

Chapter 2

Elasmobranchs of the Galapagos Marine Reserve

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Abstract The Galapagos Marine Reserve is home to at least 50 species of sharks and rays. Although these species are protected in the marine reserve, they are vulnerable to industrial fishing outside the protected waters, to unintentional bycatch by local fishers inside the reserve, and to illegal fishing. Our knowledge of shark ecology in Galapagos has increased dramatically in the last decade, due to the creation of an interinstitutional research program, which focuses on the spatial ecology of hammerhead and whale sharks. Hammerheads are resident at restricted locations where they school during the day and disperse to sea most nights. Alternatively, mostly large, pregnant female whale sharks visit the northern islands from June through November for only a few days, as part of a large-scale migration.

Longline fishing studies have shed light on the distribution of sharks and their vulnerability to this fishing method. A juvenile shark monitoring program has been created. Scientists have attempted to model changes in shark populations since the creation of the marine reserve. A diver-based census of sharks has been implemented at key sites. The establishment of a regional network, MigraMar, has enabled us to determine connectivity of sharks and mantas between Galapagos and other areas.

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Introduction

Class Chondrichthyes, the cartilaginous fishes, is made up of two subclasses—the Holocephali (chimaeras) and the Elasmobranchii (sharks and rays). These fish differ from the teleosts (bony fish) in many fundamental aspects of their biology (Klimley 2013). In general, they have slower growth rates, later onset of sexual maturity, lower reproductive rates, and longer life spans, all of which can make them particularly susceptible to overexploitation by humans (Myers & Ottensmeyer 2005). Four species of chimaeras have been recorded in the GMR—*Hydrolagus mccoskeri*, *H. albus*, a further unidentified species of the same genus, and one unidentified species of the genus *Chimaera* (McCosker and Rosenblatt 2010). Little is known about these largely benthopelagic species.

The list of elasmobranchs known to occur in the Galapagos is constantly being updated and revised. For example, both the grey reef shark *Carcharhinus amblyrhynchos* and the longfin mako shark *Isurus paucus* were excluded from a recent list of fish species for the Archipelago, while the white shark *Carcharodon carcharias* and the great hammerhead *Sphyrna mokarran* were included on the basis of plausible yet unconfirmed sightings (McCosker and Rosenblatt 2010). More recently, a previously unidentified species of houndshark was found to be *Mustelus albiguttatus*, and both the smalltooth sand tiger shark *Odontaspis ferox* and the deepwater spiny dogfish *Centrophorus squamosus* were recorded (Acuña-Marrero et al. 2013). In the case of rays, there is one unidentified species, *Dasyatis* sp., first photographed and identified as *D. brevipes* but now considered as a possible different undescribed species (McCosker and Rosenblatt 2010).

The updated list of elasmobranchs of Galapagos in 2013 includes 53 records, 33 sharks and 20 rays (see Table 2.1). Seventeen sharks and six rays (43.3 % of species listed) are known to have a circumtropical range of distribution; nine sharks and six rays (28.3 %) are eastern Pacific species (one of them, *Sphyrna tiburo*, also has a western Atlantic distribution); three sharks and two rays (9.4 %) are Indo-Pacific species; two sharks and three rays (9.4 %) are species from Peru and/or Chile; and two sharks and three rays (9.4 %) may be Galapagos or Galapagos/Cocos-endemic species.

Elasmobranchs are found in all marine habitats of the GMR, from coastal mangrove lagoons to the deep sea. Human interactions with elasmobranchs occur in the form of tourism—a multimillion dollar industry which attracts scuba divers and non-diving tourists from all over the world (Epler 2007)—and fishing; although sharks are protected within the waters of the GMR, they may be caught by industrial fishers operating legally outside the GMR or making illegal incursions into protected waters. They may also be caught by local fishers as bycatch in the hook and line and gillnet fisheries or as part of an illegal fishery for shark fins (Jacquet et al. 2008; Reyes and Murillo 2007). Finally, there are occasional incidents of shark attacks on humans (Acuña-Marrero and Peñaherrera-Palma 2011).

Our knowledge of elasmobranchs and the role they play in the GMR has increased greatly over the last decade, since the publication of a chapter on sharks

Table 2.1 Shark and ray species reported from the Galapagos Islands

No.	English name	Scientific name	IUCN red list*
1	Pelagic thresher shark	<i>Alopias pelagicus</i>	Vulnerable
2	Bigeye thresher shark	<i>Alopias superciliosus</i>	Vulnerable
3	Longnose cat shark	<i>Apristurus kampae</i>	Data deficient
4	Cat shark	<i>Apristurus stenseni</i>	Data deficient
5	Galapagos cat shark	<i>Bythaelurus giddingsi</i>	Not evaluated
6	Silvertip shark	<i>Carcharhinus albimarginatus</i>	Near threatened
7	Bignose shark	<i>Carcharhinus altimus</i>	Data deficient
8	Silky shark	<i>Carcharhinus falciformis</i>	Near threatened
9	Galapagos shark	<i>Carcharhinus galapagensis</i>	Near threatened
10	Blacktip shark	<i>Carcharhinus limbatus</i>	Near threatened
11	Oceanic whitetip shark	<i>Carcharhinus longimanus</i>	Vulnerable
12	Sandbar shark	<i>Carcharhinus plumbeus</i>	Vulnerable
13	Great white shark	<i>Carcharodon carcharias</i>	Vulnerable
14	Deepwater spiny dogfish	<i>Centrophorus squamosus</i>	Vulnerable
15	Combtooth dogfish	<i>Centroscyllium nigrum</i>	Data deficient
16	Prickly shark	<i>Echinorhinus cookei</i>	Not evaluated
17	Cat shark	<i>Galeus</i> sp.	Not evaluated
18	Tiger shark	<i>Galeocerdo cuvier</i>	Near threatened
19	Galapagos bullhead shark	<i>Heterodontus quoyi</i>	Data deficient
20	Cookie cutter shark	<i>Isistius brasiliensis</i>	Least concern
21	Shortfin mako shark	<i>Isurus oxyrinchus</i>	Vulnerable
22	White-margin fin smooth-hound shark	<i>Mustelus albigipinnis</i>	Data deficient
23	Speckled smooth-hound	<i>Mustelus mento</i>	Near threatened
24	Whitenose shark	<i>Nasolamia velox</i>	Data deficient
25	Smalltooth sand tiger shark	<i>Odontaspis ferox</i>	Vulnerable
26	Blue shark	<i>Prionace glauca</i>	Near threatened
27	Whale shark	<i>Rhincodon typus</i>	Vulnerable
28	Scalloped hammerhead shark	<i>Sphyrna lewini</i>	Endangered
29	Great hammerhead shark	<i>Sphyrna mokarran</i>	Endangered
30	Bonnethead shark	<i>Sphyrna tiburo</i>	Not evaluated
31	Smooth hammerhead shark	<i>Sphyrna zygaena</i>	Vulnerable
32	Whitetip reef shark	<i>Triaenodon obesus</i>	Near threatened
33	Spotted houndshark	<i>Triakis maculata</i>	Vulnerable
34	Spotted eagle ray	<i>Aetobatus narinari</i>	Near threatened
35	Pacific white skate	<i>Bathyraja spinosissima</i>	Least concern
36	Whiptail stingray	<i>Dasyatis brevis</i>	Not evaluated
37	Diamond stingray	<i>Dasyatis dipterura</i>	Data deficient
38	Longtail stingray	<i>Dasyatis longa</i>	Data deficient
39	–	<i>Dasyatis</i> sp.	Not evaluated
40	Dusky finless skate	<i>Gurgesiella furvescens</i>	Least concern
41	Pacific chupare	<i>Himantura pacifica</i>	Not evaluated
42	Giant manta	<i>Manta birostris</i>	Vulnerable
43	Spinetail mobula	<i>Mobula japanica</i>	Near threatened
44	Munk's devil ray	<i>Mobula munkiana</i>	Near threatened
45	Chilean devil ray	<i>Mobula tarapacana</i>	Data deficient
46	Peruvian eagle ray	<i>Myliobatis peruvianus</i>	Data deficient

(continued)

Table 2.1 (continued)

No.	English name	Scientific name	IUCN red list*
47	Rough eagle ray	<i>Pteromylaeus asperimus</i>	Data deficient
48	Pelagic stingray	<i>Pteroplatytrygon violacea</i>	Least concern
49	Velez ray	<i>Raja velezi</i>	Data deficient
50	Eisenhardt's skate	<i>Rajella eisenhardti</i>	Data deficient
51	Pacific cownose ray	<i>Rhinoptera steindachneri</i>	Near threatened
52	Blotched fantail ray	<i>Taeniura meyeni</i>	Vulnerable
53	Peruvian torpedo	<i>Torpedo peruana</i>	Not evaluated

Sources: Grove and Lavenberg (1997), Zarate (2002), McCosker and Rosenblatt (2010), McCosker et al. (2012), and the Charles Darwin Foundation Database Species Checklist (<http://checklists.datazone.darwinfoundation.org/> accessed May 21, 2013)

in the Galapagos Marine Reserve Baseline of Biodiversity in 2002 (Zarate 2002, in Danulat and Edgar 2002). In 1997, 2001, and 2003, experimental longline fishing was carried out by the local fishing sector within the GMR, shedding light on the relative abundance and distribution of some of the pelagic sharks (Murillo et al. 2004). In 2006, the Charles Darwin Foundation, Galapagos National Park Service, and University of California Davis began a long-term collaboration to study the movements of certain shark species to determine their spatial dynamics within the reserve and their connectivity with other oceanic islands in the region (Hearn et al. 2008, 2010a, b; Ketchum 2011). As part of this project, divers have been undertaking visual surveys of sharks and other open-water species at some sites (particularly in the northernmost islands) twice yearly since 2007 (Hearn et al. 2010a). Sharks and rays were also included in diver-based surveys carried out by the Charles Darwin Foundation across the archipelago, mainly over rocky coastal reefs at depths of 6 and 15 m since 2001 (Edgar et al. 2004). A number of smaller studies have also shed light on the importance of nursery areas for juvenile sharks (Llerena et al. 2010, 2012; Jaenig 2010) and have attempted to model the recovery of shark populations since the creation of the GMR (Wolff et al. 2012a).

Legislation

Shark legislation in continental Ecuador prohibits shark-targeted fisheries but permits the landing of bycatch taken in other fisheries. The most common species landed at ports on mainland are (in ranked order) pelagic thresher (36 %), blue shark (24 %), silky shark (15 %), smooth hammerhead (11 %), and scalloped hammerhead (5 %) (Martinez et al. 2007). These sharks, among others, are taken as bycatch by the industrial fleet and the artisanal fleet, although claims that they bring up to 30 % of total earnings for artisanal fishers suggest that they may be more of a target species (Martinez and Viteri 2005).

Over the last two decades, there has been increasing concern about the health of global shark populations. According to Bonfil (1994), 50 % of the estimated global shark catch (760,000 t in 1996) is taken as bycatch and does not appear in official

statistics and landings. Added to the problem of underreporting is that much of this catch is not identified to species level, due in part to the practice of finning—removing the fins (which fetch high prices in the Asian market) and discarding the bodies overboard. As a result of this concern, the United Nations Food and Agriculture Organization (FAO) created the International Plan of Action for Sharks (IPOA-Sharks) in 1998, which contains clear guidelines for all nations involved in shark fishing or consumption of shark-based goods and exhorts these nations to develop national plans of action for their shark resources (FAO 2010–2013). Within the Eastern Tropical Pacific, Ecuador has taken the lead in developing a coherent Plan of Action and establishing monitoring programs at major ports (Zarate and Hearn 2008; MICIP 2006).

In 2004, the Ecuadorian Government issued a decree banning the export of shark fins, yet this was overturned in 2007 by Executive Decree 486 which permits the export of fins but places technical restrictions on fishing gear, imposes a monitoring system to ensure that all sharks caught are landed whole, and stipulates that fin removal must occur on land. There has been a great deal of controversy about Decree 486, with alarm being raised by environmentalist groups that without a monitoring and control system in place, shark finning may become widespread. Arguments for the decree state that the previous decree was unenforceable and that it simply served to drive the activity underground.

The first attempts to provide protection for sharks in Galapagos date back to 1989, when the Government of Ecuador banned fishing, transport, and sale of all sharks and their products (MICIP 1989). Once the GMR was created (in 1998), the maximum governing authority of the GMR ratified the original ban in 2000. In addition to enacting regulations which were specific to sharks, the Galapagos Special Law banned all industrial fishing within the 40-nautical-mile (Nm) limits of the GMR and has the authority to ban fishing gear which results in unacceptable levels of bycatch.

In response to the deaths in Peruvian waters of manta rays tagged off the coast of mainland Ecuador, the Ministry of the Environment called for the species to be listed on the appendices of the Convention for Migratory Species Act (CMS). A protected species in Ecuador since 2010 (Ministerial Decree 093, Ministry of Agriculture, Livestock, Aquaculture and Fisheries), Ecuador put forward a proposal to list this vulnerable species on CMS to prompt cooperation with neighboring countries and to facilitate regional management efforts. In late 2011, *Manta birostris* became the first ray species to ever be listed on Appendix I and II of CMS.

To help curb international trade, Ecuador, with support from Brazil and Columbia, proposed manta rays to be listed on Appendix II of CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora). This proposal was successfully adopted in March 2013 and will help curb the unsustainable fishing of *Manta* species by requiring the international trade in manta rays come from sustainably harvested fisheries that are not detrimental to the wild populations they exploit. White sharks, whale sharks, and basking sharks were already listed on Appendix II, but in March 2013, the oceanic whitetip shark, the porbeagle shark, and the great, smooth, and scalloped hammerhead sharks were also uplisted to the Appendices of CITES.

Ecuador, well aware of the importance of hammerheads to their country, was also a co-proponent of the hammerhead proposal alongside Brazil, Costa Rica, Honduras, Columbia, the EU and the United States.

Distribution and Relative Abundance

The Galapagos Marine Reserve can be divided into four main biogeographic regions, based on the prevailing oceanographic conditions and reef fish and macroinvertebrate assemblages—far north, north, central, and west—with a further subregion nested within the western region, Elizabeth, characterized by a high degree of marine endemism (Edgar et al. 2004). Marine ecologists at the Charles Darwin Foundation have carried out reef fish surveys around the archipelago since 2001 (Edgar et al. 2004). Their surveys permit some broad observations on the presence of the benthic sharks and rays around the islands (Fig. 2.1).

Unsurprisingly for mostly large, mobile species, many of the shark and ray species are found throughout the GMR. However, the only shark species to be recorded consistently by the subtidal ecological monitoring survey teams in the western part of the archipelago is the Galapagos bullhead shark, *Heterodontus quoyi*. This shark is absent from the warmer, northern bioregions. Mantas and devil rays also appear limited to the cooler and mixed central and western bioregions, while whale sharks in contrast were only recorded in these surveys in the far north. Despite this, it must be noted that recreational and scientific divers occasionally report mantas, devil rays, and whale sharks throughout the archipelago.

While estimating true abundance of sharks and rays from these surveys is not possible, a measure of relative abundance can be obtained by calculating the number of individuals per hectare of habitat based on the transect dimensions (Fig. 2.2). From this data, we observe that the diamond stingray, golden cowray, and whitetip reef shark are most common in the mixed, central region of the reserve, whereas the Galapagos bullhead shark is common in the western region, to which it is almost exclusively limited. Marbled and eagle rays are found infrequently throughout the region, while Galapagos sharks were common in both the central and far north regions.

Underwater visual surveys, focused on large pelagic species, especially sharks, have been carried out at nine sites around Darwin and Wolf Islands at least twice a year and intermittently at sites throughout the archipelago which are generally either dive tourism locations or locations where underwater acoustic receivers have been deployed as part of a shark-tagging research program (Hearn et al. 2008). Notwithstanding the bias involved in these kinds of surveys (e.g., see Bernard et al. 2013), they have been particularly valuable in establishing the relative abundance of sharks which utilize nearshore waters and waters surrounding offshore islets. They have also been used to analyze habitat preference around Wolf Island in particular and to understand the seasonal changes in abundance of certain species in the far northern bioregion. The surveys are carried out by pairs of divers who identify and count all

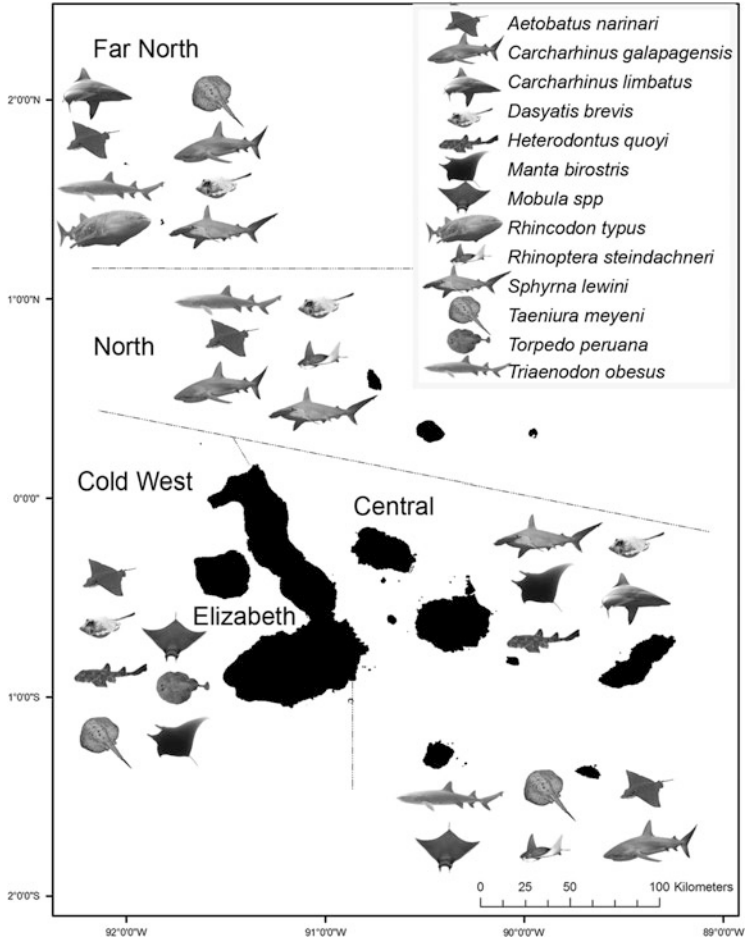


Fig. 2.1 Map showing the distribution of the sharks and rays species most commonly observed and recorded in rocky reef surveys in Galapagos divided in bioregions, as proposed by Edgar et al. (2004). The bioregions of Cold West and Elizabeth have been fused, as data from Elizabeth bioregion was scarce. The species icons are not presented in scale

sharks and other open-water species (manta rays, sunfish, tuna) over a 30-min period at a depth of approximately 15–20 m, with their backs to the coastline.

By far the most commonly encountered sharks by the dive teams were hammerhead and Galapagos sharks (Table 2.2). Hammerhead sharks school in large numbers at upstream current sites at Darwin and Wolf Islands (Hearn et al. 2010a), and these shark hotspots are undeniably populated by numbers not found elsewhere in the archipelago. The diversity of sharks in the far north is also worthy of note. It is not unusual to come across at least five species of shark in a single dive. Along with the ubiquitous hammerhead and Galapagos sharks, silky and blacktip sharks are commonly found at these hotspots, as well as occasional whitetip reef sharks. Other less common species

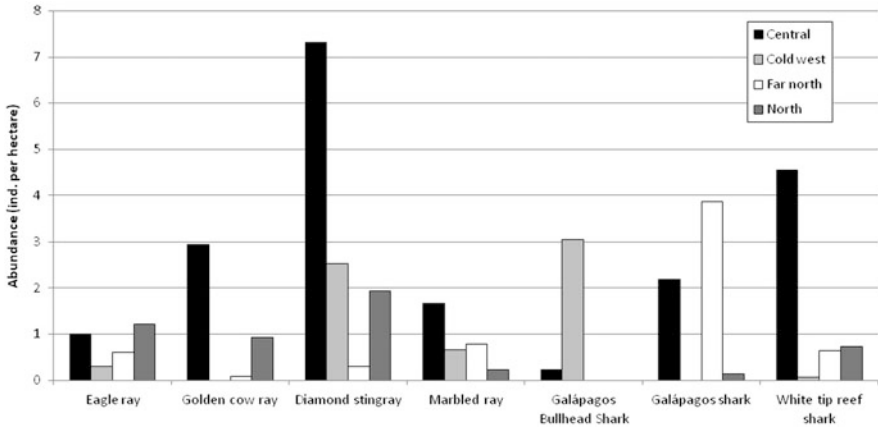


Fig. 2.2 Relative abundance (expressed as individuals per hectare) of selected elasmobranchs, by biogeographic region, from diver-based reef fish surveys from 2001 to 2010 (Source: Charles Darwin Foundation, Subtidal Ecological Monitoring Program)

include the silvertip shark, recorded only once by divers at Darwin, and the tiger shark, which was photographed by the shark-tagging team at Darwin in 2011. Divers rarely see tiger sharks, but it is likely that they are more common around the islands than would be expected based on these surveys. Five adult tiger sharks were caught within a single bay at nearby Cocos Island (Costa Rica) during a 7-day period in 2011, and a further five were caught at a single bay at Socorro Island (Revillagigedos Archipelago, Mexico) around the same time, while in neither case were tiger sharks recorded by scuba divers (Hearn, personal communication).

Whale sharks are observed rarely throughout the archipelago and were only recorded during visual surveys at the Darwin and Wolf Island hotspots, and only from June through November. Yet during this period, at least one whale shark encounter per dive can almost be guaranteed at the Arch dive site, off Darwin Island (Hearn et al. 2012).

If we examine the relative abundance of whale sharks, Galapagos sharks, and hammerhead sharks, only at the two hotspot sites in the far northern bioregion—the southeastern points of Darwin and Wolf, we find that there is a remarkably similar temporal pattern between all three species (Fig. 2.3). All three species display greater abundances in the cooler months of the year (from May through October), whereas in the warmer months, whale sharks in particular are absent, while hammerhead and Galapagos shark numbers are greatly reduced, and the large schools are rarely seen during this time.

Table 2.2 Relative abundance, expressed as individuals observed per diver hour (ind h⁻¹), of six species of sharks recorded during underwater diver surveys for open-water species from 2007 to 2012, by biogeographic region

# Dive surveys	93	483	31
Species/region	Central	Far north	West
<i>Carcharhinus albimarginatus</i>		0.008	
<i>Carcharhinus falciformis</i>	0.063	0.250	
<i>Carcharhinus galapagensis</i>	12.41	4.042	0.250
<i>Carcharhinus limbatus</i>	0.188	0.733	
<i>Sphyrna lewini</i>	2.854	125.7	6.563
<i>Triaenodon obesus</i>	1.396	0.192	
<i>Rhincodon typus</i>		0.683	

Number of surveys carried out in each region is also shown.
Source: CDF-UCD-PNG Pelagic Census Database

Key Habitats

Adult Aggregations

Research on the movement patterns of sharks in the GMR has focused mainly on the scalloped hammerhead *Sphyrna lewini*. This species is known to aggregate in large numbers around oceanic islets and seamounts (Klimley and Nelson 1984; Bessudo et al. 2011; Hearn et al. 2010a; Ketchum et al. 2011a). These act as central refuting systems from which foraging excursions take place and at which social interactions occur. Less is known about the other commonly found shark species around the island coasts, such as the silky shark *Carcharhinus falciformis* and the Galapagos shark *C. galapagensis*. No research has been carried out in the GMR directed at oceanic or deepwater sharks.

In 2006, a shark-tagging program was initiated jointly by the Galapagos National Park Service, University of California Davis, Stanford University, and the Charles Darwin Foundation. This involved placing coded ultrasonic tags on sharks (either internally by surgery or externally with a dart) and deploying an array of underwater listening stations (Fig. 2.4) that detect and record the presence of tagged sharks within a radius of approximately 200 m (Hearn et al. 2008, 2010a; Ketchum et al. 2011a).

Between 2006 and 2009, over 100 hammerhead sharks were tagged in this fashion at Darwin and Wolf. Most of these were females, as these form the large schools that predominate at oceanic islands (Klimley 1985). Between 2008 and 2012, a further 15 Galapagos sharks, and a small number of silky sharks, were also tagged at different sites throughout the archipelago.

External tags, while easy to affix to sharks, are also often rapidly shed, as observed from continuous detections of tags at receiver locations. For this reason, it is difficult to make inferences about sharks that were not detected after only a few days—they may have migrated away or simply shed their tags outside the detection range of a receiver. Yet for those tags which did provide long-term information, a high degree of site fidelity was found for almost all individuals to both Darwin and Wolf Islands (Fig. 2.5).

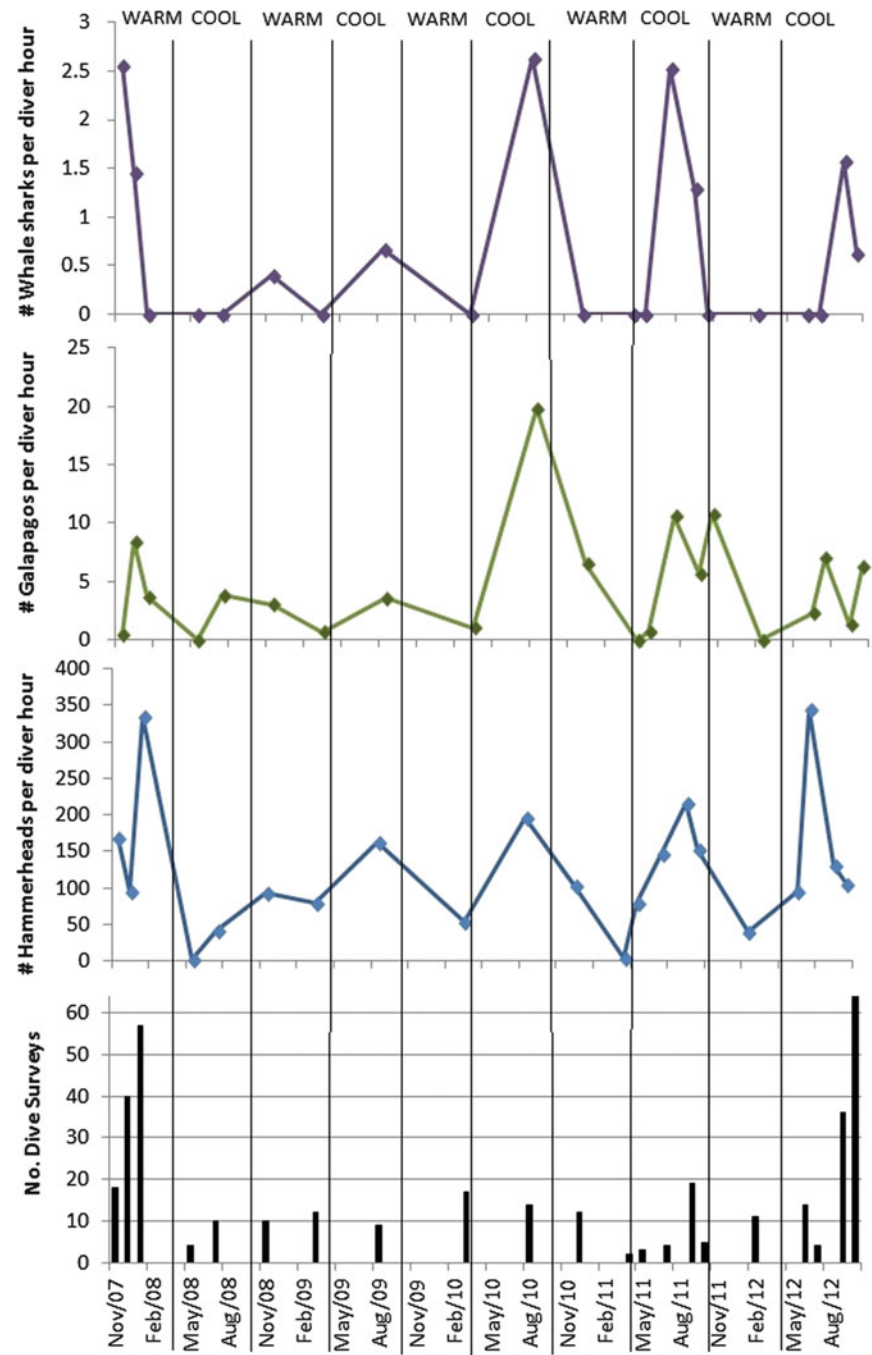


Fig. 2.3 Seasonal changes in relative abundance (expressed as the number of individuals observed per diver hour) of three shark species at the Darwin and Wolf shark hotspots, 2007–2012. From top to bottom: whale shark, Galapagos shark, and hammerhead shark. Vertical lines indicate approximate changes between warm and cool seasons. Bar chart indicates the

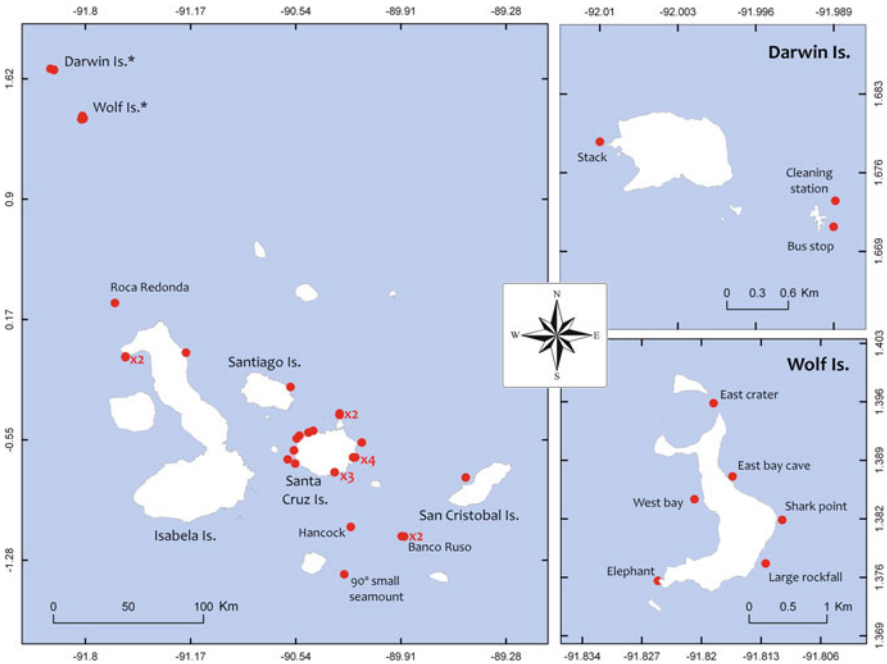


Fig. 2.4 Map showing array of underwater listening stations installed between 2006 and 2012. These stations detect and record the presence of tagged sharks and other species currently being studied in the Galapagos Marine Reserve

Hammerheads did not appear to display group cohesion, in that no clear pattern of presence at islands and movements between islands could be established. As in Mexico (Klimley and Nelson 1984), Ketchum et al. (2011b) found a strong diel signal in the presence of hammerheads at both sites, with frequent nocturnal absences of several hours duration, beginning at dusk. These are presumably foraging excursions—from dietary studies carried out on hammerheads landed at ports in continental Ecuador, it would appear that they tend to feed mainly on oceanic squid, such as *Dosidicus gigas*, that may be found in the open ocean (Castañeda-Suarez and Sandoval-Londoño 2007; Estupiñan-Montaño et al. 2009).

Hammerheads moved continuously between Darwin and Wolf, a distance of 38 km, with no clear seasonal pattern. Six individuals were detected at Roca Redonda (Fig. 2.5), 150 km south of Darwin. Four of these were detected in February 2008, and three were detected again at the island in June, after an absence from the entire array of almost three months. Yet in each case, the sharks were detected at Darwin briefly, before making the southerly movements back to Roca Redonda. Residency at

← **Fig. 2.3** (continued) number of surveys carried out at hotspots per month. Source: CDF-UCD-PNG Pelagic Census Database

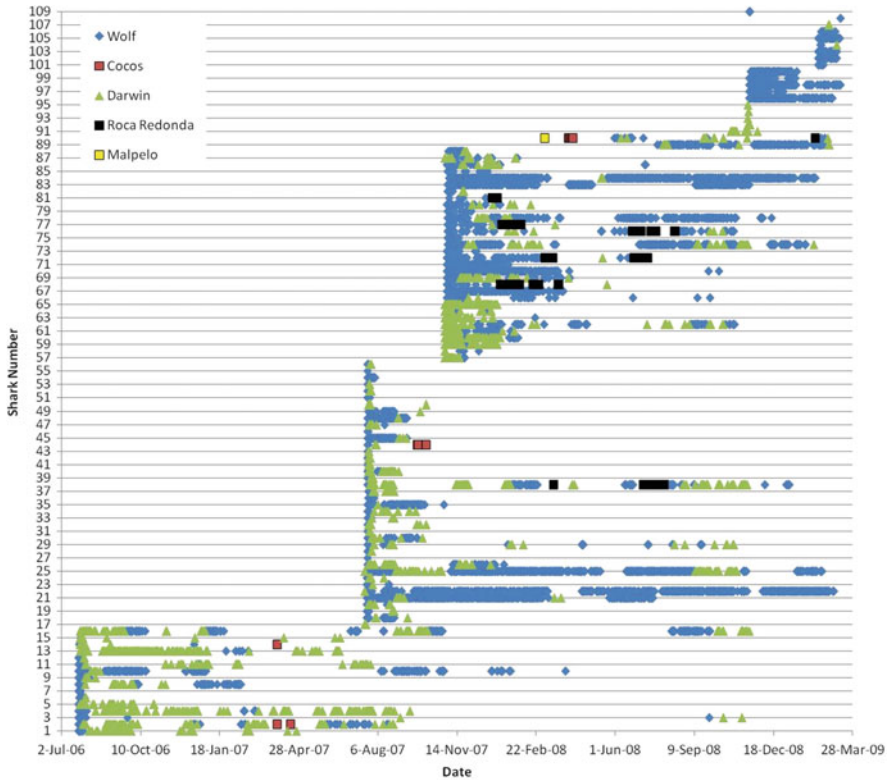


Fig. 2.5 Detection record of hammerhead sharks tagged at Darwin and Wolf from 2006 to 2009 (Source: Galapagos Shark Research Program, Ketchum et al. 2011a, b, c)

Roca Redonda was less than a month, suggesting that their migration was not further south but rather to the north. Other hammerheads that were only detected at Darwin and Wolf were also absent from March through June. In conjunction with diver surveys (see Fig. 2.3), this suggests that many female hammerheads undergo a migration at this time of year. The destination of this migration is unclear—none of the sharks were detected on the rest of the array in Galapagos, yet four were detected at Cocos Island (700 km to the northeast). Neonate hammerheads have not been found in significant numbers at Galapagos, so it is possible that this is a migration to pupping grounds. Scalloped hammerhead sharks, including some neonates, are landed in small numbers in Ecuador especially in March–April (Martinez et al. 2007), yet the largest reported landings of this species, and in particular of neonates, occur in the gulfs and bays of Costa Rica and Panama (Zanella et al. 2009; Rodriguez 2011). If a migratory route were established between Galapagos and this region, this would raise issues about regional conservation measures for this listed species.

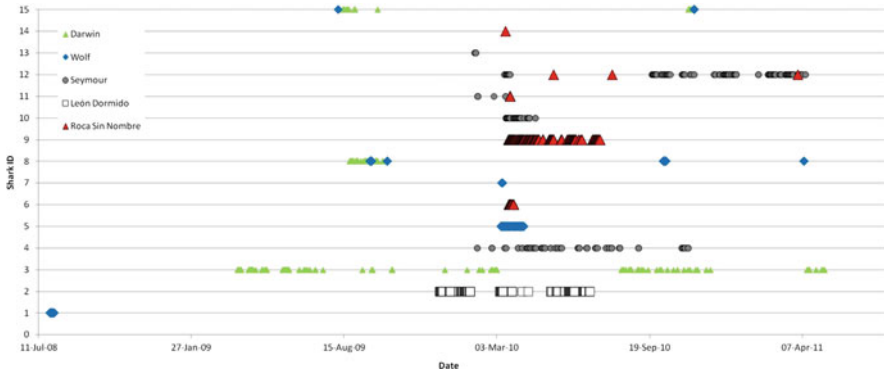


Fig. 2.6 Detection record for Galapagos sharks tagged around the Galapagos Marine Reserve 2006–2011 (Source: Galapagos Shark Research Program, Hearn et al. [in press](#))

Detections of 15 Galapagos sharks tagged at several sites throughout the GMR do not show clearly identifiable residency patterns (Fig. 2.6). Galapagos sharks seemed more loosely associated with the islets and other study sites, displaying a lower number of detections, and diel patterns which were less consistent among individuals (Hearn et al. [in press](#)). One shark (#3, Fig. 2.6) was highly residential at Darwin for 2 years but was absent for four extended periods during this time, including two 5-month periods from March to August 2010 and December 2010 to April 2011. Two other sharks moved multiple times between Darwin and Wolf, while in the central archipelago, Roca Sin Nombre and North Seymour were connected.

Both species displayed a strong preference for the current-facing coasts of Darwin and Wolf—indeed, there is greater connectivity in terms of movements of individual sharks between the two up-current sites on both islands than between upstream and downstream sites on the same island (e.g., see Fig. 2.7).

Juvenile Nursery Areas

According to Heupel et al. (2007), a nursery area is a place where neonate and juvenile fish will be more commonly encountered, where they will remain or return for extended periods of time, and that will be repeatedly used by those species in the same fashion year after year. Only three reports have been published specifically on juvenile sharks to date where a set of surveys using 3" mesh size gill nets in mangrove-fringed bays were carried out around San Cristobal (Llerena et al. 2010) and Santa Cruz Islands (Jaenig 2010; Llerena et al. 2012). During 6 months of sampling at five sites of the northwestern coast of San Cristobal Island, Llerena et al. (2010) caught 95 juvenile blacktip sharks (*C. limbatus*); 75 % were neonate or young of the year (YOY). Subadult and juvenile whitetip reef sharks (*T. obesus*) were also caught, yet only one neonate scalloped hammerhead was caught. Jaenig (2010) reported similar results but for four sites at the northwestern face of Santa Cruz. Over 6 months of

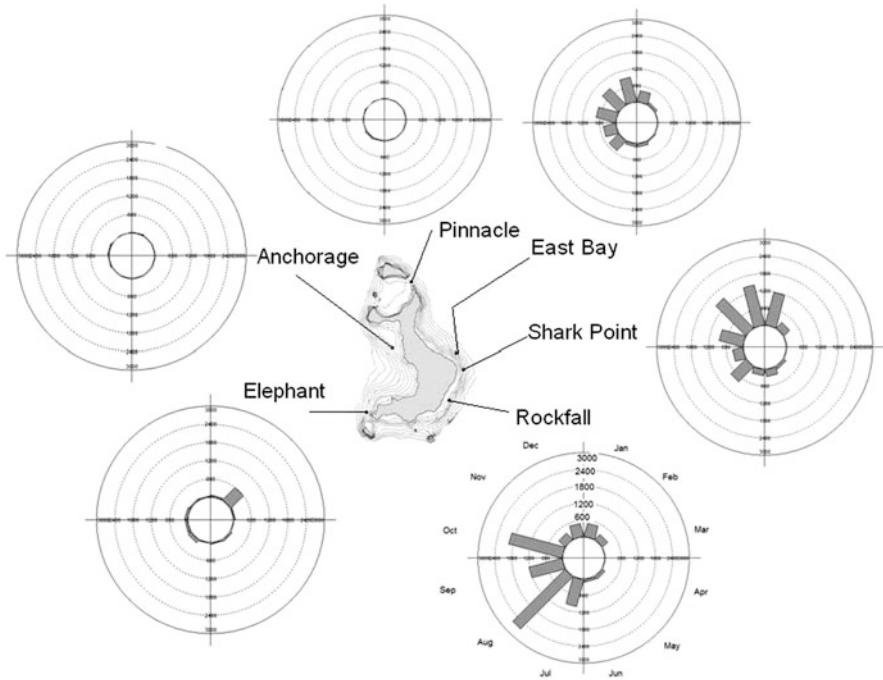


Fig. 2.7 Circular graphs showing the number of detections per month of a female hammerhead shark, tagged at Wolf, at different receiver locations around the island (from Hearn et al. 2010a)

sampling—from November 2009 to March 2010—a total of 296 sharks were caught, made up of 292 blacktips (80 % neonates and 15 % YOY), three whitetip reef sharks, and one scalloped hammerhead shark.

The Galapagos National Park Service began an extended juvenile shark monitoring program around Santa Cruz Island in 2009, yet preliminary results point towards mangrove-fringed areas as nursery grounds for blacktip sharks yet not for hammerhead sharks (Llerena et al. 2012). Although biased by the fishing gears in use, it seems unlikely that hammerhead nursery grounds such as those heavily fished in the gulfs of Costa Rica (Zanella et al. 2009) and Panama (Rodriguez 2011) exist in the Galapagos.

Young Galapagos sharks are frequently seen schooling at small islets offshore from the main islands, such as Kicker Rock (off San Cristobal) and Enderby (off Floreana). These schools are generally comprised of individuals around 1 m in length. Similar-sized Galapagos sharks are also found in the sheltered anchorage at Wolf Island—a single individual tagged here resided at the location for at least 1 month and was not detected at receivers placed elsewhere at the island (Hearn et al. [in press](#)). Of all the Galapagos and hammerhead sharks tagged at Wolf, this was the only juvenile and the only individual to display this strong fidelity to the Anchorage site.

Comparative Movement Patterns

Central refuging (Hamilton and Watt 1970), where top predators remain part of the day near their foraging grounds, is a strategy that is used by sharks (Klimley and Nelson 1984). At Wolf Island, Ketchum et al. (2011b) tracked seven hammerheads continuously for ~48 h from a small skiff using a directional hydrophone, from 2007 to 2009. Continuous tracking is labor-intensive and the results are often anecdotal due to the small obtainable sample size. However, it may provide insights into the behavior of individuals. They found that the daytime movements of most individuals were highly restricted to a narrow band of water along the up-current-facing coast of the island, referred to previously as a shark “hotspot” (Hearn et al. 2010a). They used a kernel density estimator (KDE) to measure the core movement area and found that it ranged from only 0.05 to 0.55 km² (Fig. 2.8). Possible reasons for the intensity of use of the hotspot were the abundance of food, reduced currents, and vantage location for foraging excursions into open waters (see Hearn et al. 2010a). Additionally, Klimley (1985) mentioned that hammerheads formed schools at specific locations for the purpose of sexual selection and social interactions.

Hammerheads made nighttime movements to nearby offshore locations, presumably to forage, and returned in the early hours of the morning (Ketchum et al. 2011b) in a similar fashion of movement as observed for this species in the Gulf of California (Klimley 1993). These movements were several kilometers and in some cases the shark followed the same route on the return trip back to the island. How sharks navigate is still a mystery and may involve the use of several senses, but in similar movements in the Gulf of California, Klimley (1993) found that hammerheads appeared to orient to areas where there was a high geomagnetic gradient. He suggested that sharks could detect variations in the Earth’s magnetic field caused by volcanic activity and use these to navigate between seamounts and volcanic islands.

These offshore movements did not occur every night and were not always to the same locations. Similarly, those hammerheads which had acoustic tags were sometimes present some or all of the night. There is no appreciable pattern to the sequence of nighttime absences between individuals, which suggests that their absences do not respond to an external cue such as moon phase.

One Galapagos shark tracked for 48 h made two complete circuits of Wolf Island and did not move further than 200 m from the coastline throughout the track (Hearn et al. [in press](#)).

Whitetip reef sharks are well known to aggregate in several shallow-water sites around the central, north, and far north Galapagos bioregions. A study was undertaken in a saltwater channel south of Academy Bay, Santa Cruz Island, from May 2008 to September 2009. A total of nine transmitters were attached to sharks, and ultrasonic receivers were deployed at the inner and outside areas of the creek to assess their daily behavior and site fidelity. Data from five sharks showed an elevated use of the inner area of the channel during the day, with more use of the external area during the night. However, none of the sharks were detected at the site

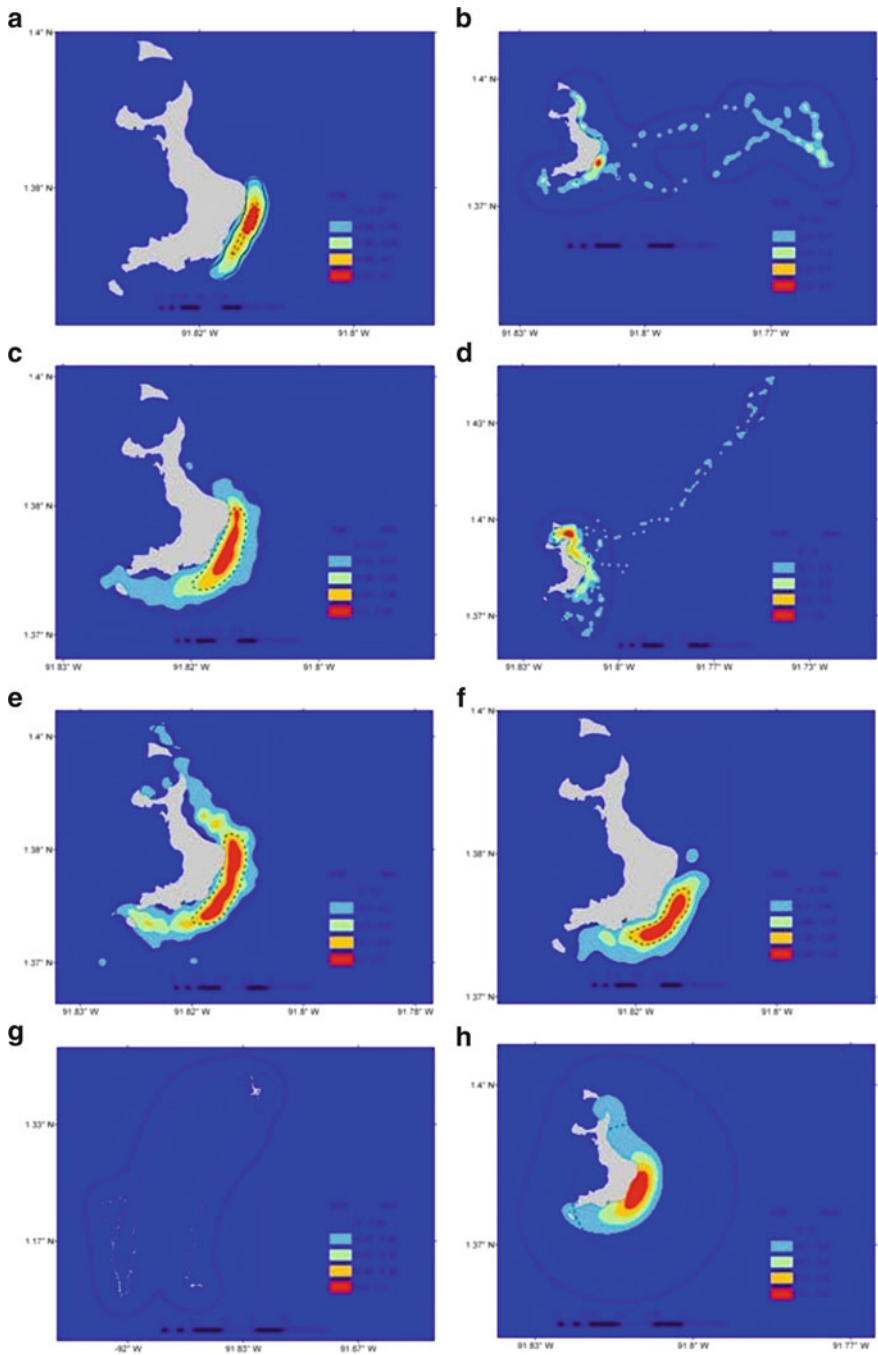


Fig. 2.8 Kernel density estimation (KDE), 50 % UD (*dotted line*) and 95 % UD (*solid line*); for (a–g) each individual hammerhead shark tracked over ~48 h; (h) entire sample of seven hammerhead sharks (from Ketchum et al. 2011b)

every day, suggesting that they may have a number of preferred sites within their home range (Peñaherrera et al. 2012).

Regional Connectivity

Tagging studies of movements of several shark species have been carried out in the Eastern Tropical Pacific as part of the MigraMar network (<http://www.migramar.org>). An array of underwater listening stations such as those used in Galapagos has been deployed by teams of researchers in Panama, Costa Rica (Cocos Island), and Colombia (Malpelo) as well as on the coast of Ecuador (Fig. 2.9). These have established the existence of connectivity between the three major oceanic island groups: Galapagos, Cocos, and Malpelo (Bessudo et al. 2011; Ketchum et al. 2011b). The first indication of connectivity occurred in 2006, when 2 from 18 hammerheads tagged in July in Galapagos were detected at Cocos Island within hours of each other in April 2007, one of which subsequently returned to Galapagos (Fig. 2.5). Since then, one or two hammerheads per year are detected at a different island group from where they were tagged. In 2008, a hammerhead tagged at Malpelo moved to Cocos and subsequently to Galapagos, where it remained for several months moving between Darwin and Wolf. No sharks tagged at oceanic islands have been detected on coastal arrays.

A small number of satellite tags have been placed on hammerhead, blacktip, and silky sharks. These tags are attached to the dorsal fins of sharks and transmit locations to the Argos (Argos 2007) satellite system when at the surface. These tags have been used in several studies around the world (Hammerschlag et al. 2011), but Galapagos is the first (and to date, only) site where these tags have been successfully placed on scalloped hammerheads (Ketchum et al. 2011c). Eight hammerheads (seven males and one female) were tagged at Darwin and Wolf from 2007 to 2009, and tracks were obtained from seven of these (Fig. 2.10). The female track lasted only 2 weeks and was tracked for approximately 350 km towards the northeast, when her signal was lost about halfway between Darwin and Cocos Island. A male tagged at the same time made a similar move towards Cocos yet returned back to Darwin after a similar distance, where its satellite transmitter ceased to function. Yet this individual also had an acoustic tag, which was later detected at Cocos. One male moved south into the central archipelago and was last detected at eastern Isabela Island, while another male moved almost 1,000 km to the northwest. Bearing in mind the small sample size and its bias towards males, preliminary kernel density estimations show that hammerheads spend significant periods outside the protected waters of the Galapagos Marine Reserve (Fig. 2.11).

Silky sharks ($N = 8$) were tagged at Darwin and Wolf in 2006–2012, with tracks obtained from seven individuals (Hearn et al. unpublished data). Only one shark made a long distance, directed movement out into the open ocean, traveling over 1,000 km to the northwest in only 25 days (Fig. 2.10). The remaining tracks lasted



Fig. 2.9 Map of regional array of underwater listening stations with a list of sharks tagged with ultrasonic tags at different sites. *Green lines* show reported movements between sites; *yellow lines* show suspected movements, as yet unconfirmed by data (from Hearn et al. 2010b)

from 16 to 127 days and all showed a high degree of residency within the reserve and close to Darwin and Wolf Islands (Fig. 2.12).

Although five Galapagos sharks were fitted with satellite tags, tracks were only obtained from three individuals, and one of these was for a single day (Shillinger et al. unpublished data). Little can be inferred from the remaining tracks; other than that, the movements were limited over 60- and 90-day periods, respectively (Fig. 2.13), and that in all cases, there were few detections, suggesting that Galapagos sharks may not spend as much time swimming at the surface as hammerhead and silky sharks.

Six adult (2–2.2 m total length) blacktip sharks (*C. limbatus*) were tagged in July 2006; and tracks were obtained from five of these (Fig. 2.14). Three of the sharks were also fitted internally with ultrasonic tags. Two satellite tracks showed sharks moving south into the central archipelago, while the remaining sharks stayed around Darwin (Shillinger et al. unpublished data). However, one of the sharks, which moved to the central archipelago, was detected at Gordon Rocks several months later and then at Leon Dormido (San Cristobal Island) over a year later. This shark has continued to be detected at receivers throughout the archipelago for almost 6 years (Fig. 2.15), ranging widely from Darwin in the far north to San Cristobal in the far south of the marine reserve.

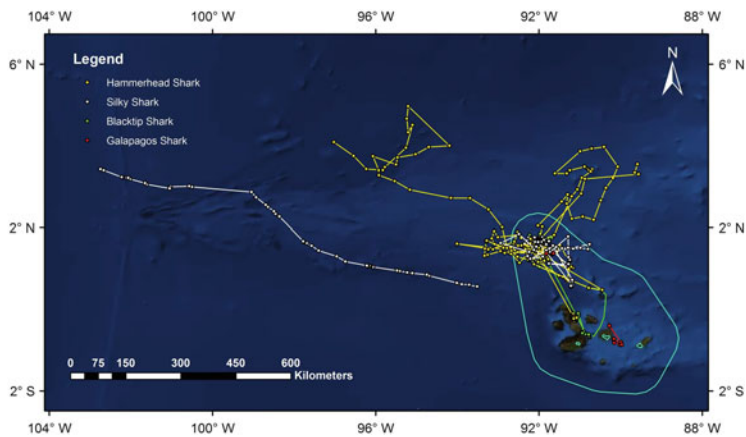


Fig. 2.10 Satellite tracks of sharks tagged at Darwin/Wolf islands 2006–2012. The Galapagos Marine Reserve boundary is highlighted in *blue*. (Source: Shillinger et al. unpublished data; Hearn et al. unpublished data; Ketchum et al. 2011c)

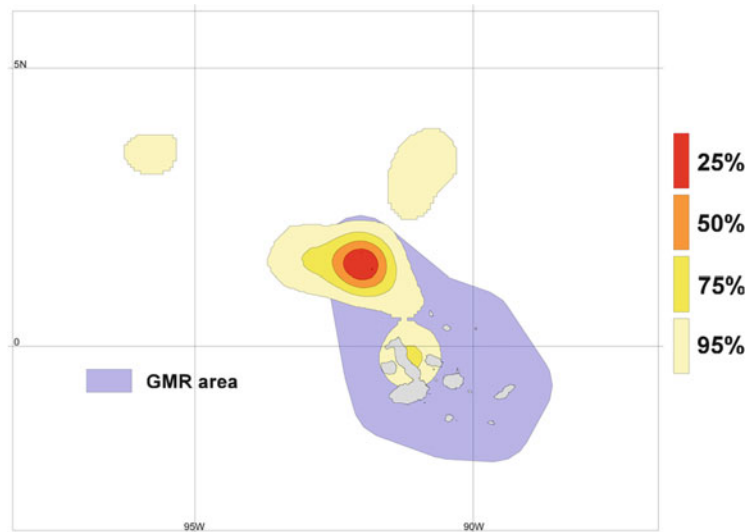


Fig. 2.11 Kernel home ranges (25, 50, 75, and 95 % UD) of the large-scale movements of hammerheads in the Galapagos Marine Reserve. Kernels of all positions from satellite tracking for all individuals ($N = 7$). Source: Ketchum et al. (2011c)

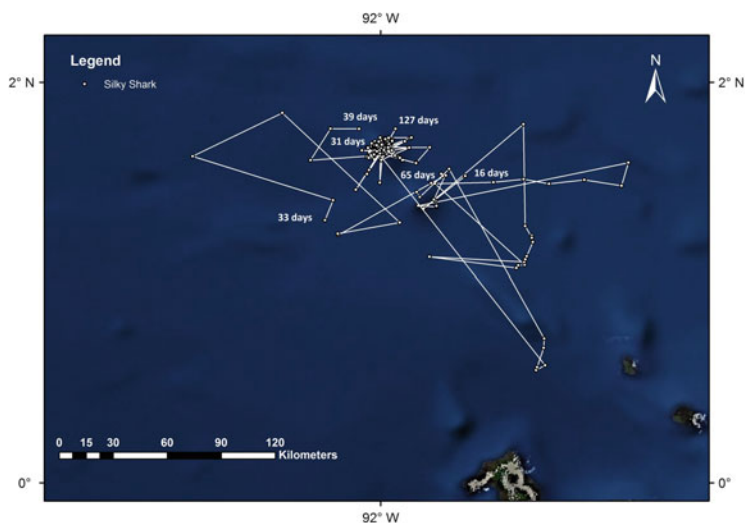


Fig. 2.12 Satellite tracks of silky sharks ($N = 6$) tagged at Darwin and Wolf Islands, which remained in the vicinity of the two islands. The long-distance track from a seventh shark is shown on a previous figure. (Source: Hearn et al. unpublished data)

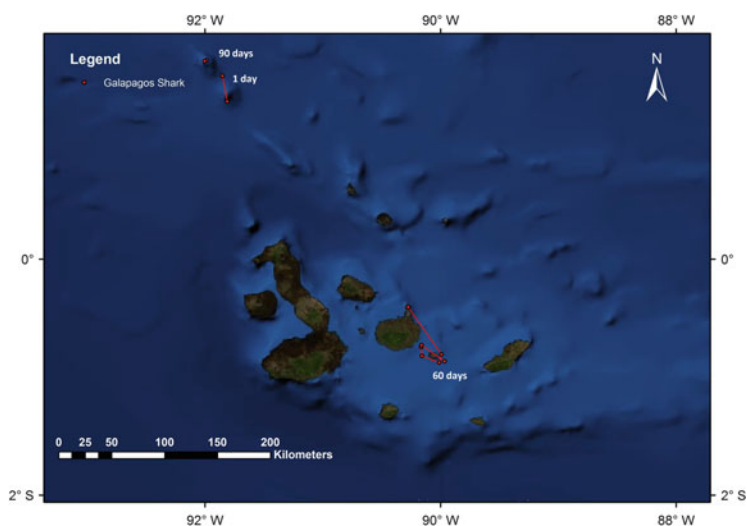


Fig. 2.13 Satellite tracks of Galapagos sharks ($N = 3$) tagged in the Galapagos Marine Reserve. (Source: Shillinger et al. unpublished data)

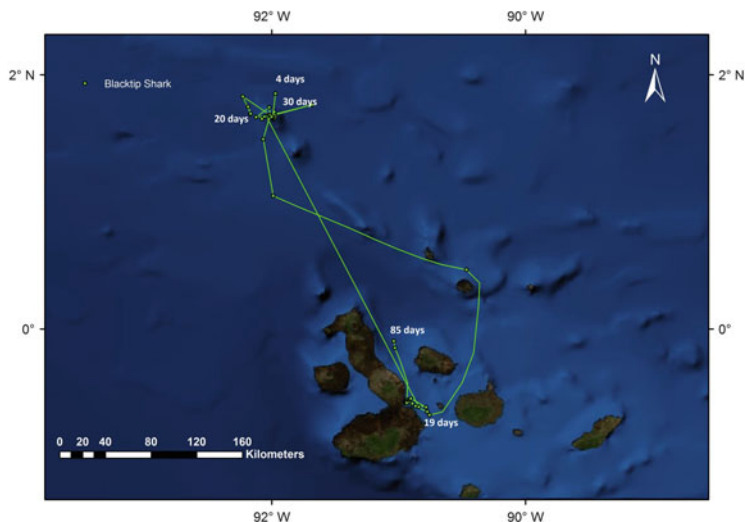


Fig. 2.14 Satellite tracks of blacktip sharks tagged in the Galapagos Marine Reserve. (Source: Shillinger et al. unpublished data)

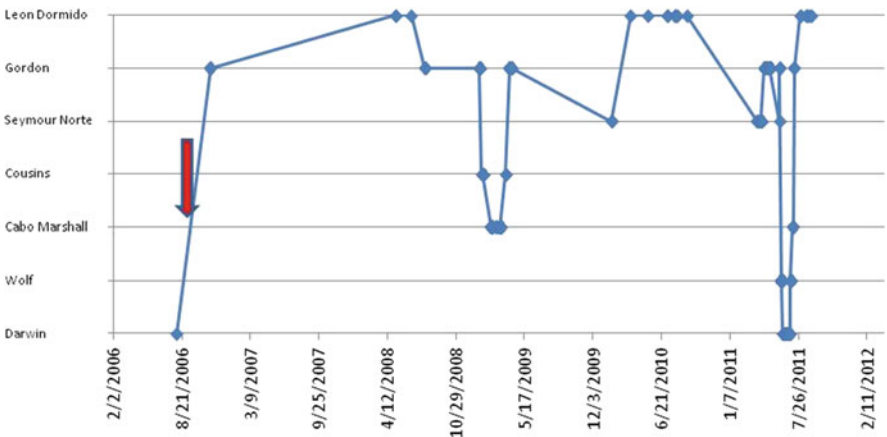


Fig. 2.15 Ultrasonic detections of a double-tagged blacktip shark on underwater receivers array from 2006 to 2012. Red arrow indicates when the satellite tag stopped transmitting (after 19 days, at eastern Isabela—see Fig. 2.14) (Source: CDF-PNG-UCD Database, unpublished)

Whale Sharks and Giant Mantas: Visiting Migrants

The whale shark *Rhincodon typus* and the giant manta ray *Manta birostris* (Fig. 2.16) are two of the world’s largest elasmobranchs. Both are known to migrate through the Galapagos Marine Reserve, although their level of residency in the reserve is uncertain.



Fig. 2.16 (Above) Female whale shark *Rhincodon typus* at Darwin Arch, Galapagos, 2011. Note the distended abdomen, suggesting pregnancy. Source: Jonathan Green. (Below) Manta ray *Manta birostris* with satellite tag from coastal Ecuador. Source: Andrea Marshall

The whale shark is the world's largest fish, reaching up to 20 m in length (Chen et al. 1997). The giant manta ray was only recently differentiated from its smaller relative, the reef manta ray (*Manta alfredi*) in 2009, when the genus *Manta* was split into two visually distinct species (Marshall et al. 2009). It is the largest extant species of ray in the oceans. The giant manta attains maximum disc widths of up to 8 m. Both species are circumglobal and often aggregate in areas of high productivity on predictable, seasonal bases (Kashiwagi et al. 2011; De la Parra-Venegas et al. 2011). Giant manta rays, like whale sharks, are known to “chase” ephemeral bursts of productivity and sometimes appear simultaneously, on mass, in groups of several hundred individuals. On these occasions, they are often exploiting a food resource like a coral- or fish-spawning event. Manta rays may also use these mass-gathering opportunities for other social behaviors like breeding, whereas almost nothing is known about the breeding dynamics of whale sharks.

Both species are predominantly filter feeders specializing in the capture of zooplankton. Highly adapted to their pelagic environment, they forage in surface waters and also at depth. Unlike whale sharks, manta rays seem to spend most of

their time in nearshore areas moving only offshore to forage or as they migrate to other areas.

Manta species have very conservative life history traits and are known to be one of the least fecund species of elasmobranchs. With small litter sizes, variable reproductive periodicity in the wild (every 2–3 years on average), and presumed high mortality in early life, manta rays are believed to be high-risk species, sensitive to anthropogenic threats (Marshall and Bennett 2010). Little information exists on the reproductive ecology of the giant manta ray, but current research in Ecuador has identified breeding sites along the mainland and in the islands of the Galapagos. Some of the first pregnant females ever seen in the wild have been sighted in the productive coastal waters off Isla de la Plata in the Machalilla National Park, while others have been reported in the GMR. To date, no one has yet witnessed a birth in the wild, and it remains unclear where these large rays give birth or even where their young spend their first few years of life.

Whale sharks are aplacental viviparous with eggs hatching within the female's uteri and the female giving birth to live young. A 9-m female was caught in Taiwan with 300 young (Joung et al. 1996) suggesting that the whale shark is the most prolific of elasmobranchs. Sparse information exists on reproductive and pupping grounds, in addition to our lack of information on migratory routes and home-range sizes.

Currently, Ecuador boasts the largest identified population of giant manta rays in the world. One of the most important aggregation areas for the species occurs along the mainland, in the waters of the Machalilla National Park. Other important aggregation areas occur within the main island group of the Galapagos National Park, where scuba divers can occasionally see them. Manta rays sighted within the GMR are often encountered within the main islands of Isabela, Floreana, Pinzon, Santa Cruz, and Santiago, with some of the biggest aggregations found in areas such as Cabo Marshall, Cuatro Hermanos, and Roca Sin Nombre.

In contrast, whale sharks have become a predictable dive tourist attraction a certain times of year at one location in particular—the Arch at Darwin Island. From observations made by a small number of long-term dive guides at the Galapagos, it became apparent that the frequency of whale shark sightings increased with the onset of the cool “garua” season and the increase in strength of both the Cromwell and Humboldt currents, usually in the month of June. Their disappearance also coincided with the weakening of these currents around December, although occasional sightings occur throughout the archipelago in all months of the year (Jonathan Green, personal communication). Perhaps one of the most significant and surprising pieces of data to emerge was the unusually high percentage of adult female sharks that form the main body of the observed population at Darwin Island. Additionally, most of the females display distended abdomens, suggesting advanced-stage pregnancy (Fig. 2.16).

As a result of two consecutive seasons of fieldwork carried out during different periods of the year, only one male was sighted by the research team (and tagged) in comparison with over 60 females (39 tagged). Males are reported occasionally by dive guides, but such sightings are rare. Even rarer was a female albino whale shark

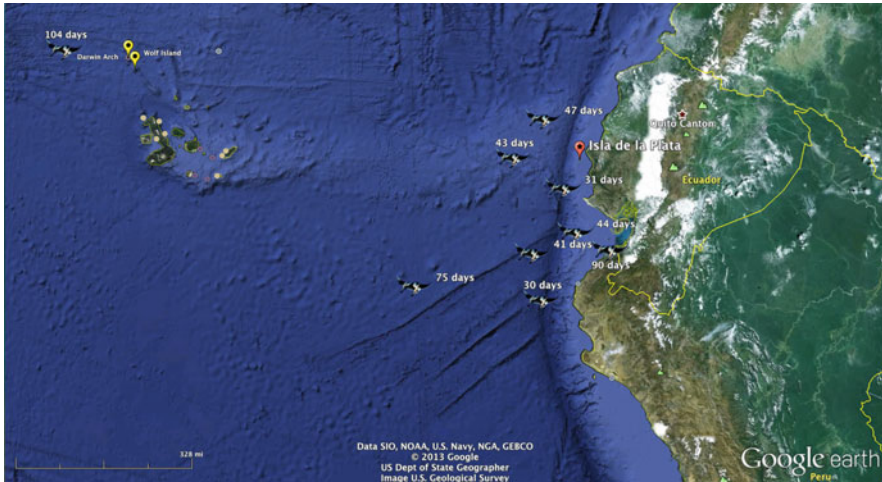


Fig. 2.17 Pop-up locations of giant manta rays tagged at Isla de la Plata in 2010 and 2011. Note that one tag was released west of Darwin Island, 104 days after attachment (Source: Andrea Marshall, unpublished data)

photographed and filmed in 2008 (Antonio Moreano, M/V Deep Blue, cited in the Daily Mail Online, UK, August 28, 2008).

In response to the paucity of information on the habits of these species in Ecuadorian waters, tagging programs were begun at known aggregation sites, of whale sharks at Darwin (Galapagos) and of giant mantas at Machalilla National Park (mainland Ecuador).

A total of 9 pop-up archival (PAT) tags were deployed on giant mantas between 2010 and 2012. The tags were programmed to stay on individuals for periods of time between 30 and 104 days. After spending limited time in the deployment area, the tagged rays radiated out from Isla de la Plata in several different directions, with some individuals making migrations of up to 1,500 km (straight-line distance) from the aggregation site where they were originally tagged (Fig. 2.17) (Marshall et al. unpublished data). Most commonly individuals moved south into Peru, resulting in some of the first international tracks of this species. Unfortunately some of these tracks were cut short when the tagged rays were killed and the tags came ashore with fishermen in Peru. Other rays tagged during the 3-year study moved distinctly west from the mainland towards the Galapagos, even establishing connectivity between the mainland and these offshore islands for the first time. The single-tagged individual that traveled all the way from the mainland of Ecuador to the Galapagos Islands was ultimately tracked to an area of the ocean just northwest of Darwin Island.

Twenty-four satellite tags were placed on whale sharks in 2011 (Hearn et al. 2012). Despite a high level of immediate tag loss (potentially caused by associated species such as jacks or blacktip and silky sharks pulling the tags out or by failure of the tag tethers), certain patterns emerged regarding the residency at

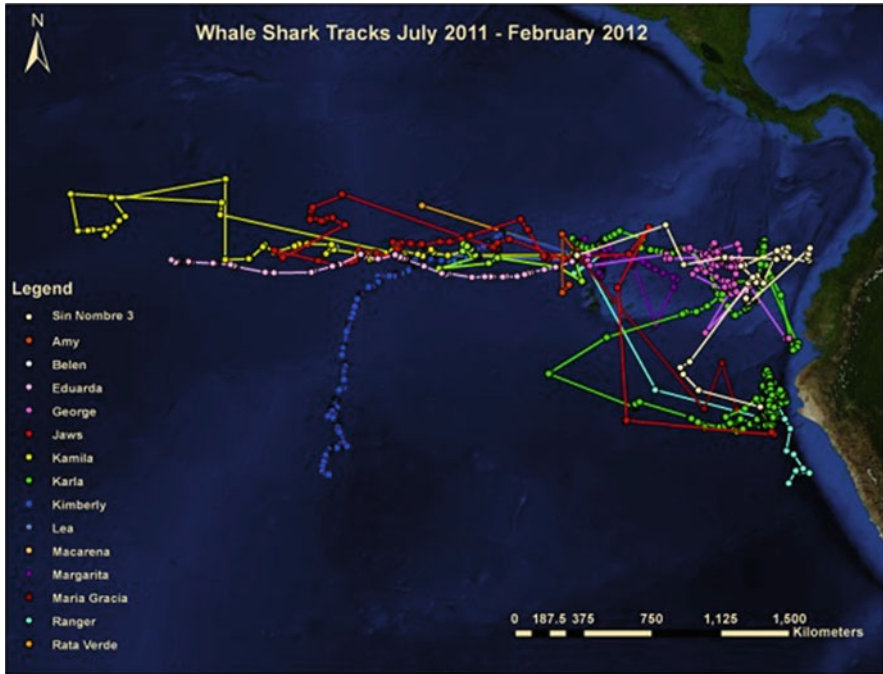


Fig. 2.18 Satellite tracks of whale sharks tagged at Darwin Island (Galapagos) in July–October 2011 (from Hearn et al. 2012)

Darwin and their final destinations (Fig. 2.18). None of the sharks tagged remained at Darwin for longer than a few days. Those sharks tagged early in the season made westerly movements of several hundred kilometers into the open ocean and then returned east late in the season, often passing close to Darwin again, and then heading towards the continental shelf. The sharks tagged later in the season moved to the continental shelf and then remained along the shelf break for extended periods (Fig. 2.18). The mean track time was 53 days, while the longest track was 177 days, which was the only male: “George” tag #108096. Whereas the females had traveled west, the male went to the east, remaining for almost 3 months midway between the Galapagos archipelago and the mainland of Ecuador.

In other words, rather than the previously held belief that a small number of whale sharks were present at Darwin for a period of several months, the reality appears to be that a steady trickle of large, apparently pregnant female whale sharks pass through Darwin for a period of a few days between June and November, continue to move out west into the open ocean, and then return later in the year through Galapagos to the continental shelf of northern Peru—a similar area to where many of the tagged manta rays are headed. The reasons for this migration over several thousand kilometers are not known—yet the predominance of large, apparently pregnant females has led to speculation about pupping grounds. However, neonate whale sharks have not been reported from Galapagos and, with a

handful of loosely distributed exceptions, are notoriously absent from studies all over the world (Sequeira et al. 2013). It may be that Darwin acts more of a waypoint than a destination en route to unknown offshore pupping areas.

Human Interactions

Fishing

In three independent studies aimed at evaluating the potential for small-scale long-lining to be permitted in the GMR, sharks, mantas, and rays were all shown to be highly susceptible to this mode of fishing (Murillo et al. 2004). Surface longlines from 3 to 19 km in length and with 80–350 hooks were deployed at depths varying between 8 and 30 m, around the southern and western part of the reserve, and left to soak overnight. In 1997, in an experimental fishing trip around Isabela, Fernandina, and Santa Cruz, sharks made up over 53.2 % of the catch. In 2001, the Ecuadorian Navy carried out an experimental fishery with a surface longline and reported that sharks made up 58 % of the catch—these were mostly blue sharks and Galapagos sharks. Mantas made up 1.3 % of the catch.

In 2003, a large-scale surface longline experimental fishery was carried out jointly by the Galapagos National Park Service, Charles Darwin Foundation, and a local fishing sector (Chasiluisa et al. 2003; Murillo et al. 2004). In order to avoid catching coastal sharks, lines were set at least 5 Nm from two polygons making up the central Archipelago and Pinta, Marchena, and Genovesa and 10 Nm from a third polygon made up of Darwin and Wolf.

Sharks made up 77 % of the catch (138 of 178 individuals) in one trip in March (one mobula ray was also caught), whereas sharks made up 27.6 % of the total catch over seven trips from October to December (mantas made up 2.5 %, rays made up 2.1 %). The most common shark in open waters was the blue shark, which at times made up more than 50 % of the shark catch. In comparison, only a handful of thresher sharks were caught (*Alopias superciliosus* and *A. pelagicus*). Galapagos, silky, blacktip, and mako sharks were also caught, along with scalloped and smooth hammerheads (the latter are rarely seen by divers). Thirty-three mantas and mobulas were caught over the seven trips (of which one died), along with 26 rays, including a specimen of *Rhinoptera steindachneri* and six *Dasyatis* sp.

Blue sharks were caught throughout the reserve; hammerheads were more predominant to the north and west of Isabela, while silky sharks were caught to the south (Fig. 2.19). Mantas were found particularly to the north of Isabela in December.

Mortality on longlines was almost three times higher for hammerhead species (32 %) than for silky and Galapagos sharks (11 %). Oceanic sharks were less vulnerable to mortality while hooked (e.g., blue sharks, 8 %), yet no post-release mortality estimations were made.

Given the paucity of the data, the experimental design, and the lack of catchability coefficients, it is hard to reach any conclusions about the relative

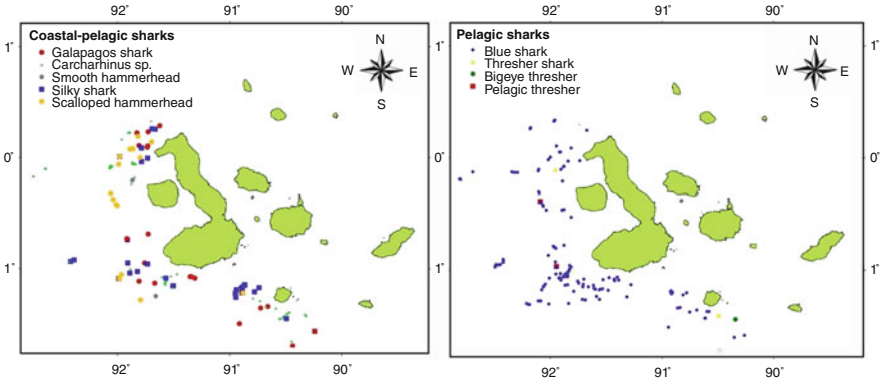


Fig. 2.19 Location of sharks caught during experimental longline fishery (from Murillo et al. 2004). Note that fishing activity was restricted to at least 10 Nm from shore

abundance and distribution of the sharks caught in this study, other than simple presence. The Murillo et al. (2004) study did not provide photographic evidence for each species caught, and therefore only the broadest of interpretations is possible.

Bycatch may also be an issue in nursery grounds. Llerena (2009) reported finding bodies of neonates blacktip sharks during surveys—probably bycatch from the gillnet fishery for mullets.

Illegal Fishing

Shark finning has occurred around the Galapagos since as early as the 1950s (INP 1964) and continues to occur illegally in the waters of the GMR, both by local fishers and by mainland Ecuador and foreign (particularly Costa Rican) industrial vessels (Reyes and Murillo 2007). Over 22,000 shark fins and 680 shark carcasses were seized between 1998 and 2006, from vessels, on the islands and at airports leaving Galapagos or arriving at mainland Ecuador (Reyes and Murillo 2007).

Jacquet et al. (2008) estimated that since 1998, almost 50 % of Ecuador's shark fin exports could not be accounted for and, based on anecdotal evidence from WildAid (2001), suggested that much of this could have originated from Galapagos. In any case, it is difficult to estimate the real extent of this activity in Galapagos, although shark fin seizures by the Galapagos National Park Service and Ecuadorian Navy continue (DPNG 2013).

Dive Tourism

In recent years, shark dive tourism has, in many places, become an economic and ecologically sustainable alternative to fishing (Rowat and Engelhardt 2007; Vianna et al. 2011; Clua et al. 2011). In Galapagos, the dive tourism industry began in the

1980s by advertising the incredible abundance of sharks and other marine megafauna. Since then, this activity has grown steadily, and the GMR is regularly listed as one of the best dive spots in the world. Scalloped hammerhead, Galapagos, whitetips, whale sharks, mantas, and mobulas are among the most commonly advertised marine species by tour operators.

Worldwide, dive guides and citizen science can be important sources of information for elasmobranch research, playing a key role in establishing relative abundance baselines and population trends in the face of scarce empirical research and fishery landings statistics (Barker and Williamson 2010; Whitehead 2001; Dudgeon et al. 2008; Holmberg et al. 2009). In Galapagos, local dive guides have reported considerable declines in shark numbers over the last decade, attributable to illegal industrial fishing and finning by local fishers (Hearn et al. 2008). Nevertheless, over the past five years, there are increasing reports of blacktip sharks (*C. limbatus*) and tiger sharks (*G. cuvier*) presence among dive sites in the south-central and far north regions. This may be a sign of recovery of those populations—supported by a recent theoretical study on trophic modeling (Wolff et al. 2012a, b). Yet the reality of trends in shark populations is clouded by the lack of a clear long-term monitoring plan.

Dive tourism is also a reliable source of revenue for local economies, and research on the economic dynamics of this activity can be a crucial step towards gaining legitimacy for the protection of these species. One study assessed the daily dive tour operation in Santa Cruz Island and estimated that 92 % of scuba divers traveling under this modality do so with the main expectation of observing sharks close-up in their natural environment (Peñaherrera et al. 2013). Their visit was estimated to generate a total gross income for the dive companies of more than 1.9 million US dollars per year, which pales in comparison with the many millions generated by the live-aboard dive vessels, which rely almost entirely on the marine megafauna at Darwin and Wolf Islands. Attitudes of tourists (both diver and non-diver) are currently the focus of several studies which aim to determine the economic contribution of sharks and rays to the local Galapagos economy (C. Peñaherrera, University of Tasmania, personal communication) and to evaluate comparative regional conservation policies for threatened charismatic species (S. Cardenas, University of California, Davis; personal communication).

Shark Attacks

There have been 17 shark attacks (all nonfatal) recorded in Galapagos waters between 1989 and 2011. Of these, 13 were verified in clinical records and/or through direct sources. The other five attacks could not be verified, but there are sufficient data to support their inclusion in the registry compiled by the Charles Darwin Foundation (Acuña-Marrero and Peñaherrera-Palma 2011).

The increased number of shark attacks in this last decade matches the growing number of visitors. Most attack events recorded in Galapagos (80 %) occurred when the victim was at the surface, which coincides with global statistics that show 82 %

of victims were at the surface (60 % surfing and 22 % swimming) (ISAF 2013). Although all attacks recorded were considered “unprovoked,” in at least seven cases, the victim’s behavior and/or a set of circumstances that surrounded the events played an important role in the attack, as victims were alone, or bathed in the evening or night, or there was organic waste in the water before and/or at the time of the event.

The majority of cases in Galapagos were “hit and run” attacks, which typically occur with swimmers and surfers in the surf zone and where the shark does not return after a single bite or hit. This type of attack is related with a case of mistaken identity by the shark, which confuses the victim with one of its usual prey, such as sea turtles or sea lions (Klimley 1974). There is only one recorded case of “sneak” attack in Galapagos which can be related with directed feeding behavior, where a surfer was attacked persistently by a shark in a low visibility zone and late in the afternoon, in 2009 at Isabela Island.

In most cases, it was not possible to identify the shark species involved in the attack, due to lack of reliable witness or photograph/video records of the event. The bull shark *Carcharhinus leucas* is often blamed for these attacks, yet it is unlikely that this species is even present in Galapagos (Acuña-Marrero and Peñaherrera-Palma 2011).

Potential Impact of the Marine Reserve

Unsustainable extractive activities are placing many shark populations across the globe at risk (Baum and Myers 2004; Myers and Ottensmeyer 2005), which in turn poses a bigger threat to the health and functioning of marine ecosystems, as the delicate balance in complex marine food webs is upset (Stevens et al. 2000; Myers et al. 2007). Marine protected areas (MPAs) are becoming important tools for limiting the removal of important species and buffering against the resultant ecosystem restructuring that can follow their removal (Agardy 1994; Friedlander and DeMartini 2002; Halpern 2003).

The Galapagos Marine Reserve (GMR) is the largest reserve in the Eastern Tropical Pacific (ETP). This creates an opportunity to examine the utility of MPAs for rebuilding shark populations and the system’s resilience in the face of severe environmental change such as El Niño events—which strongly hit Galapagos in 1982/1983 and 1997/1998.

Using the Ecopath with Ecosim modeling approach, Wolff et al. (2012a) constructed a trophic flow model of the GMR pelagic ecosystem for the period of the late 1990s when the industrial fishery was still in place. They used this reference model for simulations of a 50 % reduction in primary productivity during a 10-month El Niño period (occurred in 1998) and of the impact of the fishing ban with the reserve creation. Simulations with Ecosim showed that El Niño suppressed the positive fishery ban effect for about 3 years, showing its bottom-up forcing to be stronger than the top-down forcing by the fishery. After that, simulations on the fishery ban and considering resource-specific resident times in the GMR revealed

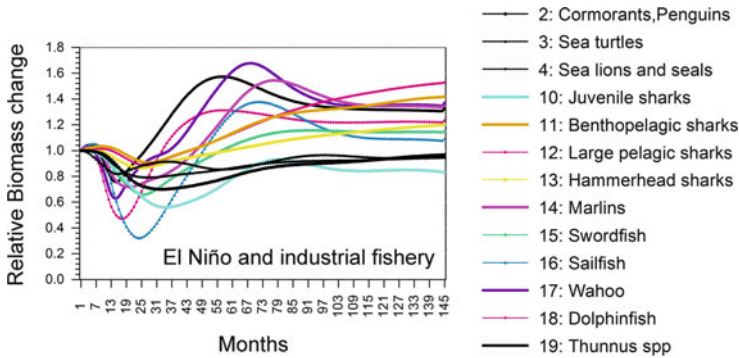


Fig. 2.20 Simulation of the GMR pelagic ecosystem response to the 1998 “El Niño” event and the industrial fishery ban after the creation of the GMR in 1998. From Wolff et al. 2012a

theoretical population increases of the following groups: benthopelagic sharks (37 %), large pelagic sharks (24 %), wahoo (13 %), tuna (13 %), hammerheads (15 %), marlins (6 %), and swordfish (2 %) (Fig. 2.20). Population increase for the above groups was still substantial even if their residence times in the GMR were assumed to be as low as 10 % of adult lifetime.

Published and unpublished monitoring data for marine mammals, birds and sea turtles confirm their population reductions simulated this model. Other trophic models focused on benthic reef systems of Galapagos reported shark-dominated trophic webs and also increased abundances of sharks when closing those systems to fisheries (Okey et al. 2004; Ruiz and Wolff 2011) and after the El Niño 1997/1998 event (Wolff et al. 2012b), suggesting a key role of sharks in the Galapagos marine ecosystems. More importantly, results by Wolff et al. (2012a) suggest that the GMR has, despite a 2–3-year system disruption caused by the El Niño 1997/1998, undergone a substantial recovery process of large pelagic fish and sharks since the industrial fishery was banned 12 years ago.

However, we do not presently have sufficient technical information to demonstrate the success of the GMR in protecting sharks, as distinct from other components of marine ecosystems. There are observational reports that blacktip and tiger sharks are becoming more frequent in the main dive sites during the last 5 years (Jonathan Green, personal communication), which would support these findings. Nevertheless, naturalist and dive guides working in Galapagos still have reported fewer sharks sighted over the last 20 years (Hearn et al. 2008). Consequently, a great uncertainty on the current state of shark populations and the impact of the GMR still exist. This theme is currently being explored as part of a PhD research thesis (C. Peñaherrera, University of Tasmania, personal communication)

A Growing Focus for Research

When the Charles Darwin Foundation and Galapagos National Park Service published their Baseline Biodiversity of the Galapagos Marine Reserve (Danulat and Edgar 2002), little was known about sharks and rays in Galapagos, other than a species list and a notion of the distribution and relative abundance of some of the more common reef-associated species, based on the CDF subtidal ecological monitoring program, on informal scuba dive records, and on seizures of illegal shark catches (Zarate 2002).

Since then, and coinciding with the development of the Eastern Tropical Pacific Seascape (Shillinger 2005) and the National Plan of Action for Sharks, there has been a consistent drive by local and international researchers in partnership, to better understand the role of the Galapagos Marine Reserve in protecting these species within a regional context and to understand their roles within the Galapagos marine ecosystem. Current and future efforts must continue to build on the developments of the past decade.

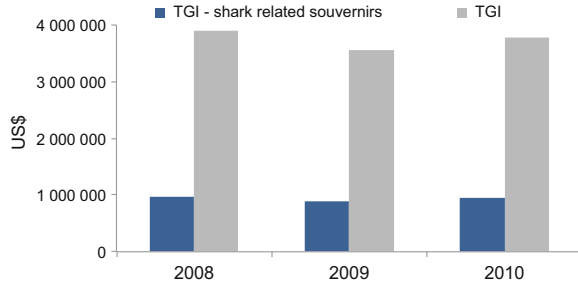
Underwater visual surveys directed at sharks and rays are currently being carried out by researchers, but the data is limited spatially and temporally. There is a clear need to engage local dive operators and tourists to expand this work via a citizen science model and to establish a baseline of distribution and abundance of the main elasmobranch species throughout the Marine Reserve. Long-term monitoring at key sites can then be established to track changes over time, and various sources of past data, such as old dive logs, photos, and underwater footage, can be explored to attempt to reconstruct past distribution and abundance.

The spatial dynamics of hammerhead and Galapagos sharks are now better understood—and the importance of remote islands and offshore islets to their ecology. Yet with tagging studies, sample size always becomes an issue, and efforts to understand and map potential long-distance migratory routes for these and other species (including whale sharks and giant manta rays) must continue. Other key habitats, such as juvenile rearing grounds, must be identified and mapped.

Genetic studies have shown that scalloped hammerheads form at least three distinct populations in the Eastern Pacific (Nance et al. 2011), yet this analysis was based entirely on samples taken from mainland sites. Further work must incorporate samples from the Galapagos and other island sites (such as Cocos and Malpelo). A similar regional approach should also be taken to integrate movement studies and fishery bycatch data, so that more formal stock assessments of the most vulnerable species can be carried out.

Our growing knowledge of the ecology of elasmobranchs in Galapagos provides a valuable tool for the management of the reserve. Modeling studies suggest that hammerheads can be used as umbrella species to represent the entire communities (Ketchum et al. 2011c). The GMR is managed as a multiuse reserve based on zonation (Heylings et al. 2002). A coastal zonation scheme was agreed upon and implemented in 2002, yet a key component of the scheme—the legal width of the coastal zone—was never decided. Based on the daytime schooling behavior of

Fig. 2.21 Estimated total gross income (TGI) in Santa Cruz Island from small souvenir stores from shark-related merchandise (*blue bars*) and overall (*gray bars*). Source: Peñaherrera et al. (2013)



hammerheads around Wolf Island (Fig. 2.8), a width of approximately half a nautical mile would ensure that the school was protected from offshore fishing activities, and this would encompass the entire shallow reef community. Similarly, ongoing satellite tagging studies aim to inform decision makers and stakeholders on an open-water zonation scheme, which is part of the GMR Management Plan (Registro Oficial no. 173, April 20, 1999).

It is likely that the threats to sharks and rays in the Galapagos Marine Reserve will continue in the foreseeable future. While there is a market for shark fins, the risk of local illegal target fisheries for sharks remains. The local fishing sector continues to lobby for permission to use longlines. Industrial fishing vessels continue to cross the reserve boundaries, and while the use of satellite and radio monitoring systems may help, a range of enforcement issues must still be addressed (WildAid 2010).

Yet overall, there has been a change in paradigm in Galapagos, which is reflected around the world—sharks are now iconic species. Based on tourist expenditure values published by Epler (2007) and Ordóñez (2007), Peñaherrera et al. (2013) estimated that shark-related souvenir purchase may reach 25 % (US\$940,000 average) of the total gross income generated by the small souvenir shops located at Santa Cruz Island in the 2008–2010 period (Fig. 2.21).

At present, Ecuador is leading the way in Latin America with its implementation of a National Plan of Action for Sharks (Zarate and Hearn 2008) and calls for greater protection for sharks and rays. It is playing a key role in the coordination of regional management for sharks, hosting the first and third regional workshops for shark conservation. Galapagos National Park technical staff recently participated at the CITES meeting where giant mantas and hammerhead sharks were placed on Appendix II. Ultimately, as is the case with transboundary migratory species, the status of sharks and rays in the Galapagos Marine Reserve will depend on the actions of Ecuador and its neighboring states.

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References

- Acuña-Marrero D, Peñaherrera-Palma C (2011) Human-shark interactions in Galapagos: first compilation and analysis of shark attacks since 1989. Charles Darwin Foundation, Technical report. Puerto Ayora, Ecuador
- Acuña-Marrero D, Zimmerhackel JS, Mayorga J, Hearn A (2013) Three new species of shark recorded at the Galapagos Islands. *Marine Biodiversity Records* 6:e87 doi: [10.1017/S1755267213000596](https://doi.org/10.1017/S1755267213000596)
- Agardy MT (1994) Advances in marine conservation: the role of marine protected areas. *TREE* 9 (7):267–270
- Argos-CLS (2007) Argos User's Manual. Worldwide tracking and environmental monitoring by satellite. Ramonville Saint-Anne, France (Updated 2011)
- Barker SM, Williamson JE (2010) Collaborative photo-identification and monitoring of grey nurse sharks (*Carcharias taurus*) at key aggregation sites along the eastern coast of Australia. *Mar Freshw Res* 61:971–979
- Baum J, Myers M (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecol Lett* 7:135–145
- Bernard ATF, Gotz A, Kerwath SE, Wilke CG (2013) Observer bias and detection probability in underwater visual census of fish assemblages measured with independent double-observers. *J Exp Mar Biol Ecol* 443:75–84
- Bessudo S, Soler GA, Klimley AP, Ketchum JT, Hearn A, Arauz R (2011) Residency of the scalloped hammerhead shark (*Sphyrna lewini*) at Malpelo Island and evidence of migration to other islands in the Eastern Tropical Pacific. *Environ Biol Fish* 91:165–176. doi:[10.1007/s10641-011-9769-3](https://doi.org/10.1007/s10641-011-9769-3)

- Bonfil R (1994) Overview of the world elasmobranch fisheries. FAO Fisheries Technical Paper 341, Rome
- Castañeda-Suarez JD, Sandoval-Londoño LA (2007) Feeding habits of the hammerhead shark *Sphyrna lewini* (Griffith & Smith, 1834) in the Ecuadorian Pacific. In: Martinez J, Galvan F (eds) Sharks in Ecuador: case studies. EPESPO-PMRC, Manta, Ecuador
- Chasiluisa C, Moreno J, Bautil B, Villalta M, Vizcaíno J (2003) Informe del B/P Vanesa, Plan Piloto Experimental de Altura para Galápagos. Fundación Charles Darwin y Servicio Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador
- Chen CT, Liu KM, Joung SJ (1997) Preliminary report on Taiwan's whale shark fishery. TRAFFIC Bull 17:53–57
- Clua E, Buray N, Legendre P, Mourier J, Planes S (2011) Business partner or simple catch? The economic value of the sicklefin lemon shark in French Polynesia. Mar Freshw Res 62:764–770
- Danulat E, Edgar G (eds) (2002) Reserva Marina de Galápagos. Línea Base de la Biodiversidad. Fundación Charles Darwin/Servicio Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador
- De la Parra-Venegas R, Hueter R, Gonzalez Cano J, Tyminski J, Remolina JG, Maslanka M, Ormos A, Weigt L, Carlson B, Dove A (2011) An unprecedented aggregation of whale sharks *Rhincodon typus*, in Mexican Coastal Waters of the Caribbean Sea. PLoS One 6(4):e18994
- DPNG (2013) DPNG captura barco pesquero y siete fibras dentro de la RMG. Press Bulletin 2013-03-01 – No. 025. Accessed 22 Mar 2013. <http://galapagospark.org/boletin.php?noticia=750>
- Dudgeon CL, Noad MJ, Lanyon M (2008) Abundance and demography of a seasonal aggregation of zebra sharks *Stegostoma fasciatum*. Mar Ecol Prog Ser 368:269–281
- Edgar GJ, Banks S, Fariña JM, Calvopiña M, Martínez C (2004) Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos Archipelago. J Biogeogr 31:1107–1124
- Epler B (2007) Turismo, economía, crecimiento poblacional y conservación en Galápagos. Fundación Charles Darwin
- Estupiñán-Montaño C, Cedeño-Figueroa LG, Galván-Magaña F (2009) Hábitos alimenticios de la cornuda común *Sphyrna lewini* en el Pacífico ecuatoriano. Rev Biol Mar Oceanogr 44(2): 379–386
- FAO (2010–2013). International plan of action for the conservation and management of sharks – web site. International plan of action for conservation and management of sharks. FI Institutional Websites. In: FAO Fisheries and Aquaculture Department [online], Rome. Updated. [Cited 27 April 2013]. <http://www.fao.org/fishery/ipoa-sharks/en>
- Friedlander A, DeMartini E (2002) Contrast in density, size and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. Mar Ecol Prog Ser 230:253–264
- Grove JS, Lavenberg RJ (1997) Fishes of the Galapagos Islands. Stanford University Press, Stanford, CA
- Halpern B (2003) The impact of marine reserves: do reserves work and does reserve size matter? Ecol Appl 13(1):S117–S137
- Hamilton WJ III, Watt KEF (1970) Refuging. Annu Rev Ecol Syst 1:263–286
- Hammerschlag N, Gallagher AJ, Lazarre DM (2011) A review of shark satellite tagging studies. J Exp Mar Biol Ecol 398:1–8
- Hearn A, Ketchum J, Shillinger G, Klimley AP, Espinoza E (2008) Programa de Investigación y Conservación de Tiburones en la Reserva Marina de Galapagos. Reporte Anual 2006-7. Fundación Charles Darwin, Santa Cruz, Galapagos, Ecuador
- Hearn A, Ketchum JT, Klimley AP, Espinoza E, Peñaherrera C (2010a) Hotspots within hotspots? Hammerhead shark movements around Wolf Island, Galapagos Marine Reserve. Mar Biol 157:1899–1915. doi:10.1007/s00227-010-1460-2
- Hearn A, Utreras E, Henderson S (eds) (2010b) Informe sobre el estado de los tiburones del Pacífico Este Tropical. Conservation International, Quito, Ecuador

- Hearn A, Green J, Peñaherrera C, Acuña D, Espinoza E, Llerena Y, Klimley AP (2012) Proyecto de Investigación de tiburones en la Reserva Marina de Galápagos: Marcaje de Tiburón Ballena. Reporte Final Parque Nacional Galápagos, Galápagos, Ecuador
- Hearn A, Ketchum JT, Arauz R, Hoyos M, Bessudo S, Soler G, Peñaherrera C, Espinoza E, Peterson M, Klimley AP (in press) Long term movements of Galapagos Sharks (*Carcharhinus galapagensis*) in the Eastern Tropical Pacific
- Heupel M, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. *Mar Ecol Prog Ser* 337:287–297
- Heylings P, Bensted-Smith R, Altamirano M (2002) Zonificación e historia de la reserva marina de Galápagos. In: Danulat E, Edgar GJ (eds) Reserva marina de Galápagos Línea base de la biodiversidad. Fundación Charles Darwin/Parque Nacional Galápagos, Santa Cruz, Galápagos
- Holmberg J, Norman B, Arzoumanian Z (2009) Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo identification. *Endanger Species Res* 7:39–53
- INP (1964) Apuntes e informaciones sobre la situación de la producción pesquera ecuatoriana y sus mercados, Instituto Nacional de Pesca vol 1. Guayaquil, Ecuador
- ISAF (2013) Archivo Internacional de Ataques de Tiburón (ISAF), administrado por la Sociedad Americana de Elasmobranchios (AES) y el Museo de Historia Natural de Florida. Disponible en: <http://www.flmnh.ufl.edu/fish/sharks/isaf/isaf.htm>.
- Jacquet J, Alava JJ, Pramod G, Henderson S, Zeller D (2008) In hot soup: sharks captured in Ecuador's waters. *Environ Sci* 5(4):269–283
- Jaenig M (2010) Sharks (Selachii) in mangrove-fringed habitats of the Galápagos Marine Reserve (GMR) with implications for management and conservation. M.Sc. thesis in International Studies in Aquatic Tropical Ecology. University of Bremen, Faculty for Biology and Chemistry. Bremen, Germany
- Joung SJ, Chen CT, Clark E, Uchida S, Huang WYP (1996) The whale shark, *Rhincodon typus*, is a livebearer: 300 embryos found in one 'megamamma' supreme. *Environ Biol Fish* 46:219–223
- Kashiwagi T, Marshall AD, Bennett MB, Ovenden JR (2011) Habitat segregation and mosaic sympatry of the two species of manta ray in the Indian and Pacific Oceans: *Manta alfredi* and *M. birostris*. *Marine Biodivers Rec* 4:e53
- Ketchum JT (2011) Movement patterns and habitat use of scalloped hammerhead sharks (*Sphyrna lewini*) in the Galapagos Islands: Implications for the design of marine reserves. PhD dissertation, University of California, Davis, CA
- Ketchum JT, Hearn A, Klimley AP, Peñaherrera C, Espinoza C, Bessudo S, Soler G, Arauz R (2011a) Chapter 1. Diel and seasonal movements of scalloped hammerhead sharks (*Sphyrna lewini*) in the Galapagos Marine Reserve and connectivity in the Eastern Tropical Pacific. In: Ketchum JT (ed) (2011) Movement patterns and habitat use of scalloped hammerhead sharks (*Sphyrna lewini*) in the Galapagos Islands: implications for the design of marine reserves. PhD dissertation, University of California, Davis, CA
- Ketchum JT, Hearn A, Klimley AP, Espinoza E, Peñaherrera C, Largier J (2011b) Chapter 2: Movement patterns, home range, and habitat preferences of the scalloped hammerhead shark (*Sphyrna lewini*) near Wolf Island, Galapagos Marine Reserve. In: Ketchum JT (ed) (2011) Movement patterns and habitat use of scalloped hammerhead sharks (*Sphyrna lewini*) in the Galapagos Islands: implications for the design of marine reserves. PhD dissertation, University of California, Davis, CA
- Ketchum JT, Hearn A, Klimley AP, Espinoza E, Peñaherrera C, Bessudo S, Soler G, Arauz R (2011c) Chapter 3: Shark movements and the design of pelagic marine reserves. In: Ketchum JT (ed) (2011) Movement patterns and habitat use of scalloped hammerhead sharks (*Sphyrna lewini*) in the Galapagos Islands: implications for the design of marine reserves. PhD dissertation, University of California, Davis, CA
- Klimley AP (1974) An Inquiry into the causes of shark attacks. *Sea Frontiers* 20(2):66–75
- Klimley AP (1985) Schooling in *Sphyrna lewini*, a species with low risk of predation: a non-egalitarian state. *Zeitschrift fur Tierpsychology* 70:297–319

- Klimley AP (1993) Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Mar Biol* 117:1–22
- Klimley AP (2013) The biology of sharks and rays. University of Chicago Press, Chicago
- Klimley AP, Nelson DR (1984) Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuting central position social system. *Behav Ecol Sociobiol* 15:45–54
- Llerena Y (2009) Identificación de tiburones juveniles y caracterización de sus hábitats en las zonas costeras de pesca de la isla San Cristobal – Reserva Marina De Galapagos. BSc dissertation, University of Guayaquil, Ecuador
- Llerena Y, Murillo JC, Espinoza E (2010) Identification of rearing areas for blacktip sharks *Carcharhinus limbatus* in the mangrove stands of coastal San Cristobal Island. Galapagos report 2009–2010. Puerto Ayora, Galapagos, Ecuador
- Llerena Y, Peñaherrera C, Espinoza E (2012) Nursery grounds of juvenile sharks in three coastal mangrove areas of Santa Cruz Island, Galapagos Marine Reserve. In: Proceedings of the III Colombian workshop on Chondrichthyan, Oct 28–Nov 3 2012, Santa Marta, Colombia
- Marshall AD, Bennett MB (2010) Reproductive ecology of the reef manta ray (*Manta alfredi*) in southern Mozambique. *J Fish Biol* 77:169–190
- Marshall AD, Compagno LJ, Bennett MB (2009) Redescription of genus *Manta* with resurrection of *Manta alfredi* (Kreff, 1868) (Chondrichthyes; Myliobatoidei; Mobulidae). *Zootaxa* 2301:1–28
- Martinez C, Viteri C (2005) Estudio socioeconómico de la captura de tiburones en aguas marinas continentales del Ecuador. UICN, Quito, Ecuador
- Martinez J, Galvan F, Carrera M, Mendoza D, Estupiñan C, Cedeño L (2007) Seasonal abundance of shark landings in Manta-Ecuador. In: Martinez J, Galvan F (eds) Sharks in Ecuador: case studies. EPESPO-PMRC, Manta, Ecuador
- McCosker JE, Rosenblatt RH (2010) The fishes of the Galápagos Archipelago: an update. *Proc Calif Acad Sci Ser 4 vol 61 Supp II No 11*:167–195
- McCosker JE, Long DE, Baldwin CC (2012) Description of a new species of deepwater catshark, *Bythaelurus giddingsi* sp. nov., from the Galapagos Islands (Chondrichthyes: Carcharhiniformes: Scyliorhinidae). *Zootaxa* 3221:48–59
- MICIP (1989) Acuerdo Ministerial 151 del 21 de marzo de. Ministerio de Industrias, Comercio, Integración y Pesca, Quito, Ecuador
- MICIP (2006) Plan de Acción Nacional para la Conservación y el Manejo de Tiburones de Ecuador (PAT-Ec). Ministerio de Industrias, Comercio, Integración y Pesca, Ecuador
- Murillo JC, Reyes H, Zarate P, Banks S, Danulat E (2004) Evaluación de la captura incidental durante el Plan Piloto de Pesca de Altura con Palangre en la Reserva Marina de Galápagos. Fundación Charles Darwin y Servicio Parque Nacional Galapagos, Santa Cruz, Galapagos, Ecuador
- Myers RA, Ottensmeyer CA (2005) Extinction risk in Marine Species. In: Norse EA, Crowder LB (eds) Marine conservation biology: the science of maintaining the sea's biodiversity. Island Press, Washington, DC
- Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effect of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846–1850
- Nance H, Klimley AP, Galvan-Malgaña F, Martinez-Ortiz J, Marko PB (2011) Demographic processes underlying subtle patterns of population structure of the scalloped hammerhead shark, *Sphyrna lewini*. *PLoS One* 6(7):e12459
- Okey TA, Banks SA, Born AF, Bustamante RH, Calvopiña M, Edgar G, Espinoza E, Fariña JM, Francisco V, Garske LE, Salazar S, Shepherd S, Toral V, Wallem P (2004) A balanced trophic model of a Galapagos subtidal rocky reef for evaluating marine conservation strategies. *Ecol Model* 172:383–401
- Ordóñez A (2007) Determinación de la oferta actual y el potencial turístico de las islas Galápagos. Banco Interamericano de Desarrollo y Cámara Provincial de Turismo de Galápagos

- Peñaherrera C, Hearn AR, Kuhn A (2012) Diel use of a saltwater creek by white-tip reef sharks *Triaenodon obesus* (Carcharhiniformes: Carcharhinidae) in Academy Bay, Galapagos Islands. *J Trop Biol* 60(2):735–742
- Peñaherrera C, Llerena Y, Keith I (2013) Perceptions on the economic value of sharks for the daily diving tourism industry and the souvenir commerce in Santa Cruz Island. In: Galapagos report 2012. Charles Darwin Foundation, Galapagos National Park Directorate and Consejo de Gobierno de Galapagos, Galapagos, Ecuador
- Reyes H, Murillo JC (2007) Esfuerzos de control de pesca ilícita en la Reserva Marina. In: Informe Galapagos 2006-7. Fundacion Charles Darwin/INGALA/Parque Nacional Galapagos, Galapagos, Ecuador
- Rodriguez YN (2011) Impacto de la pesquería artesanal en la disminución de las poblaciones de tiburones en el Pacifico Oriental de Panama. Autoridad de los Recursos Acuaticos de Panama, Julio 2011, Panama
- Rowat D, Engelhardt U (2007) Seychelles: a case study of community involvement in the development of whale shark ecotourism and its socio-economic impact. *Fish Res* 84:109–113
- Ruiz DJ, Wolff M (2011) The Bolivar Channel ecosystem of the Galapagos Marine Reserve: energy flow structure and role of keystone groups. *J Sea Res* 66:123–134
- Sequeira AMM, Mellin C, Meekan MG, Sims DW, Bradshaw CJA (2013) Inferred global connectivity of whale shark *Rhincodon typus* populations. *J Fish Biol* 82:367–389
- Shillinger GL (2005) The Eastern Tropical Pacific Seascape: an innovative model for transboundary marine conservation. In: Mittermeier RA, Kormos CF, Mittermeier PRG, Sandwith T, Besancon C (eds) Transboundary conservation: a new vision for protected areas. Conservation International, Washington, DC
- Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthys), and the implications for marine ecosystems. *ICES J Mar Sci* 57: 476–494
- Vianna GMS, Meekan MG, Pannell D, Marsh S, Meeuwig JJ (2011) Wanted dead or alive? The relative value of reef sharks as a fishery and an ecotourism asset in Palau. Australian Institute of Marine Science and University of Western Australia, Perth, Australia
- Whitehead H (2001) Analysis of animal movement using opportunistic individual identifications: application to sperm whales. *Ecology* 82:1417–1432
- WildAid (2001) The end of the line? WildAid, San Francisco, CA
- WildAid (2010) An analysis of the law enforcement chain in the Eastern Tropical Pacific Seascape. WildAid, San Francisco, CA
- Wolff M, Peñaherrera-Palma C, Krutwa A (2012a) Food web structure of the Galapagos Marine Reserve after a decade of protection: insights from trophic modeling. In: Wolff M, Gardener M (eds) The role of science for conservation. Routledge, London
- Wolff M, Ruiz D, Taylor M (2012b) El Niño induced changes to the Bolivar Channel ecosystem (Galapagos): comparing model simulations with historical biomass time series. *Mar Ecol Prog Ser* 448:7–22
- Zanella I, Lopez A, Arauz R (2009) Caracterización de la pesca de tiburón martillo, *Sphyrna lewini*, en la parte externa del Golfo de Nicoya, Costa Rica. *Rev Mar y Cost* 1:175–195
- Zarate P (2002) Tiburones. In: Danulat E, Edgar G (eds) Reserva Marina de Galápagos. Línea Base de la Biodiversidad. Fundación Charles Darwin/Servicio Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador
- Zarate P, Hearn A (2008) Estado de conservación de los tiburones de Nicaragua, Costa Rica, Panama, Colombia y Ecuador. Charles Darwin Foundation/IUCN, Ecuador