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Long term residence, diel patterns and site preferences of *Carcharhinus falciformis, Carcharhinus limbatus, Carcharhinus galapagensis, Sphyrna lewini* and *Galeocerdo cuvier* in the Galapagos Marine Reserve, Ecuador.

Disertación previa a la obtención del título de Licenciada en Ciencias Biológicas

MISHELL STEFANÍA GARCÍA ZAMBRANO

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Long term residence, diel patterns and site preferences of *Carcharhinus falciformis, Carcharhinus limbatus, Carcharhinus galapagensis, Sphyrna lewini* and *Galeocerdo cuvier* in the Galapagos Marine Reserve, Ecuador.

Stefanía García-Zambrano[1], Alex Hearn[2], Santiago Burneo[1]

[1]Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

[2]Red de Investigación y Conservación Marina MigraMar, Ciudad de México, México.

Correspondence

Stefanía García

sgarciazambrano@outlook.es

ABSTRACT

Over 14 years the MigraMar scientific network has obtained valuable information on the movement of five species of sharks of high scientific interest in the Eastern Tropical Pacific through acoustic biotelemetry. This technology has allowed long-term monitoring of 56 individuals with external and internal acoustic transmitters inside and outside the Galapagos Marine Reserve. This study demonstrates their long-term residence in the reserve and the connectivity between Darwin, Wolf, Roca Redonda and Central south-eastern, and external connectivity between Malpelo, Cocos, Revillagigedo and Clipperton islands, showing their diurnal/nocturnal activity and site preferences throughout the GMR.

KEY WORDS

Biotelemetry, Carcharhinidae, Eastern Tropical Pacific, Galapagos Marine Reserve, Long – Term Residency, Sphyrnidae.

INTRODUCTION

The Eastern Tropical Pacific (ETP) covers an area of two million hectares between Southern Baja California, Mexico and North of Peru (Ketchum et al., 2014). The region hosts several marine protected areas including UNESCO Natural World Heritage Sites such as the Galapagos Marine Reserve (Ecuador), Malpelo Marine Sanctuary (Colombia), Cocos National Park (Costa Rica) and Revillagigedo National Park (Mexico), all of which emphasize protecting sharks and other highly mobile threatened marine species (Bessudo et al., 2011).

Many pelagic sharks are highly migratory predators (Camhi et al., 2008, Stein et al., 2018), however, some species (in particular from the Carcharhinidae and Sphyrnidae families) are temporally resident at coastal and island locations for feeding, mating and breeding (Heithaus, 2007). Their migratory nature, bringing them into contact with different fishing fleets, has caused their populations to decline severely over recent decades (Lisney et al., 2012; Coffey et al., 2020).

Increased global fishing effort, together with an increasing demand for shark fins, has led to higher concern about shark populations across the world's oceans. Annual average catches of sharks are around 595 metric tons, 33 % of them corresponds to Pacific Ocean catches (Dent and Clarke, 2015; Okes and Sant, 2019). Ecuador is one of the twenty countries with greatest shark capture reports worldwide, with two highly-affected genera: *Sphyrna* and *Carcharhinus* (Okes and Sant, 2019). Both are top predators, and have an important ecological role, providing a link between oceanic and coastal habitats (Hearn et al., 2017).

Although Ecuador has developed a National Action Plan for sharks, and is a signatory of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Pazmiño Manrique et al., 2018), over 200,000 sharks are landed each year as by-catch, many of which come from the waters surrounding the Galapagos Marine Reserve (GMR) (Martínez-Ortiz et al., 2015).

The GMR is located 1000 km from the Ecuadorian coast encompassing 133 000 km^2 of protected area (González et al., 2008). Researchers have studied the short-term movements of some shark species in and around the GMR for 15 years (Hearn et al., 2010, 2017; Ketchum et al., 2014; Peñaherrera-Palma et al., 2018). Many of these studies have focused on the use of ultrasonic telemetry to address residency and site fidelity of sharks around the islands. This technique comprises the use of coded transmitters either attached externally with darts or implanted in the peritoneal cavity of sharks, which emit a signal at 69 kHz frequencies which can then be detected when within 200 m (Hearn et al at 2010) of a network of passive receivers deployed in the area (Webber, 2009).

The receivers deployed in the GMR are part of a region-wide array managed by the MigraMar network of scientists studying the movement ecology of sharks and turtles throughout the ETP. However, to date, most studies have focused on time-scales of weeks to months, partly due to tag retention issues.

This study aims to analyze *C. falciformis*, *C. limbatus*, *C. galapagensis*, *S. lewini* and *G. cuvier* residency indices at the GMR with particular interest in Darwin and Wolf islands in the far northern bioregion and Baltra in the central - southeastern bioregion in order to

determine whether they move around the marine reserve or stays at a single island, follows rhythmic and synchronized patterns and what are their preferred sites.

METHODOLOGY

Study Area

At the time of its creation in 1998, the GMR was the world's second largest MPA (currently it is the 33rd) and was declared a Natural World Heritage site by UNESCO in 2001 and a Mission Blue Hope Spot in 2020 (Burbano et al., 2020). The GMR is divided into four bioregions. Far Northern includes Wolf and Darwin, Northern includes Pinta, Marchena and Genovesa islands; Western includes Fernandina and Isabela while Central – Southeastern includes Santiago, Santa Cruz, Baltra, Floreana, San Cristobal and Española as major islands (>10 km^2) (Edgar et al., 2004) (Figure 1). The convergence of a system of currents and countercurrents gives rise to considerable environmental variability in oceanographic conditions, such as the difference in water temperature between islands, within same time intervals (Edgar et al., 2004). The Equatorial Undercurrent flows east and the South Equatorial current flows west at the surface increasing the nutrients concentration, the Panama current is associated with warm temperatures and Humboldt current is associated with cool temperatures (Humphreys et al., 2018). As a result, the GMR has a unique environment with high endemism and seasons divided over two seasons, from December to May hot water temperatures prevail (21°C – 26°C), while from June to November the coolest water temperatures prevail (18°C – 24°C). There is also considerable inter-annual variation based on the El Niño Southern Oscillation (ENSO): when the "El Niño" event occurs (every 4 – 7 years), the surface ocean temperature reaches 28°C and sea level increases by up to 45 cm (Elias, 2020).

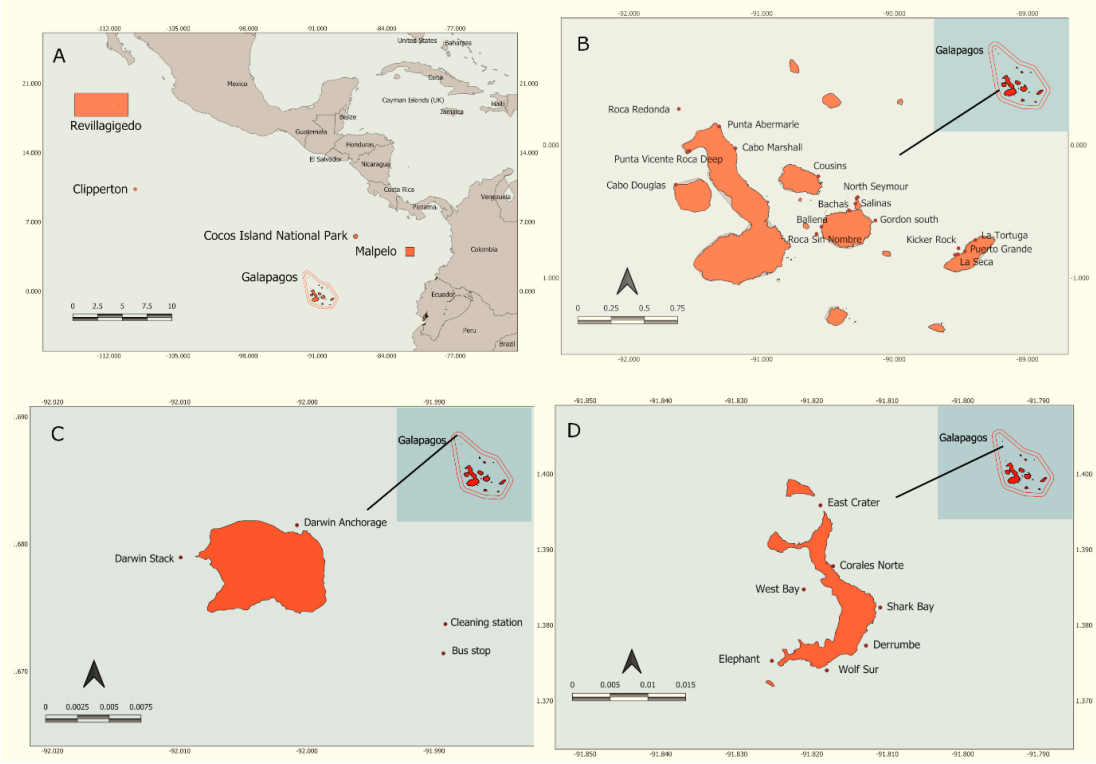


Figure 1. Study sites **A)** Bottom up: Galapagos Marine Reserve, Malpelo's Fauna and Flora Sanctuary, Cocos National Park, Clipperton island and Revillagigedo Archipelago **B)** Central islands receivers. **C)** Darwin island receivers **D)** Wolf island receivers.

Study species

Carcharhinus falciformis (Müller & Henle, 1839) - Carcharhinidae

The Silky shark is a solitary epipelagic species associated with deep water reefs (18–500 m) with a circumglobal distribution in tropical and subtropical waters along the eastern Pacific. It's found from southern Baja California to northern Chile (Froese and Pauly, 2020) and has been regarded as dangerous due to its potential size (0.87 m at birth and 3.3 m in maturity) and occurrence offshore near land (Compagno, 1984)

The species feeds mainly on fishes and squids and are commonly associated to tuna schools, mature females can have between 2 – 14 offspring (viviparous with a yolk – sac placenta), (Compagno, 1984), and is considered vulnerable by the IUCN due to direct and bycatch fishing (Clarke et al., 2015; IUCN, 2020).

Carcharhinus limbatus (Müller & Henle, 1839) - Carcharhinidae

The Blacktip shark is a pelagic species with preferences to estuaries, lagoons and coral reef drop–offs (0–100 m), is cosmopolitan and can be found in Western Atlantic, Eastern Atlantic, Indo – Pacific, and Eastern Pacific from Mexico to Peru including the Galapagos islands (Froese and Pauly, 2020).

Their diet is based on pelagic, benthic fishes, and small sharks and rays; females are viviparous, with a yolk-sac placenta and have up to ten young per litter (max. length 2.75 m, size at birth 0.38 - 0.72 m) (Compagno, 1984; Froese and Pauly, 2020), however, is a Near Threatened species (IUCN, 2020).

Carcharhinus galapagensis (Snodgrass & Heller, 1905) - Carcharhinidae

The Galapagos shark is a circumtropical pelagic species founded at rocky bottoms (30–180 m) with presence at Western Indian Ocean, Western Pacific and Eastern Pacific including Galapagos islands (Froese and Pauly, 2020).

Their diet includes fishes, squids and octopi, however in the GMR it preys on sea lions and iguanas as well, the species maximum length reported is 3.70 m, and females are viviparous with a yolk – sac placenta (litters can have up to 16 offspring), (Compagno, 1984; Froese and Pauly, 2020) with a Near Threatened status (IUCN, 2020).

Galeocerdo cuvier (Péron & Lesueur, 1822) - Carcharhinidae

The Tiger shark is a circumtropical species associated to the bottom that can be found from surface to 140 m depth, is present in tropical waters that includes Western Atlantic, Eastern Atlantic, Indo Pacific and Eastern Pacific including Revillagigedo, Cocos and the Galapagos islands (Froese and Pauly, 2020).

Is a nocturnal predator, as Near Threatened by IUCN (2020). that feeds mainly on fishes, marine mammals and reptiles, however it has been reported that can consume garbage such as metal pieces and carrion, females are ovoviviparous and their litter can have up to 82 young (max. length reported is 7.5 m) (Compagno, 1984; Froese and Pauly, 2020).

Sphyrna lewini (Griffith & Smith, 1834) - Sphyrnidae

The Scalloped hammerhead shark is a Critically Endangered species due to commercial illegal fisheries for its fins (IUCN, 2020). Is pelagic with a circumglobal distribution and can be found from surface to 1,000 m depth (mostly present at 25 m) in tropical zones, including Western Atlantic, Eastern Atlantic, Indo Pacific, and Eastern Pacific from USA to Ecuador (including Galapagos islands) (Froese and Pauly, 2020).

Juveniles are present on large schools and adults can be found either solitary, in pairs or schools, their diet includes teleost fishes and cephalopods and females are viviparous, placental with litters up to 23 young (max. length is 4.3 m, size at birth is 0.5 m) (Compagno, 1984; Froese and Pauly, 2020).

Fieldwork

Receiver deployment

VEMCO VR2W underwater receivers were deployed at 28 stations across the archipelago. Each receiver was affixed to a 25 kg concrete base to which was attached a 2-3 m rope or cable with a sub-surface buoy. Receivers were attached to the cable using a combination of clamps and plastic cable-ties approximately 1.5 m from the seabed at depths ranging from 28 to 40 m. Range testing carried out by Hearn et al (2010) suggested that, in general, 50 % of tag transmissions are detected at a distance of 250 m. Similar arrays were deployed by the MigraMar network (available at http://www.migramar.org) at Cocos National Park, Malpelo's Sanctuary, Archipelago of Revillagigedo and Clipperton island (Fig.1).

Tagging

28 transmitters (VEMCO, V16, 69.0 kHz). were attached externally to the dorsal musculature of sharks with pole spears by free divers and internally by insertion into the peritoneal cavity by means of a small incision, which was then closed using 2-3 degradable sutures (these individuals were capture by a local fisherman using hook and line) (Hearn. et al., 2014).

56 individuals with over 300 days of detections were tagged since 2006 with acoustic transmitters. Our sample consisted of the following:

- Hammerhead shark (*Sphyrna lewini*): 24 females, 1 unknown and 1 male (n=26), with sizes between 1.4 -2.8 m, four individuals were tagged in Cocos National Park, five in Darwin, one in Malpelo and sixteen in Wolf (between 2006 - 2017).
- Silky shark (*Carcharhinus falciformis*): 9 females and 2 males (n=11), with sizes between 1.8–2.26, one individual was tagged in Cocos National Park, three in Darwin and seven in Wolf (between 2010 - 2014).
- Blacktip shark (*Carcharhinus limbatus*): 8 females (n=8), with sizes between 1.91 – 2.15, four individuals were tagged in Baltra, one in Darwin, one in Mosquera and two in North Seymour (between 2006 - 2014).
- Galapagos shark (*Carcharhinus galapagensis*): contains 6 females and 2 males (n=8), with sizes between 1.7 – 2.45, two individuals were tagged in Darwin, two

in Malpelo, one in Santa Cruz, one in Revillagigedo and two in Wolf (between 2009 - 2016).

- Tiger shark (*Galeocerdo cuvier*): 3 females (n=3), with sizes between 2.52 – 3.84, all were tagged in Baltra (2014).

Residency index (RI)

The Residency Index (RI) was calculated as the number of days that a shark was detected on any given receiver, divided by the total track length (number of days from tagging to the last detection). For this study, we only used sharks with overall track lengths equal to or greater than 300 days. The Galapagos residence index (GMR RI) was calculated as a proportion between the total detected days and the track length. Darwin, Wolf and Baltra RIs were calculate as a proportion between the total detected days at each island and the total track length. Monthly RI was calculated as a proportion between the detected days and the total days per month, and the annual RI was calculated as a proportion between the total detected days per year and 365 days (with an exception on leap-year where 29 days were considered in February).

Seasonal patterns

GMR seasons were divided in two semesters, warm season begins in December and finish at May, while cold season begins in June and finish at November. A Shapiro - Wilk test was performed with each species monthly and seasonal residence index values, considering 0.05 as significance value at R Studio software (R Foundation: www.rproject.org).

Residency events

The acoustic detection data was analyzed with V-Track R package, in order to identify ecological events such as residence, through the synthesis of location points and movements data provided by VEMCO acoustic tags (Dwyer et al., 2015).

Habitat preferences

A density point map was elaborated with each receiver station residency index through QGIs 3.16.0 software.

Diel patterns

In order to understand species daily cycles, time data (24 hours) was analyzed by Oriana software, a Microsoft Windows program that analyzes circular data by calculating basic statistics, circular histograms and Rayleigh's Uniformity Test were perform, considering Z and P values (Aldana-Moreno et al., 2020; Ketchum et al., 2020).

RESULTS

Residency Index (RI)

The summary of individual detections is shown in Table 1 and Residency index (RI) values for each species are shown in Figure 2. Hammerhead sharks (*S. lewini*) GMR RI value is 0.245 and has the higher Wolf RI value (0.55) (zero detections at Baltra), eighteen individuals showed movements between Darwin & Wolf, and other seven individuals have been detected at Darwin, Wolf and others GMR islands. Individual#22, 24, 25 and 26 (Tag ID 38087 - 31016 – 31037 - 30574) showed movements between Cocos National Park and Wolf, their Cocos residency index are 0.04, 0.002, 0.008 and 0.06 respectively.

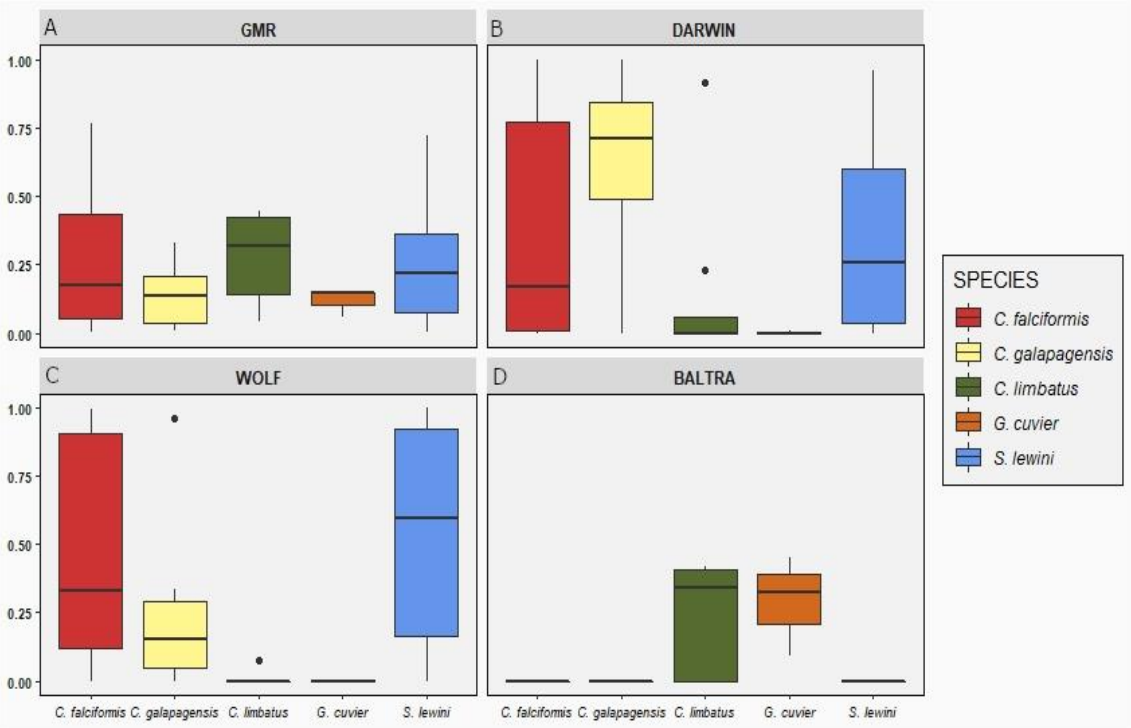


Figure 2. Residency index per species by study site. From left to right: C. falciformis, C. galapagensis, C. limbatus, G, cuvier and S. lewini. A) Galapagos (GMR), B) Darwin's Residency index C) Wolf's Residency index D) Baltra's Residency index

Individual#2 (Tag ID 1206) showed movements from Wolf island to Darwin and Cocos National Park with a Cocos RI of 0.04, and Individual#18 (Tag ID 6962) showed movements from Malpelo to Darwin, Wolf, Roca Redonda & Cocos National Park with a Malpelo RI of 0.02 and Cocos RI of 0.02.

Silky sharks (*C. falciformis*) GMR RI is 0.25, six individuals showed movements between Darwin & Wolf only, one was detected only at Darwin, one only at Wolf and one included central islands within its range (Baltra and Santa Cruz), individual#28 (Tag ID 46665) was tagged at Cocos Island and included few detections in Wolf and Roca Redonda (Cocos RI value is 0.2), finally individual#27 (Tag ID 55955) showed movements from Wolf to Clipperton islands (Figure 3), stayed for 38 days, and move back to Darwin and Roca Redonda (Clipperton RI value is 0.05).

Galapagos shark (*C. galapagensis*) GMR RI value is 0.138, two individuals were tagged at Malpelo and detected at Darwin and Wolf only, one stayed at Darwin, and the other five, include Isabela, Mosquera, North Seymour, Santa Cruz and Roca Redonda, individual #45 (Tag ID 22687) was tagged at Socorro, and included movements from Clipperton to Darwin with 88 days of detections at Clipperton islands, its Clipperton RI value is 0.01.

Blacktip shark (*C. limbatus*) GMR RI value is the highest (0.28), four individuals showed movements between Santa Cruz, Baltra and North Seymour, three included also Darwin, Cousins, Mosquera and Venezia, and one individual included movement between Darwin, Wolf and central - southeastern bioregion.

Tiger shark (*G. cuvier*) GMR RI value is the lowest (0.12). All three individuals showed movements from Baltra to Santa Cruz and North Seymour; individual #56 (Tag ID 27484) includes Wolf island as part of its detection and individual #55 (Tag ID 27483) showed recent movements from GMR to Cocos Island (Dos Amigos, Punta Maria, Dirty Rock and Manuelita) for a 30 days period in 2020.

Table 1. Tagging and detections overviews

#	Tag ID	Species	Sex	Size	Island	Tag Date (local)	Track Length (days)	Detection (days) GMR	Residency index (GMR)	Islands detected
1	1207	*S. lewini*	F	1.8	Wolf	2006-07-21	421	111	0.2637	Darwin & Wolf
2	1206	*S. lewini*	F	2	Wolf	2006-07-21	400	88	0.2200	Darwin, Cocos & Wolf
3	1217	*S. lewini*	F	1.5	Wolf	2006-07-23	2000	202	0.1010	Darwin & Wolf
4	1218	*S. lewini*	F	2	Wolf	2006-07-23	369	48	0.1301	Darwin & Wolf
5	1223	*S. lewini*	F	1.5	Darwin	2006-07-24	847	182	0.2149	Darwin & Wolf
6	1220	*S. lewini*	F	1.5	Darwin	2006-07-24	329	127	0.3860	Darwin & Wolf
7	5520	*S. lewini*	F	2.2	Wolf	2007-07-21	1646	895	0.5437	Darwin & Wolf
8	5515	*S. lewini*	F	1.5	Wolf	2007-07-21	363	243	0.6694	Darwin & Wolf
9	5616	*S. lewini*	F	2.3	Wolf	2007-07-23	2331	207	0.0888	Darwin & Wolf
10	5619	*S. lewini*	F	1.5	Wolf	2007-07-23	533	151	0.2833	Darwin & Wolf
11	5608	*S. lewini*	F	2	Wolf	2007-07-23	463	31	0.0670	Darwin, Wolf & Roca Redonda
12	7281	*S. lewini*	F	1.5	Darwin	2007-10-29	366	85	0.2322	Darwin & Wolf
13	7285	*S. lewini*	i	1.4	Wolf	2007-10-31	333	34	0.1021	Darwin & Wolf
14	7265	*S. lewini*	F	1.8	Wolf	2007-11-01	811	365	0.4501	Darwin & Wolf
15	7270	*S. lewini*	F	1.8	Wolf	2007-11-01	410	171	0.4171	Darwin, Wolf & Roca Redonda
16	7267	*S. lewini*	F	2	Wolf	2007-11-01	362	79	0.2182	Darwin & Wolf
17	7278	*S. lewini*	F	1.8	Wolf	2007-11-04	462	334	0.7229	Darwin & Wolf
18	6962	*S. lewini*	F	2.2	Malpelo	2008-03-03	397	25	0.0630	Darwin, Wolf, Cocos, Malpelo & Roca Redonda
19	52941	*S. lewini*	F	2	Wolf	2009-02-16	864	202	0.2338	Darwin, Wolf & Roca Redonda
20	52938	*S. lewini*	F	2	Darwin	2009-03-15	888	56	0.0631	Darwin & Wolf
21	55947	*S. lewini*	F	1.6	Darwin	2009-08-06	456	28	0.0614	Darwin & Seymour Norte

22	38087	*S. lewini*	F		Cocos	2010-07-02	166	39	0.2349	Darwin & Wolf
23	63853	*S. lewini*	M	2.3	Wolf	2012-02-22	760	411	0.5408	Darwin & Wolf
24	31016	*S. lewini*	F	2.8	Cocos	2017-01-06	456	5	0.0110	Wolf
25	31017	*S. lewini*	F	2.8	Cocos	2017-05-31	238	1	0.0042	Wolf
26	30574	*S. lewini*	F		Cocos	2017-07-08	550	23	0.0418	Darwin & Wolf
27	55955	*C. falciformis*	F	1.87	Wolf	2010-03-05	782	13	0.0166	Darwin, Clipperton, Roca Redonda & Wolf
28	46665	*C. falciformis*	F	2.26	Cocos	2011-01-23	961	5	0.0052	Cocos, Wolf & Roca Redonda
29	46678	*C. falciformis*	F	1.8	Wolf	2012-02-15	2743	58	0.0211	Darwin, Wolf & Isabela
30	46670	*C. falciformis*	M	2.14	Wolf	2012-02-15	849	652	0.7680	Darwin & Wolf
31	46672	*C. falciformis*	M	2.17	Wolf	2012-02-16	1106	532	0.4810	Darwin & Wolf
32	46674	*C. falciformis*	F	2.24	Darwin	2012-02-19	980	381	0.3888	Darwin
33	25718	*C. falciformis*	F	1.98	Darwin	2014-01-17	1802	954	0.5294	Darwin & Wolf
34	25715	*C. falciformis*	F	1.8	Wolf	2014-01-17	818	65	0.0795	Darwin & Wolf
35	25720	*C. falciformis*	F	1.83	Wolf	2014-01-18	2078	367	0.1766	Darwin & Wolf
36	25721	*C. falciformis*	F	2.23	Wolf	2014-01-18	1027	198	0.1928	Darwin & Wolf
37	25726	*C. falciformis*	F	2.16	Darwin	2014-01-19	1278	120	0.0939	Santa Cruz, Darwin, Fernandina, Wolf, Isabela & Baltra
38	52948	*C. galapagensis*	F	2	Darwin	2009-03-15	782	78	0.0997	Darwin
39	55929	*C. galapagensis*	M	2.45	Darwin	2009-08-06	874	33	0.0378	Darwin, Wolf & Roca Redonda
40	55953	*C. galapagensis*	F	2	Wolf	2009-08-07	559	16	0.0286	Darwin, Isabela & Wolf
41	55935	*C. galapagensis*	F	1.7	Santa Cruz	2010-03-13	686	224	0.3265	Santa Cruz, Wolf, Mosquera & Seymour Norte
42	46663	*C. galapagensis*	F	1.94	Wolf	2012-02-18	2438	578	0.2371	Darwin, Wolf & Roca Redonda
43	44584	*C. galapagensis*	F	2.27	Malpelo	2014-12-13	219	38	0.1735	Darwin & Wolf
44	44583	*C. galapagensis*	M	2.09	Malpelo	2014-12-13	417	3	0.0072	Darwin & Wolf
45	22687	*C. galapagensis*	F	1.81	Socorro	2016-02-27	1312	258	0.1966	Darwin, Isabela, Clipperton & Wolf
46	1225	*C. limbatus*	F	2.04	Darwin	2006-07-24	1865	82	0.0440	Darwin, Santa Cruz, Isabela, Wolf, Cousins, Mosquera, Seymour Norte & San Cristobal
47	63855	*C. limbatus*	F	2.1	Seymour norte	2010-10-15	2000	308	0.1540	Darwin, Cousins, Mosquera & Seymour Norte
48	63859	*C. limbatus*	F	1.91	Seymour norte	2010-10-15	435	193	0.4437	Mosquera, Seymour Norte & Venezia
49	32392	*C. limbatus*	F	2.15	Baltra	2014-01-25	1078	120	0.1113	Santa Cruz, Baltra, Mosquera & Seymour Norte
50	46679	*C. limbatus*	F	2.13	Mosquera	2014-01-28	496	169	0.3407	Santa Cruz, Baltra & Seymour Norte
51	25728	*C. limbatus*	F	1.93	Baltra	2014-01-29	1086	455	0.4190	Santa Cruz, Baltra & Seymour Norte
52	25730	*C. limbatus*	F	2.13	Baltra	2014-01-29	1086	318	0.2928	Santa Cruz, Baltra & Seymour Norte

53	25723	*C. limbatus*	F	2.03	Baltra	2014-01-30	1083	471	0.4349	Santa Cruz, Baltra & Seymour Norte
54	27482	*G. cuvier*	F	2.52	Baltra	2014-01-30	374	22	0.0588	Santa Cruz, Baltra & Seymour Norte
55	27483	*G. cuvier*	F	2.74	Baltra	2014-01-30	2473	364	0.1472	Santa Cruz, Baltra & Cocos
56	27484	*G. cuvier*	F	3.84	Baltra	2014-01-30	1746	254	0.1455	Santa Cruz, Wolf, Seymour Norte & Baltra

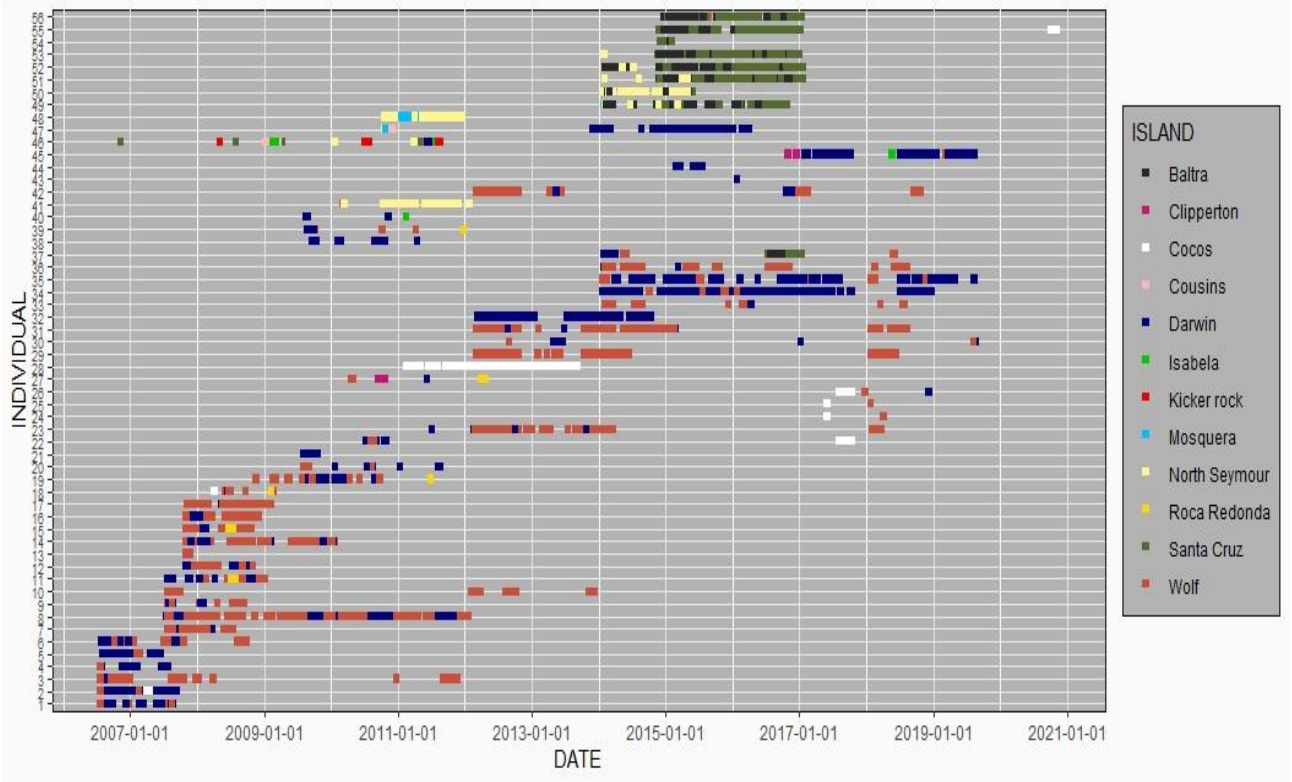


Figure 3. Individual monitoring. S. lewini: 1 – 26, C. falciformis 27 – 37, C. galapagensis 38 – 45, C. limbatus 46 – 53, G. Cuvier 54-56.

Seasonal patterns

Shapiro wilk test values for each species accept the null hypothesis (Table 2), showing normal distribution. Hammerhead sharks follow a clear pattern at Wolf during warm and cold seasons (Figure 4). As the warm season progresses, their presence decreases, a female tagged at Wolf moves to Cocos National Park during March and April, a female tagged at Malpelo moves from there to Cocos at April and a female tagged at Darwin swam to North Seymour from March to November.

During the cold season, 22 individuals move between Darwin and Wolf and four of them move to Roca Redonda (Tag ID 5619 - 7267 - 52941 detected during cold season and Tag ID 6962 during warm season). Peak detections at Wolf occur during July and October (RI = 0.34) and August, September and November (RI = 0.36) (Table 2).

Silky shark movements in the warm season follows a pattern between Darwin and Wolf islands from December to February, while Darwin's residency index decrease, Wolf's

residency index increase (Figure 4), in one case, a female (2.24 meters) have no detections at Wolf island, however between February and June this individual has also no detections at Darwin island.

March and April showed the lowest warm RI values at both islands, but two individuals (Tag ID 46665 and 55955) were detected at Roca Redonda during that period. At the beginning of cold season, silky shark presence at Darwin increases, but shows similar residency index values from July to November at Darwin and Wolf.

This was not the case of a female (1.87 meters) tagged at Wolf that showed movements to central GMR islands during that period, and a female (2.16) tagged at Darwin that moved to Clipperton islands from September to October.

Galapagos sharks showed no clear patterns at Darwin and Wolf islands in either season. Individuals are detected at different islands such as North Seymour, Mosquera and Isabela, throughout the year.

However, two individuals (Tag ID 46663 and 55929) were detected in Roca Redonda during warm season in December and April, and a female tagged at Revillagigedo moved to Clipperton at the beginning of warm season and then swam to Darwin, where it remained for ten months.

Blacktip sharks (all females) have a high residency index at GMR, which highest peak is February when seven individuals show presence only at central islands. The species have no detections at Wolf island with an exception of one individual (Tag ID 1225 - 2.04 meters, tagged at Darwin) that moves around far northern bioregion during June and July, and moves to central islands during cold season.

One individual (tagged at North Seymour) stayed around the central bioregion during October and November, between Cousins, Mosquera and North Seymour and then appeared in Darwin (Bus stop station) 2 years later in December where stays for 9 months; five from eight total individuals move constantly to Baltra all over the year, with no obvious patterns.

The smallest of the tiger sharks (#54) spent most of its time (79% of detections) in Bachas station (Santa Cruz from December 2014 to February 2015), after which it was absent for 306 days. Two other females moved around Bachas and Baltra island stations all year long. These stations are all fairly close to one another (Baltra to Salinas point = 4.68 km; Salinas to Bachas station = 7.61 km), and that Bachas station had 136 more detections during track length. Individual #55 appeared in Cocos in October after 3 years of absence.

Table. 2 Shapiro wilk test values. H0: normal distribution. H1: not normal distribution, Significance value: 0.05

SPECIES	**MONTH p-value**	**SEASON p-value**
C. falciformis	0.194	0.694
C. galapagensis	0.715	0.489
C. limbatus	0.441	0.687
G. cuvier	0.271	0.319
S. lewini	0.300	0.344

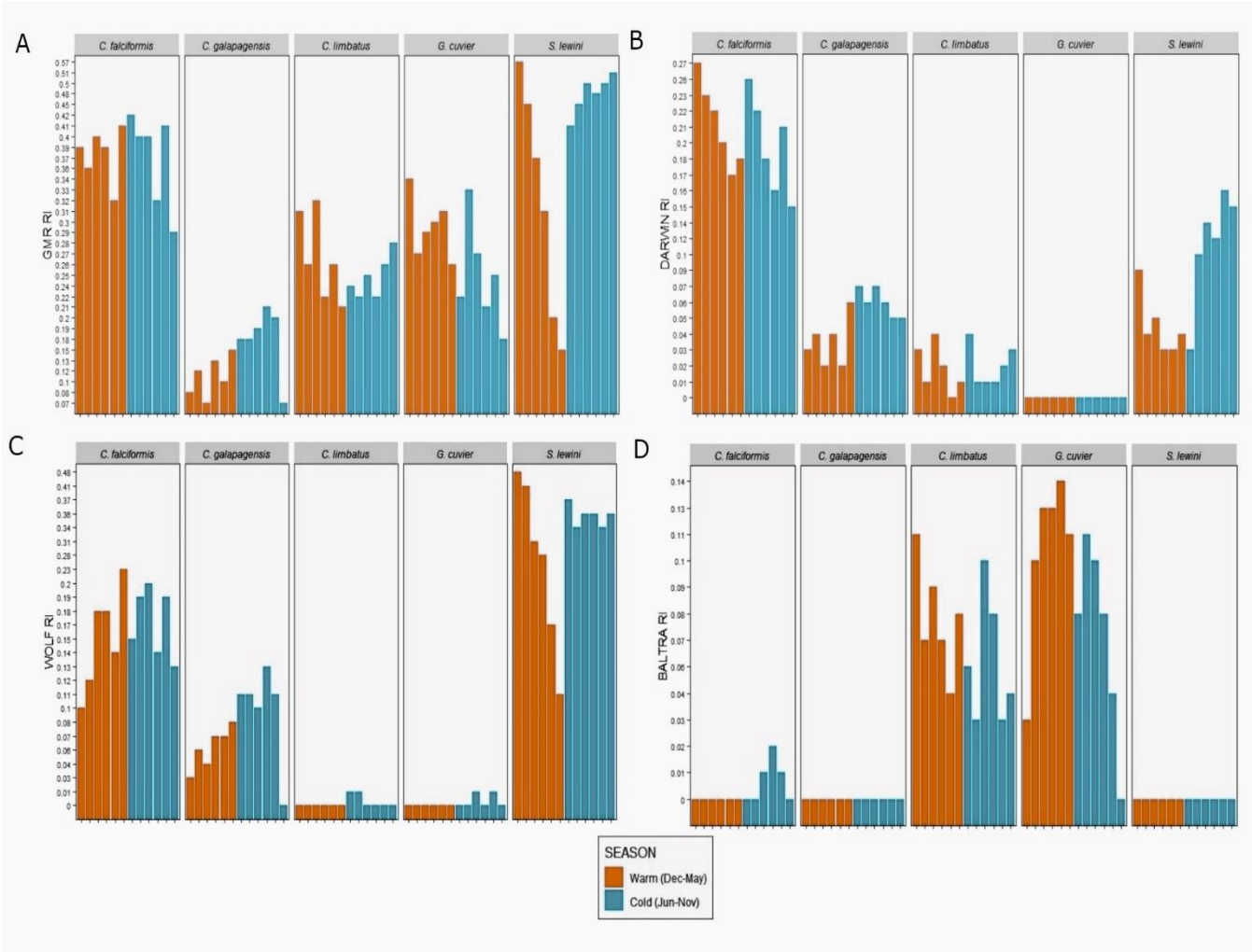


Figure 2. Seasonal patterns by study site. From left to right: December, January, February, March, April, May, June, July, August, September, October and November. A) Galapagos Marine Reserve's monthly residency index. B) Darwin's monthly residency index

Residency events and habitat preferences

In the GMR, 4,450 residency events were detected for *C. falciformis*, 1,409 for *C. galapagensis*, 2,029 for *C. limbatus*, 13,451 for *S. lewini* and 558 for *G. cuvier*. Each residency event lasted up to 12.98 hours. In Darwin island, Cleaning station receiver had the higher residency index for *C. falciformis* and *C. galapagensis* (Figure 5), in Wolf island, Shark bay receiver had the higher residency index for *S. lewini* (Figure 6), while Bachas receiver at Santa Cruz had the higher index for *G. cuvier* (Figure 7).

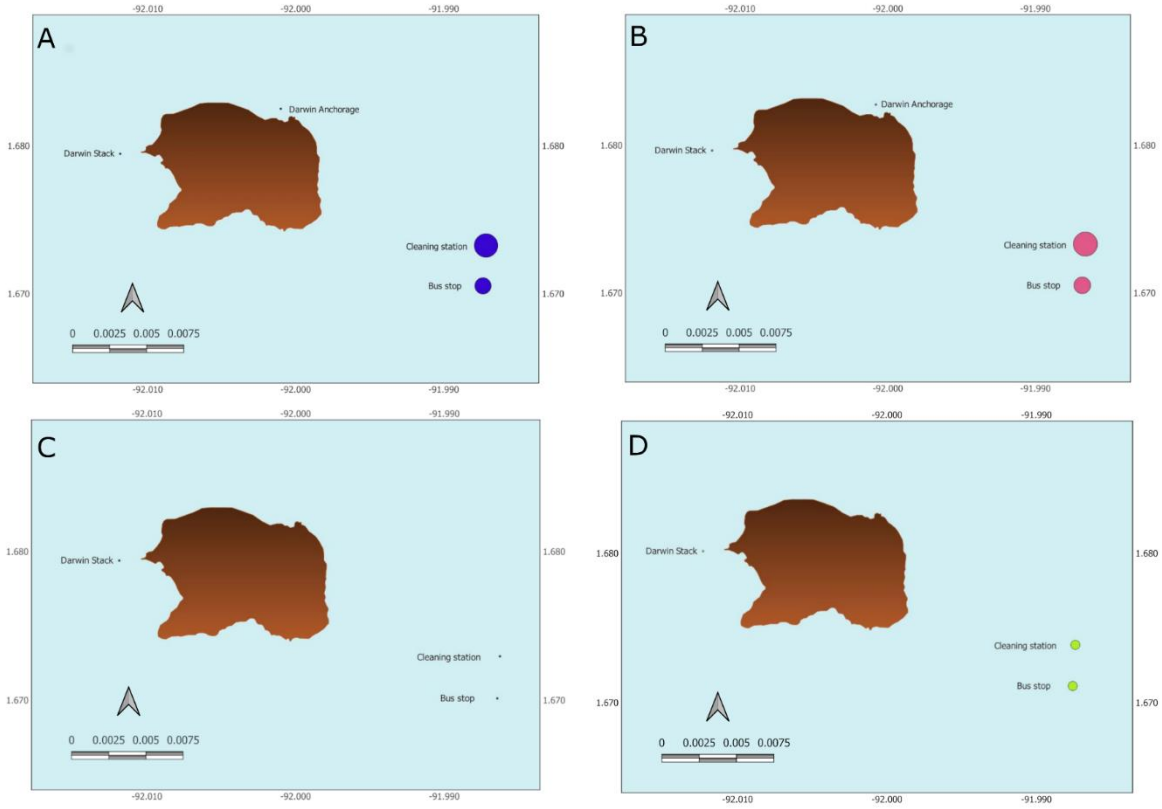


Figure 3. Darwin's receiver preferences. **A**) *C. falciformis* – higher residency index at Cleaning station (0.33) **B**) *C. galapagensis* – higher residency index at Cleaning station (0.25) **C**) *C. limbatus* – all receivers with values lower than 0.1 **D**) *S. lewini* - Cleaning station and Bus stop residency index (~0.1).

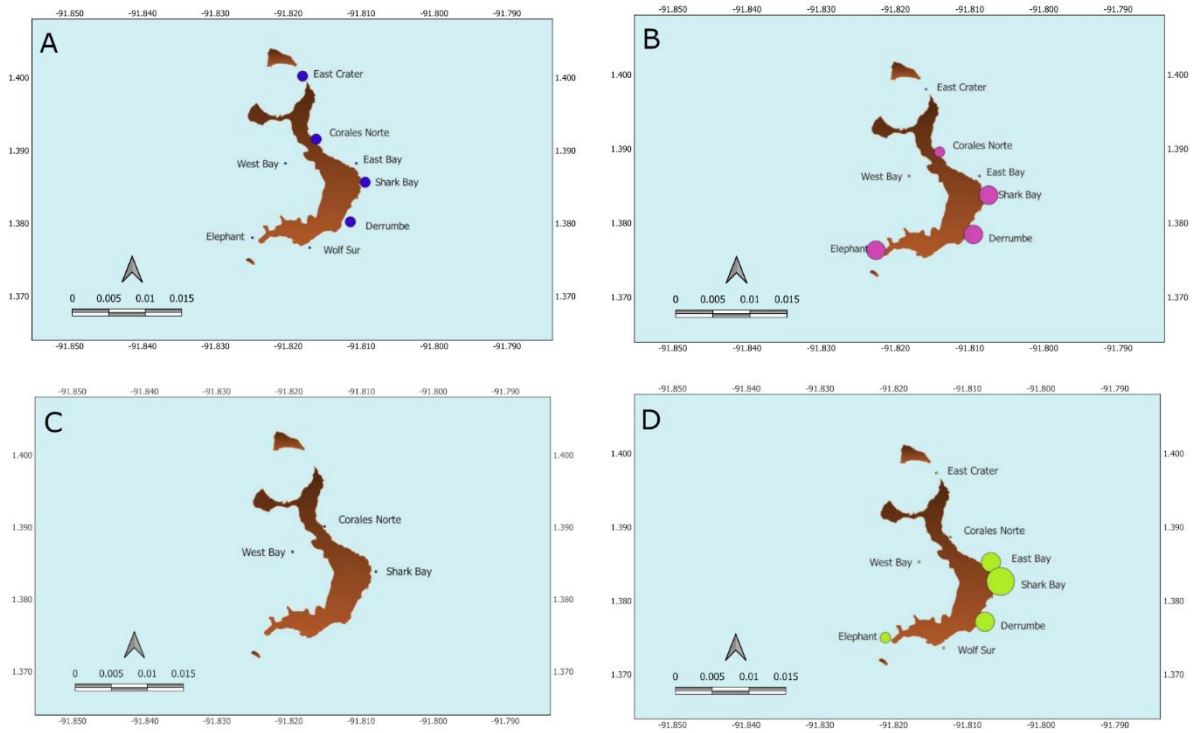


Figure 4. Wolf's receiver preferences. **A**) *C. falciformis* – smallest circles show residency indexes from 0.001 – 0.05, others from 0.06 - 0.11 (0.13) **B**) *C. galapagensis* – higher frequency at Shark Bay (0.15) **C**) *C. limbatus* – all receivers with frequencies lower than 0.1 **D**) *S. lewini* – higher frequency at Shark Bay (0.3).

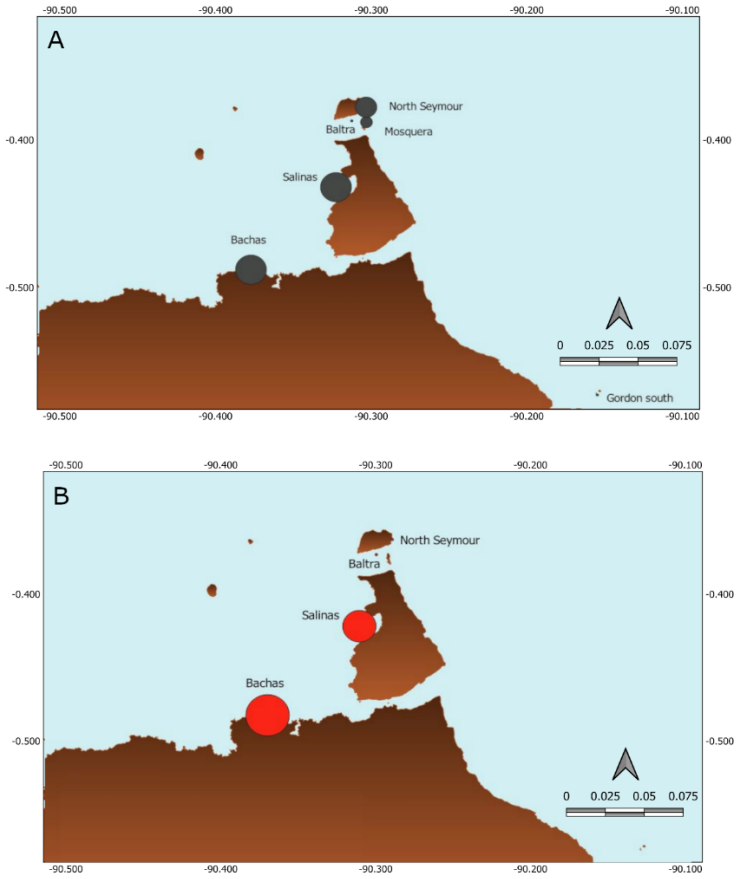


Figure 5. Baltra's receiver preferences. **A**) *C. limbatus* - higher frequency at Bachas station (0.4) **B**) *G. cuvier* – higher frequency at Bachas station (0.7).

Diel patterns

Rayleigh's test shows the probability of uniformity all along time data with Z (nr2) and P (follows Fisher's equations) values, in this study the uniformity one-sample test results rejected the null hypothesis for all species (Table 3), establishing that the data were not uniform cause species didn't follow the same preference of direction (Figure 8) (Kovach, 2011).

Oriana software statistics are based on mean vector (μ) concept (in this case each detection can be relate as an individual vector), *C. falciformis*, *C. limbatus* and *C. galapagensis* shows different mean vectors (μ) between themselves at Darwin, Wolf and Baltra (Figure 8), showing opposites directions in the graph (divided into 24 hours).

C. falciformis shows higher detections at Darwin between 6:00 AM–6:00 PM, at Wolf between 6:00 PM–6:00 AM and Baltra shows highest peak between 12:00 AM–1:00 AM. *C. limbatus* highest detections in Darwin are between 6:00 AM–12:00 PM, in Wolf between 12:00 PM–6:00 PM and Baltra between 6:00 PM–6:00 AM. For *C. galapagensis* highest Darwin detection number is between 7:00 AM–9:00 AM, but in Wolf is between 7:00 AM–7:00 PM (No detections at Baltra).

S. lewini shows similar mean vectors (11:06 AM and 11:15 AM) at Darwin and Wolf, with higher detections between 6:00 AM–6:00 PM at both islands (diurnal cycle), however there is a difference in the number of detections by island, Darwin has 1,983 detections and Wolf 11,428. *G. cuvier* detections are in Baltra only, its highest detections are between 6:00 PM – 6:00 AM, with a mean vector at 22:37, showing a nocturnal cycle.

Roca Redonda is also included for three species *C. falciformis* shows higher peak at 11:00 PM, *C. galapagensis* shows higher peak at 4:00 AM with several detections between 5:00 PM – 9:00 PM and *S. lewini* shows higher detections from 10:00 AM – 5:00 PM.

Table 3. Circular statistics – Rayleigh's uniformity test, z value (nr^2, n = observations number and r = length of the mean vector); p significance value (0.05).

SPECIES	**ISLAND**	**RAYLEIGH'S (Z)**	**RAYLEIGH'S (P)**
C. falciformis	Darwin	141.849	<1E-12
	Wolf	38.076	<1E-12
	Baltra	5.553	0.003
C. galapagensis	Darwin	10.29	3.40E-5
	Wolf	16.975	4.24E-8
C. limbatus	Darwin	19.802	2.51E-9
	Wolf	4.162	0.015
	Baltra	16.348	7.95E-8
S. lewini	Darwin	503.674	<1E-12
	Wolf	2855.468	<1E-12
G. cuvier	Baltra	35.478	<1E-12

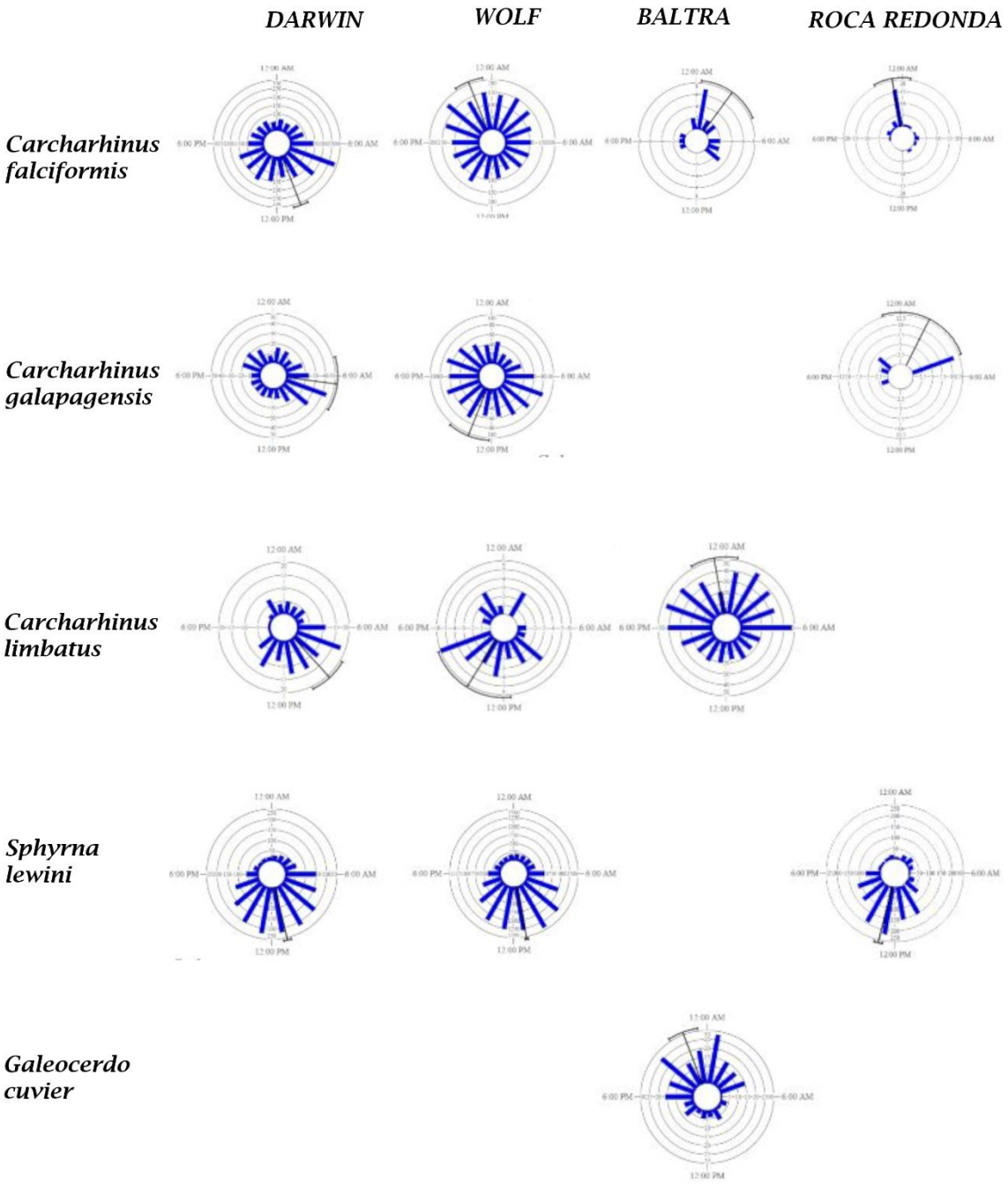


Figure 6. Diel movements. Circular histograms of detections per day and night hour – Axis divided into 6:00 hours

DISCUSSION

The long-term residence of each species provides information that supports previous results of short-term studies that have been taking place (Hearn et al., 2010; Meyer et al., 2010; Bessudo et al., 2011; Soler et al., 2013; Gallagher and Klimley, 2018; Peñaherrera-Palma et al., 2018; Ajemian et al., 2020; Ketchum et al., 2020), the Galapagos Marine Reserve represents an important point of contact between Eastern Tropical Pacific MPAs.

Each species shows an increase in abundance at different seasons over 10 islands of all bioregions, 47 individuals have the Far Northern bioregion as the zone with the highest incidence of detections, while 9 individuals were constantly present at Central–Southeastern bioregion. Although the general residence values of the reserve may seem low, it must be considered that on days when an individual was not detected in any ETP receiver, it could have been present in offshore areas for feeding, reproductive or migratory behavior.

The scalloped hammerhead shark (*S. lewini*) is a highly mobile species, however, on the islands of the Far Northern bioregion it displays the highest rate of residence, 81% of the study sample was tagged in Darwin or Wolf, and consistent with the information by Ketchum et al., (2014), their movements have been recorded only between both islands of the GMR.

Highest residency index value for Wolf (0.6) corresponds to 22 individuals, this sample mean RI is a significant value that prove that those individuals are resident of the island and their movements to Darwin can be related exclusively to the cleaning station receiver zone (the presence of individuals on Bus stop is due to their proximity to the cleaning station point) (Nalesso et al., 2019).

The scalloped hammerhead sharks showed movements between the GMR and other MPAs during their extended track length (166 – 2331 days), this external connectivity confirms that their range is much broader than the limits of the reserve and that long-distance movements might be triggered for reproductive purposes or prey availability throughout the lives of several individuals (Clarke, 1971; Nalesso et al., 2019).

Individual #18 is a great example: the female moved from Malpelo to Cocos, Wolf and Roca Redonda, and never came back to its tagging site, this behavior is consistent with the hypothesis proposed by Bessudo et al., (2011), that individuals tagged in Malpelo FFS and detected in other MPAs are not part of local populations.

According to Ketchum et al., (2014), fishes prefer to reside at specific locations during certain times of the year, which is consistent to the seasonal patterns showed at this study (Fig. 4). Hammerheads decrease their presence at Darwin and Wolf islands during March and April and similar occurs in Malpelo when sharks appear to leave to pupping areas (Bessudo et al., 2011).

The behavior of specimen #18 and the information previously established for Malpelo, shows synchronicity with the presence of the individual in Roca Redonda during March and few days of April, a year before those detections, the female started its journey to Cocos Island. Specimens #11, #15 and #19 (tagged at Wolf) use Roca Redonda from June

to August. This circular islet with a diameter of 300 meters, is a high productivity site, with nearby vertical walls that are extremely similar to Wolf and Darwin islands, despite the fact that is not resting over the Galapagos platform (Standish et al., 1998; Berkenbosch, 2006).

The individuals # 11, 15, 18 and 19 (previously mention), are females and have a size that is consistent with the range of sexual maturity reached by the species (Froese and Pauly, 2020). Roca Redonda may represent a site with the right conditions over those months to increase foraging with lower energy expenditure for potential pregnant females (Heithaus, 2014).

The scalloped hammerhead sharks have a strong diel pattern with diurnal activity nearby the receivers at Darwin, Wolf and Roca Redonda, this behavior is shown in all ETP MPAs and the reason for this might be related to the preference of places nearby their feeding zones and their high site fidelity to oceanic seamounts (Hearn et al., 2010; Gallagher and Klimley, 2018).

The silky shark (*C. falciformis*) shows a wide variety of individual residence values, 9 specimens have a high rate of residence in the Far Northern bioregion and these values may be linked to site productivity, the model of Lopez et al., (2017) demonstrates a correlation between high productivity and abundance of silky sharks.

Darwin and Wolf islands have the presence of two currents that adjoin the southern edges, which has proven to be the oceanographic factor that improves productivity, increasing the number of benthic communities and prey for apex predators (Salinas-De-León et al., 2016).

Individual #27 (Tag ID 55955) was tagged at Wolf, but showed external connectivity with Clipperton islands, this movements can be related to feeding, although, benthic communities are limited, biodiversity around Clipperton fracture zone is still high (Volz et al., 2018). Conversely, individual #28 (Tag ID 46665) shows a noticeable preference for Cocos islands, its movements to the GMR are not evident in Figure 3, due to the low detections at Wolf and Roca Redonda (5 detections in both islands), evidently, this specimen can be considered as a long-term resident of Cocos island considering that was tagged in Cocos and moved to the GMR for few days only.

An important point is the presence of sharks #27 and #28 at Roca Redonda during warm season, between same months at same year (Figure 1). Roca Redonda is an emergent tip of a submarine volcano, and represents the youngest phase of Galapagos constant creation of volcanic islands (Standish et al., 1998). The silky shark presence in the islet might be related to productivity and not water temperature, since between Roca Redonda and the far northern bioregion the temperature remained similar over this period (according to INOCAR data).

Diel movements have a notable pattern of diurnal activity in Darwin and nocturnal activity in Wolf (Figure 8), the diet of *C. falciformis* in the Ecuadorian Pacific includes tuna fish as main prey. Estupiñán-Montaño et al., (2018) suggest that the silky shark is a specialist predator, so movements between the two islands may be related to the movement of tuna schools.

The highest residency value for *C. galapagensis* (Galapagos shark) occurred at Darwin. Little is known about Galapagos shark ecology, but Pazmiño et al., (2017) demonstrate the presence of two genetically distinct populations of the species from the sampling of 22 sharks in Santa Cruz, San Cristobal and Isabela islands.

Individuals #43 and #44 of this study were tagged at Malpelo Flora and Fauna Sanctuary, so the possibility that they are from a different genetic population is not ruled out, due to their short stay over at the GMR.

Individual #45 shows external connectivity with Clipperton islands at the beginning of warm season and four individuals show internal connectivity between GMR islands (including Roca Redonda during warm season), however, there was no clear pattern linked to seasons for the species.

Wetherbee et al., (1996) suggest that Galapagos shark prefer strong current habitats, and they tend to move when the conditions change drastically, so they are regarded as extreme (Soler et al., 2013). Because of this, their presence in different receivers does not present clear evidence of synchronization between all individuals, and could be determined as a behavior related to external factors such as currents, temperature or other environmental values.

Diel movements have not been previously described for Galapagos sharks in the GMR, Darwin's activity increased significantly at 7:00 AM, while Wolf's activity is significantly reflected among the 7:00 AM–7:00 PM, the species is a non-specialist predator, so it has many preys available along the bioregion, why its broad spectrum of diel detections in Wolf may be related to constant foraging throughout the island (Papastamatiou et al., 2006).

Blacktip shark (*C. limbatus*) has the highest value of the sample mean in the GMR, considering that this is the most abundant species of the order Carcharhiniformes (Acuña-Marrero et al., 2018) and that the study sample is represented only by females, this value can be related to its philopatric behavior with females returning to their birthplace to give birth (Keeney et al., 2003).

The species individuals did not demonstrate external connectivity, but they did demonstrate connectivity internally, their residency index in Baltra of 0.24 and the constant presence of the species between points of the central–southeastern bioregion may be related to mangrove nursery areas previously monitored (Llerena et al., 2015).

Three individuals had connection between Kicker Rock, Santa Cruz, Baltra, Mosquera, Cousins and North Seymour until 2012. The first week of 2012 had a temperature of ~25°C at central–southeastern bioregion, but during year 2013 temperature rounded the 20°C and there are no detections during that period time. Heupel, (2019) explains that migratory species such as blacktip sharks, constantly swim to warmer waters as a response to physiological tolerance and behavior survival.

In 2014, the other 5 individuals showed connectivity between Baltra and North Seymour, and from 2015 to 2016 individuals moved only between Santa Cruz and Baltra (during first week of 2014 and 2015 temperature increased to 25°C again) (Fig.2).

Year 2016 had the highest temperature of tracking period time, with a 27°C value, following year had a significant decrease of 7°C reason why they may have migrated to another place with higher temperature outside the reception range of the acoustic waves emitted by the transmitters.

The case of individual #47 is an example, since in 2014 is detected in the GMR after two years of inactivity and its return point is Darwin island, where reported temperature was 26°C (+1°C higher than central–southeastern islands).

According to Diatta et al., (2001) and Tavares, (2008), temperature is related to the presence or absence of the specimens (preferred temperature between 25°C – 30°C), the species is found in warmer waters in order to feed or reproduce, hence, considering that in the reserve the hot season has the highest residency index (Figure 3). Páez-Rosas et al., (2021) explained that females usually feed across coastal regions before giving birth, which is consistent to the relationship between residence, nursery areas and temperature along the receptors found in Baltra and its surroundings (Figure 7).

Blacktip's diel movements showed different high-activity schedules on each island. Central-Southeastern bioregion has a high level of nocturnal activity while far northern bioregion has a high level of diurnal activity. This pattern is evident in Dávalos and Hearn, (2007) and Legare et al., (2018) studies, where the evidence is clear that in elasmobranchs, the variability of diel activity between points is mainly due to foraging, reproduction or predation.

For Darwin and Wolf islands, the daily behavior may be directly related to the risk of predation (Dahlgren and Eggleston, 2000), considering that in the far northern bioregion, only two individuals were detected, and that one of them was present for longer in Darwin, it can be determined that in fact, the risk of predation was higher, since this island does not have a high rate of residence at any of its points (Figure 5).

Despite Baltra's diel movement show higher nocturnal activity, there are several detections during daylight time, and considering that six individuals move between four receivers overnight all year and that the distance between receivers is minimal. These diel results can be related to a central point foraging, this strategy follows a pattern with a central resting zone during the day, and dispersal movements at night for feeding as it's described in Speed et al., (2010).

Tiger shark (*G. cuvier*) is the species with the highest residency index in Baltra, however, Baltra does not represent its preferred habitat (Figure 7), the species has a high residency index in the receiver Bachas (Santa Cruz). By the acoustic monitoring reflected in Fig.2 is evident the internal connectivity between Baltra and Santa Cruz receivers separated by a straight-line distance of 7.8 kilometers. Patterns previously described around the Hawaiian Islands show similarity to the patterns shown in this study (Meyer et al., 2018).

There is a clear temporary site fidelity to central–southeastern bioregion where inter-island movements are observed, and may be highly related to foraging (Ajemian et al., 2020), and feeding of sea turtles near their nesting areas, as in Ecuadorian waters, tiger shark has been showing a possible dietary specialization (Estupiñán-Montaño et al., 2017).

One female showed external connectivity with Cocos island (30 days-period), but for three years, the individual showed no activity in any of the receivers placed by the MigraMar research network, so its location is unknown during this time, however, it is interesting to check through this behavior its role as an apex predator.

The tiger shark is considered a species with a wide distribution worldwide and therefore, a wide home range, this has led to it being a key species for marine ecosystem balance, by regulating communities through top-down trophic effects so this behavior can be related to interoceanic connectivity (Afonso et al., 2017).

The presence of the tiger shark in the GMR increases during warm season and decreases considerably with the arrival of the cold season, similar to previous reports (Ajemian et al., 2020). A correlation between catch rate and water temperature has been reported, when the temperature drops to values between 20°C–22°C, the presence of the species declines significantly. This decrease has been evident between the months of May and June in the Heithaus, (2001) study, and is consistent with the inter-season changes presented in this research.

Seasonal changes of the species may be directly related to green turtles (*Chelonia agassizii*) hatch seasons (Zárate et al., 2013; Dicken et al., 2017), and their return to the same nesting area during warm months and not necessarily with the temperature variation.

Although the sample of the tiger shark is low, the three individuals exhibit similar nocturnal activity in the receivers of Baltra Island, and the relationship is even more evident considering that green turtle lays its eggs overnight (Zárate et al., 2013).

The results reported by this work demonstrates the importance of the Galapagos Marine Reserve as an important temporary point of residence for the five species of sharks analyzed. The values of their residency indices take into account the number of days that have been detected on each Galapagos island, however, their apparent inactivity between their monitoring periods are evidence that all individuals move beyond the boundaries of the reserve, with evidence of connectivity through migration movement between different MPAs and possible movements between oceans as well.

It is vitally important to expand the GMR, so that the conservation status of sharks that are in force in the Ecuadorian government regime can exercise de law over possible entities that attack their well-being through their illegal fishing and sale. Finally, the information established in this research can be used as evidence of the importance of the protection of the marine corridor that connects Galapagos with Cocos island, in order to achieve a total protection not only for sharks, but for all migratory marine species that make use of the Eastern Tropical Pacific as is the case with Malpelo Flora and Fauna Sanctuary expansion and successful Revillagigedo conservation processes (EFE, 2017; Garzón, 2017).

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