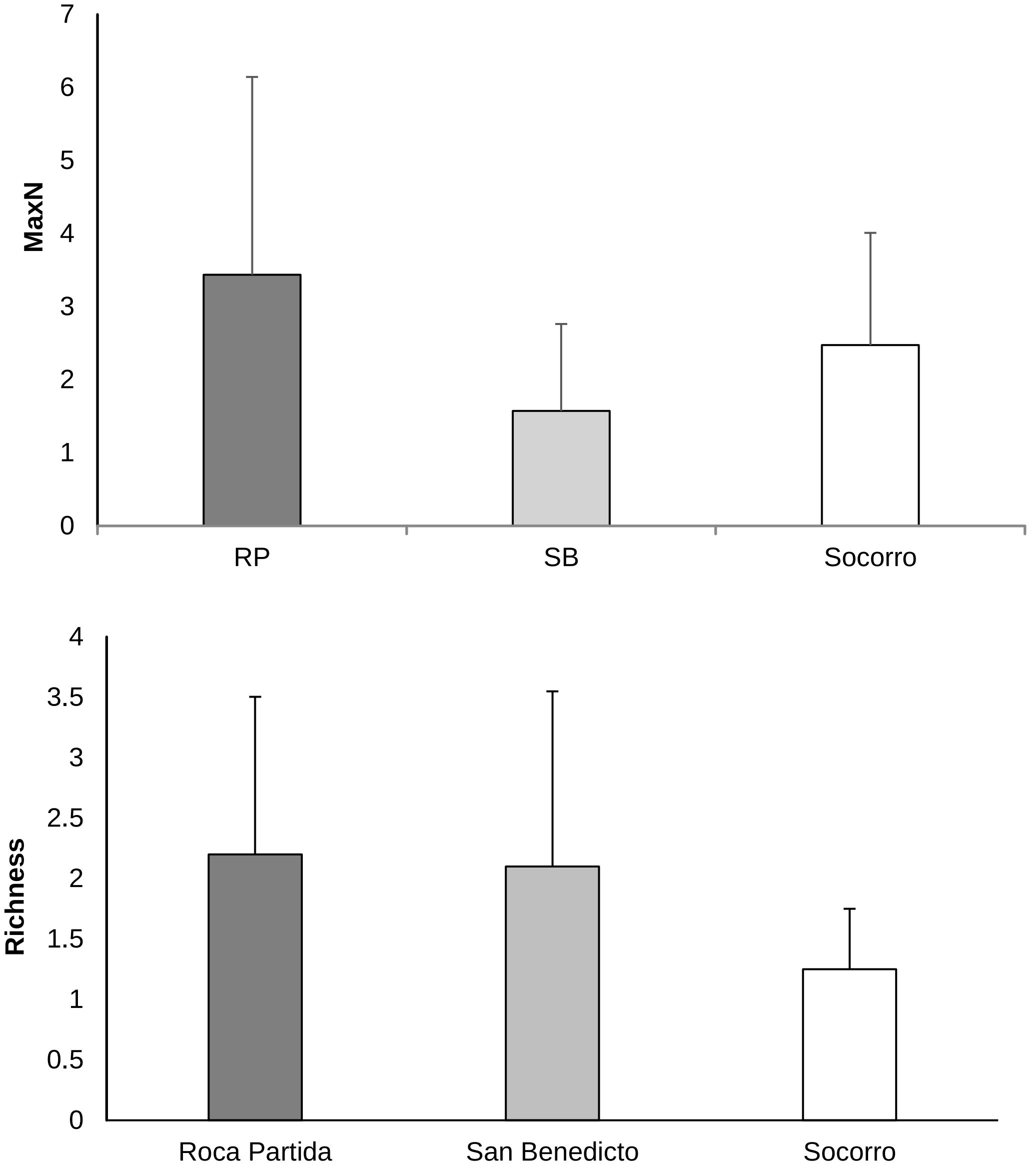


Figure 16. Relative abundance (MaxN) and average shark species richness (S) according to the BRUVS deployed in three islands of the Revillagigedo Archipelago.

In a comparison of the average relative abundance per site, it is shown that Roca Partida (X = 2.46, DE = 4.491) has the highest values, followed by Cabo

Pearce (X = 2.5, DE = 1.5) and Canyon (X = 2, DE = 2.1) (Figure 16). Roca Partida presented the highest relative abundance (MaxN) compared to the rest of the sampling sites (mean ±SD: 2.46 ± 4.19). The differences of the relative abundance of sharks in the different sites (KW X^2 = 32.104, DF= 13, p<0.005) and islands (KW X^2 = 13.761, DF= 2, p<0.001) were significant.

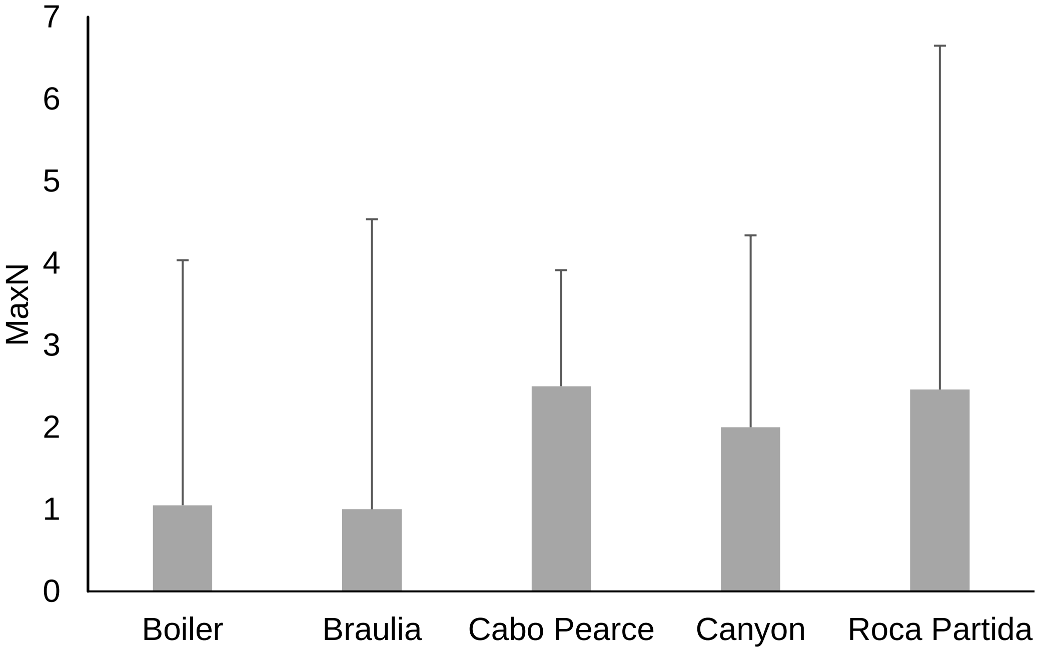


Figure 17. Relative abundance (MaxN) of sharks in the different sites according to the BRUVS deployed in Revillagigedo Archipelago.

In terms of maturity stage, the proportion of adults and juveniles were classified on 123 sharks, which were able to measured (using stereo-video). Sites like Punta Tosca (1 adult:11 juveniles) and Cabo Pearce (3:14) showed a higher proportion of juveniles than adults. Whereas, the sharks recorded in Roca Partida were mainly adults (Table 4).

Table 4. Number of the sharks divided by their maturity recorded by BRUVS in the Revillagigedo Archipelago.

	Adults	Juveniles	Proportion	Total
Site				
Boiler	6	8	0.75:1	14
Cabo Pearce	3	14	0.2:1	17
Canyon	22	15	1:0.68	37
Braulia	12	3	1:0.25	15
Punta Tosca	1	11	0.11:1	12
Roca Partida	26	2	1:0.07	28
Total	69	54	1:0.78	123

In Las Cuevitas, three juvenile tiger sharks (*G. cuvier*) of 1.5 m total length (measured by stereo video) were recorded. Showing that potentially this area represents an important habitat for the species in the first’s life stages (Figure 18).

Figure 18. First record of juvenile tiger sharks (*G. cuvier*) of 1.5 m total at Las Cuevitas, San Benedicto Island, Revillagigedo Archipelago.

All environmental and spatial variables were significant in a redundancy analysis using constrained eigenvalues, and the model explained about 19% of the total variation in the species occurrence at each BRUVS site (Figure 19; Appendix 2). The first axis accounted for 47.6% of the total variation (19%) explained by all the axes in the model, indicating that BRUVS sites were separated first by the temperature and then (on the second axis) by the type of substrate and environment. Especially *C. falciformis* showed a relation with the pelagic environment. The rest of the sharks showed correlation mainly with the current. Despite topography (slope angle) were related to the type of BRUVS (benthic deployments had a higher diversity), they did not show a relation to the shark presence.

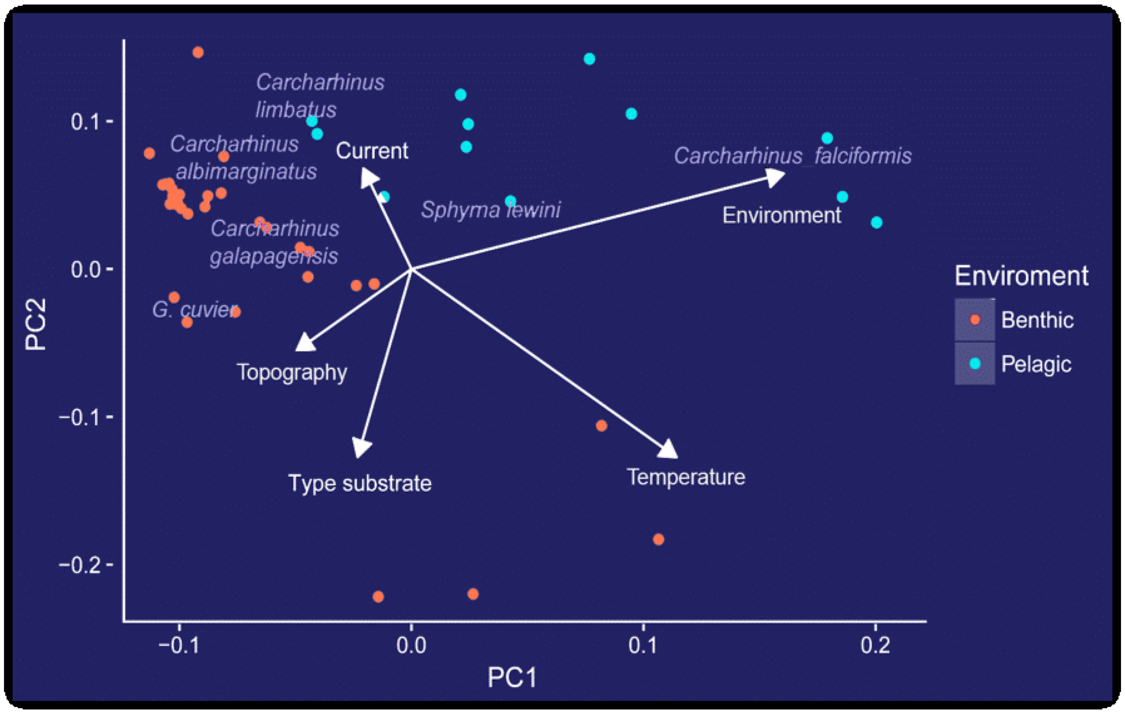


Figure 19. A principal component analysis (PCA) performed by constraining the BRUVS scores to showing the variation among BRUVS that could be explained by the percent cover of major habitat types, the current and the type of substrate. Dots represent the deployments and their color represents the type of BRUVS according to the environment: benthic (1 m up of the bottom) and pelagic (in the column of the water, 10 m below the surface).

6.4. DISCUSSION

Previous studies have recorded 28 shark species in the Revillagigedo Archipelago (Fourriere *et al.*, 2016). Of those, at least eight were observed during this study recorded in 400 hours of recorded video on BRUVS (90 minutes per set). Differences are potentially related with our limited depth sampling area, associated only to the shallow water of a maximum depth of 40 m. It is expected that sampling on the pelagic zone will increase the number of species recorded.

The average standardized shark abundance (mean of the maximum number of sharks recorded in a video frame (MaxN) / hour) in the Revillagigedo Archipelago was 4.16 (± 1.80 SD). Silky sharks (*Carcharhinus falciformis*) and Whitetip reef sharks (*Triaenodon obesus*) were the most common species 1.92 (± 1.25 DE), followed by Galapagos (*Carcharhinus galapagensis*) and silver tip (*Carcharhinus albimarginatus*) sharks. Other recorded species were hammerhead sharks (*Sphyrna lewini*), tiger (*Galeocerdo cuvier*), black tip (*Carcharhinus limbatus*), dusky (*Carcharhinus obscurus*) and white nose (*Nasolamia velox*). At least one species of shark was detected in most of the cameras (n = 32). Whitetip reef sharks were the most common species (87.5% of the sets), followed by the Galápagos (62%) and silvertip sharks (56%). Species richness by BRUVS varied between 1 and 5 (mean ± SD, 2.5 ± 0.84), with 43% of BRUVS with at least 3 species present.

The BRUVS sampling protocol was found to be an efficient and cost effective means of monitoring shark populations. The advantages of BRUVS are that compared to other methods used to assess shark populations (i.e. long lines, etc.), produce the greatest accuracy of results, are fisheries independent and thus are the least invasive to shark populations, are non-destructive to habitat, maximize range of use and carry the fewest additional bias (Harvey *et al.,* 2011; Dorman *et al.,* 2012; Santana-Garcon *et al.,* 2014).

The classification of the functional groups within each site enables to compare the differences between the habitats. We found that areas exposed to currents presented a high abundance and diversity of pelagics and sharks, such as Roca Partida and Canyon. Others presented a diverse group of reef fishes associated to the shallow and more protected areas, such as Punta Tosca and Cuevitas. Interestingly, this also reflects changes on the proportion of juveniles and adult sharks. More exposed sites presented a higher proportion of adults than juveniles.

All studies emphasize the importance of avoiding pseudo replication, and for this it is established that the devices must be separated by at least 250 meters. Ellis and DeMartini (1995) proposed that the distance between the devices should be greater than 100 m and with replicates 10 minutes apart. In this study, we followed this method respecting 100 m between the cameras. In the case of Roca Partida, replicates were taken with at least two hours between them. The main goal is that the deployments are totally independent from each other. However, previous experiences in the Galapagos, showed us that even setting the cameras 700 m away between them, some sharks like, tiger sharks were identified in two different deployments.

As for the type of bait, most of the studies have used sardine (*Sardinops sagax*), in quantities ranging from two kilos to 200 grams. However, according to the study by Hardinge *et al.,* (2013), the diversity and abundance observed with 200 g is the same as with 1 kg or 2 kg. Cappo *et al.,* (2007) mentioned that although the amount of bait is increased, the influence pen still has an area of constant influence, only increases the concentration. In this study, we used 500 g of bait, having successful results, attracting sharks during the 90 minutes of the sampling.

BRUVs have been found to sample greater species richness and obtain greater estimates of relative biomass of generalist carnivores than diver-operated video methods (Langlois *et al.*, 2012). This may be as a result of one of the main advantages of BRUVs: the absence of shark diver-avoidance behavior, which may confound abundance estimates, and is inherent to underwater visual census (UVC) techniques (Cappo and Speare, 2007). In this study, the no- shark diver-avoidance behavior allows to record first life stages for many shark species (silky, Galapagos, silvertips and tiger sharks) that are not commonly observed during the dives.

6.4.1. Contributions of the BRUVS

The knowledge of the movement patterns of highly migratory species like sharks and other pelagic species have been studied for many years. Some of the limitations of monitoring that are often mentioned in previous studies are the observations in field. BRUVS can be used to document fish species richness along geographic gradients (Cappo *et al.,* 2007; Harvey *et al.,* 2013), quantify elasmobranch abundances and distribution patterns (Bond *et al.,* 2012; White *et al.,* 2013), and compare fish densities inside and outside marine reserves (Malcolm *et al.,* 2007; Ruppert *et al.,* 2013).

BRUVS have been used to quantify biodiversity, relative abundance, behavior, and using stereo-video, size and biomass (Cappo *et al.,* 2011; Dorman, Harvey, and Newman, 2012; Santana-Garcon *et al.*, 2014). They can be used to evaluate the fish community in a variety of environments, estuaries, and tropical and temperate reefs (Ghazilou *et al.*, 2016). This technique is non-invasive and offers several sampling advantages, such as (Santanta-Garcon *et al.*, 2014):

1. Longer observation time, with sampling in deep areas (50 m) for longer time intervals
2. Statistically robust databases, comparable in time and space
3. Reduction of bias in sampling, recording both large and small species.

6.4.2. Limitations of the BRUVS

These include the potential inflation of density estimates due to fish being drawn from outside visible sampling areas, unknown areas of attraction as a byproduct of variable bait plume dispersion, alteration of fish behaviors, competitive exclusion, and/or preferential sampling of predator and scavenger populations with corresponding reductions to other functional groups (Hardinge *et al.*, 2013; Santana-Garcon *et al.*, 2014). However, comparisons between baited and unbaited camera stations have shown that while carnivore and scavenger abundances tend to increase in the presence of bait, no commensurate changes are typically detected in herbivore or omnivore abundances (Harvey *et al.*, 2011).

Notably, the ‘area of attraction’ to the bait bag is unknown, thus making highly accurate density calculations impossible (Cappo *et al.,* 2007). It is also not known whether sharks exhibit bait-preference or altered behavior in interactions in the presence of a bait-bag, thus this technique can only provide a relative estimate of abundance of shark populations. Potential bias also exists in the data analysis component of the study. Tape analysis by different enumerators has the potential to cause inconsistency in the data collected through misidentification of species or counting, but the tapes are a permanent record of data and can be independently interrogated to ensure this does not occur. A greater limitation is the time requirement for the BRUV tape interrogation and data archival, although new software is available and advancing to make this process more efficient (Cappo *et al.,* 2007).

Although stereo-video can accurate measures of fish size, Santana-Garcon *et al.* (2014) found highly mobile pelagic species, such as sharks, were difficult to measure with great accuracy due to their observance farthest from the camera systems. Stereo-video systems are also more complicated, requiring multiple specialized cameras and additional three-dimensional calibration software and expertise, and as such represents highly increased costs, neither of which are practical for application in this region at this time.

6.4.3. Comparing results with other studies

According to Aburto *et al.* (2016), Revillagigedo Archipelago has the highest biomass of sharks compared to other MPA’s in the world. This characteristic top predator community is mainly formed by white tip sharks, *T. obesus,* galapagos sharks*, C. galapagensis*, Silvertip sharks*, C. albimarginatus,* and others. Acuña-

Marrero (2018) found that the Darwin and Wolf harbored distinct shark assemblages than the rest of the Galapagos Archipelago, characterized by high abundances of large and highly mobile species and a low diversity of sharks. Also, by the dominance of large and highly mobile semipelagic shark species with broad distributions (Figure 20).

In this study, finding a similar number of shark species indicates the importance of Revillagigedo. Pelagic sites such as, Roca Partida presented lower numbers of species than Canyon and Boiler, dominated by semi-pelagic sharks. In contrast, species such as, tiger (*G. cuvier*) and white nose shark (*N. velox*) were only observed in San Benedicto.

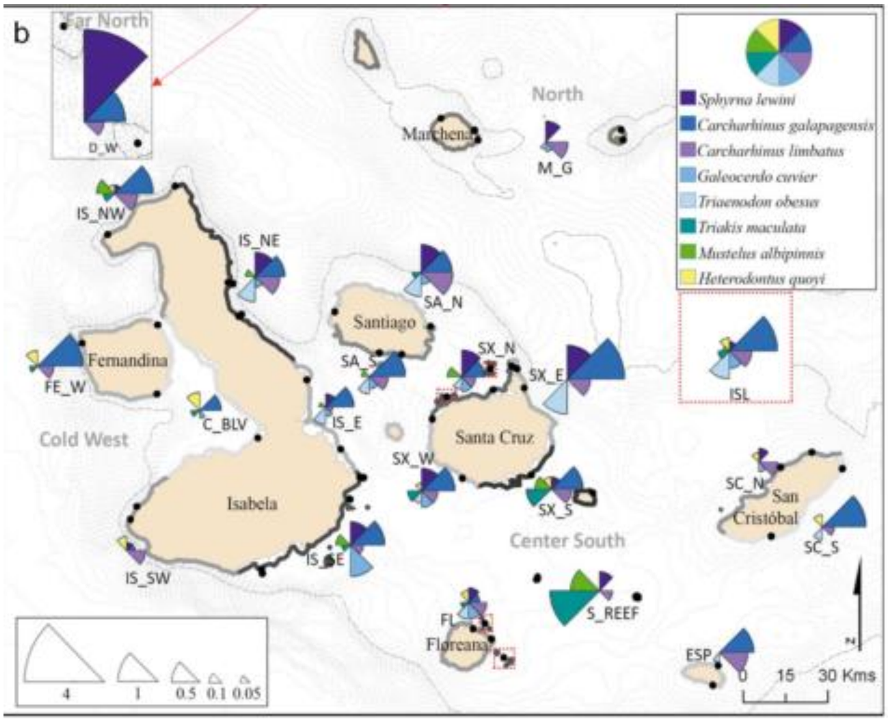


Figure 20. Distribution and abundance of coastal sharks recorded by BRUVs within the Galapagos. Presence and relative abundance of coastal sharks is indicated using segmented bubble plots where in each shark species is represented by a circle segment corresponding to a given colour and whose size is proportional to its average relative abundance per stratum (no. sharks per BRUV, taken from Acuña Marrero *et al., 2018*).

Espinoza (2015) determined a relative abundance of *C. albimarginatus* of 98 individuals in Western Australia, which is higher of what we recorded (12 MaxN) for the same species. In the Indo-Pacific, reproductive aggregations of grey reefs (*C. amblyrhinchos)* and silvertips sharks have been well documented. In Revillagigedo, juvenile sharks tend to appear together, adult silvertips are not commonly observed schooling together.

Salinas de León *et al.*(2016) found that sharks, mainly hammerhead and galapagos sharks, dominated the fish assemblage, but other predators like the bluefin trevally, black jack (*Caranx lugubris*) and bigeye jack (*C. sexfasciatus*) were also common at several of the sites surveyed. In Revillagigedo, we observed that the abundance of predators was also very remarkable and followed in abundance by planktivores (*P. colonus*).

In the Galapagos, a marked concentration of sharks and planktivores fish biomass at the southeast corners of Darwin and Wolf, something previously documented by acoustic telemetry studies (Hearn *et al.*, 2010). Apex predators (sharks, jacks, and groupers) accounted for 75% of the total biomass, followed by planktivores (primarily gringos) at 20%, lower level carnivores (4%), and herbivores (1%).

The remarkable diversity of sharks in Revillagigedo was recorded in many sites. This interaction between species is very interesting, because it implies competition in terms of potential preys and habitats. According to White *et al.* (2015), silvertip sharks, *C. albimarginatus*, may be in direct competition with blacktip, *C. limbatus*, and galapagos sharks, *C. galapagensis*.

In the Cocos Island, records of increases in the presence of blacktip and galapagos could be due to working effectively for these largely reef-restricted species. Shifts reflect the changing community assemblage that has occurred at Cocos Island over the past 21 years and are not necessarily an indication of the MPA's effectiveness (Baskett *et al.,* 2007). Tiger sharks also have showed significant increases in their odds of occurrence over time, arising from the abrupt increase observed since 2007. It is possible that within this system of strong fishing pressure, tiger sharks have an advantage over other elasmobranch species because of their relatively high intrinsic rate of increase (Hutchings *et al.,* 2012) and high post-hooking survival rate (Gallagher *et al.,* 2014).

The deep waters are scarce documented ecosystems in Revillagigedo. During 2016 Pristine Seas expedition, conducted biodiversity surveys using remote cameras (the National Geographic Dropcams) and dives on board of manned submarines with the aim of filling this knowledge gap. Four phyla, composed of 28 families and 29 species were observed during a total of 15 Dropcam launches in deep habitats between 50 and 2285 meters deep. The most abundant recorded species of fish was the grouper (*Epinephelus cifuentesi*); sharks and deep rays were also numerous. Deep-sea species of Elasmobranch were recorded: Pacific sleeper shark (*Somniosus pacificus*), purple chimera (*Hydrolagus purpurescens*), long-nosed cat shark (*Apristurus nasutus*), black shark (*Centroscyllium nigrum*) and the deep sea skate (*Bathyraja abyssicola*).

Thenty three dives on board of submarine to depths of more than 200 m, registered 70 families and 117 species. The carangids (horse mackerel) and chondrichthyans (sharks) were common in the deep dives in the Revillagigedo. Of these, the silky shark (*C. falciformis*) was the most abundant (56 sightings) and was frequently recorded (73% of the censuses), followed by the galapagos shark (*C. galapagensis*) with 56 sightings in 43% of the censuses and the hammerhead shark with 42 sightings in 13% of the censuses. A record of a great abundance of reef species in mesophotic reefs (50-200 m) with large abundances of the grouper olive (*E. cifuentesi*), red snapper of the Pacific (*Lutjanus peru*), black horse mackerel (*Caranx lugubris*) and palometas (*Seriola rivoliana*), all of them fish species of great commercial value and whose abundance in other places of the continental coast of Mexico has been greatly reduced due to overfishing.

6.4.4. Relation between environmental variables and shark relative abundance

In this study, environmental and spatial variables were significant, exposure to currents, temperature, type of substrate and environment. Especially *C. falciformis* showed a relation with the pelagic environment. The rest of the sharks showed correlation mainly with the current. According to Salinas de León *et al.,*(2016) the higher fish abundance at these SE locations may be related to local oceanographic features, dominated by a unidirectional current from the southeast to the northwest that collides with the southeast corner of both islands. This current may enhance productivity that supports rich benthic communities and large numbers of planktivores fishes, mainly gringos, which may serve as a food source to carnivorous fishes and sharks (Hamner *et al.*, 1988; Hearn *et al.*, 2010).

Another factor is that, both hotspots in Revillagigedo and Galapagos are important for nightly foraging excursion to adjacent pelagic areas; and/or for the cleaning stations (Hearn *et al.*, 2010). Seasonal changes in fish assemblages and biomass are likely since hammerheads are known to migrate from these islands between February and June (Ketchum *et al.*, 2014). Future studies should focus on seasonal trends and depth gradients (Lindfield *et al.*, 2014) in shark abundance and distribution.

This is one of the first studies using BRUVS in the north of the Eastern Tropical Pacific. The results show interesting patterns and provide a baseline in terms of shark distribution patterns in Revillagigedo Archipelago. To improve the results, it is necessary a larger sampling effort in the rest of the localities, that did not were monitored, such as, Clarion Island and the north of the Socorro Island. We were able to demonstrate that Revillagigedo habitats are important for a wide range of shark species. The use of BRUVS as a fishery-independent tool allowed quantification of shark species richness and occurrence for the entire area, including areas where visual surveys are restricted by depth.

7. CHAPTER 2. DIEL AND SEASONAL MOVEMENTS AND RESIDENCY INDEX OF *C. falciformis* AND *C. galapagensis* IN THE REVILLAGIGEDO ARCHIPELAGO

Figure 21. Silky shark (*C. falciformis*) passing by the Canyon cleaning station in San Benedicto Island. Photo by: Rodrigo Friscione.

7.1. INTRODUCTION

With technological advances, new methodologies allow scientists to elucidate the distribution of highly mobile and generalized pelagic species such as sharks. It has been determined that oceanic islands provide rest and breeding areas, (Montoya and Thorson, 1982; Veech and Crist, 2007; Figure 21). With the technological advances, there is a powerful technique that elucidates the distribution of very mobile and widespread pelagic species such as sharks. Acoustic telemetry consists of a series of acoustic receivers that record the presence of animals marked with an acoustic transmitter within the detection range (Sundström *et al.,* 2001).

The use of this technique offers wide advantages, such as monitoring periods on a large time scale (+ 10 years), low field monitoring costs (since data are collected every 6 months) and provides a large amount of information on the patterns of distribution in space and time. As well as establishing the patterns of interconnectivity between sites, islands, etc. Sharks were tagged with acoustic tags (VEMCO V16) that send a unique signal, identifying the individual and detected by a stationary receiver (Chapman *et al.*, 2015). When an individual return to a specific location where it previously resided after having left it for some defined period of time is known as site fidelity (Speed *et al.*, 2016).

The abundance and distribution of the species can vary from meters to kilometers, and on temporary scales from minutes to decades, incorporating daily patterns such as vertical migrations (Hoyos-Padilla *et al.*, 2014; Sundström *et al.,* 2001), time cycles (Espinoza *et al.*, 2015) and inter-annual trends (Hook *et al.,* 2006; Ketchum *et al.,* 2014). These tendencies to be distributed in a previously used locality, which is determined by biotic (i.e. food availability, competition, predation risk, and behavior) and abiotic (i.e. temperature and light) conditions (Young and Wiersma, 1973; Heithaus *et al.,* 2002).

To study the preference of habitats that sharks use during stationary or movement periods it is necessary to define the stages. To determine if sharks and other pelagic species are directed to a specific habitat, the proportion of movements of each area are calculated for each individual, such as the number of movements within an area divided by the total number of movements (Meyer *et al.,* 2010). Current population assessments based on fishing rates are scarce and trends are not species-specific (Bennett *et al.*, 2003). Therefore, they determine how sharks use their habitat over time to support effective management strategies (Heupel *et al.*, 2004).

The knowledge of the area of activity is a useful tool for the management of the fauna because it provides us with information about the approximate area needed to maintain a viable population (Bruce *et al.,* 2005). Home ranges provide basic information on movement patterns and contribute to species ecological analyzes for habitat preference (Bruce and Bradford, 2007). The non-random use of a site, resulting in voluntary movement of an organism as a response to a broad combination of factors has been defined as habitat selection (Sims, 2003). Stock assessment is necessary to create strategies at the national level and later they are integrated in analysis on the connectivity of the islands (Peñaherrera *et al.,*2018). It has been recommended that operational restrictions during the migration periods point out the need to create international cooperation means such as Migramar (www.migramar.org).

Differences in biological processes along the nocturnal/diurnal variety, for example, have long been of interest to science posing questions of central importance to ecology and evolution about how environments may affect animal physiology and behavior (Panda *et al.*, 2002, Panda and Hogenesch 2004). Whitetip reef sharks (*Triaenodon obesus*), are normally nocturnally active but show increased levels of diurnal vertical activity at dive sites during daytime provisioning tourism operations (Fitzpatrick *et al.,*2011). It is possible that such alterations in nocturnal activity could have energetic or fitness consequences; however, this remains unknown (Gallagher *et al.,* 2015). It is also feasible that the loss of elasmobranch prey or predators could alter diel behaviors.

7.2. MATERIALS AND METHODS

7.2.1. Tagging procedure

a) Internal tagging

Sharks captured by hook and line were lifted into a sling and kept alive in water while being tagged (Figure 22). The gender (presence of claspers or not), maturity stage (juvenile, sub-adult, adult), and total length (estimated by scuba or free diver taggers or measured for sharks which were captured), were recorded for all sharks when possible. A pump may be placed underwater and water introduced through mouth and out of gills of the shark while in sling where operation will be performed. The tag and the equipment used during the surgery were immersed in a disinfectant before the procedure (Klimley and Nelson, 1981).

Figure 22. Tagging procedure for the implantation of an acoustic transmitters internally. A surgery on a juvenile silver tip shark (*C. albimarginatus*).

The technique of tagging selected was the one that enabled us to complete the operation most quickly and less stressful. The ultrasonic tags were inserted into the peritoneum of the sharks. Sharks were placed on their backs to induce tonic immobility as in other published studies elsewhere (Klimley *et al.*, 1983; Hearn *et al.,* 2010). To introduce the transmitter, an incision 3-cm long was performed to the side of the midline of the stomach. Then either surgical staples or, more likely, sutures to close the wound were used. Prior to release, the hooks were carefully removed from the shark's mouth while still in tonic immobility. This whole procedure, from retrieval from the long line to release should not take longer than 3-6 minutes (Klimley and Nelson, 1981).

b) External tagging

The external tagging procedure was made by SCUBA and free-divers using a pole spear and a special dart that was introduced in the skin located in the base of the dorsal fin. As it has been showed in previous studies, probable dislocation of the tag is expected due the natural friction of the tag; fishes that confuse the tag as an ectoparasite or corrosion of the tether (Kohler and Turner, 2001).

In total, thirty-nine sharks (21 *C. falciformis* and 18 *C. galapagensis*), were fitted with ultrasonic tags (Vemco, Ltd., V16), during cruises to those five insular systems from 2008 to 2015 (Appendix 3). All the tags emit a coded signal at 69 kHz with a random delay of 40–140 s to avoid successive signal collisions between two tags. The MigraMar Ultrasonic Receiver Network (http://www.migramar.org/), registered the signals emitted by the ultrasonic tags using the VR2. Ten receivers were used for this analysis which were placed on Socorro (Cabo Pearce, Punta Tosca), San Benedicto (Boiler, Canyon and Cuevitas), and Roca Partida (North, East; Figure 23).

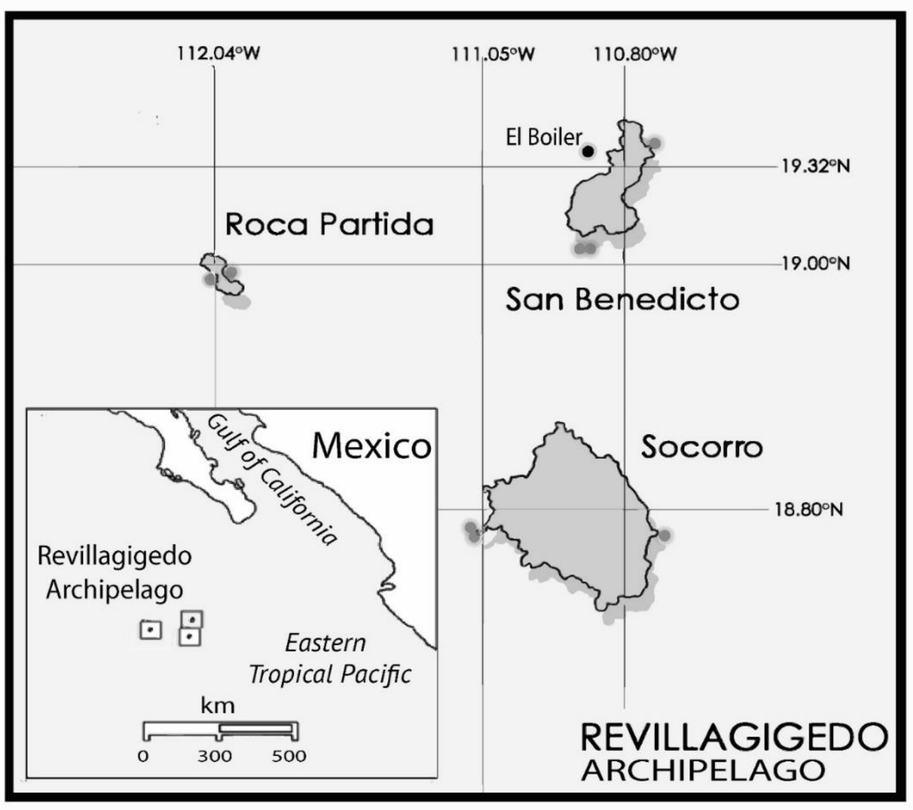


Figure 23. Map showing the receiver array with in the Revillagigedo Archipelago. Gray dots indicate the location of each station.

Receivers were affixed with heavy-duty cable ties to a mooring line with chain or cable to attach to the bottom anchor and a buoy for flotation (Figure 24). Detection range tests of the ultrasonic receivers were previously performed at several of the study areas in the ETP, varying from 200 to 800 m, depending on many variables but mostly on the topography, (Hearn *et al.,* 2010; Bessudo *et al.,* 2011).

Figure 24. Image of an internal tagged Silvertip shark, *C. albimarginatus* (see stitches on right, isn't that the left, side) swimming near to an acoustic receiver VRW2 located at the Canyon, San Benedicto Island, Revillagigedo Archipelago (Photo by Jesús Ballesteros).

7.2.2. Data analysis

The residency index (RI) was calculated as the ratio between the number of days an animal is present in sites to the number of days from the first to the last detection with a value of 1 indicating it is detected every day and 0 indicating it was never detected. The number of consecutive days each individual resided will be calculated and divided by the total visits by all sharks to gain an average residency time per visit (Daly *et al.*, 2014; Espinoza, *et al.,* 2015). To test for normality the following tests were performed: Kolmorov- Smirnov Significance Test, Wilcoxon Rank Sum, Chi^2 test or Kruskal-Wallis Ranked- Sum, respectively Mann- Whitney U tests. For the analysis of the daily presence patterns circular plots were created using the R packages circular (Lund, 2012), lubridate (Grolemund and Wickham, 2013), and ggplot2 (Wickham, 2006).

The number of detections recorded for each shark during diurnal and nocturnal periods was collated separately for each receiver to examine diel patterns of activity. For each shark, the detection records were also plotted versus time of the day and month to further investigate diel and seasonal patterns of use of primary sites (Espinoza *et al.*, 2015). In addition, a Rao's test was performed to test uniformity of the daily detection patterns with those packages (Lund, 2012).

For sharks tracked for more than one consecutive year, a comparison was made between their detection history during the first and second half of the study to verify if a change in activity space; e.g., a shift in the location of the primary detection site, an increase in the overall number of sites where it was detected, a reduction in time spent within the array, occurred as the animal aged. Residency histories were plotted by day to provide a visually interpretable timeline of animals present in the study site. The number of continuous days that individuals were resident in the study site was calculated each time they entered the study site and compared among years using one factor analysis of variance (ANOVA). For all statistical analyses, the assumptions of normality and homogeneity of variance were tested using normal probability plots of residuals and plots of residuals vs. predicted values. If the data did not meet the assumptions, log transformations were performed following recommendations in Zar (1984). Total numbers of days monitored and number of continuous day presence were calculated for each individual. Data were checked for normality with Quantile-Quantile plots and either log(x) or log (x + 1) transformed if required. Two factor analysis of variance (ANOVA), was used to test for differences in total days present and continuous days monitored between years and age classes. Test were performed using the R package and the library AOV (Wickham, 2006).

7.3. RESULTS

The presence of twenty-four *C. falciformis (*22 females; 1 male; 1 unknown), and eighteen *C. galapaguensis* (9 females; 2 male; 7 unknown), were recorded within the marine reserve from 11th of April 2010 to 13th of November 2015 (Figure 25 and 26). The shark total length ranged from 111 to 300 cm (mean= 203.36 cm TL; Table 1). Based on the Length at first maturity, five of the *C. falciformis* were immature and nineteen were adults. In contrast, fourteen *C. galapagensis* were immature and four were adults. The average recording period was 430 days (±349.25), since the shark was tagged to the last day of record with an average presence of 50.53% of the recording days. Significant differences were observed between external and internal transmitters ($T_{(1,40)} = -4.24$, $P>0.05$).

In terms of residence index, April (0.94 ± 0.2) and May (0.76 ± 0.2), presented the highest values, while lowest RI occurred in August (0.24 ±0.15) and September (0.3 ± 0.5) (Figure 28). Significant differences were found between the months for *C. falciformis* (f=3.45, DF=11, $p<0.05$) and *C. galapagensis* (f=2.35, DF=11, $p<0.05$).

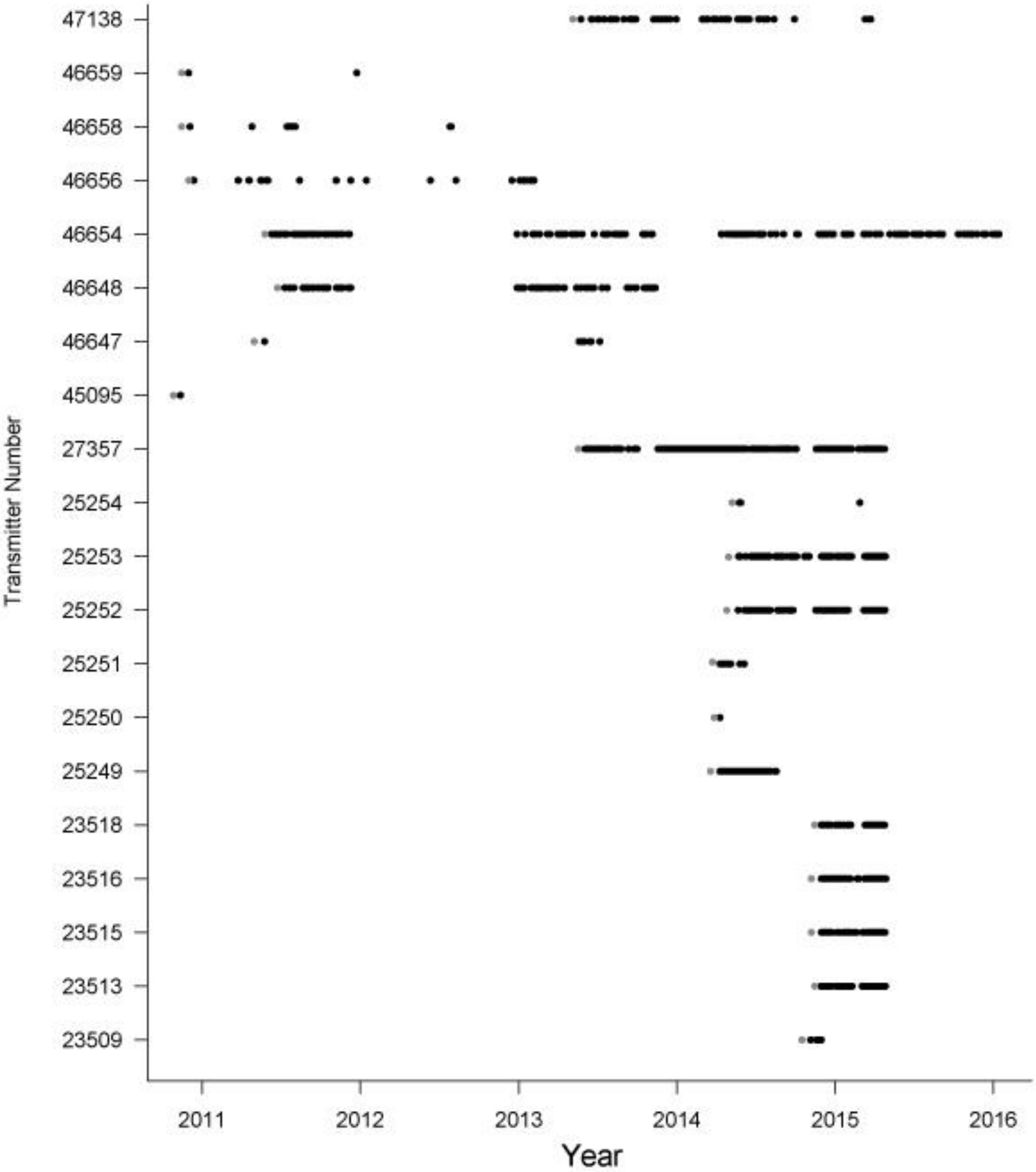


Figure 25. Detection plot of Silky sharks (*C. falciformis*) recorded in the Revillagigedo Archipelago.

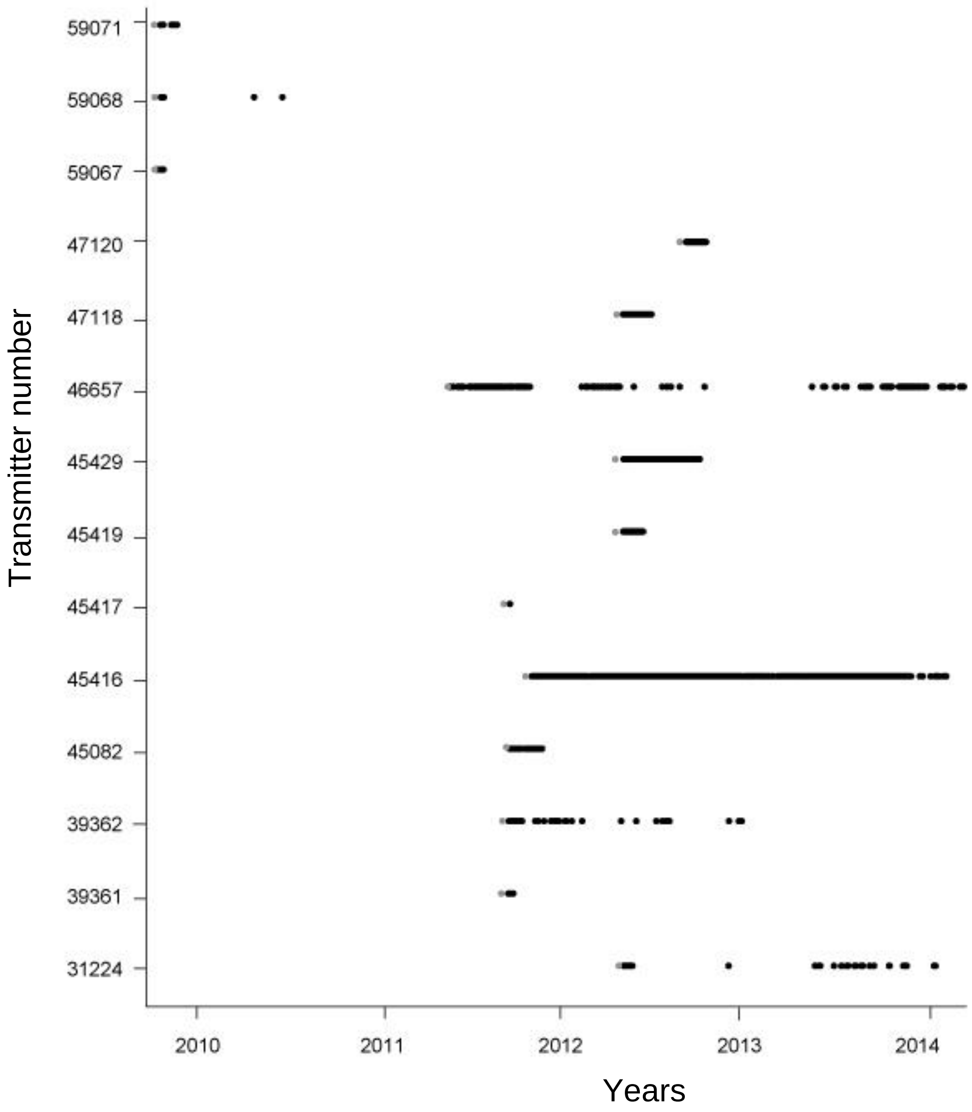


Figure 26. Detection plot of galapagos sharks (*C. galapagensis*) recorded in the Revillagigedo Archipelago.

The number of detections per day during the years showed a strong presence of *C. galapagensis* during the first's years. Since 2012, *C. falciformis* increased their detections and showed more residence than *C. galapagensis* (Figure 27).

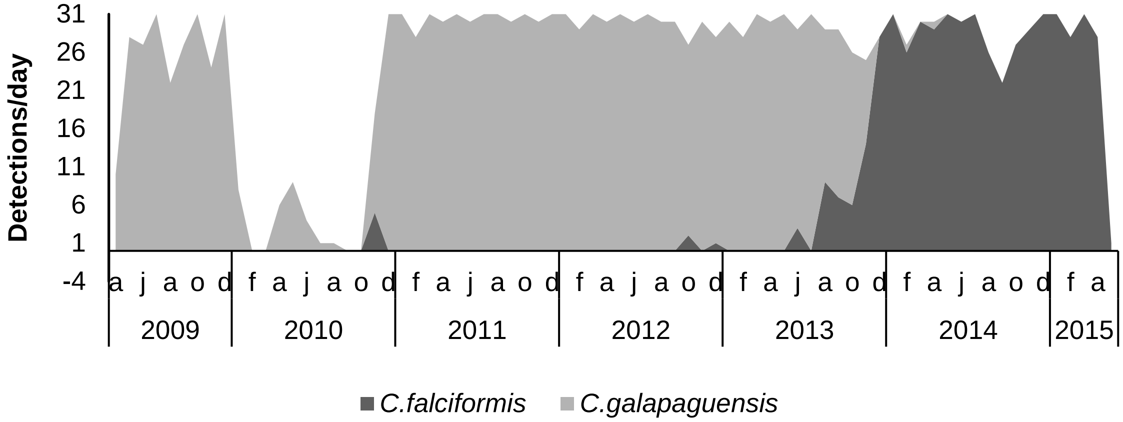


Figure 27. Number of detections per day (number of detections recorded at the receiver/number of days the receiver recording) accumulated in 7 monitoring sites.

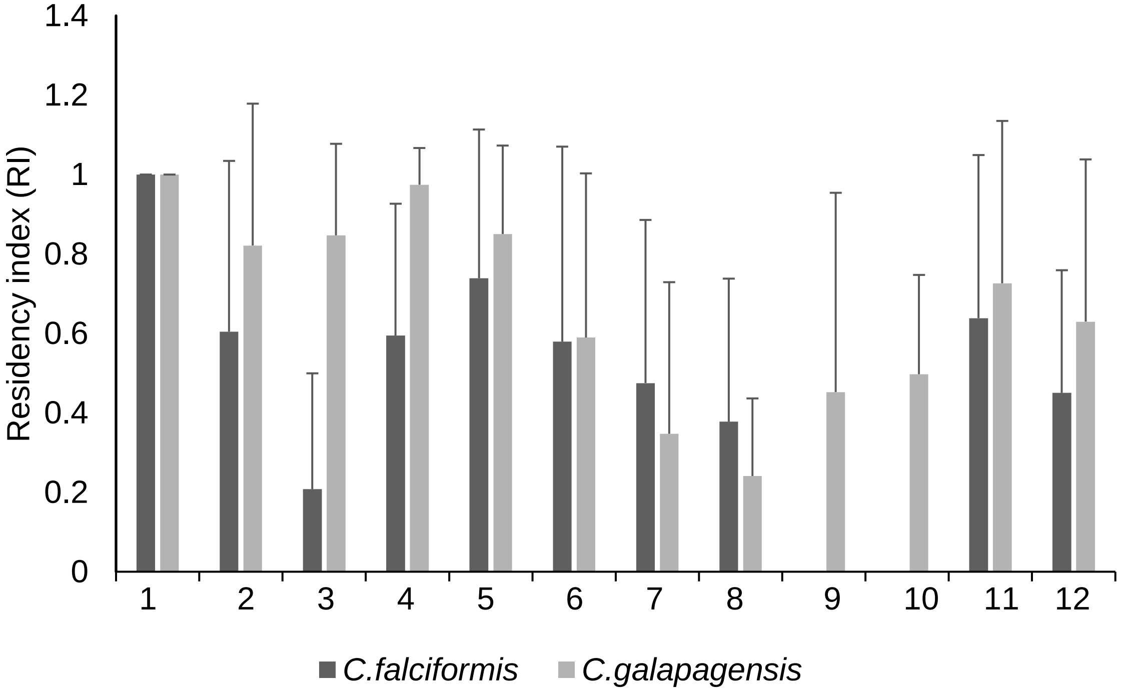


Figure 28. Residency index (RI) per month for *C. falciformis* and *C. galapagensis* in the Revillagigedo Archipelago.

In terms of the mean residence index between stations, the Canyon was the site with the highest residence index for *C. falciformis (*RI= 0.6 ±0.2), while *C. galapaguensis (*RI= 0.45 ±0.15), was mainly recorded in Roca Partida (Figure 29). Thirteen *C. falciformis* and seven *C. galapagensis* presented at the Canyon as the main area of distribution. Six of them (*C. falciformis*) were also distributed in adjacent areas of Boiler, Cabo Pearce and Punta Tosca. Fifteen *C. falciformis* and nine *C. galapagensis* were recorded mainly in Roca Partida. One *C. falciformis* was recorded in Clarion and two *C. galapagensis* were distributed in the Canyon and Punta Tosca; the rest (13) remained in Roca Partida. Differences between sites were significant (ANOVA f=4.2, DF=6, p<0.05).

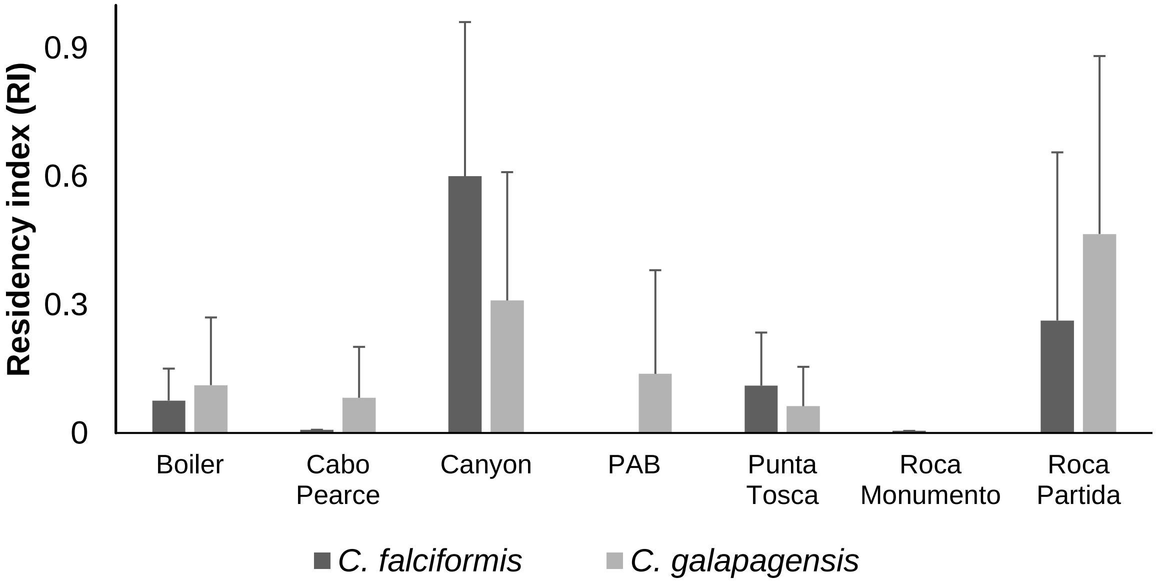
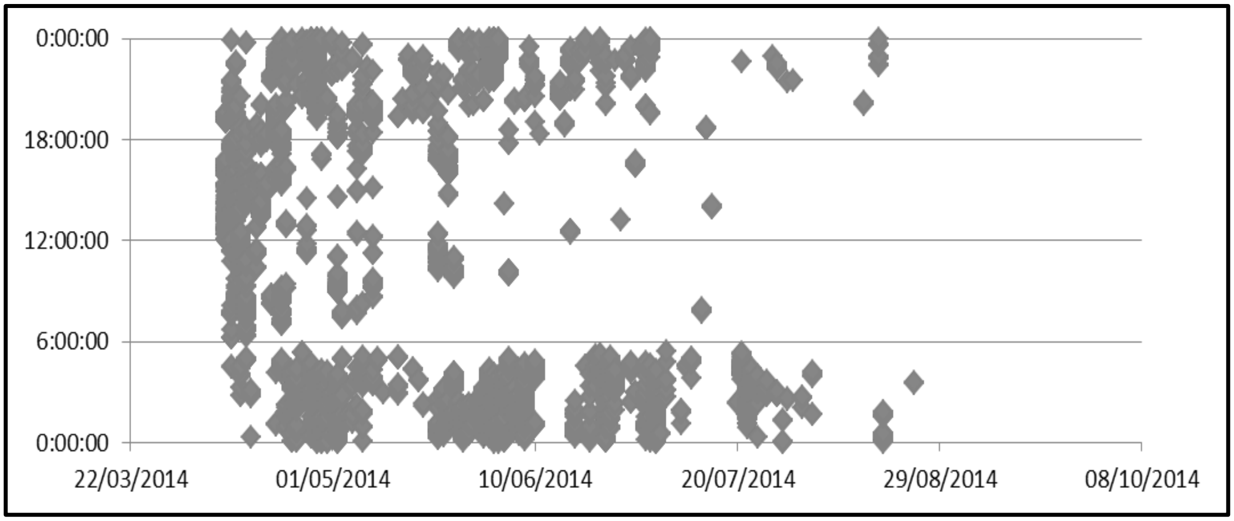


Figure 29. Residency index (RI) per site for *C. falciformis* and *C. galapagensis* in the Revillagigedo Archipelago.

7.3.1. Ontogenic changes in the distribution patterns

The changes of distribution patterns in relation to the years showed high site fidelity in the first years and then its presence decreased to became almost absent individuals, such as a *C. galapaguensis (*young male of 111 cm total length). Another *C. galapaguensis* (adult male of 250cm total length), showed more constant presence with a high fidelity in winter of 2012 to 2013. A female *C. galapagensis* (LT 210cm), recorded some visits in 2010 and 2011 and then was absent for almost two years and present again in the fall of 2013. To determine the changes in the long-term residency of sharks, the detections of sharks were plotted using the time of the day and the dates. In the following figure two examples are shown. During the first months, sharks presented a high residence, then their presence is decreased until they are absent (Figure 30).

A) C. falciformis



B) C. galapagensis

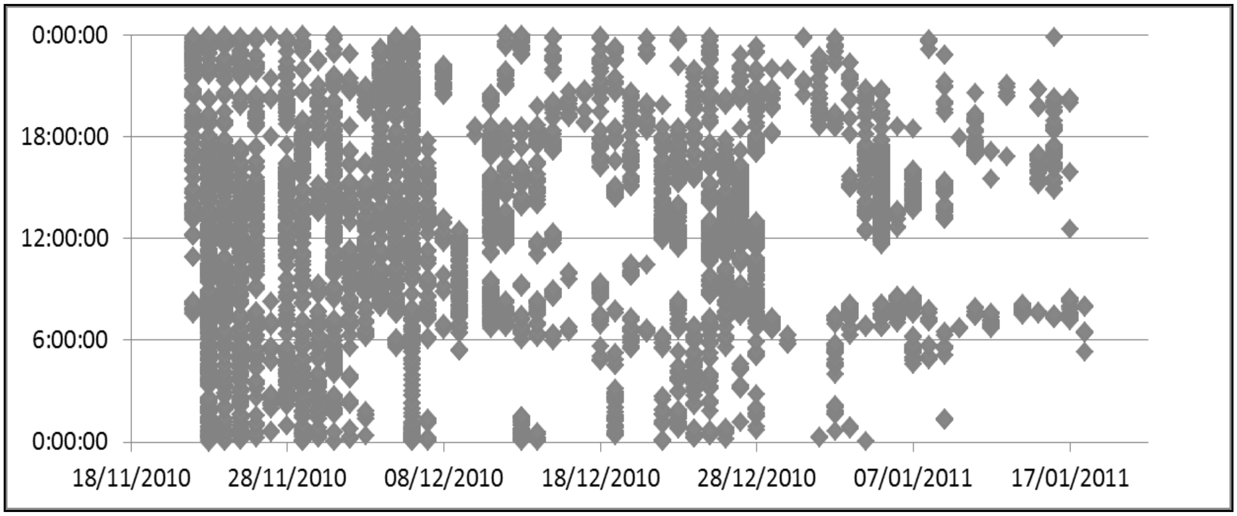


Figure 30. Daily detections of two individuals (A) *C. falciformis*; B) *C. galapagensis*) over a year monitored in the Revillagigedo Archipelago. In the *y* axis it is shown the time of the day and in the *x* axis the dates. The dots represent the detections.

7.3.2. Dial presence and residency patterns

Despite both species overlap in terms of space, they do not show the same pattern in a daily basis. While *C. falciformis* were recorded mostly during night hours (2:00-5:00 hrs; Figure 31), *C. galapagensis* showed a diurnal presence with the highest records just before sunset (12:00 to 17:00hrs; Figure 32). In both cases, the Rao’s test of uniformity showed a significant *p-value (*p<0.001). This means the detections during the day were not random and that some hours are more important than others.

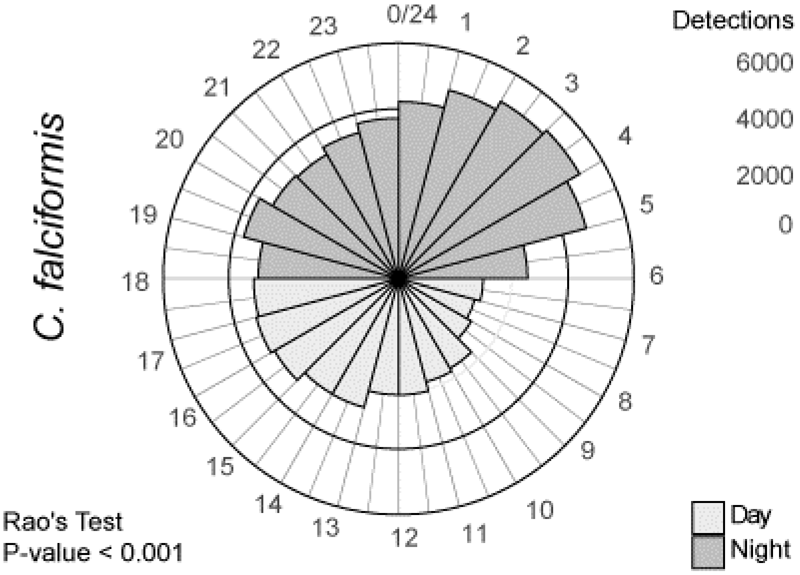


Figure 31. Daily detections of *C. falciformis* divided by hour. Circles indicate the number of detections per hour (6000, 4000, 2000 or 0 detections).

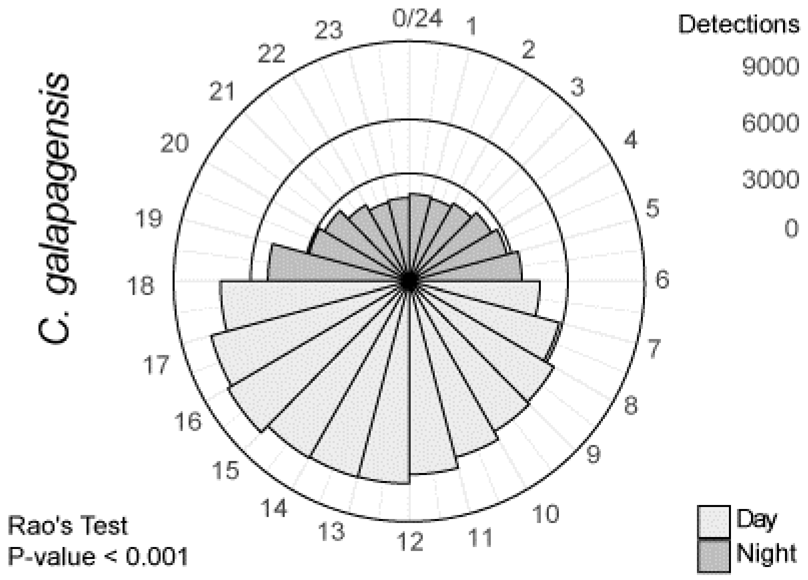


Figure 32. Daily detections divided by hour of *C. galapagensis* monitored in the Revillagigedo Archipelago. Circles indicate the number of detections per hour (9000, 6000, 3000 or 0 detections).

7.4. DISCUSSION

In this section, the variability of the residency index of *C. falciformis* and *C. galapagensis* in the Revillagigedo Archipelago was determined. The first predictions are that both species exhibit high site-fidelity to the reserve areas. In terms of detections, March (1 ± 0.1, mean ± SD) and April (0.94 ± 0.2, mean ± SD), presented the highest values while lowest RI occurred in August (0.24 ±0.15, mean ± SD), and September (0.3 ± 0.5, mean ± SD) (Figure 28).

Significant differences were found between the months for *C. falciformis (*f=3.45, DF=11, p<0.05), and *C. galapaguensis (*f=2.35, DF=11, p<0.05). Comparing the number of detections with the average temperature recorded by *in situ* data loggers, we can observe that during the warmest months sharks tend to be less detected. These months also coincide with the storm season when drastic temperature changes are recorded.

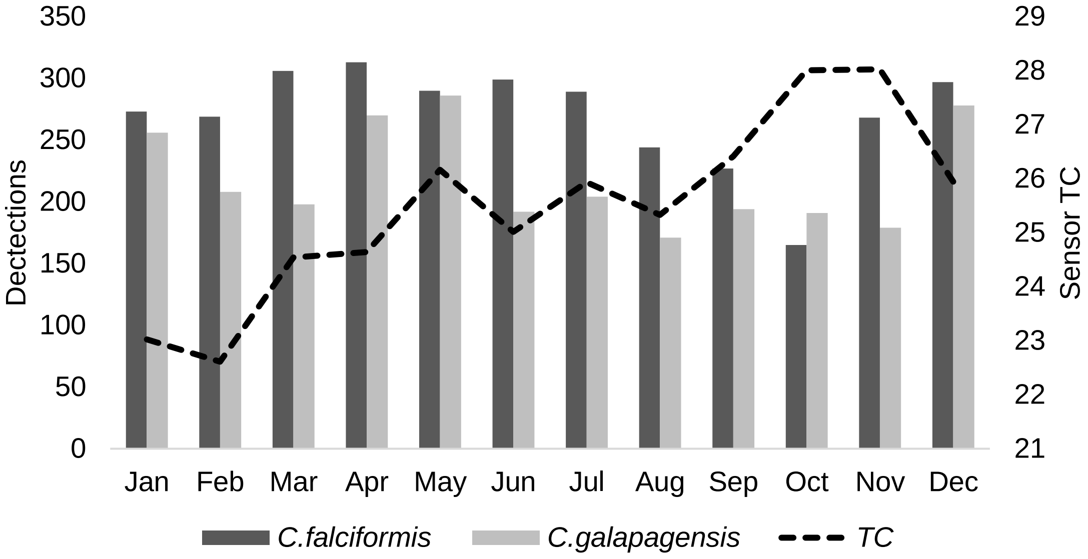


Figure 33. Average daily detections per month compared to average temperature recorded by the sensors *in situ* for *C. falciformis* and *C. galapagensis* in the Revillagigedo Archipelago.

These areas are characterized by numerous schools of cleaner fishes (i.e. *Chaetodon clarionensis* and *Johnr*and*allia nigrirostris*). Kimbley, *et al* (1983), proposed that other sharks, like the scalloped hammerhead sharks (i.e. *Sphyna lewini*), could use seamounts as cleaning stations. As we proved in the first section, large schools of cleaners were present at the Canyon and El Boiler. Therefore, there is a potential use of these areas as cleaning stations.

On the other hand, shallow zones have been recognized as nursery areas (Heupel *et al.,* 2007). There should be strong selection for the utilization of shallow habitats by shark pups in predator-dominated ecosystems. Similarly, juvenile lemon sharks select for shallow inshore mangrove habitats or tidal pools to obtain protection from predation by larger sharks (Morrissey and Gruber, 1993, Wetherbee *et al.,* 2007). According to Muntaner (2016), the presence of neonate and juvenile *C. albimarginatus* sharks in San Benedicto Island and Socorro Island suggests that both islands could be nursery areas for this particular species finding refuge in the shallow area around the islands. A great abundance of prey and a low density of predators agrees with the definition of shark breeding area (Heupel *et al.,* 2007).

Ontogenic changes in the distribution patterns

Changes in the habitat use in the time can be related to ontogenic expansion where juveniles and subadults home ratios are delimited within the shallower waters. When they reach certain length they start to spend more time in deeper waters. This is the case of a subadult male *C. galapaguensis (*LT=111cm), which after a few years changed the home range to areas outside of the receiver arrange.

Evidence that these islands function as a nursery area is the presence and movement of pregnant females (*C. falciformis, C. galapagensis* and *C. albimarignatus*), observed during the tagging procedures and the BRUVS. Especially, silvertip sharks (*C. albimarginatus*), have been reported by Muntaner (2016), who described adult females present in Roca Partida, already pregnant, that migrated to San Benedicto and Socorro for a short period of time before returning to

Roca Partida. This suggests that they are using the islands as birth areas and therefore the movements between the islands can be partly attributed to their biological cycle.

Bond *et al* (2012) observed the same ontogenic expansion with the Caribbean reef shark, *C. perezi* in the Gulf of Mexico. In terms of sexual segregation, Villoro and Rivera (1994) reported that the ratio between males and females is 1:1 in El Salvador. The same ratio is reported by Del Rosario (1998) in Guatemala and Ronquillo (1999) in Chiapas, Mexico. However, Hoyos (2003) found a ratio of 1F:0.6M in Baja California.

Guttridge *et al.* (2012) determined that predation risk imposed by the presence of subadult sharks can influence habitat use in juvenile lemon sharks (*Negaprion brevirostris*), whereas biological features such as mangroves and seagrass beds can provide shelter and abundant prey resources, (Munroe, Simpfendorfer, and Heupel, 2014).

Home range size has been found to increase with increasing body size in other elasmobranch species, including *Rhinoptera bonasus* in a Florida estuary (Collins *et al.,* 2007), and the lemon shark, *Negaprion brevirostris,* in the Bahamas (Morrissey and Gruber 1993). The juvenile galapagos sharks regularly utilize shallow lagoon habitats (Lowe *et al.,* 2006), while adults prefer deeper fore-reef habitats (Wetherbee *et al*., 1996).

According to Muntaner (2016), adult *C. albimarginatus* showed a high residence to Roca Partida while juveniles and neonates showed their greatest residence in the Canyon, Isla San Benedicto (Figure 34). The neonates tagged did not present any movement between islands; they only moved between the sites El Boiler and Canyon, both located in San Benedicto while four of the juveniles had migratory movements between islands. Three of them moved between San Benedicto Island and Socorro Island, which are separated by 83.3 km. On the other hand, the fourth juvenile shark that presented movement between islands migrated to Roca Partida 2.9 years after being marked (Muntaner, 2016). This species of shark shows an annual growth rate of up to 30% of total length (Kato *et al.,* 1967), which indicates that it made its migration to Roca Partida upon reaching maturity (Muntaner, 2016).

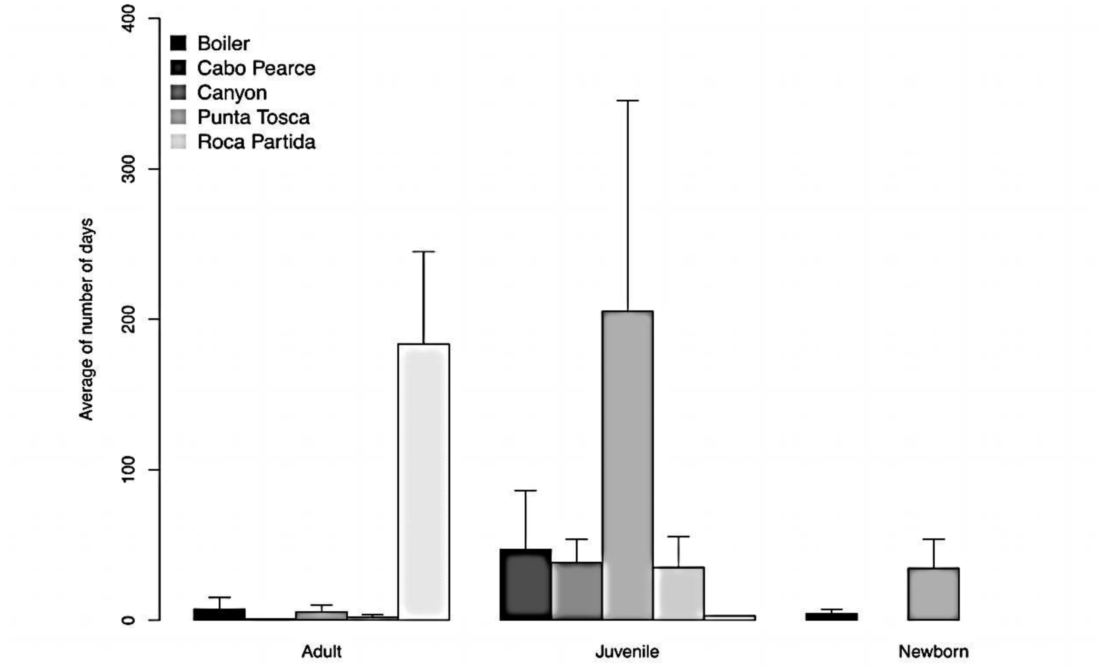


Figure 34. Average days present by adults, juveniles and newborn *C. albimarginatus* in different sites of the Revillagigedo Archipelago. Error bars represent the standard deviation (By Muntaner, 2016).

Foraging and breeding areas must have high prey densities, as well as high current, deep water and high productivity conditions associated with upwelling (Hearn *et al.,* 2010). Therefore, it is considered that Roca Partida is a potential site for feeding and reproduction of silver tip sharks, especially for pregnant females which present high energy requirements (Muntaner, 2016). For this reason, all the islands of the Revillagigedo Archipelago are of vital importance for the management of this species.

Diel residence patterns

It is commonly assumed that elasmobranchs (sharks, skates, and rays) are most active during dark periods (dawn, dusk, night). However, this assertion has not been critically evaluated. It is also unclear whether dark periods are primarily utilized for the performance of important life history events, such as mating (Hammerschlag *et al.,* 2017). In this study, Galapagos and silky sharks overlap in terms of space, but not in time. While *C. falciformis* were recorded mostly during night hours (2:00-5:00 hrs; Figure 31), *C. galapagensis* showed a diurnal presence with the highest records just before sunset (12:00 to 17:00hrs; Figure 32). In both cases, the Rao's test of uniformity showed a significant *p-value* (p<0.001), this means the detections during the day were not random, and some hours are more important than others.

Filmarter *et al.* (2015) found a similar pattern across all *C. falciformis* tracked, where median depths were significantly shallower at night than during the day. Sharks also spent short periods of time descending to greater depths than during daylight hours. During the day, the sharks exhibited a more consistent vertical behavior, seldom undertaking large vertical movements. Musyl *et al.* (2011) also found significant differences between day and night depths of silky sharks tagged with PATs in the Pacific Ocean, and reported that sharks spent the majority of their time (95%) in the surface layers (above 120 m). The nocturnal presence could be related with the fact that *C. falciformis* feed mainly on Giant squids, *Dosidiscus gigas,* which get close to surface during the night. On the other hand, Galapagos sharks primarily utilize the mixed layer (0–100 m). They feed on pelagic fishes and were mainly detected during the day around the islands. Direct observations showed that the Galapagos sharks feed in the morning and dust hours in Roca Partida.

There are significant management implications of nocturnal or crepuscular changes in elasmobranch behavior, although they are rarely discussed. Some elasmobranch species may be more or less vulnerable to exploitation at dark (Gallagher *et al.,* 2015). Individuals that use marine protected areas during the day but disperse across larger areas at dark may be more vulnerable to fishing pressure at night (Hearn *et al.,* 2010). Similarly, elasmobranchs that exhibit vertical migration at night may become more vulnerable to interacting with fishing gear at or near the surface (Hammerschalg *et al., 2017*). For instance, *C. falciformis* is the primary elasmobranch bycatch species in tuna purse seine fisheries throughout the world's major oceans. Juveniles of this species commonly associate with drifting fish aggregating devices (FADS) deployed to enhance tuna catches in these fisheries (Filmalter *et al.,* 2011). Therefore, the knowledge of the distribution patterns of both species has a remarkable importance in terms of management.

8. CHAPTER 3. CONNECTIVITY BETWEEN REVILLAGIGEDO AND THE GULF OF CALIFORNIA

Figure 35. Image of a whitenose shark, *Nasolamia velox,* recorded in the El Boiler, San Benedicto Island (6 March 2015; taken by Frida Lara).

8.1. INTRODUCTION

The whitenose shark (*Nasolamia velox*) is an endemic species of the Eastern Tropical Pacific (ETP), however very little is known about the biology and distribution of this species. The whitenose shark was previously known as *Carcharhinus velox* (Figure 35). Compagno and Garrick (1983) determined that the species differs externally from all other carcharhinids by very wide, transversely oriented nostrils placed close together so that the internarial width is only slightly greater than the width of each nostril, hence, they proposed a new genus Nasolamia.

Recent molecular phylogenetic studies suggest that this species might be closely related to *Carcharhinus acronotus* (Naylor *et al.,* 2012). *N. velox* (Gilbert, 1898) is a medium-sized shark that reaches a maximum of 165 cm TL (Ruiz *et al.,* 2009). The species is viviparous, with a yolk-sac placenta (Ruiz-Alvarado and Mijangos-López, 1999; Compagno, 2001). It feeds mainly on anchovies and crabs. The size at birth is about 53 cm TL. Size at maturity in the male is 114 cm and in the female 130–162 cm (Compagno, 2001). The usual reproduction, mating and birth season for *N. velox* is May– July, although recent births have been observed toward the end of March (Ruiz-Alvarado and Mijangos-López, 1999; Mendizábal *et al.,* 2000; Villavicencio, 2000; Bizzarro *et al.,* 2009). *N. velox* is classified as highly vulnerable and its conservation is critical as it requires very specific nursery areas and has a low fecundity rate (four individuals per female with 9 months' gestation period; Soriano-Velásquez *et al.,* 2006). *N. velox* is commonly reported among fishery landings of the Eastern Pacific Coast, such as Mexico (Saucedo- Barrón, 1982; Cabrera, 2000; Soriano *et al.,* 2006; Bizzarro *et al.,* 2009; Walther-Mendoza *et al.,* 2013), Panama (Compagno and Garrick, 1983), Costa Rica (Garro *et al.,* 2011), Peru (Kato *et al.,* 1967), Colombia (Mantilla, 1998; Mejía-Falla *et al.,* 2010) and Ecuador (Bearez, 1996).

In Mexico, the distribution of *N. velox* ranges from Baja California (Walther-Mendoza *et al.,* 2013), south of Sinaloa (van der Heiden and Findley, 1988), east coast of Baja California Sur (Bizzarro *et al.,* 2009), Michoacán (Madrid-Vera *et al.,* 2007), Oaxaca (Alavez-Jiménez, 2006) to the Gulf of Tehuantepec, Chiapas (Soriano-Velásquez and Acal-Sánchez, 2003). In the Gulf of California, the whitenose shark, *N. velox* has also been reported in the outer Gorda Banks, Cabo San Lucas, and Santa Maria Bay in Baja California Sur, San Felipe, Bahia Las Animas in Baja California, Guaymas in Sonora, Mazatlan and Bahia Topolobampo in Sinaloa (Compagno and Garrick, 1983).

Some reports have been published about the presence of this species in insular areas of the ETP. In Galapagos, reports show evidence of records at the northern end of Isabela (1987) and Baltra Island (1989) (Grove and Lavenberg, 1997). In Guadalupe Island, tourists and fishermen have reported the presence of *N. velox*, however there are no records in the formal literature (Walther-Mendoza *et al.,* 2013).

In this chapter we were also able to describe other evidences of the connectivity between Revillagigedo to the Gulf of California, based on other sharks and mantas. The movements of *C. falciformis* in the coastal areas of Baja California Sur could be related to the increase of the superficial sea temperature in the summer, showing movement seasonality, where, only adults (179- 200 cm TL) migrate to the coastal areas. In the ETP, tropical cyclones arise over the eastern Pacific warm pool. Once formed, the cyclonic storms move with the easterly trade winds and often curve northward over cooler waters, sometimes impacting the Revillagigedo Archipelago (Fiedler and Lavín, 2017; Carter 2017).

8.2. MATERIALS AND METHODS

8.3. Fieldwork

During a study on shark movements and residency in Cabo Pulmo National Park, Mexico in March 2013, a *N. velox* was captured using hand-lines baited with fish. The individual shark was fitted with a coded acoustic transmitter (V16, 69.0 kHz, Vemco, Halifax), which emitted a uniquely coded acoustic signal at random intervals between 60–120 s. The shark was brought onto a small fishing boat, immobilized on the deck, and a hose placed in the mouth with running saltwater to pump through the gills while the shark was manipulated. The coded transmitter was implanted surgically into the body cavity of the shark through a small 2 cm incision and then the wound was closed with three sutures. In addition, total, fork and precaudal lengths of the shark were measured, sex determined by the presence of claspers, and location recorded with a GPS.

The identification of *N. velox* was determined on the basis of videos and pictures that highlighted the diagnostic characters (Figure 36, described by Compagno and Garrick, 1983). Since 2009, Pelagios Kakunjá and The University of California, Campus Davis have set an array of eight autonomous acoustic receivers (VR2W, Vemco, Halifax) in different sites around the Revillagigedo Archipelago at depths easily reached by scuba divers (average 25 m below the surface). These receivers were designed to listen for coded transmitters and to record the date and time of arrival and departure of individual sharks.

The acoustic range of each receiver varied depending on water depth, tide and neighboring reef structure. Range tests at other sites indicated transmitter detection ranges of 200–300 m. Therefore, if a shark tagged (with a unique acoustic signal code) was within the detection range of one of the acoustic receivers, we were able to determine the presence of this shark. If the shark was recorded in two or more receivers, we knew that the individual was moving between two or more of the monitored sites (Figure 36).

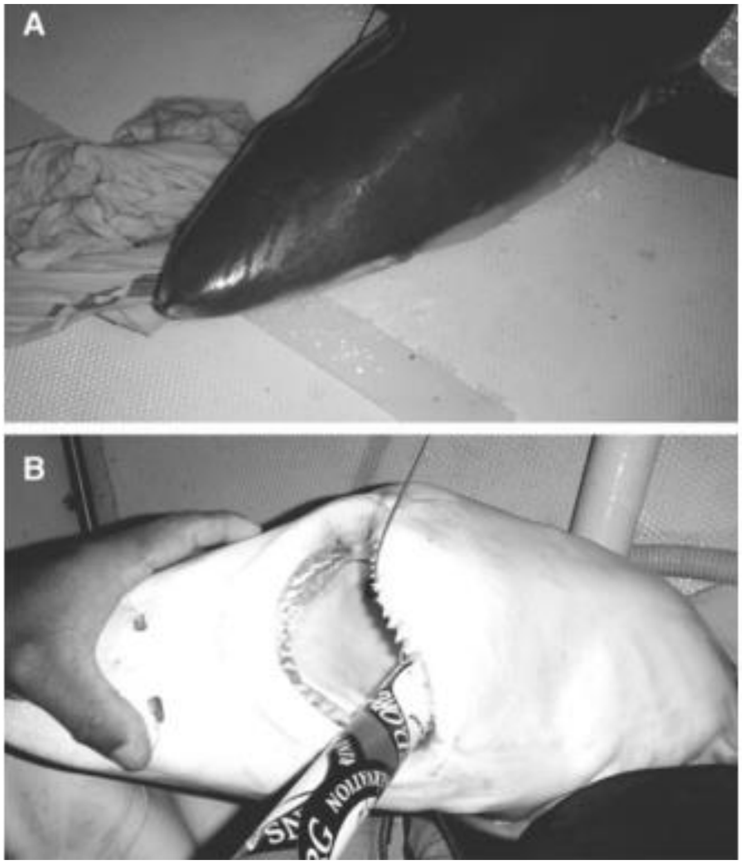


Figure 36. Whitenose shark (*Nasolamia velox*) tagged in Cabo Pulmo National Park, Mexico (March 2013). (a) Dorsal view showing the white coloration in the tip of the snout (b) Ventral view showing the particular nostrils position that differentiated the genus Nasolamia from other Carcharhinidae.

Other highly migratory species of sharks and mantas have been previously tagged since 2010 in the Revillagigedo Archipelago during different expeditions (Figure 37), such as: tiger shark (*G. cuvier*), silky sharks (*C. falciformis*) and Pacific giant manta (*M. birostris*).

Figure 37. Satellite and acoustic tagging of an adult female tiger shark (*G. cuvier*) during the Ocearch expedition to Revillagigedo in 2010 (388 cm TL).

The sighting recorded on video

During a shark survey performed on 5–13 March 2014, visual censusing was conducted by scuba divers. A total of 22 observations were taken at six different areas of the Archipelago: Socorro Island (Punta Tosca and Cabo Pearce), Roca Partida and San Benedicto (Cuevitas, El Boiler and El Canyon). Each survey lasted 45 minutes. Information on depth and temperature were recorded and a number of images and videos of the sharks were taken using a GOPRO 3+ camera. The identification of the whitenose shark was made on the basis of photographs and videos that documented diagnostic evidence of this species (Figure 38). Once the species was confirmed, we verified its geographic range using specialized literature and revised data on collected specimens from worldwide museums in order to confirm that there was no existing record of this species from the Revillagigedo Archipelago. This specialized literature and revised data were available on the International Centre for Living Aquatic Resources Management website (htttp://www.fishbase.org; Froese and Pauly, 2016).

Figure 38. The shark *N. velox* sighting during a survey at El Boiler, San Benedicto Island (6 March 2015). Individual of 120 cm TL.

8.4. RESULTS

The presence of *N. velox* was recorded by acoustic telemetry and video in the Revillagigedo Archipelago. The first record occurred at the receiver located at the east side of Roca Partida Island (18899′186″N 112808′44″W) at a depth of 33 m. The individual was tagged In Cabo Pulmo National Park on March 3, 2013 and it was first detected on 12 May 2014 and last detection was on 22 February 2016. The total duration of monitoring was 646 days, however this individual was only present 14% of the time (96 days; Figure 39).

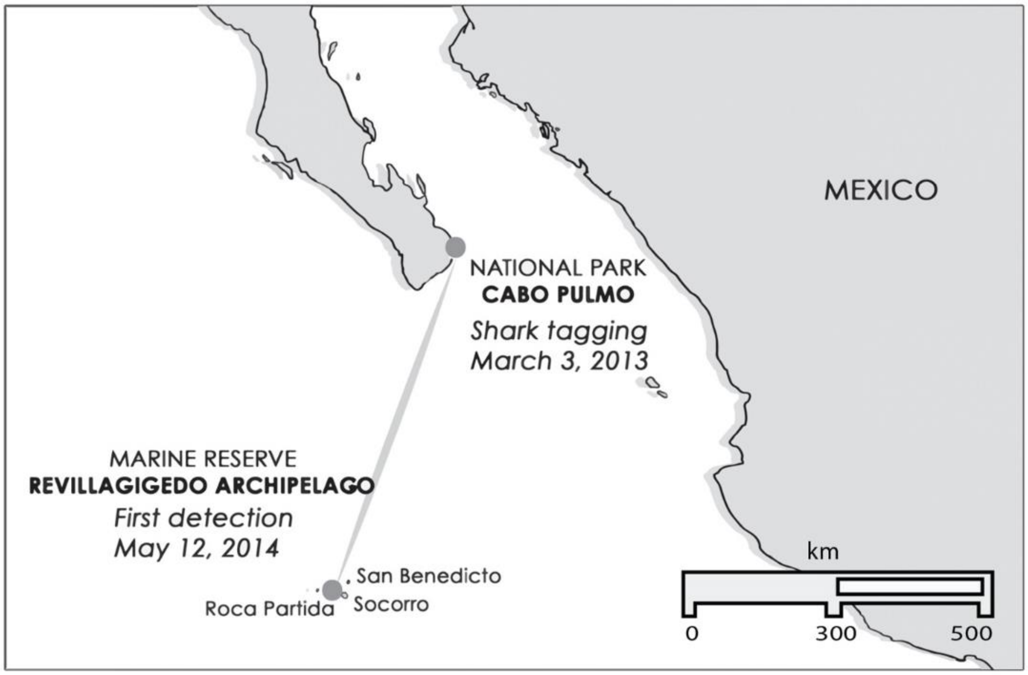


Figure 39. Map showing the movement from where the adult *N. velox* was tagged (National Park Cabo Pulmo, March 2013) to where it was first detected (Roca Partida, Revillagigedo Archipelago, May 2014).

. The first record was at the receiver located at the east side of Roca Partida Island (18º 99’ 186” N 112º 08’ 44” W) at a depth of 33m (12th May 2014). Then, a total of 126 acoustic detections were recorded in the same islet. The last detection recorded was the 22nd February 2016. According to the time of the detections, *N. velox* was present mostly during sunset and nightime (11:00 pm to 2:00 pm) (Figure 40).

The second record occurred at San Benedicto Island at 24 m on 6 March 2015, at the dive site known as 'El Boiler'. Water temperature was 25.58 C°. The identified specimen was 120 cm in length. In both cases (telemetry and video records) the sharks were not collected, but positive identification was based on a single high-definition video of one of the sharks by observing diagnostic characteristics (Compagno, 2001).

During this project have also found other species such as silky shark (*C. falciformis*), tiger shark (*Galeocerdo cuvier*), moving between Cabo Pulmo and Revillagigedo (Ketchum, pers. Com.), and the giant manta (*M. birostris*), which was photo-identified using both areas as part of their life cycle (Rubin, Pacific Manta Research Group, Pers. Com., 2015; Figure 41).

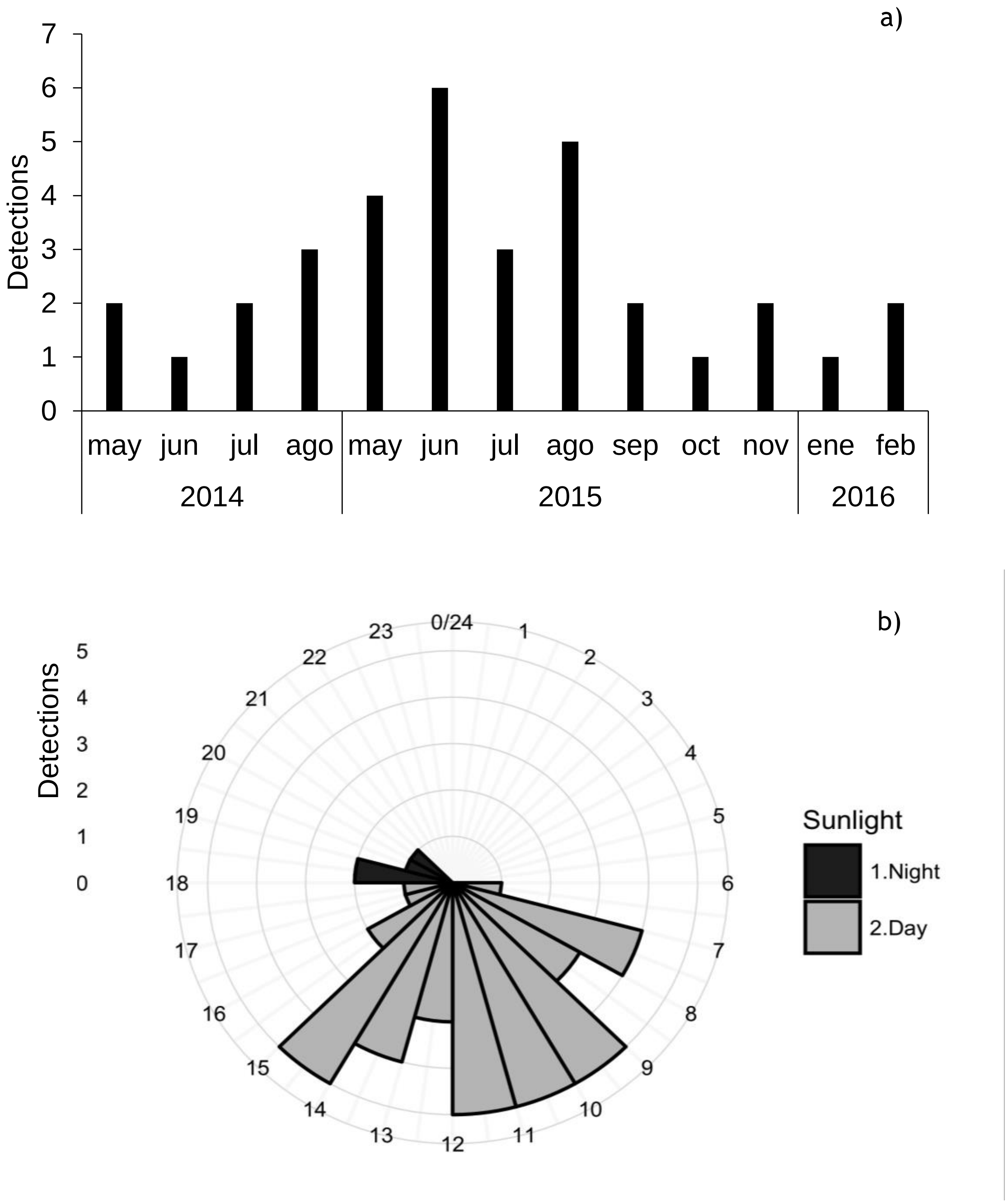


Figure 40. Individual records of *N. velox* using acoustic telemetry a) Comparing the detections during different months b) time of the day, where the bars indicate the number of detections during the sunlight (light gray) and night (dark gray).

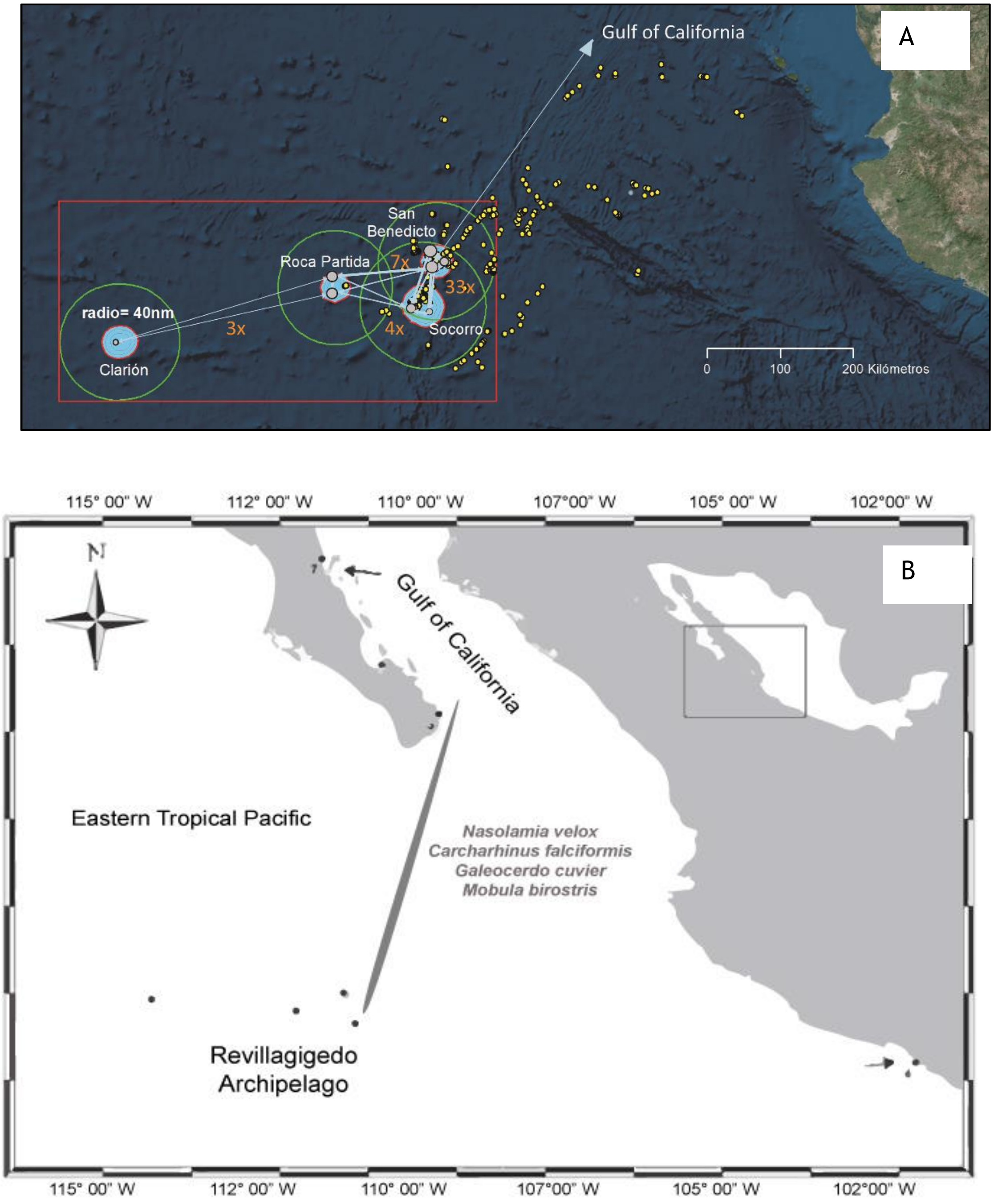


Figure 41. Long distances movements recorded between Revillagigedo Archipelago and the Gulf of California. A) Satellite tracking of *C. falciformis* tagged in Revillagigedo Archipelago B) Summary of the recorded sharks and mantas using the swimway Revillagigedo-Gulf of California.

8.5. DISCUSSION

We report here for the first time, the occurrence of *N. velox* in Cabo Pulmo and the Revillagigedo Archipelago, and movements from a coastal location (Cabo Pulmo reef) to a group of oceanic islands (Revillagigedo). We provide evidence that the movement patterns of *N. velox* are longer and more complex than what was previously considered for this species, and its distribution range is extended over 487 km. We also describe the evidences of potential connectivity between these two locations based on the movements of other three species: tiger sharks (*G. cuvier,*) and silky shark (*C. falciformis)* acoustically tagged in Revillagigedo and mantas (*M. birostris)* photo- identified.

According to the literature and museum records, the distribution range of *N. velox* is restricted to the Eastern Pacific, from Mexico (Saucedo-Barrón, 1982; van der Heiden and Findley, 1988; Gilbert, 1898; Cabrera 2000; CONANP 2017; Soriano *et al.,* 2006; Bizzarro *et al.,* 2009; Walther-Mendoza *et al.,* 2013; Madrid-Vera *et al.,* 2007) to Panama (Compagno and Garrick, 1983), Costa Rica (Garro *et al.,* 2011), Peru (Kato *et al.,* 1967), Colombia (Mejía-Falla *et al.,* 2010) and Ecuador (Bearez, 1996). Previous records at insular locations of the Eastern Pacific included the Galapagos Archipelago, 3150 km south of Revillagigedo Archipelago. There were no previous records from the Revillagigedo Archipelago, and the closest records were from Cabo San Lucas, 487 km north-east of the Revillagigedo Archipelago (Bizzarro *et al.,* 2009).

The whitenose shark is frequently classified as a tropical inshore shark, normally found over the continental shelves in shallow coastal waters at depths of 15–24 m, but occasionally it can be found down to 192 m (Compagno, 2001). In Guatemala, this species has been reported 30–100 km off the coastline on the continental slope (Porras, 1997; Ruiz-Alvarado and Mijangos-López, 1999). In Costa Rica, *N. velox* is found in offshore fisheries 80–120 km off the coast and in demersal fisheries on the slopes of the continental shelf (Garro *et al.,* 2011). Our findings show evidence that there may be potential connectivity of sharks between the Gulf of California and the Revillagigedo Archipelago, however population level observations are needed to confirm this idea.

Very little is known about the biology, reproduction and ecology of *N. velox*, therefore, future research on this species is necessary. It has been reported that the species has a low fecundity rate and very specific nursery areas (Compagno, 1988; Ruiz-Alvarado and Mijangos-López, 1999). Because of these characteristics this species has been classified as vulnerable to habitat degradation and marine pollution (Alavez-Jiménez, 2006). Responses to the El Niño–Southern Oscillation (ENSO) were documented with high catch per unit effort (CPUE) in landings off the Pacific Coast of Mexico during 1998, prompting the dispersal of a larger number of whitenose sharks (Soriano-Velásquez *et al.,* 2004). It is necessary to increase our understanding of this species and to generate effective management strategies for vulnerable shark species in the region.

The observed movements between two important marine protected areas suggest that these species are vulnerable to domestic fisheries as well as multinational fisheries on the high seas, as these species are highly associated with commercial pelagic species such as the yellowfin tuna, *Thunnus albacares.* Even when not targeted, these sharks often comprise a high proportion of landings in line-based fisheries (Megalofonou, 2005). There is strong evidence that *C. falciformis* is summited by the fisheries pressure. The average mature sizes for the species is higher in other parts of the world, but in Baja California and the Mexican Tropical Pacific the populations mature in smaller lengths. According to Ronquillo (1999) the species exposed to high fishing pressure can reach sexual mature lengths smaller to compensate the stock exploitation by the effect of a mechanism denso-dependent. Del Rosario (1998) reported that *C. falciformis* represent the most exploited species in the shark fisheries in Guatemala. Castillo-Géniz *et al.,* (1997) reported that also it is the most common species in Chiapas, Mexico. Chong-Robles and Alejo-Plata (2002) mentioned that *C. falciformis* represents more than 90% of the fisheries in

Oaxaca, Mexico. All the mentioned studies also reported that most of the individuals were immature.

Regular movement across state boundaries highlights the need for cooperation between jurisdictions to ensure sharks receive sufficient protection throughout their migrations. This may include the need for regulations related to the habitats in each jurisdiction where individuals spend time, as well as movement corridors (Peñaherrera *et al.,* 2018), such as the proposed swimways (see www.migramar.org). According to Bigue *et al.,* (2010) the region has poor level of enforcement of the laws and regulations. There is a low capacity to detect and intercept offenders, poor preparation for effective legal cases, difficulties in both administrative and judicial processes, and finally, obstacles which prevent sanctions from being imposed upon violators.

New management strategies are necessary, these should ensure that the sharks and mantas travelling between Revillagigedo to the Gulf of California are fully protected. To determine which is the most effective measures is necessary to study the migration routes, by using satellite tags, and define the seasonality for each species. At moment, the temporal fishing ban (from May to August) could have a positive effect on the highly migratory species, which are travelling to the Gulf during the hurricane season (June to October).

9. CHAPTER 4. SHARK CONNECTIVITY IN THE EASTERN TROPICAL PACIFIC

Figure 42. Large adults *C. falciformis* aggregation in Roca Partida, probably for mating reasons (June, 2017, Photo by Erick Higuera).

9.1. INTRODUCTION

Many MPAs have been designated around oceanic islands to protect marine coastal and pelagic species such as sharks. Among notable MPAs are the Galapagos Marine Reserve (138,000 km^2), Malpelo Island Flora and Fauna Sanctuary (9,584 km^2), Revillagigedo Archipelago National Park (148,087 km^2) and Cocos Island National Park (1,997 km^2). The ETP is renowned for its high ecological value, providing habitat for endangered species, and for its inherent cultural value: four of the five MPAs have been designated as UNESCO World Natural Heritage Sites. UNESCO first recognized Cocos Island National Park in 1997, then the Galapagos Marine Reserve in 2001, Coiba National Park in 2005, Malpelo Flora and Fauna Sanctuary in 2006, and Revillagigedo Archipelago in 2016 (Bigue *et al.,* 2010).

Current literature shows that inter-island movements of sharks in the ETP are common. Evidence suggests that sharks may use islands as ‘stepping stones’ for long distance oceanic dispersal (Bessudo *et al.*, 2011, Ketchum *et al.,* 2014). Scalloped hammerhead sharks (*Sphyrna lewini)* at Wolf and Darwin islands in the Galapagos moved over 100 km to Roca Redonda and Seymour Norte within the marine reserve, and others made longer-distance movements across the ETP to other isolated islands, such as Cocos and Malpelo Islands (Bessudo *et al.,* 2011; Ketchum *et al.,* 2014).

The knowledge of the area of activity is a useful tool for the conservation of the fauna because it provides us with information about the approximate area needed to maintain a viable population (Bruce *et al.*, 2005). Home ranges provide basic information on movement patterns and contribute to species ecological analyzes for habitat preference (Bruce and Bradford, 2007).

Despite to the renowned importance, all these marine reserves are threatened by the following human activities: Poorly regulated legal and illegal fishing, overexploitation of coastal and oceanic marine resources, inadequately regulated tourism growth, pollution from commercial vessels (marine transport), habitat loss and degradation; and the introduction of exotic species (Bigue *et al.,* 2010). The movements in and out of marine protected areas imply that these species are vulnerable to domestic fisheries within Exclusive Economic Zones (EEZs) and multinational fisheries on the high seas (Stevens, 2000; Ketchum *et al.,* 2014;). Regular movements across state boundaries highlight the need for cooperation between jurisdictions to ensure sharks receive sufficient protection throughout their migrations. This need includes regulations focused on the habitats in each jurisdiction where individuals spend time, as well as movement corridors (Pendoley *et al.,* 2014).

The silky shark is globally distributed (40°N and 40°S) and is a highly migratory species (Hoyos-Padilla *et al.,* 2012; Sánchez-de Ita *et al.*, 2011; Figure 42). It is found from the surface to depths of >200 m (Last and Stevens, 2009). Based on carbon (δ13 C) and nitrogen (δ15 N) isotope analysis, it was found that the species feeds in the open ocean, consuming oceanic pelagic prey (9–12), normally at night or in the early morning (González and del Socorro, 2005). It consumes squid, such as *Dosidicus gigas* during its vertical migration to the surface during the night (Stewart *et al.,* 2014). The Galapagos shark has a similar geographical (39°N-33°S) and depth distribution from the surface to 180 m, but mostly <80 m, (Papastamatiou *et al.,* 2009), yet it is highly associated to seamounts, oceanic islands and continental shelf environments (FAO, 1997). Galapagos sharks feed primarily on demersal teleosts (Wetherbee *et al.,* 1996), but it can also consume cephalopods, elasmobranchs, crustaceans, small marine mammals (e.g. sea lions), and even other elasmobranch species (Heupel and Simpfendorfer, 2007).

The definition of the extent and occurrence of long-range movements and population connectivity are necessary for a full understanding of the ecology of a species and hence for designing effective management action (Heupel and Simpfendorfer, 2007). By assessing the movement frequency, Network analysis (NA) can be used to identify important swimways between core habitats of a species (Chetkiewicz *et al.,* 2006). NA provides a new insight into the importance and connectivity of specific habitat features on the animal moving between them. It also proves valuable in revealing important information on distinct spatial and temporal changes in animal movement (Jacoby *et al.,* 2012). For example, an area with a high degree centrality, would suggest strong site fidelity by wide-ranging animals, hence the animals may return from many different areas but always back to the same location.

Movement and residency patterns of key marine animals are still poorly understood, particularly within and between insular locations. Therefore, in this study based on the movement patterns and habitat use of Galapagos and silky sharks we describe the connectivity within and between insular sites in the ETP, the differences in the dispersal ranges of each species, the most important stepping stones and swimways between them.

9.2. MATERIALS AND METHODS

9.2.1. Study area

The study area included five MPAs within the ETP. The Revillagigedo Archipelago (18º49´N 112º46´W), located 400 km south from Baja California, consists of four volcanic islands (Socorro, Clarion, San Benedicto and Roca Partida) that emerge from a volcanic floor along the Clarion Fracture Zone, west of the union of the Pacific, Rivera, and Cocos geologic plates (Snodgrass and Heller, 1905).

Clipperton Island (10°17’N 109°13’W) is the only coral atoll in the eastern Pacific. It lies about 965 km from mainland Mexico. Clipperton is positioned at the edge of the Eastern Pacific Barrier (Snodgrass and Heller, 1905). Cocos Island (5º31’N 87º04’W) is located more than 500 km from mainland Costa Rica. It is the only point above sea level on the Cocos Ridge, which originates in the Galapagos Spreading Center. The 24 km^2 island is surrounded by an insular platform that deepens to around 180 m, with an area of about 300 km^2, then drops to several thousand meters deep (Cortés, 2008). Malpelo Island (3°58´N and 81°37´W) is located 490 km from the Colombian Pacific coast. The 1.2 km^2 Island is surrounded by eleven pinnacles and its highest point is 300 m above sea level (López-Victoria and Rozo, 2008).

The Galapagos Archipelago (0º40’S 90º33’W) is located 1,000 km from the coast of continental Ecuador. The archipelago is made up of 13 major islands and over 100 islets and emergent rocks, along with an unknown number of shallow and deep seamounts. These five marine reserves are characterized by their complex oceanography, high diversity and abundance of pelagic species with high economic value for fisheries and tourism (Smith, 1984).

Receiver array for the regional scale analysis (ETP)

The receivers (Vemco Ltd., VR2 and VR2W) were located within all oceanic MPAs across the ETP, spanning a straight-line distance of 4000 km from Revillagigedo to Galapagos. The arrays were deployed at the following sites: Revillagigedo (Roca Partida, Clarion, Socorro and San Benedicto Islands), Clipperton Atoll, Cocos Island, Malpelo Island and Galapagos Archipelago (Darwin, Wolf, Santa Cruz, Isabela, San Cristobal; Figure 43). Receivers were affixed with heavy-duty cable ties to a mooring line with chain or cable to attach to the bottom anchor and a buoy for flotation. Range tests of the ultrasonic receivers were previously performed at several of the study areas, varying from 200 to 300 m (Hearn *et al.,* 2010; Bessudo *et al.,* 2011).

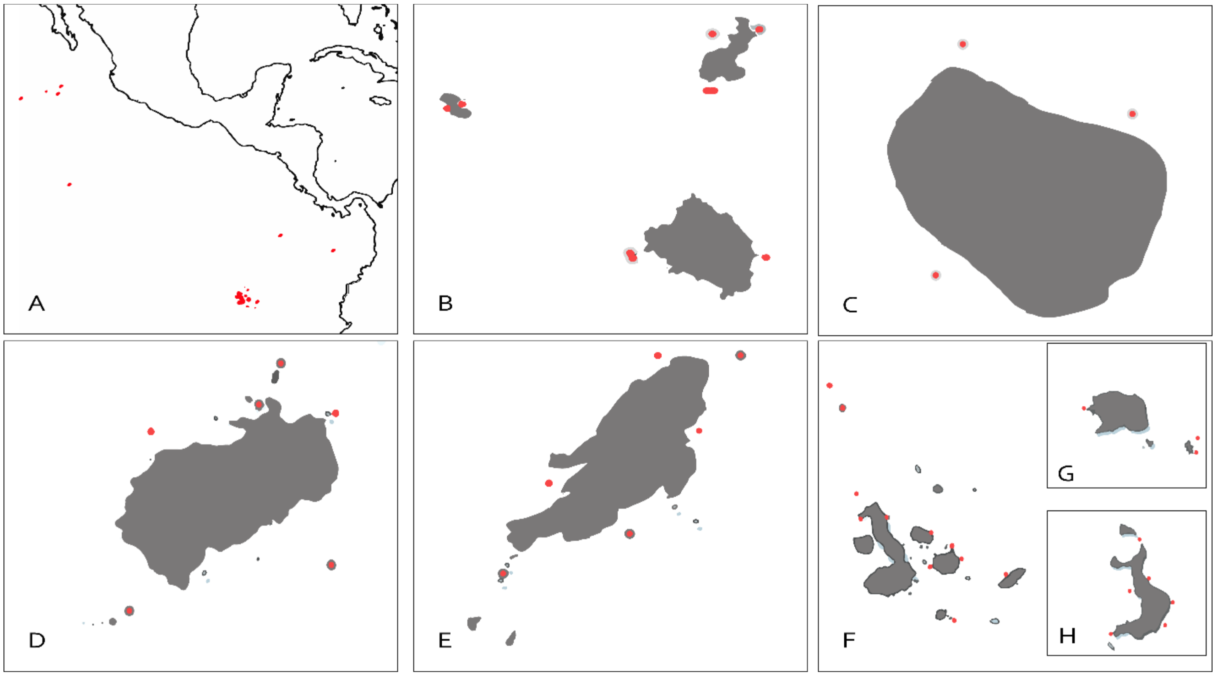


Figure 43. Map of the study sites showing the location of acoustic receivers used to monitoring shark movements in the insular sites of the ETP. A. Insular sites of the ETP; B. Revillagigedo Archipelago, C. Clipperton Atoll; D. Cocos Island; E. Malpelo; F. Galapagos; G. Darwin Island; and H. Wolf Island. Red dots indicate the receiver locations.

Ultrasonic tag detection

Seventy-eight sharks (44 *C. falciformis* and 34 *C. galapagensis;* Appendix 4) were fitted with ultrasonic tags (Vemco, Ltd., V16, frequency, 69 kHz, power 5-6H, life 1800 to 3,650 days) during cruises to those five insular systems from 2006 to 2016. Tags emit a coded signal at 69 kHz with a random delay of 40–140 s to avoid successive signal collisions between two tags. Tags were fitted externally on sharks by scuba and free diving using pole spears or spear guns, inserting a stainless-steel barb into the dorsal musculature at the base of the dorsal fin.

Other tags were implanted in the peritoneal cavity of sharks caught using hook and line. The gender (presence of claspers or not), maturity stage (juvenile, sub-adult, adult) and total length (estimated by free diver taggers or measured for sharks which were captured) were recorded for all sharks when possible.

9.2.2. Data analysis

To evaluate the dispersal range of each species (Hijmans et al., 2012) we measured the straight-line distances between acoustic receivers using the library geosphere in R.2.3.1 (R Core Team, 2017), we perform frequency histograms for the distance of each movement and we compare the results by each species.

To describe the movement behavior of each species along the ETP we used network analyses (NA) using the igraph 1.2 package (Csardi and Nepusz, 2006) available in the R programing language (R Core Team, 2017). The NA describe the local and global structure of networks constructed from pairwise interactions of connected elements in a graphic format node linked by one or a series of edges (Jacoby *et al.,* 2012). In our analysis each node represented the physical location of the acoustic receivers (hereafter sites). Edges were equally variable and represented the mobility of organisms between nodes. Each individual tagged represented a unique observation of the network.

A number of quantitative metrics were calculated from the interconnected network to describe the local and global network structure (Jacoby *et al.,* 2012): (i) number of edges (ii) number of vertices (iii) degree of centrality and (iv) density. The density defined as the proportion of edges actually present in the network among all possible edges in the data (White and Harary, 2001).The degree of centrality defined as the overall level of connectedness within the network.

The NA was based on movements between receiver locations, which was graphically displayed using the library igraph in R 2.3.1 (Csardi and Nepusz, 2006; Espinoza, *et al.,* 2015), where the size of the node represented the degree centrality (Jacoby *et al.,* 2012). To determine the relative importance of each node with in the marine reserves, we calculated the eigenvalues, defining the centrality of each node as a proportional to the sum of the centralities of those nodes to the ones which is connected. In general, nodes with high eigenvector centralities are those which are connected to many other nodes which are, in turn, connected to many others (Jacoby *et al.,* 2012).

To reconstruct the patterns in spatial distribution of Network Analysis, we used Generalized Additive Mixed Models (GAMMs), using the *gamm* function of the *mgcv* R package mgcv (Wood, 2006). GAMMs are capable of modeling non-linear relations between the covariates and response variables (fixed effects) in a semi-parametric way (Maunder, M.N. and Punt, 2004), while accounting for differences in the measured parameters observed for different individuals (random effects; 31). Given the distribution of our response variable, and because Network metrics are integers ("counts"), we decided to use Poisson-based models(Zuur and Elphick*,* 2010; Zuur and Smith, 2007). Optimal smoothing is automatically performed by the mgcv package, using cross-validation. Models were built using a forward stepwise technique, starting from the model that only included length as a covariate, and adding one covariate at a time. To minimize the potential problems associated with stepwise-model building, we decided to enter the covariates in an order established prior the start of the model-building process, based on our experience of the study system (Table 1), keeping only those covariates that resulted both in a significant contribution to the explained deviance and in a decrease of the Akaike Information Criterion (AIC) by at least two units (Burnham and Anderson, 2003). Standard validation methods for regression-based models (histogram of residuals, Q-Q plot, scatter plots of residuals vs. fitted values, etc.) were used to assess the pertinence of the modeling approach (Zuur and Elphick, 2010).

Table 5. Summary of the variables included in the GAMM, with a brief justification and corresponding references.

Variable	Why?	Type of variable	Citation
Total length	To determine the effect of ontogenic changes in the movements. Ontogenic differences in migrations have been reported for different shark species.	Continuous	(E. Hoyos-Padilla et al., 2014; Lowry and Motta, 2008; Yannis P. Papastamatiou et al., 2009)
Sex	Differences among sexes have been reported due their differences in diet and reproduction.	Categorical (F, M)	(E. M. Hoyos-Padilla et al., 2012; Joung, Chen, Lee, and Liu, 2008; Y P Papastamatiou et al., 2009)
Species	Differences in the distribution patterns of both species have already been described.	Categorical (CGAL, CFAL)	(J. J. Dale et al., 2011; Meyer et al., 2010; Yannis P. Papastamatiou et al., 2009)
Island	Each island has different habitats and environmental conditions that could determine shark affinity. differences among them.	Categorical (12 levels)	(Bessudo, Soler, Klimley, Ketchum, Hearn, et al., 2011; Bigue et al., 2010; Hearn et al., 2010; Ketchum, Hearn, Klimley, Peñaherrera, et al., 2014)

9.3. RESULTS

We obtained data from seventy-eight sharks (44 *C. falciformis* and 34 *C. galapagensis*) from 43 receivers (Appendix 2). Of the 457,390 detections analyzed, 13.8% represented movements within the same island, 9.5% were inter-islands (i.e. Figure 44) and less than 1% were across jurisdictional boundaries between MPAs in different countries. Our results show that the ETP is an interconnected system, based on the movements of *C. falciformis* and *C. galapagensis* (Figure 45,Figure 46).

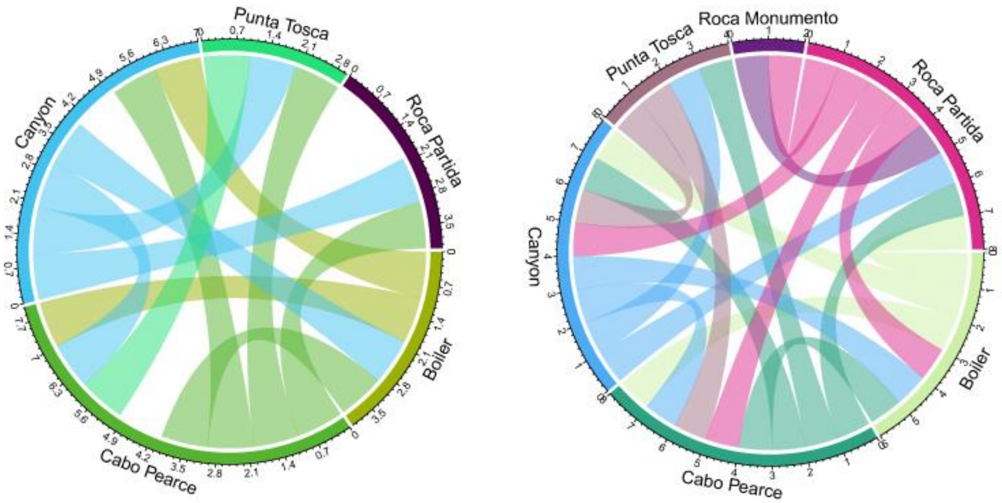


Figure 44. Inter-Island movements by *C. galapagensis* and C. *falciformis* recorded in the Revillagigedo Archipelago (respectively).

A *C. falciformis* female of 187 cm TL tagged in Anchorage, Wolf Island Galapagos on April 5th 2010, travelled to Clipperton Atoll (2,200 km north), representing the largest movement recorded for this study (Figure 45). In contrast, the largest movement of *C. galapagensis* was a 180 cm TL female tagged in February 2016 in Socorro Island, Revillagigedo, later detected in Clipperton Atoll and Darwin Arch, Galapagos (3,300 km southward) (Figure 46).

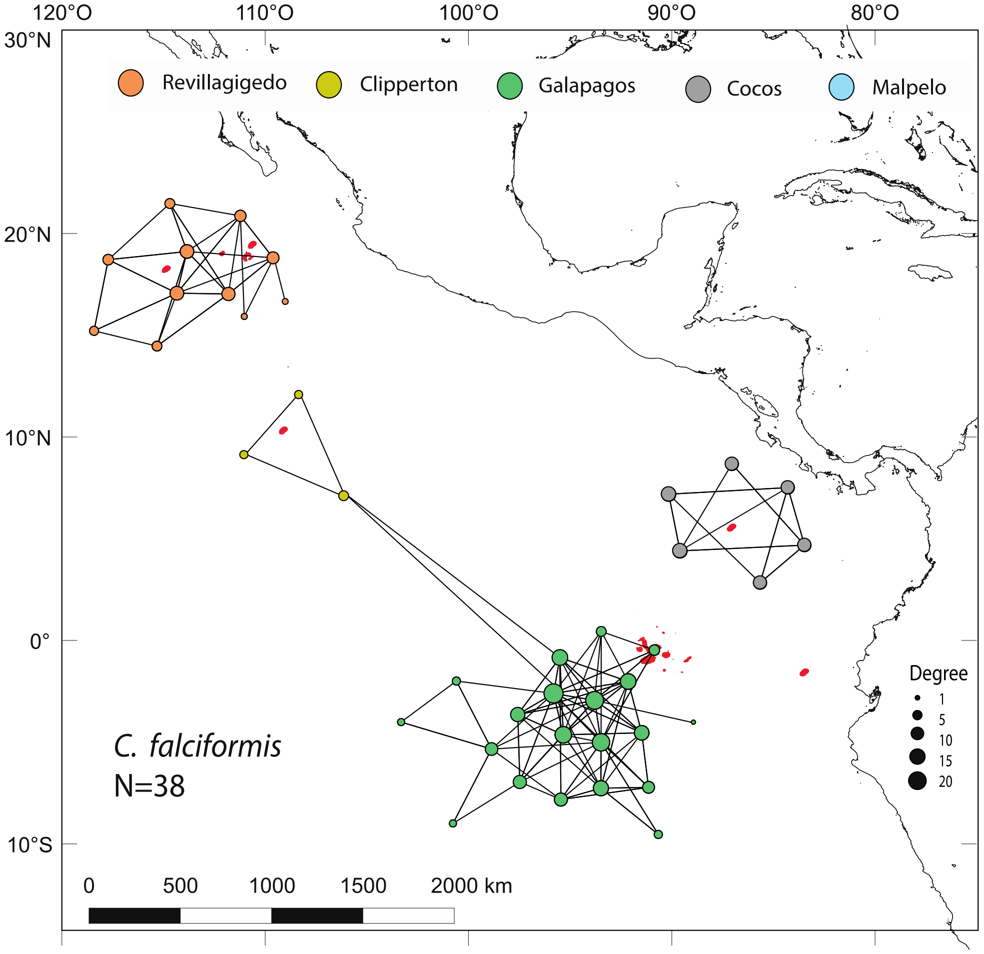


Figure 45. Network analysis of *C. falciformis* monitored the ETP. Circles represent the nodes and the arrows indicate the edges or movement paths. The size of the circles represents the degree, the number of links for each receiver.

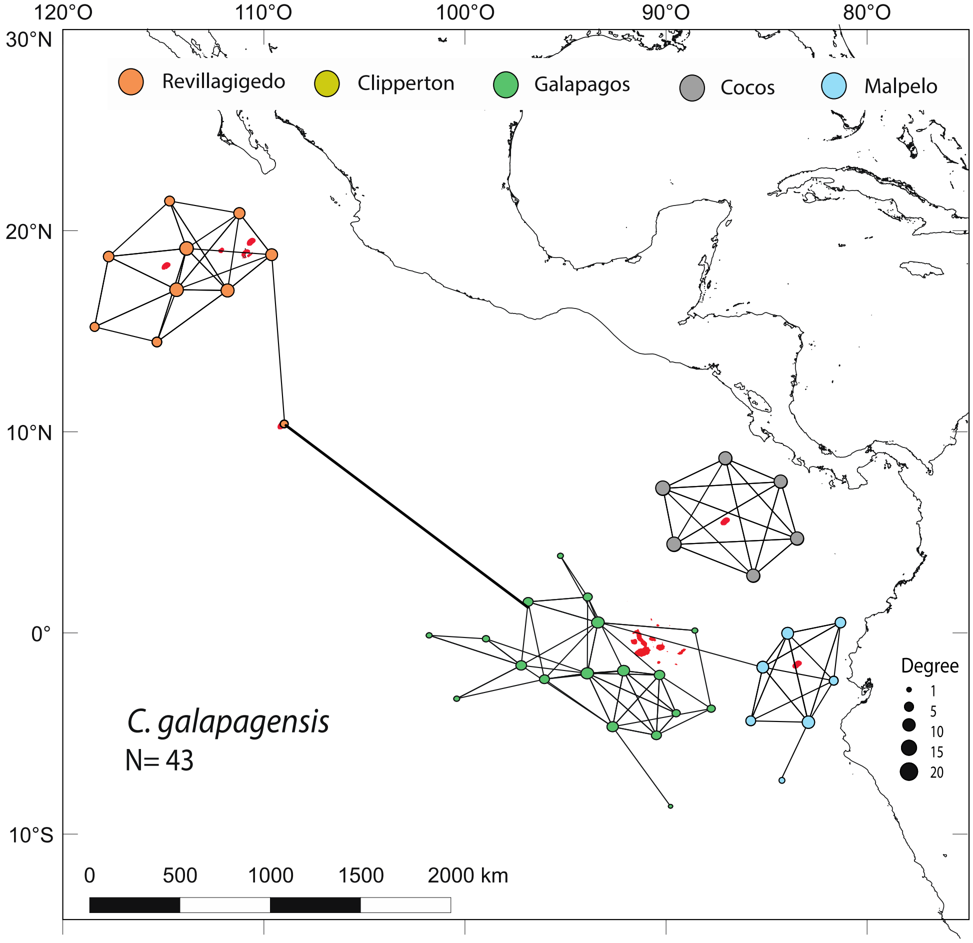


Figure 46. Network analysis of *C. galapagensis* monitored the ETP. Circles represent the nodes and the arrows indicate the edges or movement paths. The size of the circles represents the degree, the number of links for each receiver.

Despite these large-scale movement, as we expected, 90% of the movements of both species were observed in a range of < 50 km, showing high residence to the tagging site (Figure 47).

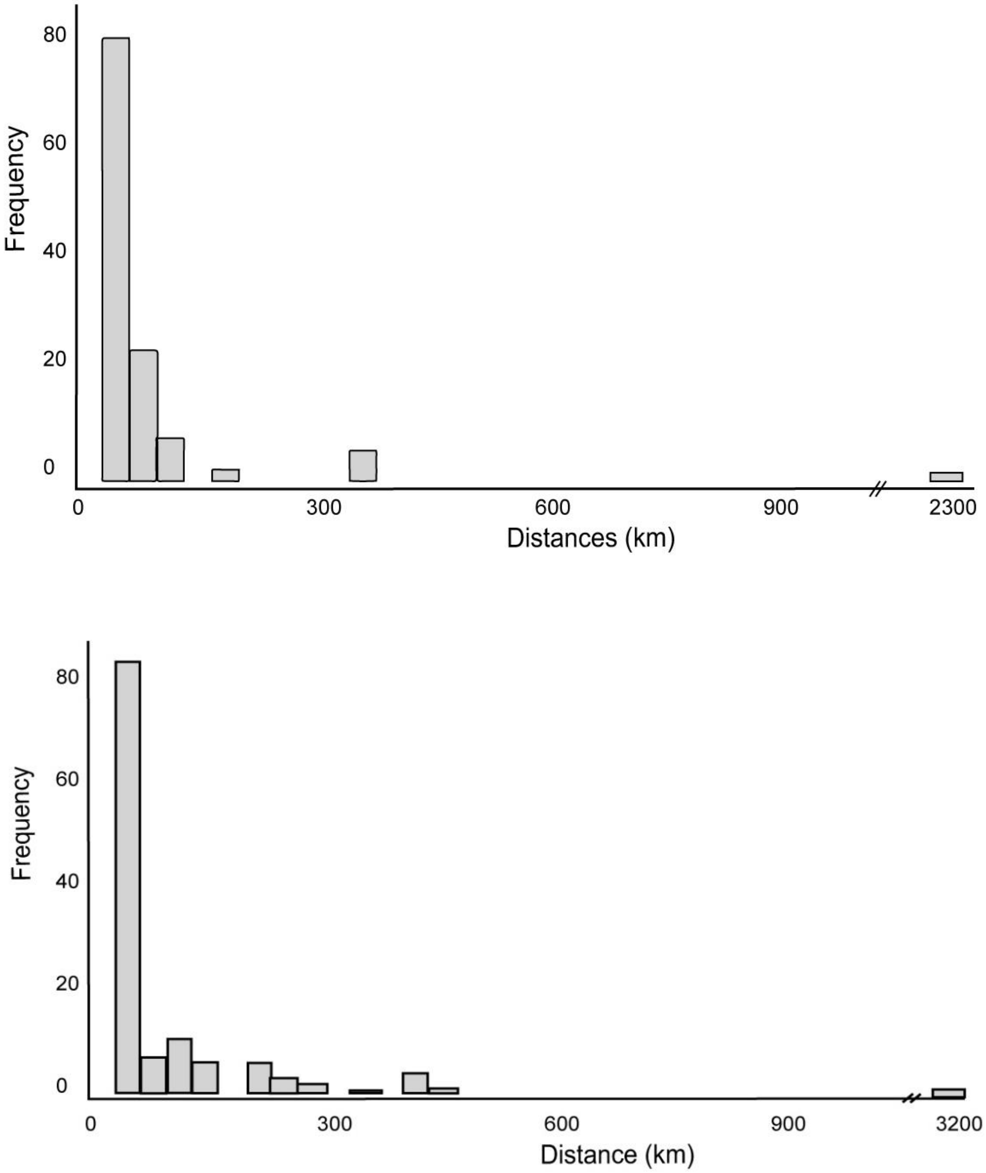


Figure 47. Frequency of sharks' *C. falciformis* (on the top) and *C. galapagensis* (on the bottom) movements per distance (kilometers).

Network analysis and *metrics*

C. falciformis had significantly higher values than *C. galapagensis* in terms of the number edges (X^2= 44.714, DF=1, p<0.5), degree of centrality (X^2= 40.164, DF=1, p<0.5) and density (X^2= 14.238, DF=1, p<0.5), whereas the number of nodes did not show a significant difference between the two species (X^2= 0.10001, DF=1, p= 0.75).

The relative importance of the site with the highest number of movements and the effect of site isolation on networks were investigated by performing a site removal analysis. Networks for *C. falciformis* were typically more complex than *C. galapagensis*, as most individuals used a larger number of sites and exhibited a higher frequency of inter-reef movements. This was more evident after removing sites from the system, which resulted in smaller and less variable changes in metrics from the full network (either positive or negative) in *C. galapagensis* compared to C. *falciformis* (Figure 48). However, network metrics were affected in different ways after each removal scenario. While removing sites from the network negatively impacted the number of edges and density, degree had a positive change (Figure 48). Therefore, removing sites from the network reduced the size and also the number of inter-habitat movements in both species, but also increased the number of components of isolated sites. In many cases, the scenarios could not be estimated due the low number of movements between sites.

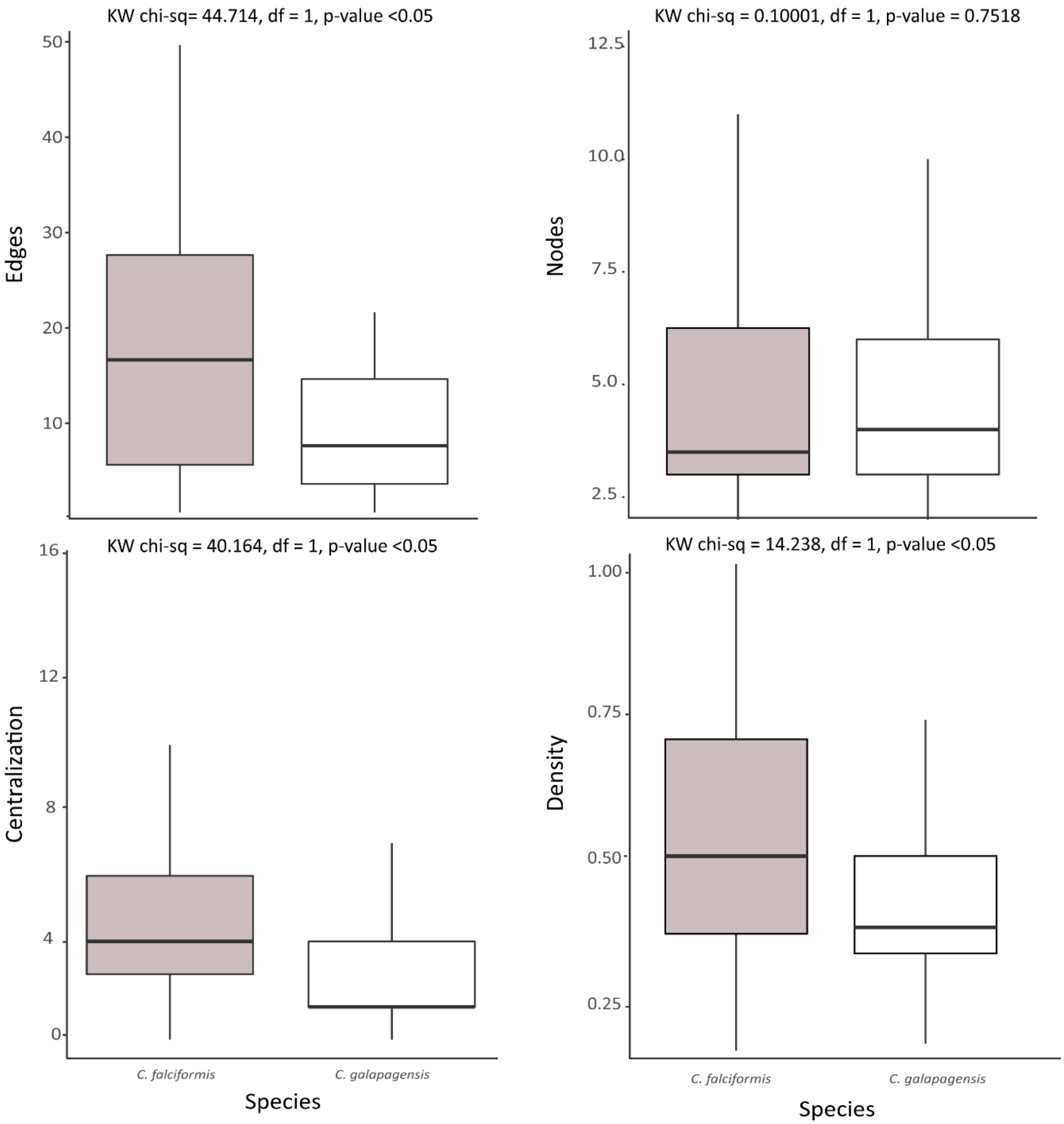
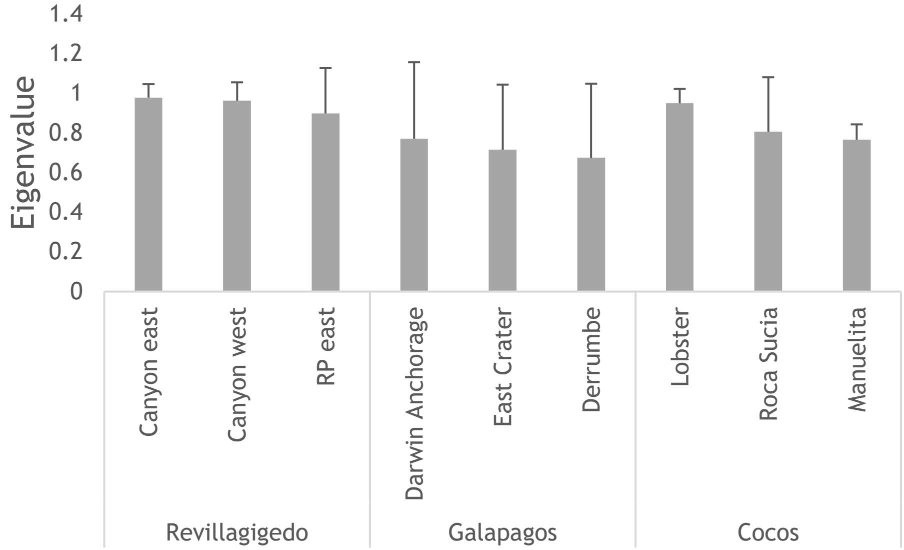


Figure 48. NA metrics of *C. falciformis* and *C. galapagensis* of the ETP comparing the species.

The most important sites in terms of eigenvalues varied according to the species. For *C. galapagensis*, Roca Partida (Revillagigedo), Nevera (Malpelo), Roca Elefante (Galapagos) and Corales Norte (Cocos) were the most connected. Whereas the most important for *C. falciformis* were The Canyon (Revillagigedo), Darwin Anchorage (Galapagos) and Lobster (Cocos) (Figure 49).

C. falciformis



C. galapagensis

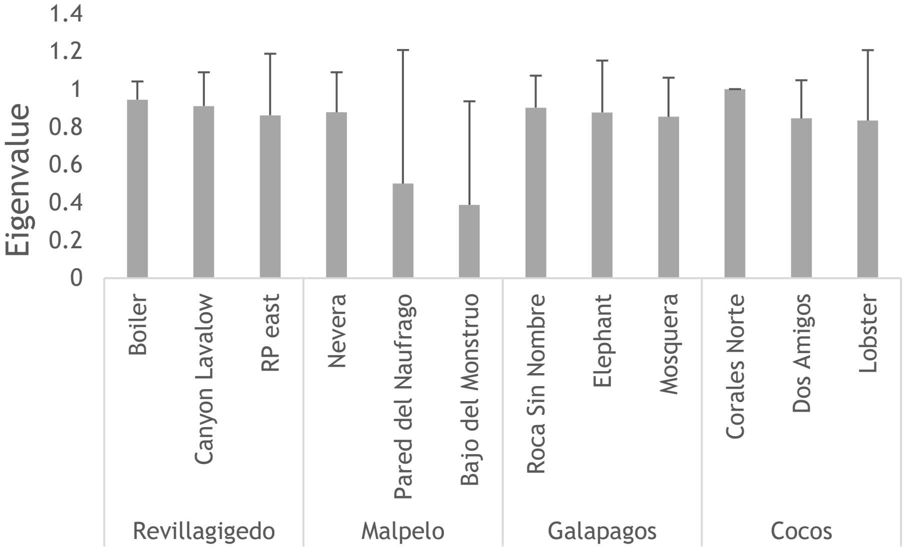


Figure 49. Eigenvalues of *C. falciformis (*top graph) and *C*. *galapagensis* (bottom graph) showing the importance of each sites according to the connectedness.

As it was expected, GAMMS model showed that the density of the nodes decreased when sharks were larger, whereas the number of nodes and edges increased. The model was significant (r=0.68, p<0.05). The residuals showed the model fitted with the variability of data (Figure 50).

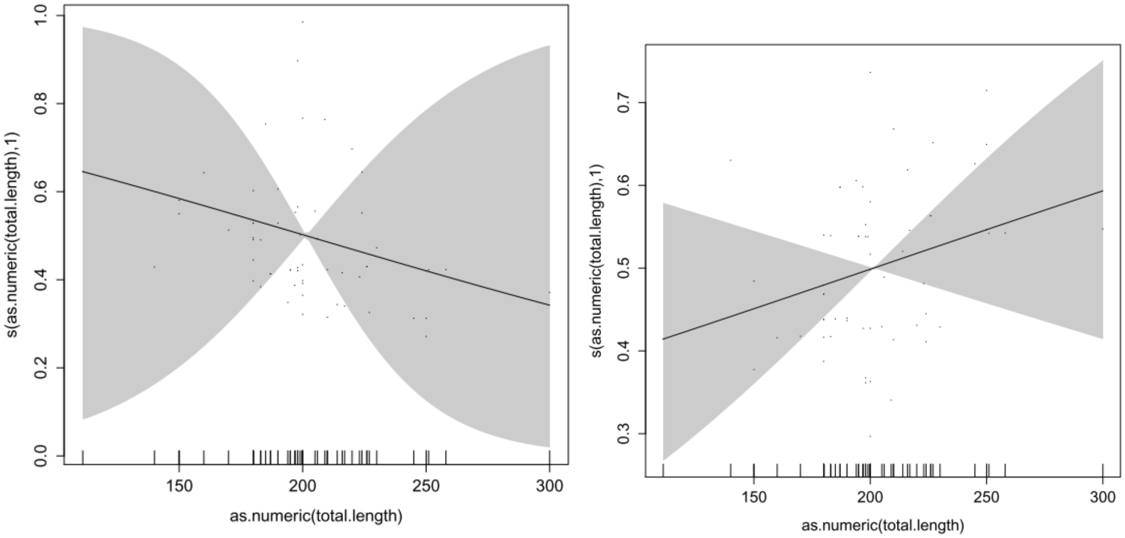


Figure 50. Graphs of the General Additive Mixed Model (GAMMS) using the metrics Density (left) and number of Nodes (right) as a response to the total length.

During this study, one of the longest movements for *C. galapagensis* has been recorded. A sub adult female of 181 cm TL was tagged in Socorro Island the 26th of February 2016, then was detected 945 km south in the Clipperton Atoll for three months and finally was located in the Darwin Island, Galapagos (2,300 km). Therefore, this single individual showed a movement of at least 3,200 km south, passing by three marine reserves (Figure 51).

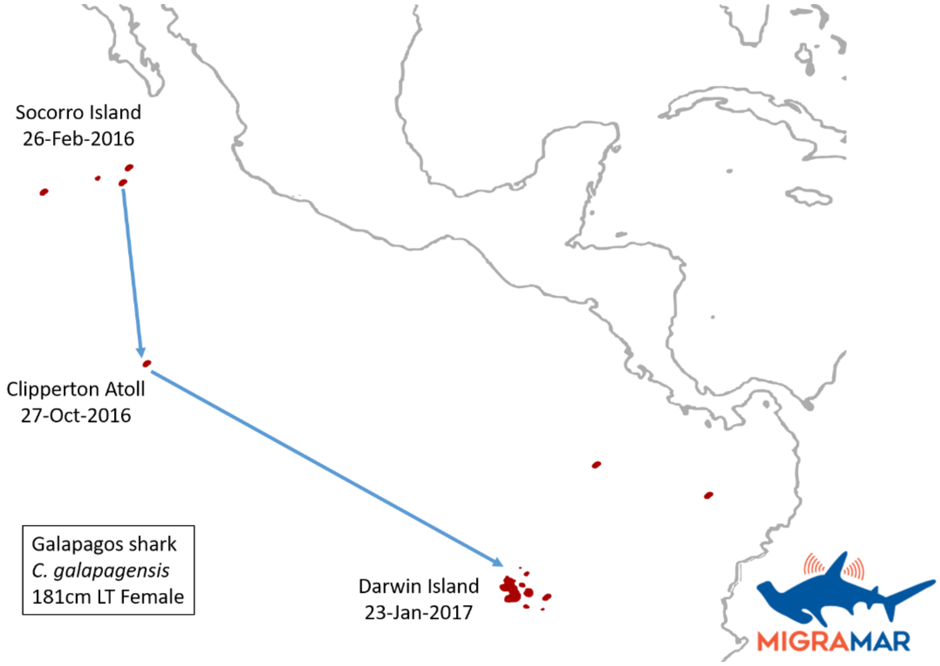


Figure 51. Long distance movement by an sub-adult female tagged in Revillagigedo Archipelago and detected in Clipperton Atoll (995 km south) and Darwin Island, Galapagos (2,300 km away) a year later.

9.4. DISCUSSION

The results of this study have shown that continental scale acoustic telemetry systems can provide useful data on long-range movements and connectivity of highly mobile species. The NA allowed us to observe large-scale spatial and temporal connectivity. However, differences in tagging effort, receiver network deployment and acoustic coverage affected the results. The analyses did not consider the distance between the receivers, therefore the probability of detecting more movements in short distances was expected. Using acoustic telemetry, it was possible to record the longest movements ever described for *C. galapagensis*.

The previous records showed that a *C. galapagensis* tagged in Bermuda moved 2,859 km away of the coast of Suriname, but most recaptures (12 of 14) were within 100 km of the original capture sites (Kohler and Turner, 2001).

The movements of *C. falciformis* and *C. galapagensis* between Revillagigedo to Clipperton, and from Clipperton to Galapagos recorded in this study are an example of the importance of defining biological corridors between MPAs. According to the NA, *C. falciformis* presented significantly higher values than *C. galapagensis* in terms of the number edges, the centralization and the density ($p<0.5$), whereas the number of nodes did not show a significant difference ($p= 0.75$). The most important sites in terms of the eigenvalue varied according to the species, for *C. galapagensis* Roca Partida (Roca PArtida, RP), Nevera (Malpelo, MP), Elephant (Galápagos, GLP) and Corales Norte (Cocos, CC) were the most connected. Whereas for *C. falciformis* the most important were Canyon east (RA), Darwin Anchorage (GLP) and Lobster (CC).

Heupel *et al.,* (2010) determined that for wide-ranging species, there is an under-estimation of the connectivity, because some individuals can appear to be absent from receiver locations for long periods while actually remaining within the general study area but outside the detection range of the receivers. However, the long distances movements also recorded in this study are very relevant because, they show the potential population connectivity within the ETP.

Previous studies have also shown that shark populations are not homogenously distributed in different habitats of the ecosystem that can support a higher diversity and abundance of sharks (Dale *et al.,* 2006). Many shark species are known to aggregate on outer parts of reef slopes that are generally exposed to stronger current flow (Hearn *et al.,* 2010), where productive foraging grounds are present (McCauley *et al.*, 2012). Currents probably shape the shark community and define spatial and temporal patterns of habitat use.

Hearn *et al.,* (2010) and Ketchum *et al.,*(2012) provided evidence to support this hypothesis by showing that the areas around Wolf Island (GLP) with stronger current flow were generally ‘hotspots’ for hammerhead sharks and for other pelagic species, including galapagos sharks. Based on the NA results, sharks are not just highly residential; they also tend to begin long dispersal from these sites to other islands and marine reserves (more than 100 km). We determined that the stepping-stones are sites, where previous studies have found high abundance of sharks.

In Cocos, previous studies have shown that there are less sharks in shelter bays, than the islets and seamounts (Sibaja-Cordero, 2008). Dos Amigos, Roca Sucia, and Alcyone are the sites with the highest abundance. Manuelita also is important, but it varies according to the habitats within the site (Bessudo *et al.,* 2011). In the Galapagos and Revillagigedo Archipelago, sharks seem to show a similar behavior as in Malpelo, with the largest aggregations found up-current in the side of the island where the current flows into, for example, Shark Point and Rockfall at Wolf Island (Hearn *et al.,* 2010). Ketchum *et al.,* (2014) also mentioned that Darwin Island may be a stopover site for hammerheads that perform long-distance movements.

Few inter-island movements were observed within the marine reserves (9.5%), and most of the movements were within 50 km. Previous studies have shown that female galapagos sharks display high site-fidelity, while males are less resident (Kohler and Turner, 2001). In general, they present movements of less than 100 km (Dale *et al.*, 2001). However, Pazmiño *et al.* (submitted) showed that there are areas where *C. galapagensis* and *C. obscurus* co-occur across the Pacific Ocean and with nuclear genome-wide markers they showed hybridization between the two species. Four hydrid individuals (~1%) were detected bi-directional between *C. galapagensis* and *C. obscurus* in the Gulf of California along the east Pacific coast. The presence hybrid at Clipperton Atoll and Galapagos Islands suggests movement of female Galapagos sharks (potentially hybrid mothers) from the primary area of contact (Gulf of California or Revillagigedo) towards the Galápagos Islands using Clipperton Atoll as a stepping-stone.

Genetic and physical evidences agreed that *C. galapagensis* is travelling from the Northern Eastern Tropical Pacific to the Surthern ETP. These findings are very relevant, because highlight the necessity of multi-national collaboration and shark management.

10. GENERAL DISCUSSION

9.1. DISTRIBUTION PATTERNS AND THE EFFECTS OF THE ENVIRONMENTAL VARIABLES

The Revillagigedo Archipelago is located in the north of the eastern tropical Pacific (ETP), an oceanic region located between the subtropical gyres of the North and South Pacific, containing the eastern Pacific warm pool and the eastern terminus of the Pacific equatorial current system (Lavín *et al.,* 2006). The islands lie in in the transitory zone of the Northern Equatorial Current (NEC) and the California Current and therefore oceanic conditions are highly influenced by the seasonal dynamics of these two current systems (Brattstrom, 1990). The annual range of SST is from 23.7 °C to 28.6 °C (Carter, 2017; Figure 51). Generally, Socorro experiences the highest sea surface temperatures, followed by San Benedicto, Clarion and Roca Partida. Minimum SST occur from January until June, reflecting the dominance of the California current in transporting cool waters from higher latitudes south along Baja California, and turning west where they converge with the NEC (Carter, 2017). In June the California Current weakens and the NEC becomes the more dominant influence on SST at the archipelago. At this time the NEC is predominantly fed by the warmer waters of the Northern Equatorial Counter Current (NECC), causing SST to increase (Kessler, 2006; Carter, 2017).

We observed that *C. falciformis* and *C. galapagensis* were less present during the summer (July and August), whereas the highest presence is recorded in the winter (January to March), indicating that temperature and productivity of currents could drive the seasonal migrations. Why some sharks leave the reserve in summer while others remain is unknown.

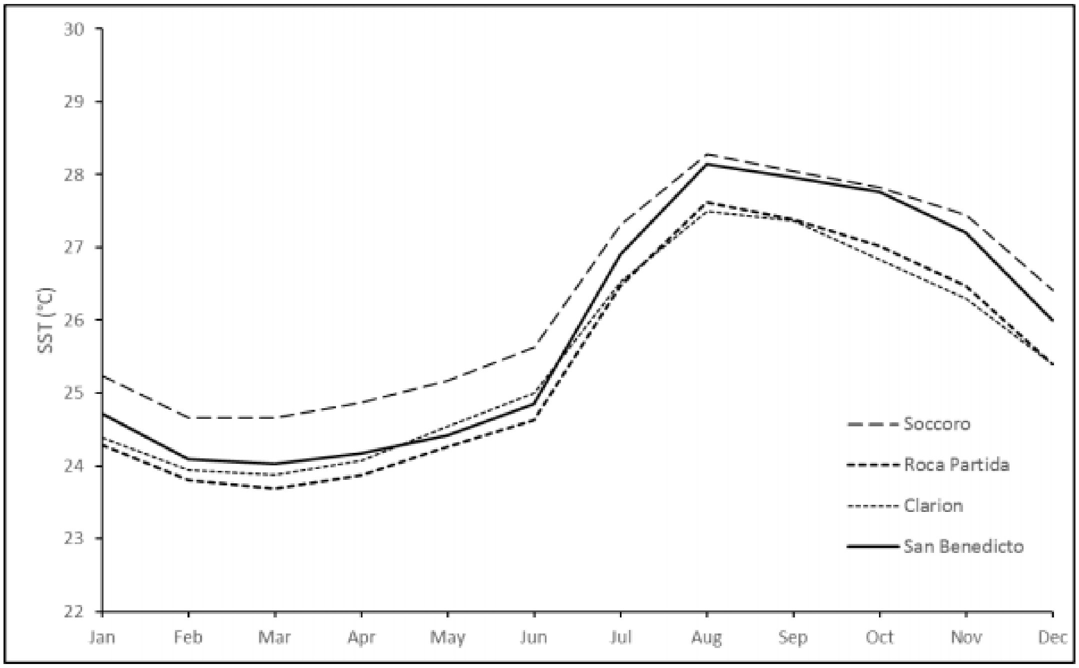


Figure 52. Monthly climatology SST for the Revillagigedo Archipelago from 1982-2016 (IGOSS; Carter, 2017).

The thermocline at the Revillagigedo Archipelago is shallowest in September; this is caused by northward migration of the Inter Tropical Convergence Zone (ITCZ) and the subsequent upwelling lift, which causes the thermocline shoal across the ETP. The thermocline deepens as ITCZ moves south, reaching its maximum depth (70 m) between January and March. Surface salinity in the Revillagigedo Archipelago ranges from 34.3 to 34.7 psu. Despite the influence of low salinity California Current, the halocline is most pronounced and salinity values are highest in spring and summer months when there is very little precipitation (Carter, 2017).

The oxygen minimum layer is positioned between the pycnocline and subpycnocline waters. In the ETP the oxygen minimum layer is remarkable for its size and degree of hypoxia (Karstensen,Stramma and Visbeck, 2008). This can be attributed to a highly productive photosynthetic layer at the surface and the sharp and permanent pycnocline, which impedes the exchange of oxygen-rich water from the surface (Fiedler and Lavin, 2017). The oxygen minimum layer is at its shallowest from January to March. The variability can be explained as being related to seasonal changes in offshore wind patterns and thermocline depth. When the thermocline is shallow, increased upwelling allows for increased primary production and thus a deepening of the oxygen minimum layer (Carter, 2017).

According to Carter (2017) the satellite data of the SST could predict 49% to 62% of temperature variability at the islands on a weekly timescale, indicating the moderate overall influence of wider scale oceanographic processes on the island conditions. The *in situ* temperature measurements very seldom exceed open water temperatures but exhibit a larger seasonal range in temperature compared to satellite-derived SST. Lower temperature ranges of the *in situ* measurements are likely to be attributable to the fact they were recorded at depth compared to satellite-derived data which measures the temperature of a very thin layer on the ocean's surface (Sheppard, 2009). Roca Partida had the lowest annual temperature range, which reflects the fact it was the deepest set temperature logger (38 m) and that there is the presence of a strong thermocline in the water column. The largest fluctuation over one day, recorded by Carter (2017), was 9 °C at San Benedicto and Roca Partida on 16 th January 2017 (Figure 52). Fluctuations of this size and frequency indicate the presence of large amplitude internal waves (LAIW) causing a rapid change in depth of the thermocline. In any stably stratified body of water, internal waves can be produced by a variety of mechanisms which can cause them to occur at a range of frequencies (Leichter *et al.,* 1996). The present data does not allow a determination of the ultimate source of the internal waves.

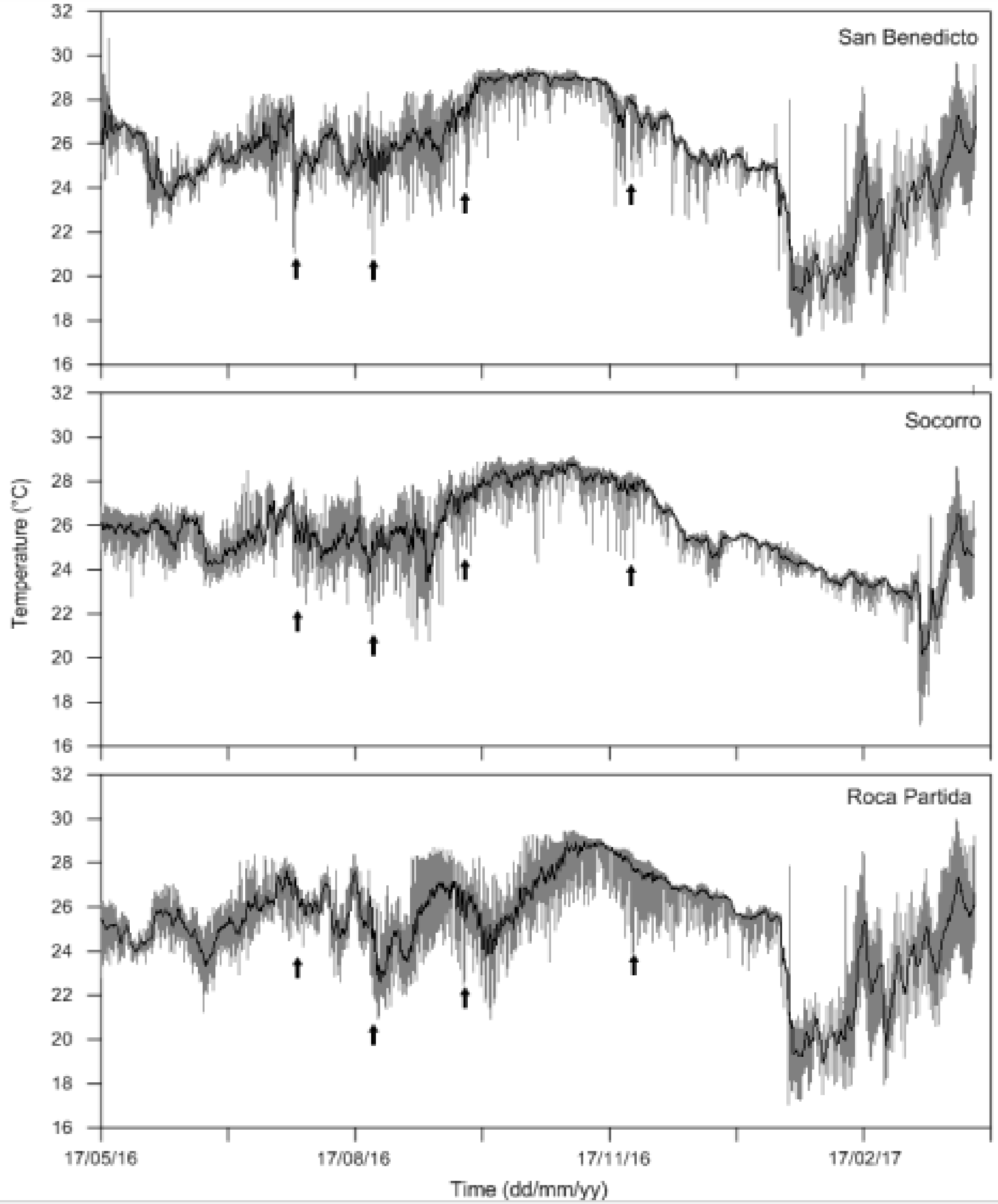


Figure 53. *In situ* temperature records at San Benedicto (23 m), Socorro (28 m) and Roca Partida (38 m) from 17th May 2016 to 25 th March 2017: raw data (grey) taken at 13-minute intervals and daily running average (black). Black arrows mark the occurrence of a tropical cyclone within a 200 km radius of the islands (Plot taken from Carter, 2017).

Other species that have been shown to exhibit variability in patterns of residency within bays include bonnethead sharks (*Sphyrna tiburo*) (Heupel *et al.,* 2006), bull sharks *Carcharhinus leucas* (Heupel and Simpfendorfer 2008), and cownose rays *Rhinoptera bonasus* (Collins *et al.,* 2007). According to Papastamatiou *et al.,* (2008) there are shark populations characterized by partial migrations, part of the population like juveniles could stay longer in shallower waters or when pregnant females spend more time in the nursery grounds.

The studies also reported a high seasonality in the fisheries. Ronquillo (1999) reported that during May to June the number of females in the landings is much higher than males. In an annual basis, there is no strong evidence of sexual segregation. According to Strasburg (1958), Fourmanoir (1961), Stevens (1984), and Stevens and McLoughing (1991) the populations of *C. falciformis* and *C. galapagensis* do not present sexual seasonality. Therefore, the pregnant females could visit the nursery grounds during the whole year. However, the abundance of *C. falciformis* in the coastal areas of Baja California Sur could be related to the increase of the superficial sea temperature in the summer, showing movement seasonality, where, only adults (179- 200 cm TL) migrate to the coastal areas.

In the ETP, tropical cyclones arise over the eastern Pacific warm pool. Once formed, the cyclonic storms move with the easterly trade winds and often curve northward over cooler waters, sometimes impacting The Revillagigedo Archipelago (Fiedler and Lavín, 2017: Carter 2017). The Revillagigedo Archipelago is impacted on average by 3 tropical cyclones per year, typically between May and November (https://coast.noaa.gov/hurricanes/). The tropical cyclones can have episodic effects on oceanographic conditions in the form of increased wind and wave energy, and cool SST anomalies (Carrigan and Puotinen, 2011). Cooling effects of up to 6 °C have been recorded in their wake, caused by the upwelling and mixing of cold subsurface waters (Price *et al.*, 2008). The magnitude of each cooling impact is likely to be related to the proximity and strength of each storm and the duration it's in the zone of influence of the island (Carrigan and Puotinen, 2011). For example, at San Benedicto, the largest cooling event, which coincided with a tropical cyclone, occurred when the cyclone track passed directly over the island (Storm Frank). It is suggested that the occurrence of tropical cyclones during the period of warmest SST may disrupt the annual SST warming cycle at the islands and could play a significant role in regulating average SST.

10.1. CURRENT POPULATION STATUS AND RISKS

There is strong evidence that *C. falciformis* and *C. galapagensis* are summited by the fisheries pressure. The average mature sizes for both species are higher in other parts of the world, but in Baja California and the Mexican Tropical Pacific the populations mature in smaller lengths. According to Ronquillo (1999) the species exposed to high fishing pressure can reach sexual mature lengths smaller to compensate the stock exploitation by the effect of a mechanism denso-dependent. Del Rosario (1998) reported that *C. falciformis* represent the most exploited species in the shark fisheries in Guatemala. Castillo-Géniz *et al.,* (1997) reported that also it is the most common species in Chiapas, Mexico. Chong-Robles and Alejo-Plata (2002) mentioned that the silky shark represent more than 90% of the fisheries in Oaxaca, Mexico. All the mentioned studies also reported that most of the individuals were immature.

According to Carter (2017), a linear trend analysis of SST in the Revillagigedo Archipelago region indicates relative moderate warming of 0.7 °C from 1880 to 2010 (HADISST) (Figure 16). This could suggest that it is a region that will exhibit a slower rate of San Benedicto Socorro Roca Partida Clarion increasing SST. However, the eastern Pacific warm pool has also been suggested to be an area of concentrated ocean warming (Jimenez *et al.,* 2017). This may influence the SST at Revillagigedo Archipelago on a seasonal basis, when the NEC is the dominant influence on the oceanographic conditions and SST temperature.

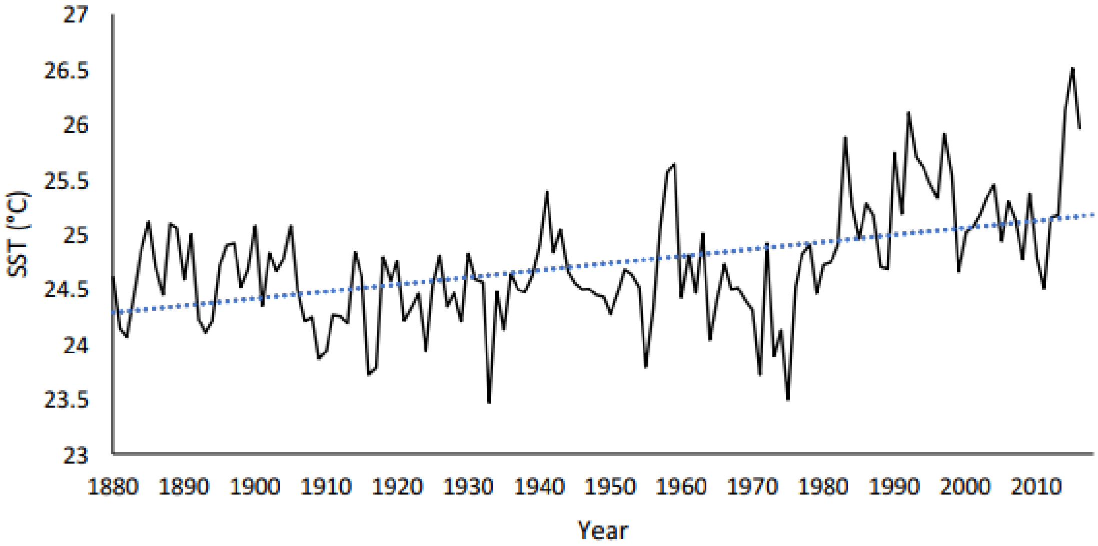


Figure 54. Monthly SST in Revillagigedo Archipelago from 1880-2016 (HADISST; by Carter, 2017).

10.2. EFFECT OF CLIMATE CHANGE ON SHARKS IN PARTICULAR

Reducing the impacts of climate change on sharks and rays requires a variety of approaches, including mitigating climate change, habitat degradation and ensuring sustainability. According to predictions, the group of sharks compared to others such as birds, fish and marine mammals will be the most affected by climate change (Hazen *et al.,* 2012). For example, mako sharks, *Isurus oxyrinchus* would lose most of the habitat, since they are extremely sensitive to temperature variation (for example, they may respond to changes of <0.001 ° C, Brown, 2010).

Many aspects of shark physiology are regulated by temperature (Sims 2003), which could explain fine-scale movement patterns and close association with the specific temperature ranges observed for some species (Simpfendorfer and Heupel 2004). Few studies have shown the effect of temperature and acidification on sharks.

Heuter *et al.,* (2001) describes that blacktip sharks (*Carcharhinus limbatus*) are directed to deeper waters due to a decrease in barometric pressure associated with the approach of storms. This response was consistent for all individuals, who returned to the shallow zone after the storm passed, suggesting that it was an innate behavior.

Ketchum *et al.* (2014) using active acoustic telemetry showed that there is a preference for the eastern side of Wolf Island, in Galapagos, in both the warm and cold seasons. However, the depth of the sharks varied with the season, apparently in response to seasonal changes in the vertical structure of temperature. The hammerheads made vertical movements above the thermocline during the high seas, preferring temperatures of 23-26 °C. The results provided evidence that the hammerheads are highly selective of location and depth during their resting periods (following refuge theory), where they can perform essential activities such as cleaning and thermoregulation and perform vertical exploratory movements towards the mixed layer and occasionally below the thermocline in search of food.

The oceanic whitetip shark (*C. longimanus*) also exhibits behavioral thermoregulation, performing short duration dives (mean = 13.06 minutes) in the mesopelagic zone (up to 1082 m and 7.75 °C), which occurs significantly more often overnight. The rates of climb during these dives were significantly slower than the rates of decline, suggesting that these dives are for foraging (Howey-Jordan *et al.,* 2013).

Organisms typically have some capacity to acclimate to potential stressors either by altering aspects of their physiological, behavioral or morphological characteristics to enable them to cope with changes. Some are more permanent alterations (developmental acclimation) whereas others are reversible. Rosa *et al.,* (2014), showed that the tropical shark *Chiloscyllium punctatum*, is significantly affected in the projected scenarios of ocean acidification (ΔpH = 0.5) and heating (+ 4 °C, 30 °C). Pistevos *et al.,* (2015) conducted a combination of experiments to assess how warming and acidification affects the development, growth and behavior of *Heterodontus portusjacksoni*. Although embryonic development was faster due to temperature, high temperature and CO_2 had detrimental effects on sharks not only increasing energy demands, also decreasing metabolic efficiency and reducing their ability to locate food through smell. The combination of these effects led to considerable reductions in shark growth rates sustained in natural environments with high CO_2, alone or in combination with higher temperatures. The results suggest that ocean acidification reduces its ability to hunt effectively and exercise strong control in food webs.

11. RELEVANCE OF THE STUDY

Defining these movements between habitats is important to identify critical environments or corridors that may be important for population connectivity zonation (Fletcher *et al.*, 2011) and developing management strategies that ensure protection (Bond *et al.,* 2012). Clipperton is an area with unusual assemblages of both Indo-Pacific and Panamic flora and fauna, and it is possible that it is an important stepping-stone for connection between the two bioregions, Northern ETP (Revillagigedo and Gulf of California) and Sothern ETP (Malpelo, Cocos and Galapagos)(Allen and Robertson, 1997).

It is becoming increasingly clear that some species can benefit from investments in local management measures nested within broader international efforts. However, Brewster-Geisz and Miller (2000) determined that nursery closures or size limits that protect only neonates and young juveniles are unlikely to promote population recovery; effective management must involve protection for older age classes along with nursery-using life stages.

The ideal MPA design provides protection for all life stages of the species of concern, which is impractical for the majority of shark species because they are wide ranging. According to the results, management strategies within insular zones of the ETP region may have broad geographic benefits, because these reserves may be efficient protective zones. The observed movements between marine protected areas suggest that these species are vulnerable to domestic fisheries as well as multinational fisheries on the high seas, as these species are highly associated with commercial pelagic species such as the yellowfin tuna, *Thunnus albacares.* Even when not targeted, these sharks often comprise a high proportion of landings in line-based fisheries (Megalofonou, 2005).

According to Bigue *et al.,* (2010) the region has poor level of enforcement of the laws and regulations. There is a low capacity to detect and intercept offenders, poor preparation for effective legal cases, difficulties in both administrative and judicial processes, and finally, obstacles which prevent sanctions from being imposed upon violators.

Kohin *et al.,* (2006) determined that silky sharks tagged in Costa Rica ranged into the Exclusive Economic Zone (EEZ) of 6 countries and beyond into international waters. Increased protection of reefs and inter-reef habitats along the inner shelf may provide a greater management benefit. Definition of the extent and occurrence of long-range movement and population connectivity is necessary for a full understanding of the ecology of a species and hence for designing effective management action (Heupel *et al.,* 2015).

Regular movement across state boundaries highlights the need for cooperation between jurisdictions to ensure sharks receive sufficient protection throughout their migrations. This may include the need for regulations related to the habitats in each jurisdiction where individuals spend time, as well as movement corridors (Espinoza *et al.,* 2015), such as the proposed swimways (see www.migramar.org).

12. CONCLUSIONS

The diversity and distribution patterns of sharks in the Revillagigedo Archipelago differ in time and space and regarding to the environmental conditions and habitat use. Boiler (Figure 54) and Roca Partida (Figure 56) and are potential sites ideal for mating aggregations, whereas Canyon (Figure 54) and Punta Tosca (Figure 55) present conditions for nursery areas of silvertip and galapagos sharks. Juvenile and adult tiger sharks, *Galeocerdo cuvier* are mainly distributed in sandy bottoms and are highly associated the substrate, being almost absent in the pelagic environment.

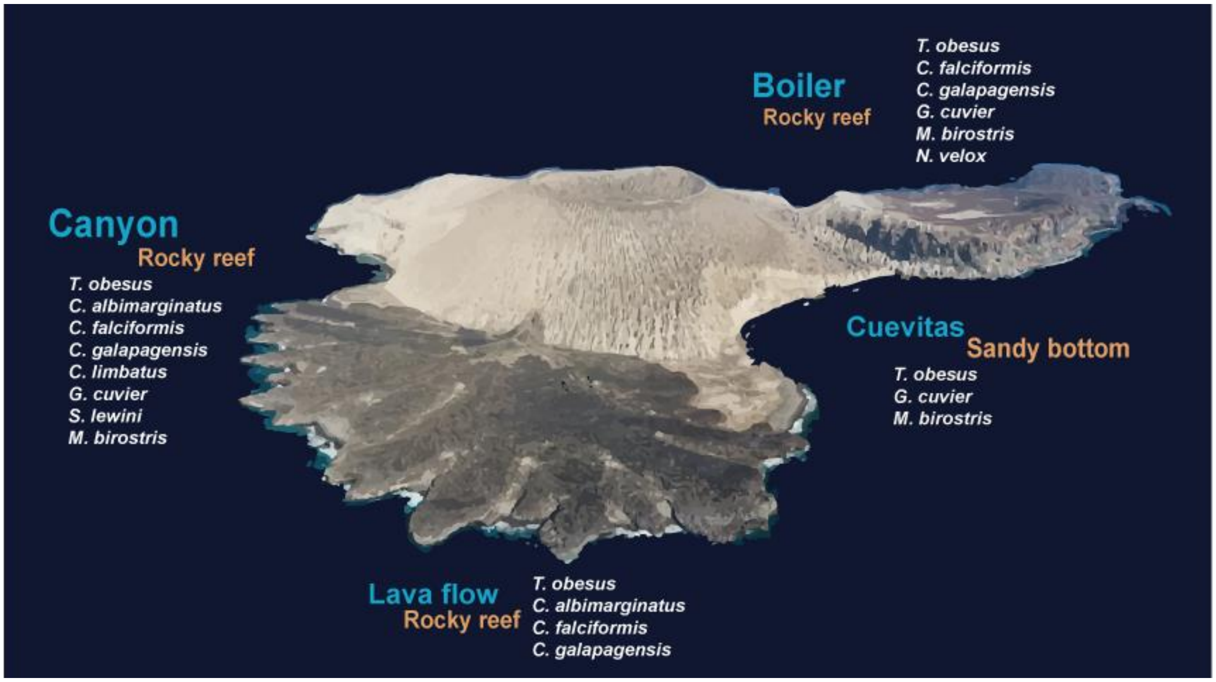


Figure 55. Summary of the BRUVS records in San Benedicto Island: Sites, habitats and shark species found in each site.

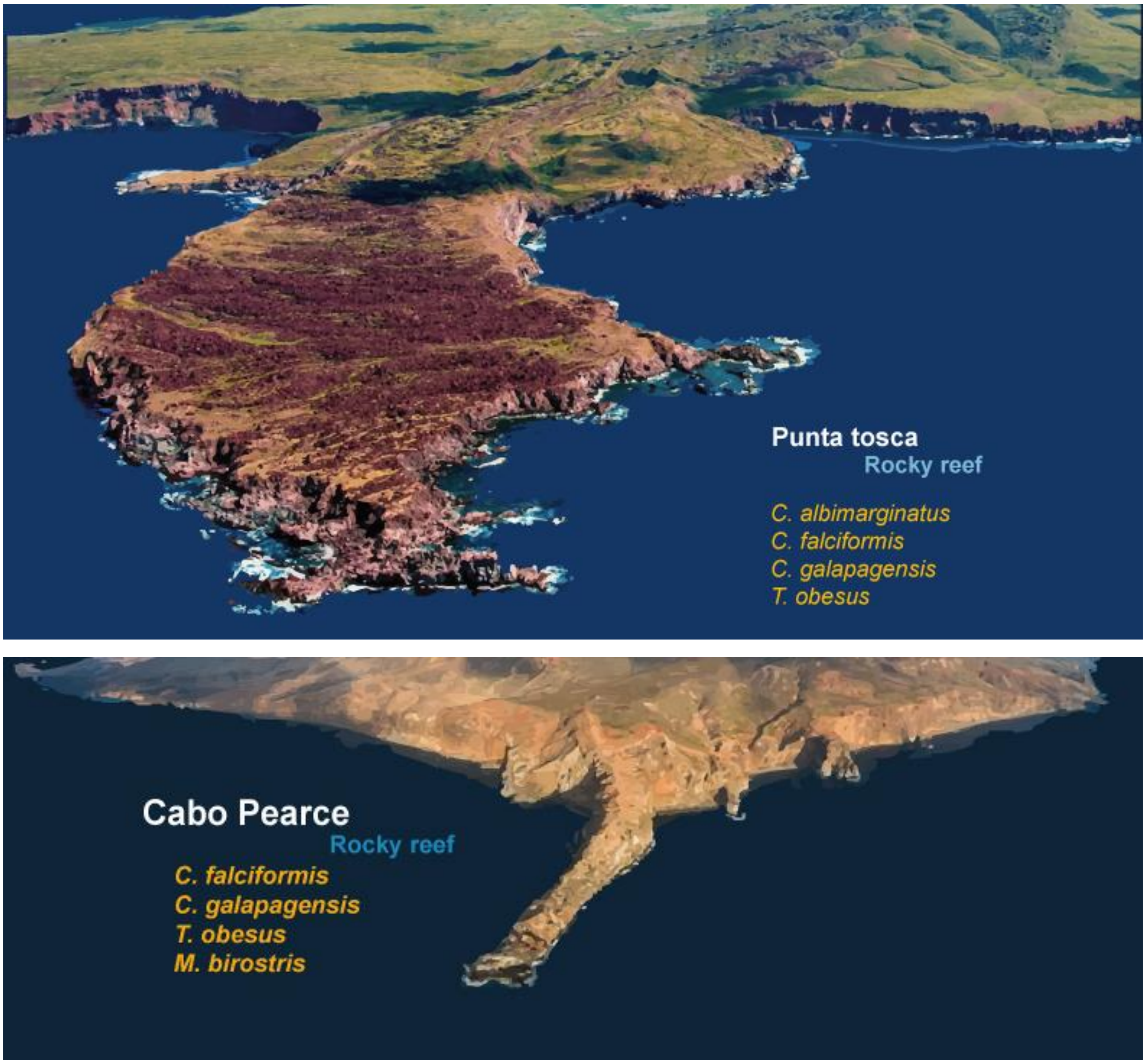


Figure 56. Summary of the BRUVS records in Socorro Island (Top image: Punta Tosca, bottom; Cabo Pearce): Sites, habitats and shark species found in each site.

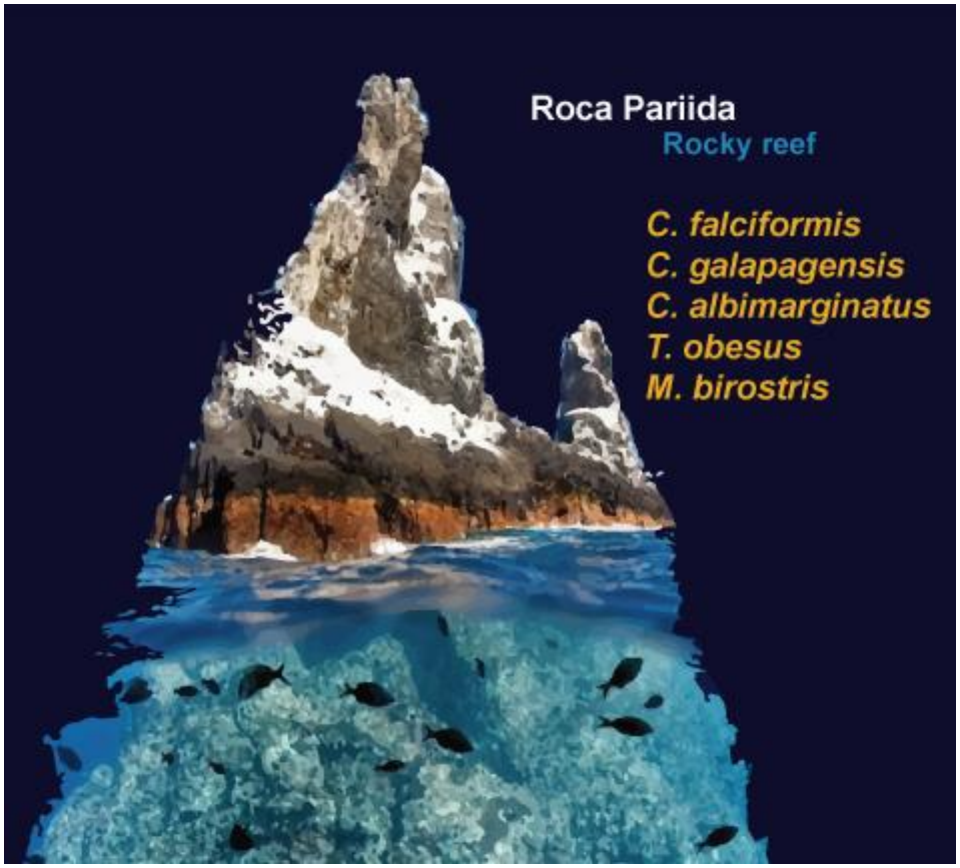


Figure 57. Summary of the BRUVS records in Roca Partida: Site, habitat and shark species recorded.

The patterns of residence and habitat use of the sharks of Revillagigedo Archipelago are different according to the site and the season of the year. For *C. falciformis* and *C. galapagensis*, we found that the highest residency where observed during May to April and then they probably move to the open ocean or continental waters during the warm season (July- October), when the hurricane season and extreme temperature changes occurred (~9 TC variation over a day).

Shark species showed segregation by sex and size, most of the monitored sharks were female due to their habit to remain close to the islands. The distribution patterns of sharks are dependent to maturity and development of sharks, obtaining significant differences in the presence of sharks in space and time. We observed a tendency of decreasing residency index (RI) over the year in both species, which also coincide with more inter-insular and large-scale movements, as a result of differences in eating habits, distribution patterns, demand for energy expenditure, competition and risk of predation.

Due the unique oceanographic and biological conditions in each site, differences in the connectivity were recorded in terms of time and space. The metrics from the Network analysis showed differences between the species and between MPAs. Environmental variables and distribution patterns of the sharks of the Revillagigedo Archipelago were related, especially in terms of current exposure, environment (pelagic/ benthic), type of substrate, temperature and overall community richness (S). *C. falciformis* and *S. lewini* were present in the pelagic BRUVS. Whereas, *T. obesus, C. albimarginatus* and *C. galapagensis* and other less common species were observed in the benthic BRUVS.

The observed movements between marine protected areas suggest that these species are spending periods in the non protected areas, which potentially make them vulnerable to domestic fisheries as well as multinational fisheries on the high seas, as these species are highly associated with commercial pelagic species such as, yellowfin tuna, *Thunnus albacares.* The preference of *C. galapagensis* to remain at or above 50 m depth makes the species much more vulnerable when moving offshore between reserves. Furthermore, even when not targeted, these sharks often comprise a high proportion of landings in line-based fisheries. Regular movement across state boundaries highlights the need for cooperation between countries to ensure that sharks receive sufficient protection throughout their migrations. This may include the need for regulations related to the habitats in each jurisdiction where individuals spend time, as well as movement corridors.

Finally, we defined the critical areas of management for sharks in the Revillagigedo Archipelago, determined by the habitat use, connectivity, residence rates and abundance. Management strategies within insular zones of the ETP region are necessary, because these reserves may be efficient protective zones, as long as they have a minimum size of 70,000 km^2 established around each island, where persistence is highest and vulnerability is lowest.

13. RECOMMENDATIONS

Before 2017 Revillagigedo was a Biosphere Reserve that had a limited no-fishing zone of 9 nautical miles around each island. Using our results and other studies undertaken in the area, the Mexican authorities determined that was necessary to expand the marine reserve to 14.8 million hectares, which include the 40 nautical miles that were recommended for protecting inter-insular movements. The new National Park regulations establish that there is no fishing allowed within the reserve. However, surveillance and enforcement are very important to ensure that the reserve is fully protected and ensure that the illegal fishing is finally controlled.

Further research

1. To determine the presence of more shark species within the Revillagigedo Archipelago, it is necessary to keep the monitoring efforts focused on the pelagic habitats. It is recommended the use of innovative techniques, such as, Mid-water BRUVS which are deployments that are able to drift in the ocean and record the species in the areas between the islands.
2. In terms of acoustic monitoring, It is recommended to keep the tagging efforts, and ensure that a large number of silky and Galapagos sharks are constantly being detected by the large-scale arrange. Then, the network analysis would show more complete patterns of the movements of the sharks within different areas.
3. I would also recommend the use of satellite tracking, like SPOT and MiniPATs in order to described long distance movements that are not determined by the acoustic telemetry. That will allow us to understand in a better detail how sharks are moving from Revillagigedo to the Gulf of California and the Eastern Tropical Pacific.
4. Complementary techniques, such as, trophic ecology using stable isotopes to determine the differences and overlapping between individuals and

species in terms of how they share their prey and habitats are also recommended

5. To determine the connectivity, it is also recommended to start genetic studies of the silky and galapagos sharks. Then, it would be possible to determine if the findings described in this study are comparable to the genetic perspective.

Management strategies

1. As we determine in this study, sharks have complex distribution patterns, using the marine reserves for different activities during the life cycle. Therefore, it is important to ensure the sustainability of each critical habitat and recover the areas that are already impacted by human activities, such as, fishing pressure and not regulated eco-tourism.
2. More efforts to create frameworks for international collaboration that will ensure the protection of highly migratory species are essential. As it has been shown in this thesis, sharks are moving across national boundaries, therefore is necessary collaboration between different countries and ensure the protections the shark populations.
3. Expanding marine reserves can have a positive effect on some shark species. However, a deeper understanding of how the sharks use different areas will allow us to use ocean resources in more effective ways.
4. It is important to understand the nature of the swimways, their dynamicity and how they are affected by external factors, such as environmental variables and biological cycles. It is also important to determine which the best ways to protect them are.

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15. APPENDICES

14.1. SPECIES LIST FROM BRUVS

Appendix 1. Species recorded by BRUVS in the Revillagigedo Archipelago: General groups of interest, fishbase classes (environment), vulnerability and trophic level.

General groups	Fishbase Habitat Class	Latin name	Vulnerability (FishBase)	Trophic level
Cleaner fishes				2.64
	Reef-associated			2.64
		Holacanthus clarionensis	26.64	2.64
		Johnrandallia nigrirostris	15.01	2.97
Groupers				4.33
	Demersal			4.25
		Epinephelus labriformis	39.82	4
		Mycteroperca olfax	56.43	4.5
	Reef-associated			4.5
		Cephalopholis panamensis	39.06	4.5
		Dermatolepis dermatolepis	63.97	4.5
Manta				
	Reef-associated			3.46
		Mobula birostris	78.25	3.46
Pelagic				4.10
	Benthopelagic		60.08	4
		Caranx lugubris	60.08	4
	Pelagic-neritic		34.03	4.05
		Caranx caballus	34.03	4.05
	Pelagic-oceanic			4.45
		Acanthocybium solandri	46.16	4.42
		Thunnus albacares	50.67	4.48

	Reef-associated			3.992
		Carangoides orthogrammus	37.95	4.01
		Caranx melampygus	50.49	4.28
		Caranx sexfasciatus	45.19	3.58
		Elagatis bipinnulata	50.69	3.59
		Seriola rivoliana	73.55	4.5
Rays				3.84
	Demersal			3.84
		Dasyatis brevis	75.76	3.84
Reef fishes				3.09
	Benthopelagic			2
		Kyphosus analogus	40.97	2
	Demersal			3.65
		Bothus leopardinus	34.72	3.65
	Reef associated			3.10
		Abudefduf troschelii	30.38	2.95
		Acanthurus nigricans	33.71	2
		Acanthurus triostegus	16.26	2.78
		Acanthurus xanthopterus	37.08	2.87
		Aluterus scriptus	69.33	3.02
		Anisotremus interruptus	57.63	3.5
		Arothron hispidus	34.01	3.09
		Arothron meleagris	34.01	3.06
		Aulostomus chinensis	33.78	4.24
		Balistes polylepis	53.94	3.34
		Balistes vetula	36.2	3.33
		Bodianus diplotaenia	61.24	3.44
		Cantherhines dumerilii	37.03	3.07
		Canthidermis maculata	44.41	3.47
		Canthigaster punctatissima	10	
		Chaetodon humeralis	19.78	2.72
		Chilomycterus reticulatus	26.2	3.45
		Cirrhitus rivulatus	28.28	4.02
		Fistularia commersonii	68.33	4.28

		Forcipiger flavissimus	16.69	3.38
		Gymnothorax castaneus	78.17	4.03
		Halichoeres dispilus	31.66	3.85
		Halichoeres nicholsi	37.49	4
		Halichoeres notospilus	32.15	3.52
		Kyphosus elegans	42.49	2.94
		Melichthys niger	44.41	2.73
		Microspathodon dorsalis	46.07	2.1
		Mulloidichthys dentatus	29.09	3.69
		Ophioblennius steindachneri	34.92	2.74
		Paranthias colonus	34.58	3.76
		Plagiotremus azaleus	20.93	4.42
		Prionurus laticlavius	38.55	2.72
		Prionurus punctatus	38.55	2
		Scarus compressus	39.38	2
		Scarus ghobban	37.31	2
		Scarus perrico	42.72	2
		Scarus rubroviolaceus	51.54	2
		Stegastes acapulcoensis	12.86	2
		Sufflamen verres	35.08	3.27
		Thalassoma grammaticum	35.18	3.5
		Thalassoma lucasanum	24.31	3.45
		Xanthichthys mento	34.44	4
		Zanclus cornutus	11.94	2.49
Sharks				4.36
	Benthopelagic		63.83	4.42
		Galeocerdo cuvier	63.83	4.42
	Demersal		60.91	4.18
		Nasolamia velox	60.91	4.18
	Pelagic-oceanic		81.26	4.21
		Sphyrna lewini	81.26	4.21
	Reef-associated			4.41
		Carcharhinus albimarginatus	75.92	4.48
		Carcharhinus falciformis	79.03	4.4
		Carcharhinus galapagensis	84.46	4.34
		Carcharhinus limbatus	55.45	4.46

		Carcharhinus obscurus	87.58	4.42
		Triaenodon obesus	82.54	4.36
Snnapers				4.09
	Reef-associated			
		Lutjanus argentiventris	55.83	4.03
		Lutjanus viridis	26.59	4.16

Appendix Ib. Results of the analysis of similarities (ANOSIM) using different scales

ANOSIM	**R:**	**0.1919**			
	Significance:	0.001			
	0%	25%	50%	75%	100%
Between	118.5	419	700	1104	1431
Flat	118.5	118.5	419	1001.5	1395.5
Pelagic	118.5	265	700	906	1414
Wall	118.5	579	968	1194	1426
Island	R:	0.1882			
	Significance:	0.001			
Dissimilarity	ranks	between	and	within	classes:
	0%	25%	50%	75%	100%
Between	118.5	419	700	1104	1429
RP	237	669.75	1085	1346	1431
SB	118.5	419	700	906	1367
Socorro	118.5	118.5	419	987.75	1395.5
Ambiente	R:	-0.03414			
	Significance:	0.667			
Dissimilarity	ranks	between	and	within	classes:
	0%	25%	50%	75%	100%
Between	118.5	419	700	1015	1429
Benthic	118.5	419	700	1168.5	1431
Pelagic	118.5	265	419	700	1339

Appendix 2. Summary of the results from the principal component analysis (PCA) of the six major habitat types. This analysis was performed the RDA function in the "vegan" library of R statistical package v.3.0.2 (R Development Core Team 2008).

	PC1	***PC2***	***PC3***	***PC4***
Standard deviation	3.1158	1.6846	1.0499	0.87408
Proportion of Variance	0.6219	0.1818	0.07061	0.04894
Cumulative Proportion	0.6219	0.8037	0.87431	0.92325
Temperature	0.521185	-0.58081	0.240202	0.046596
Current	-0.09457	0.310376	-0.17133	-0.22078
Topography (Slope)	-0.2257	-0.25188	-0.1592	-0.39854
Type of substrate	-0.10585	-0.57997	0.066441	-0.28179
Pelagic/Benthic BRUVS	0.116935	0.122828	0.013882	0.165079
Carcharhinus albimarginatus	-0.09041	0.20378	0.804167	-0.26794
Carcharhinus falciformis	0.73188	0.294798	-0.14073	-0.52656
Carcharhinus galapagensis	-0.10519	0.12362	0.427912	-0.12884
Sphyrna lewini	-0.01403	0.06923	0.073172	0.105016

14.2. Shark tagging information

Appendix 3. Individuals of *C. falciformis* and *C. galapagensis* monitored since April 2009 to November 2015 in the Revillagigedo Archipelago.

Code trans	**Species**	**Date**	**Int/Ext**	**Total length**	**Monitoring period**

23509	*C.falciformis*	19/11/2014	External	185	169
23513	*C.falciformis*	25/11/2014	Internal	214	163
23515	*C.falciformis*	21/11/2014	Internal	195	167
23516	*C.falciformis*	17/11/2014	Internal	214	171
23518	*C.falciformis*	21/11/2014	Internal	202	167
25249	*C.falciformis*	10/04/2014	External	190	392
25252	*C.falciformis*	22/05/2014	Internal	203	350
25253	*C.falciformis*	22/05/2014	Internal	224	350
27357	*C.falciformis*	28/05/2013	Internal	191	709
31224	*C.galapagensis*	12/12/2011	Internal	111	1242
36476	*C.galapagensis*	22/11/2010	External	300	1627
36478	*C.galapagensis*	29/04/2010	External	175	1834
39359	*C.galapagensis*	21/11/2010	External	220	1628
39360	*C.galapagensis*	22/11/2010	External	250	1627
39362	*C.galapagensis*	22/04/2011	External	200	1476
45416	*C.galapagensis*	18/04/2011	External	250	1480
45417	*C.galapagensis*	19/04/2011	External	200	1479
46648	*C.falciformis*	15/11/2010	Internal	198	1634
46654	*C.falciformis*	15/11/2010	Internal	198	1634
46657	*C.galapagensis*	14/11/2010	Internal	210	1635
47138	*C.falciformis*	11/04/2013	Internal	199	756
59067	*C.galapagensis*	06/05/2009	External	200	2192
59068	*C.galapagensis*	05/05/2009	External	175	2193
59071	*C.galapagensis*	06/05/2009	External	180	2192
59073	*C.galapagensis*	06/05/2009	External	UN	2192

Appendix 4. Tagging information of the sharks monitored in the ETP

MRE	**Species**	**# Sharks detected**	**# Receivers**	**Total detections**
Cocos	*C. falciformis*	2	7	3642
Cocos	*C. galapagensis*	9	7	28225

Galapagos	*C. falciformis*	17	24	48640
Galapagos	*C. galapagensis*	19	24	59119
Malpelo	*C. galapagensis*	4	7	4243
Revillagigedo	*C. falciformis*	24	11	122757
Revillagigedo	*C. galapagensis*	18	11	190561
Clipperton	*C. falciformis*	1	3	203
	Total	78	94	457390

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