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Identification of critical habitats of 10 pelagic shark species



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SOMMAIRE

INTRODUCTION	1
1. MATÉRIEL ET MÉTHODE	3
1.1 MATERIEL	3
1.1.1 Vidéo sous-marine à distance à l'aide d'appât, Stéréo-BRUVS à mi-eau	3
1.1.2 Collection des données	3
1.2.1 Traitement des différences entre milieux et espèces selon les âges	4
1.2.2 Identification nurserie	4
2. RÉSULTATS	7
2.1 DISTRIBUTION DES REQUINS	7
2.2 RESULTATS DES DIFFERENCES ENTRE MILIEUX ET ESPECES SELON LES AGES	9
2.2.1 Fréquence par lieu	9
2.2.2 Fréquence par espèce	0
2.3 Spectre de proie des requins1	.1
3. INTERPRÉTATION ET DISCUSSION1	.2
CONCLUSION ET PERSPECTIVES1	.7
RÉFÉRENCES BIBLIOGRAPHIQUES1	.9
ANNEXES	5

TABLE DES ILLUSTRATIONS

FIGURES

Figure 1 : Schéma de configuration d'une BRUVS (a) plateforme et (b) dans l'eau.

Figure 2 a-b : Exemples de requins bordés détectés sur des BRUVS au niveau de l'archipel des Chagos, avec (a) le segment pour mesurer la longueur à la fourche et (b) le requin de plus près.

Figure 3 : Nom et localisation des sites sur lesquels les BRUVS ont été déployés, et un cercle marron représente le positionnement d'un requin enregistré.

Figure 4 : Histogramme de la pression de pêche sur les sites de cette étude, avec les sites n'étant pas protégés par des aires marines et les sites étant protégés par des aires marines, pas de différence significative.

Figure 5 : Histogramme de la pression de pêche des sites de l'étude sur les juvéniles, des sites qui subissent une grosse pression de pêche sur les juvéniles et des sites ou il y a peu de pression de pêche. Différence significative entre a et b (p = 0,009).

Figure 6 : Chaque point représente l'effort de pêche par site et par tous les requins enregistrés de l'étude, avec en vert électrique très peu d'effort de pêche (0), vert fade peu d'effort de pêche(1), en rouge fade présence de pression de pêche(2) et rouge électrique grosse pression de pêche (3) sur le milieu. Les noms des sites en bleu sont les sites protégés pas une aire marine et les sites en noir, les sites pas protégés.

Figure 7 a-d : Graphiques radars montrant les pourcentages de proies classées comme proies nouveau-nés, proies juvéniles / adultes et « non proies» par log de l'abondance totale, en fonction de la taille maximale des nouveau-nés et des juvéniles/adultes pour le requin bleu, le requin bordé, le requin mako et le requin soyeux. Les axes sont mis à l'échelle à 80% par incrément de 20%.

TABLEAUX

Tableau 1: Taille de la longueur à la fourche (LF) et maximum des proies ingérées pour un nouveau-né et un adulte/juvénile de chaque espèce.

Tableau 2 : Le nom commun et latin des 10 espèces de requins de l'étude, le pourcentage de distribution sur les sites par espèce et leur statut de conservation.

Tableau 3 : Pourcentage des juvéniles et des adultes observés, avec l'intensité de la pêche (pêche, forte pêche, pas trop de pêche), le niveau correspondant (haut, moyen, bas, très bas) et le marquage entre 1 et 3 de chaque localisation.

GLOSSAIRE

ADULT : individual at sexual maturity and therefore reproductive HOMES : Critical habitat for breeding, denning, nursery and feeding JUVENILE : individual that has not reached sexual maturity Neonates : Individual who has less than 1 year old NURSERIE : Habitat côtoyé par les nouveau-nés POINT CHAUD : Rassemblement important de requins PRISE ACCESSPOIRE : Capture d'espèces non ciblées due à la pêche REQUIN D'INTÉRÊT : Requin traité dans l'étude

LISTE DES SIGLES ET ABRÉVIATIONS

MPA : Marine Protected Areas ADT : Adult BRUVS : Baited Remote Underwater Video Systems CAL : Progiciel event measure JUV : Juvenile LF : Fork length YOY : Young of the year, neonate, newborn

Abstract

Sharks are among the most endangered groups of marine animals on earth. They are part of many species for which there is few information on their abundance and distribution. Protection and good management of nurseries habitats and places of refuge are essential to the survival and the recovery of endangered sharks. Very few studies have been carried out to find out these areas. Indeed, there is few identifications of nurseries or even places identified as important for migratory sharks. We collected data on the diversity, abundance and size of pelagic organism from 5587 recordings made by underwater stereoscopic video using half-water bait (BRUVS) during the period of 2012 to 2019 at 31 locations known for having productivity. Places were in the Atlantic, Indian and Pacific Oceans. One thousand five hundred and twenty four sharks, coming from 6 families with : 124 blue sharks Prionace glauca, 215 blacktip sharks Carcharhinus limbatus, 57 copper sharks Carcharhinus brachyurus, 190 sandbar sharks Carcharhinus plumbeus, 110 silvertip sharks Carcharhinus albimarginatus, 116 dusky sharks Carcharhinus obscurus, 41 shortfin mako shark Isurus oxyrinchus, 399 silky shark Carcharhinus falciformis, 66 scalloped hammerhead shark Sphyrna lewini and 55 great hammerhead shark Sphyrna mokarran. Adults and juveniles were recorded mostly in the sites of: Ascension Island; Chagos archipelago: Ningaloo; Long reef; Pilbara and Shark bay, and young of the year only rerecorded within the blue, blacktip, mako and silky sharks in: Research archipelago; Bremer; Chagos archipelago; Tristan; Ningaloo; Long reef and Azores island. Data showed that the distribution of neonates was adapted to the availability of appropriately sized prey (prey <36 cm), they have been seen also in the presence of larger animals potentially predators. Comparison of observed and expected relative abundance in sharks on the basis of habitat quality indicated abnormally low levels of species in the majority of sampled sites, confirming that pelagic sharks were wiped out by the overfishing in much of their range habitat.

Key words: pelagic sharks, distribution, nursery, refuge, overfishing, BRUVS

INTRODUCTION

Sharks first appeared on planet earth 430 million years ago (Curtis et al. 2014). They have survived the five major mass extinctions, yet currently a quarter of sharks are threatened with extinction according to the IUCN1 Red List of Threatened Species and half of coastal and pelagic sharks are vulnerable, endangered, or critically endangered.

Pelagic sharks are complex migrants, using ill-defined habitats separated by large distances (Game et al. 2009, Worm & Tittensor 2011, Vandeperre et al. 2014). This makes it extremely difficult to study their behavior, and as a result, very few studies exist on their choice of distribution. Indeed, relatively few critical areas for pelagic shark survival have been identified. Critical habitat is defined as habitat necessary for reproduction, pupping, growth, and feeding (Heithaus 2007). Nurseries where newborns spend the first months of their lives are important areas for population survival (Villafaña et al. 2020). A habitat can be termed a nursery when the distinct area is inhabited by neonates where their abundance is highest relative to other areas (Heithaus 2007). Nurseries are also critical habitats for adult and juvenile sharks. Identifying and understanding the selection of these habitats is fundamental to halting and reversing precipitous declines in elasmobranchs (Ducatez 2019, Nosal et al. 2019). Indeed, for a long time the protection of areas for shark conservation has been focused on nurseries often inferred from the migratory patterns of tagged adult females, rather than by direct observation of newborns, and little progress on population evolution has followed (Campana et al.2010, Howey-Jordan et al. 2013). Thus, it is important to look beyond nursery areas to older sharks living in homes outside of nurseries to allow populations to rebound (Kinney & Simpfendorfer 2009).

The blue shark Prionace glauca, the mako shark Isurus oxyrinchus, the silky shark Carcharhinus falciformis are all pelagic, while the bordered shark Carcharhinus limbatus, the copper shark Carcharhinus brachyurus, the sandbar shark Carcharhinus plumbeus, the whitetip shark Carcharhinus albimarginatus, the osbcur shark Carcharhinus obscurus, the scalloped hammerhead shark Sphyrna lewini and the great hammerhead shark Sphyrna mokarran are coastal and pelagic. They are all large migratory sharks (Bessudo et al. 2011, Calich et al. 2018, Dulvy et al. 2008, Hoffmayer et al. 2014). They migrate into areas often occupied by surface longlines of fishing gear targeting other species (Calich et al. 2018). As a result, they are fatally prey to bycatch (Queiroz et al. 2016). In addition from their meat or fins, they are fierce victims of overfishing (Smith et al. 1998, Cortés 2002). As such and having relatively slow growth, maturity late and low fecundity, migratory shark populations are declining (Bessudo et al. 2011, Calich et al. 2018, Dulvy et al. 2008, Hoffmayer et al. 2014). 7 of the 10 sharks studied are classified as threatened on the IUCN Red List. The goal of this study is to understand the movements of these sharks in order to help researchers better predict their presence and thus be able to subsequently identify areas where they are most vulnerable to fishing.

¹ International Union for Conservation of Nature

In this study, a global dataset was analyzed using underwater video bait systems (BRUVS). This analysis was conducted at 31 locations across the Atlantic, Pacific and Indian Oceans, throughout the range of migratory sharks. The objective of this study is to improve our understanding of the distribution of these species and to identify critical habitats and habitats under heavy fishing pressure. BRUVS generate estimates of diversity, abundance, size, and biomass of pelagic fauna (Letessier et al. 2013, Bouchet et al. 2017).

Using the collected data and mapping systems, it was hypothesized that sharks would show strong associations with highly productive locations qualified as "nurseries" or locations qualified as "homes". Then, using organism size data by location, it was predicted that neonate-rich locations would have greater availability of appropriately sized prey (<36 cm), based on prey ingestion limitation theory (Bethea et al.2004, Barley et al. 2019). Whereas co-occurrence of neonates with large predators, including adult sharks of each species, would be minimal to reduce the threat of inter- and intraspecific predation.

Finally, in order to assess the extent to which overfishing has affected population size, observed shark abundance was compared to expected abundance, predicting that many locations with favorable conditions would be characterized by observed under-abundance of sharks and that current marine protected areas (MPAs) with little fisheries management will not be home or nursery locations for sharks in this study.

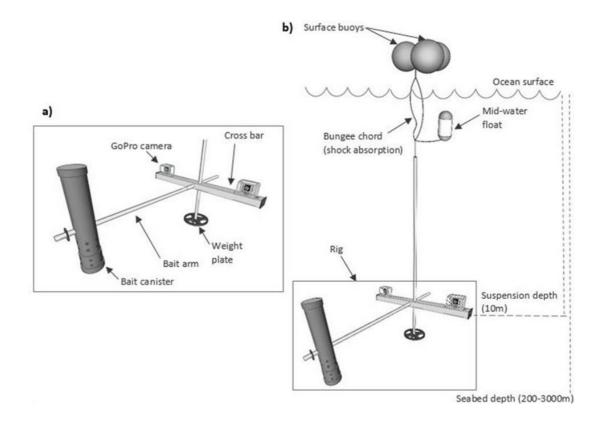


Figure 1 : BRUV configuration

1. MATERIAL AND METHOD

1.1 Material

1.1.1 Mid-water stereo BRUVS

Mid-water stereo-BRUVS identify pelagic fish assemblages. BRUVS are a variant of benthic BRUVS, which are themselves a tool for identifying benthic fish assemblages (Cappo et al. 2006, Whitmarsh et al. 2017). BRUVS are more efficient than traps and provide better samples (Harvey et al. 2012). They are placed at a depth of 10 m below the sea surface and film all pelagic organisms. They consist of surface floats (Figure 1; Bouchet & Meeuwig 2015), each tether is complemented by a pair of underwater floats and a turnbuckle to absorb wave shock and optimize image quality (Bouchet & Meeuwig 2015). The BRUVS also have an aluminium crossbar on which two high-definition GoPro HD cameras are mounted, converging inward at a 4-degree angle. The crossbar is attached by a 1.8 m long stainless-steel rod at the end of which is a 0.45 m long perforated PVC canister containing 1 kg of locally sourced Sardinops spp. sardines, creating a bait with a slow-release frequency. The camera pairs were previously calibrated in a pool using CAL in the Event Measure software package which is a stereoscopic camera calibration tool (Harvey & Shortis 1998). They are then synchronized with a hand clap before deployment. The platform containing the cameras and PVC canister was deployed on longline ropes of 5 (90% of the ropes), with the remaining 10% deployed in sets of 3 due to technical or environmental conditions. The platforms were separated by 200 m of line for at least 2 hours of soaking.

1.1.2 Data collection

Stereo-BRUVS were deployed at 31 sites in the Atlantic, Pacific, and Indian Oceans between 2012 and 2019 (n = 1163 strings) with repeat surveys at 13 sites. All platforms were deployed with knowledge of migratory shark distribution. All platforms were deployed based on a generalized stratified random tessellation (GRTS) approach (Stevens & Olsen 2004). Sampling took place during the day to minimize the effects of twilight behavior (Axenrot et al. 2004, Birt et al. 2012).

1.2 Method of data processing

The BRUVS videos were processed using SeaGis Event Measure software. Data collection began once the platforms had reached stability and a depth of 10 m and was completed after 2 hours of processing. All animals were identified to the lowest taxonomic level possible, sometimes down to species if not to genus or family. The fork length (FL) (Figure 2;a) was measured using also Event Measure (Figure 2;b).

1.2.1 Processing differences between environments and species according to age

1.2.1.1 Mapping

In order to get an idea of the geolocation of sharks, a map with the sites visited by the different shark species was made using the latitudes, longitudes and time periods of the data provided by the BRUVS. The map was created on QGIS and the world map was downloaded to Natural Earth2.

² https://www.naturalearthdata.com

¹ https://www.floridamuseum.ufl.edu/discover-fish/species-profiles/prionace-glauca

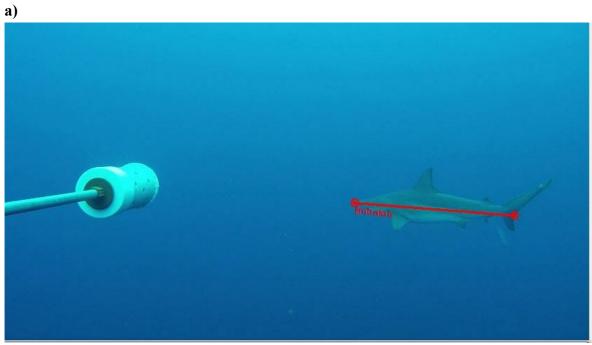






Figure 1 a-b : Examples of edged sharks detected on BRUVS in the Chagos Archipelago, with (a) the segment to measure fork length and (b) the shark up close.

1.2.1.2 Data analysis

To test the differences in abundance between adults and juveniles, and then between adults/juveniles and neonates for each species and then by site, the Chi-squared statistical test was used. Each site was marked with a level of fishing pressure; noted "0" for a site with very little fishing up to "3" for a site with strong fishing pressure. The data were then analyzed with an analysis of variance ANOVA to first test for differences in life history and environment, but also for differences in fishing effort between sites with marine protected areas and sites without.

Environments with less than 5 sharks were considered too small samples, so they were excluded from the study.

1.2.2 Nursery identification

The aim is to analyze the presence of newborns in environments adapted in terms of prey size. This could only be observed on 4 sharks (Blue shark, Spotted shark, Mako shark and Silky shark). The others did not have any pups recorded..

1.2.2.1 Sharks

- Blue sharks are born between 35-50 cm (IUCN 2005)¹ with a growth rate of 30 cm/year for the first 5 years (Skomal & Natanson, 2002). Newborns (YOY), were defined as having a LF < 67 cm, juveniles (JUV) < 153, 5 and adults (ADT) beyond this size.
- The bordered shark has an average birth size of 53-65 cm2 with a growth rate of approximately 30 cm in the first year (Smart 2017). Neonates were defined with a LF of < 66.2 cm and juveniles < 107, 6 cm, above this size individuals are considered adult.
- Mako sharks can measure up to 69.8 cm at birth (Duffy and Francis 2001) and grow at a rate of 50-61 cm during their first year (Maia et al. 2007). Neonates were defined as individuals < 70 cm in length, juveniles < 152 cm and beyond that adults.
- Silky sharks can be 70-76 cm at birth, with a growth rate of 30 cm in the first few years (Joung et al. 2008). This rapid growth is thought to improve their survival (Frazelle 2005). YOYs were defined with a LF of < 80 cm and juveniles < 148, 4 cm, larger individuals are adults.

Details on the other sharks (Copper shark, Grey shark, Great hammerhead, Scalloped hammerhead, Obscure shark and Whitetip shark) are in the Appendix (Appendix 1).

	Neonates		Adult/ Juvenile	
Species	Length FL	Size Preys Limited	Length FL	Size Preys limited
Mako shark	100 cm	< 36 cm	300 cm	< 108 cm
Blue shark	67 cm	< 24,1 cm	279,7 cm	< 100,7 cm
Silky shark	80 cm	< 28,8 cm	207,1 cm	< 74,5 cm
Edge shark	66,2 cm	<23, 8 cm	124,2 cm	< 44,7 cm

Table 1: Fork length (FL) size and maximum prey ingested for a neonate and adult/juvenile of each species

1.2.2.2 Prey spectrum

Due to their dentition, many shark species must swallow their entire prey and as a result can only consume prey at approximately 36% of their fork length (Bethea et al.2004, Barley et al.2019). We measure the abundance of appropriate prey size classes. Then, we examine whether this differs between sites occupied by neonates, juveniles/adults, and sites where the treated shark is not present. FL was used to obtain consumable prey sizes for neonates, as well as juveniles/adults for each species. The size values in **Table 1** were calculated with 36% of the LF and predict for neonates and adults/juveniles, the maximum consumable prey sizes.

Prey with a FL greater than the maximum that adults can ingest were designated as 'non-prey'. For make sharks, "non prey" are prey > 108 cm, for blue sharks > 100.7 cm, for silky sharks > 74.5 cm and finally, for sandbar sharks > 44.7 cm.

1.2.2.3 Prey abundance

On each platform, the abundance and biomass of individuals in each of the three groups (neonates, juveniles/adults, and non-sharks of interest) were transformed to log10 (x + 1). These data are then summed across all platforms in each string to generate total abundance (TA), followed by mean TA values for each line.

Since neonates never appeared with juveniles or adults on a given string, each string was defined as neonates only, juveniles/adults only, or no sharks of interest.

Logs of average AT values of potential prey were then calculated for the strings in each category. These values were then divided by the total abundance of all animals in each category to control for variation in total prey quantity.

Radar graphs containing the percentages of prey classified as neonate food, juvenile/adult food, and non-prey were then generated. Visualization of these percentages indicates the degree of overlap between the size distribution of prey versus the presence of neonates or juveniles/adults or non-prey.

² https://www.floridamuseum.ufl.edu/discover-fish/species-profiles/carcharhinus-limbatus/

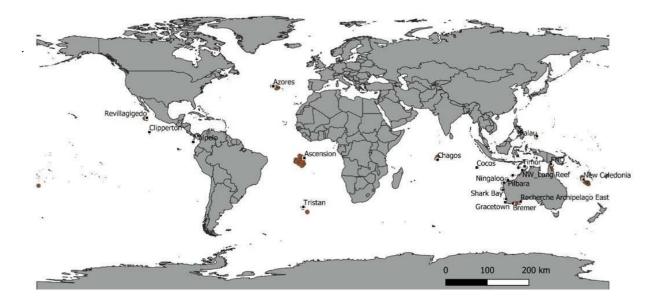


Figure 3 :Name and location of the sites where BRUVS were deployed, and a brown circle represents the position of each sharks recorded

Specices	Vernacular name	% of distribution	Statut red list IUCN
Blue shark	Prionace glauca	29,2 %	Near threatened
Edge shark	Carcharhinus limbatus	41,7 %	Near threatened
Mako shark	Isurus oxyrinchus	45,8 %	Endangered
Silky shark	Carcharhinus falciformis	58,3 %	Vulnerable
Requin cuivre	Carcharhinus brachyurus	20,8 %	Near threatened
Requin obscur	Carcharhinus obscurus	25 %	Endangered
Grand requin marteau	Sphyrna mokarran	41,7 %	Critically endangered
Requin gris	Carcharhinus plumbeus	29,2 %	Vulnerable
Requin marteau halicorne	Sphyrna lewini	41,7 %	Critically endangered
Requin à pointe blanche	Carcharhinus albimarginatus	25 %	Vulnerable

 Table 2 : Percentage of distribution of the 10 sharks and classification in the IUCN red list

2. RESULTATS

2.1 Distribution oh sharks

A total of 101,050 teleosts, sharks, invertebrates, marine mammals and marine reptiles were observed in the 1159 samples, representing 255 different taxa and 66 families. There were 1524 sharks of 10 species representing 6 families.

They were found at 24 locations in the Atlantic, Indian and Pacific Oceans (Figure 3).

The percentages of distribution in the different locations where sharks have been observed by species vary from 20% to 60% (**Table 2**). Of the sharks with a distribution >40%, 60% are classified as threatened by the IUCN, and those with a distribution >40% are 25% threatened.

Blue sharks were recorded at 8 locations (Tristan, Azores, Ascension, Bremer, Recherche Archipelago, Perth Canyon and Tristan-Gough). There were 124 individuals observed with 17 newborns, 25 juveniles and 82 adults, with a FL ranging from 37.2 cm to 272.92 cm. They were recorded in the Atlantic and Indian Oceans and around the island of Ascension, 55 adult and juvenile individuals over the years 2017 and 2018. These data were recorded in January/February/May for these 2 ages. In the Indian Ocean, a gathering was observed in the Bremer's area, they were present in January and February 2017 (11 ADT), then the same month in 2019 (3 ADT, 6 YOY) (**Appendix** 2). For the overlap, 100% of the YOY were found at the same location, time, and year as adults and/or juveniles.

Edged sharks were recorded at 11 sites around the world (Revillagigedo, Timor, Ashmore reef, Pilbara, Shark Bay, New Caledonia, Ningaloo, Long Reef, Palau and FNQ). A total of 215 bordered sharks are distributed as follows: 11 neonates, 112 juveniles and 92 adults. FL ranged from 58.1 cm to 251.9 cm. Ten newborns were located (NW Long reef) during the Australian summer of September 2018 and the 11th in July 2017. 206 edged sharks were sighted on the Australian coasts, near Shark bay and Ningaloo where 33 adults are present in 2019 and 2018 mainly in October. 110 juveniles are observed in the years 2012, 2017 and 2018, in the month of October and September at the Long reef site (Appendix 3). There are 100% of the young of the year found at the same location, same time in the same year as adults and/or juveniles.

Mako sharks were recorded in 15 sites (Azores, Gracetown, Ascension, Shark Bay, Bremer, Recherche Archipelago, New Caledonia, Perth Canyon, Montebellos, Ningaloo and Chagos Archipelago). A total of 37 individuals were observed with 4 neonates, 7 juveniles and 26 adults with a FL ranging from 57.3 cm to 316.5 cm. They were recorded in several oceans: notably at Ascension Island where 2 adults appeared in February 2017 and 1 in January 2018. Newborns were identified on the Australian coast near the Perth Submarine Canyon between November and December 2016, near Shark bay in September 2017 and towards Bremer in March 2019 (Appendix 4). 25% of the young of the year were found in the same area, same time period in the same year as adults and/or juveniles.

Silky sharks were recorded in 16 sites (Cocos, Revillagigedo, Timor, Ascension, Pilbara, Shark Bay, Rowley Shoals, Clipperton, Perth Canyon, Montebellos, Ningaloo, Malpelo, Chagos and Palau). There are 399 individuals including 20 young of the year, 179 juveniles and 200 adults with a FL ranging from 11.2 cm to 317.8 cm. In terms of distribution, silky sharks were found in the Atlantic Ocean near Ascension Island where 88 individuals were identified during the periods of January 2017 (1 ADT, 4 JUV, 1 YOY), May and June 2017 (25 ADT, 26 JUV) and finally January

2018 (2 ADT and 8 JUV). 45 individuals were also present towards the Chagos Archipelago, in November 2012 (4 JUV), January 2015 (21 ADT, 2 JUV and 1 YOY) and February 2016, at the same period when the majority of YOY were present (7 YOY, 12 ADT) (Appendix 5). 80% of YOY were found at the same location as adults and/or juveniles, same time of year.

Copper sharks were recorded in 8 locations (Gracetown, Shark Bay, Bremer, Recherche Archipelago and Perth Canyon). A total of 57 individuals were observed, divided into 14 juveniles and 43 adults. The smallest juvenile measured 60.7 cm FL and 157.7 cm for the largest adult.

From a geolocation point of view, they were mainly recorded around the coast of southwestern Australia. On the Research Archipelago area 20 adults and 5 juveniles were observed between January and February 2019. Towards Bremer 26 adults and 2 juveniles for half in March 2017 were recorded, while the other was seen in March 2019. Finally near Gracetown 15 adults appeared between May and June 2018 and 4 juveniles in the same area in March 2019 (**Appendix 6**).

Great hammerheads were recorded in 10 locations (Timor, Ashmore, Pilbara Reef, Shark Bay, New Caledonia, Perth Canyon, Montebellos, Ningaloo, Long Reef and FNQ). A total of 52 individuals were observed, divided into 12 juveniles and 40 adults, the size at LF varied from 107 cm to 285.4 cm. They were identified at the Australian coast. Pilbara has mostly adults (22 ADT, 1 JUV), they are present in September in 2017, 2019 and August/September 2018. In the Long reef area: 6 juveniles were present in July 2017 and 4 adults in September 2018 (**Appendix 7**).

Silvertip sharks were recorded in 6 sites (Ascension, Ashmore reef, Clipperton, New Caledonia, Montebellos and Ningaloo). 110 individuals were observed: 61 juveniles and 49 adults. Their LF size varies from 72.7 cm to 221 cm. Whitetip sharks were also located in the Atlantic with 2 juveniles around Ascension Island. In the Indian Ocean, near the Chagos archipelago, 1 adult and 1 juvenile were seen in January 2015. Finally around the Australian coasts, 7 adults and 3 juveniles were observed in the South Timor Sea in September 2012 (**Appendix 8**)

Localisation	% juveniles observe d	% adults observe d	Fishing pressures	Level of fishing	Tagged fishing effort
Timor	u 40%	<u> </u>	fishing on juveniles	Meduim	2
Cocos	35%	65%	fishing on juveniles	Meduim	2
Tristan	27%	73%	fishing on juveniles	Low	1
Revillagigedo	49%	51%	fishing on juveniles	Meduim	2
Shark Bay	47%	53%	fishing on juveniles	Meduim	2
Ascension	48%	52%	fishing on juveniles	Meduim	2
Ashmore reef	53%	47%	fishing on juveniles	Low	1
Gracetown	25%	75%	fishing on juveniles	Meduim	2
Azores	21%	79%	fishing on juveniles	High	3
Pilbara	36%	64%	fishing on juveniles	Meduim	2
New Caledonia	17%	83%	intense fishing on juveniles	Meduim	2
Clipperton	23%	77%	intense fishing on juveniles	Meduim	2
Perth Canyon	11%	89%	intense fishing on juveniles	Low	1
Ningaloo	26%	74%	intense fishing on juveniles	Meduim	2
Rowley Shoals	4%	96%	intense fishing on juveniles	meduim	3
Recherche	15%	85%	intense fishing on juveniles	Meduim	2
Bremer	13%	88%	intense fishing on juveniles	Meduim	2
Montebellos	9%	91%	intense fishing on juveniles	Meduim	2
Tristan -					
Gough	71%	29%	not too much fishing	Very low	0
FNQ	66%	34%	not too much fishing	Meduim	1
Chagos	58%	42%	not too much fishing	Very low	0
Palau	76%	24%	not too much fishing	Very low	0
Malpelo	76%	24%	not too much fishing	Meduim	2
Long Reef	83%	17%	not too much fishing	Low	1

Table 3: Percentage of juveniles and adults observed, with fishing intensity (fishing, intense fishing, not too much fishing), corresponding level (high, medium, low, very low) and marking between 1 and 3 of each location.

Grey sharks were recorded in 7 locations (Ashmore reef, Pilbara, Shark Bay, New Caledonia, Montebellos, Ningaloo and FNQ). 190 individuals were observed with 6 juveniles and 184 adults, their size FL varied between 52.8 cm and 259 cm. In the Shark bay site, 52 individuals were counted mostly adults (51 ADT + 1 JUV) in September 2017, in August 2018 and in September 2019. Towards Ningaloo there were 15 individuals all adults seen mainly in July 2018 and also in October 2019. Towards Pilbara area 110 individuals including juveniles (2) were seen in September 2019. Subsequently, in the same year, adult sharks (108 sharks) were mostly sighted at the same period as in 2018 and 2019 (**Appendix 9**).

Dusky sharks were sighted in 7 sites (Pilbara, Cocos, Pilbara, Shark Bay, Montebellos, Ningaloo and FNQ). A total of 270 individuals were observed with 175 juveniles and 95 adults. Their FL measured 83.8 cm to 344.5 cm. They were recorded in Shark Bay 116 individuals with 34 adults and 82 juveniles over 3 years in 2017, 2018 and 2019 in the month of September mostly. In the Ningaloo area, there was also aggregation between juveniles and adults with 57 individuals found (35 adults and 22 juveniles). They were present in 2 years in 2018 in July and in December 2019. In the area near Pilbara, 50 individuals (17 ADT, 33 JUV) were recorded. All adults were sighted in August 2018. As for the juveniles, they were observed in 2017, 2018 and 2019. Those of the 2017 year mainly in September, those of 2018 in April/May, and those of 2019 in April (**Appendix 10**).

Scalloped hammerhead sharks were recorded in 10 locations.66 individuals were observed with 39 juveniles and 27 adults. Their FL varied between 61.2 cm and 299.9 cm. They were identified in several oceans, with notably a spot near the island of Malpelo. This had 37 sharks (8 ADT, and 29 JUV) at the time of April 2018 (**Appendix 11**)

2.2 Results of age differences between locations and species

- 2.2.1 Frequency by location
 - 2.2.1.1 Juvenile et adult

In the study, 5 locations with less than 5 sharks were excluded from the analysis.

For the remaining 24 sites, the number of juveniles relative to the number of adults varied by location ($\chi^2 = 271.8$; p<0.001).

On average, juveniles represented 43.3% of the records. 10 locations had a similar percentage of observed juvenile abundance as expected (Timor, Cocos, Tristan, Revillagigedo, Shark bay, Ascension, Ashmore reef, Gracetown, Azores and Pilbara), assimilated to a fishing pressure on juveniles. There were 8 environments with relatively fewer juveniles observed (New Caledonia, Clipperton, Perth Canyon, Ningaloo, Rowley Shoals, the Research Archipelago, Bremer and Montebellos) than expected, The average for the level of fishing pressure on juveniles was 1.5 times higher than expected (**Table 3**) and 6 other locations (Tristan-Gough, FNQ, Chagos, Palau, Malpelo and Long Reef) with more juveniles observed than the expected average, were considered as having low fishing pressure on juveniles. The mean for the level of fishing pressure was 1.9 (\pm 0.18) for areas with expected ratios, 1.87 (\pm 0.12) for those with fewer juveniles than expected and 0.7 (\pm 0.33) for those with more juveniles than expected. There was a significant difference between sites with fishing pressure and those with low fishing pressure. (p = 0.009)(**Figure 5**). On the other hand, there was no significant difference in fishing effort between the sites with marine protected areas and the sites without (p = 0.2) (Figure 4). All sites were scored by fishing effort and protection (MPA or non-MPA) (**Figure 6**).

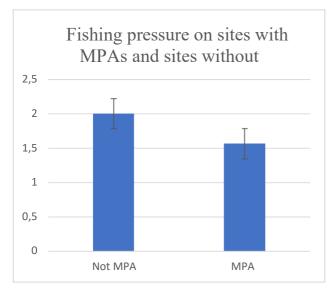


Figure 4 : Histogram of fishing pressure at the sites in this study, with sites not protected by marine areas and sites protected by marine areas, no significant difference.

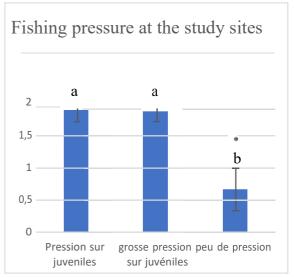


Figure 5 : Histogram of fishing pressure of study sites on juveniles, sites with high fishing pressure on juveniles and sites with low fishing pressure. Significant difference between a and b (p = 0,009).

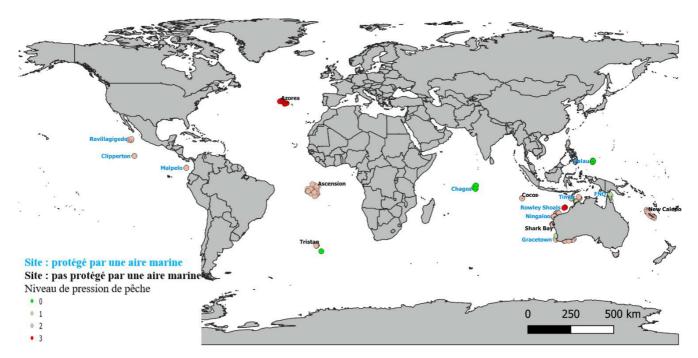


Figure 6: Each point represents the fishing effort by site and by all the sharks recorded in the study, with electric green representing very little fishing effort (0), dull green representing little fishing effort (1), dull red representing the presence of fishing pressure (2) and electric red representing heavy fishing pressure (3) on the environment. The names of the sites in blue are the sites with a marine protected area and the sites in black, the sites not protected.

2.2.1.2 Juveniles/ adults and Neonates

For the 11 sites with newborns: Ascension, Azores, Bremer, Chagos Archipelago, Malpelo, Long reef, Palau, Pilbara, Recherche Archipelago, Timor, and Tristant-Gough, the number of neonates relative to the number of juveniles/adults varied among sites ($\chi 2= 149.4$; p<0.001). On average, neonates represented 3.4% of records. 5 sites (Ascension, Malpelo, Pilbara, Timor and Tristan) have similar numbers of neonates observed as expected. 6 sites (L'Archipelago de la Recherche, Chagos Archipelago, Palau, Bremer and Long reef) are analyzed with relatively fewer pups and only Azores with more pups than expected. Locations with observed percentages of juveniles >8% are considered hot spots (Appendix 12).

2.2.2 Species frequency

2.2.2.1 Juvénile et adulte

The number of juveniles and adults varied among species ($\chi 2= 259.49$; p<0.001). On average, juveniles represented 42% of the sharks observed.

For silky shark and whitetip shark, the percentage of juveniles was similar to the overall average. For 5 species, there were fewer juveniles than expected (copper, sandbar, blue, mako and great hammerhead sharks) and 3 species with a higher percentage of juveniles (scalloped hammerhead, mako and dusky shark) than expected.Juvéniles/adultes et Nouveau-nés

The number of neonates compared to the number of juveniles and adults varied by species (χ^2 = 268,70; p<0.001). On average, young-of-the-year represented 6.6% of the sharks. The results for silky, mako and brimstone sharks were similar to the expected average, but there was a higher percentage of neonates for blue sharks.

10

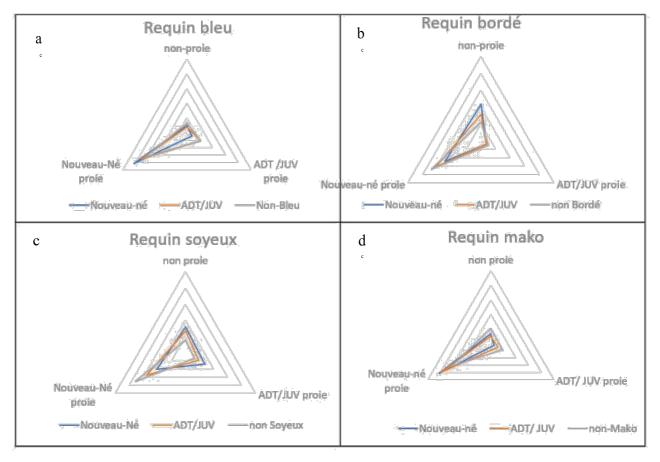


Figure 7 a-d : *Radar plots showing the percentages of prey classified as neonate prey, juvenile/adult prey, and "non-prey" per log of total abundance, as a function of maximum neonate and juvenile/adult size for blue shark (a), mako shark (b), and silky shark (c). Axes are scaled to 80% in 20% increments.*

2.3 Spectrum of shark prey

Mako shark : The percentage of TA recorded from the different prey size classes (neonate prey, juvenile/adult prey, and animals too large to be prey) differed between neonate, juvenile/adult, and non-mako strings.

On strings with neonates, there was a higher proportion of appropriately sized prey (i.e., < 36 cm LF; 83% of individuals) compared to strings with juveniles/adults (79%) or without makos (61%) (Figure 7; a).

Strings with neonates also had a lower percentage of large non-prey animals (e.g. 13.1% of individuals) but also a low percentage of prey adapted to ADT / JUV (4.8%; potential predator). On strings with food suitable for neonates, both ADT / JUV (73.5%) and non-prey (65%) are present. Radar provides a visualization of these percentages.

Edged shark : For total abundance, neonates are in a higher percentage associated with prey adapted to them (i.e. < 23.8 cm FL; 49.0% of individuals) compared to non-proy (43.7%) and adult/juvenile (7.5%). Despite this, non-bordered sharks and adults/juveniles have higher percentages of prey adapted to neonates (**Figure 7 ; b**).

Blue shark : The percentage of TA recorded from the different prey size classes (prey neonates, prey juveniles/adults, and animals too large to be prey) differed between strings with neonates, juveniles/adults, and non-blue. For strings with newborns, there was a high proportion of prey size appropriate to (i.e., < 24.1 cm FL; 75.5%) compared to areas with prey size appropriate to juveniles/adults (2.8%) and "non-prey" (21.7%) (**Figure 7 ; c**).

Silky shark : Total abundance contains in the case of neonates a higher percentage of food with adapted size 41% than percentage at the level of adapted prey for ADT/JUV (27.3%) and than "non-prey" (31.7%).

Prey foods suitable for juveniles remain highest for "non-silkies" (71%) and ADT / Juv (54.8%) (Figure 7 ; d).

3. DISCUSSION

Sharks are the apex predatory of the marine pelagic ecosystem. They act as regulators of biodiversity by directly influencing the abundance of other species through trophic levels (Friedrich et al. 2014). Unfortunately, many shark populations are in decline (Shepherd & Myers 2005), especially due to overfishing and bycatch (Dulvy et al. 2014).

Few studies have been conducted on habitats suitable for their survival, this lack of knwoledge is due in particular to their complexity of movement (Brannen 2013, Speed et al. 2010). Migratory tracking provides greater insight into the relative extinction risk of species, which varies based on several factors: their ranges; dispersal; and the use and specificity of each habitat (Speed et al. 2010).

This study is among the first to investigate the long-term (2012 to 2019) distributional choices of 10 shark species; the coastal shark *Carcharhinus limbatus*, the blue shark *Prionace glauca*, the copper shark *Carcharhinus brachyurus*, the sandbar shark *Carcharhinus plumbeus*, the whitetip shark *Carcharhinus albimarginatus*, the oscar shark *Carcharhinus obscurus*, the mako shark *Isurus oxyrinchus*, the silky shark *Carcharhinus falciformis*, the scalloped hammerhead shark *Sphyrna lewini* and the great hammerhead shark *Sphyrna mokarran*.

Nursery areas are widely considered critical habitats for sharks. However, very few studies have identified the factors that influence the selection of these areas (Heithaus 2007). Indeed, young-ofthe-year sharks grow up according to specific distributional choices. Prey-spectrum analysis has indicated that one of the specificities and habitat choices for blue shark, mako shark, and silky shark is related to the size of prey available in the environment. Consistent with our hypothesis, newborns were present in a higher percentage on the strings with prey sizes that are suitable for them (i.e. <36cm), with 75.5% for blue shark, 49% for mako shark, 82.1% for mako shark and 41% for silky shark. Newborn sharks have high energy requirements due to their rapid growth rate (Post& Evans 1989, Maia et al.2007). In addition, they are less efficient at hunting than adults, spending more time capturing prey than their older conspecifics (Barry et al., 2008). As such, it is widely accepted that nursery areas should be rich in prey (Branstetter 1990). However, there is a counter-argument in which high food abundance is a "faux- ami" because it attracts predators (Heithaus 2007). Indeed, our results showed that adults/juveniles and "non-sharks" (i.e., potential predators), were often in locations with food suitable for young-of-the-year, with 73.5% presence for adult/juvenile blue sharks, 61.5% for adult/juvenile, 79.1% for adult/juvenile mako sharks, and finally 54.8% for adult/juvenile silky sharks. However, studies have shown that movements of neonates to certain locations may be primarily motivated by predator avoidance rather than prey distribution (Heupel & Simpfendorfer 2005). Indeed, many studies support the strong segregation that occurs between neonates and adults/juveniles. Despite this, the results contradict these studies and our hypothesis on the segregation of these life stages. The distribution results showed that the newborn sharks observed were in the presence of adults/juveniles at the same time and at the same location: 100% for the blue shark and the sandbar shark, 25% for the mako shark and 80% for the silky shark.Indeed, blue shark young of the year were recorded in the presence of older conspecifics at Bremer in January 2018, at Tristan in January 2018 but also at Azores in June 2018. The same is true for the bordered shark at Long reef in September 2018, for the silky shark at Malpelo in April 2018, at Ascension in January 2017, at the Chagos Archipelago in February 2016 and in New Caledonia in September 2014 and finally for the mako shark at Perth canyon in November 2016.

It is true that segregation can occur in the same environment. Consistent with our knowledge, some newborn shark populations may exhibit intense niche partitioning using environmental topography (Kinney et al. 2011). However, our underwater videos film at a depth of 10 m and necessarily the different ages of sharks were observed at this depth: segregation within the same environment is therefore unlikely.

All the sites in this study are considered to be frequented by migratory sharks, but some sites have periods with peaks of productivity, and therefore of prey abundance, which may have motivated the newborns to remain in the presence of their older conspecifics. Indeed, in the Bremer area in January, the concentration of nutrients increased strongly, this being linked to the warm Leeuwin current. This current flows along the Western Australian coastline, and passes over the Bremer Canyon. It creates an oceanic gyre of warm water at the surface that causes nutrient rich cold water to rise from the sea floor. This creates a very productive environment over the following weeks (Bouchet et al. 2018). Also, in the Azores region known to be an important feeding area for migratory sharks (Das & Pedro 2017), sees peaks in nutrients and productivity in the spring (April, May and June) (Schiebel & al. 2011, Abell et al. 2013). The Chagos Archipelago has a peak of productivity especially with the SWTIO upwelling during the spring and austral summer (August to February) (Hermer et al. 2008). The Tristan area on the other hand is a remote area with one of the few relatively intact ecosystems, high biomass and abundance of species present (Caselle et al., 2018).

Of course, there are specific bathymetric conditions and other specifics of habitat choice than productivity and suitable prey size. For example, studies have shown that neonates seek associations with warm water because they may be motivated by energetic trade-offs, so higher temperatures may allow them to expend less energy on endothermic reactions and invest more in growth (Casey & Kohler 1992, Maia et al.2007).

Thus, the results provide evidence that prey availability and environmental productivity may be a major factor in neonate distribution, and that predation appears to play a secondary role.

Identifying the factors stimulating and influencing the selection of newborns on critical habitats is necessary. Following on from these findings, the next step is to identify these habitats for the future implementation of mandatory management for the survival and for some species the recovery of shark populations (Ducatez 2019, Nosal et al. 2019). Eventough all of the study sites in this experiment are known to be shark friendly, the actual and expected abundance observed highlighted hot spot areas which are areas with higher percentages of young of the year (Research Archipelago, Chagos, Palau, Bremer, Long reef, Azores and Tristan). Inversly, cold spot areas were identified where few or no newborns are observed. The number of young of the year in our samples is small (only 52 in total out of 1524 sharks), the expected values are also small, so the results must be approached with caution. However, small samples on neonates are not uncommon in studies in view of the complexity of their movements (Domeier & Nasby-Lucas 2013, Thorpe et al. 2014). Although it can be argued that the rarity of neonates in the observed samples reflects a methodological bias, it is noted, however, that neonates spend 97% of their time between 0 and 40 m and 25% between 0 and 10 m, thus at mid-water. As such, the stereo-BRUVS are perfectly designed to detect this life stage. The low recorded abundance of young-of-the-year may reflect the rarity of blue, mako, edge and silky shark in the word.

Sites characterized as hot spots showing the highest percentage of young of the year are: Azores (36% juveniles) and Tristan (21% juveniles). These two sites are suitable habitats for young of the year despite the fact that they are highly coveted by the shark fishery, especially for makos and blue sharks, which are the most heavily fished sharks in the world.

Almost all young of the year are less abundant or not present at all at other locations even those associated with marine protected areas with Gracetown, Perth canyon, Ashmore reef, Clippertone, Montebellos and Revillagigedo being marine protected areas and not recording a single newborn during the 8 years of video (**Appendix 12**). Some areas continue to experience excessively high fishing quotas or high levels of illegal shark fishing making population recovery impossible (Hughes et al. 2016).

It was analyzed whether the difference in abundance of young-of-the-year was species dependent. It was found that the actual and observed abundance was the same for Mako, billfish and silky. However, in blue shark an increase in newborns was observed relative to the expected abundance. An explanation for the higher juvenile rate would not be in a greater number of spawners, or a higher survival rate, but probably in their ability to produce large litters during pupping, between 13 and 68 pups (Zhu et al., 2011) compared to an average of 15 pups for the other 3 sharks (NOAA Fisheries).

Eventough neonates are often considered the most critical age classes in terms of population stability/recovery, more and more research suggests that life stages outside the nursery may be equally important. Thus, there is an equal need for management strategies that also encompass older individuals (Kinney & Simpfendorfer 2009).

The sharks studied have a heterogeneous spatial distribution. The mako shark, silky shark and scalloped hammerhead shark were recorded in the 3 oceans (Pacific, Atlantic and Indian), the blue shark in the Indian and Atlantic Oceans, the mako shark, great hammerhead shark and sandbar shark in the Indian and Pacific Oceans and finally the copper shark and dusky shark in the Indian Ocean. The results on shark distribution percentages showed that sharks with a distribution > 40% (mako shark, silky shark, great hammerhead shark, scalloped hammerhead shark) included 60% of species classified as threatened. While those with a distribution < 40% (blue shark, copper shark, dusky shark, sandbar shark, whitetip shark) included 25% threatened species. Highly migratory sharks with their wide distributions are highly susceptible to interaction with commercial longline fishing gear and capture as targets or bycatch (Calich et al. 2018), a study by Nuno Queiroz et al in 2016 showed that the most intense longline deployment rates are focused on areas highly used by sharks, with up to 80% overlap between European longlines and areas frequented by blue, great hammerhead and mako sharks. As a result, the blue shark has a 67.3% chance of being caught in these areas and the mako 40.7%. Another study conducted by Heather et al. analyzed the mortality rate of sharks after being hooked on pelagic longlines. After being hooked for more than 3 hours, 97% of dusky sharks and 27% of sandbar sharks died. In addition, more than 36 million sharks are killed for their fins each year, with mako, blue and a few others accounting for about 42,000 tons of the European Union's catch, including 25,000 tons of blue sharks according to the European Shark Commission.

All of these consequences make elasmobranchs the most threatened groups by direct or indirect fishing worldwide (Worm et al. 2013). The sharks in our samples were 70% threatened (i.e., vulnerable, endangered or critically endangered). The results of the study allow us to understand and identify the areas where pelagic sharks are most at risk from capture.

First of all, juveniles and adults are considered to have life stages that can cohabit and therefore do not exhibit segregation behavior (Jacoby et al. 2012, Litvinov 2006), secondly, that in the logic of a stable environment there are more juveniles. The analysis of actual and expected abundance in the proportion of juveniles and adults already showed an anomalous discrepancy with proportionally less juveniles (43.3%). The analysis also highlighted the fishing pressure on sharks in some areas. Indeed, 8 sites (New Caledonia, Clipperton, Perth Canyon, Ningaloo, Rowley Shoals, the Research Archipelago, Bremer and Montebellos) had on average a smaller ratio of juveniles with a fishing pressure of 1.87. 10 sites (Timor, Cocos, Tristan, Revillagigedo, Shark bay, Ascension, Ashmore reef, Gracetown, Azores and Pilbara) had an expected number of juveniles, which was smaller than the natural ratio with a fishing pressure of 1.9. Finally, 6 sites (Tristan-Gough, FNQ, Chagos Archipelago, Palau, Malpelo Island and Long reef) significantly different with a lower fishing effort of 0.7 had more juveniles than expected. Furthermore, when comparing sites with and without MPAs, there was no significant difference in fishing effort, which is consistent with studies showing that weak management of MPAs has very little positive impact, and that it is important to implement good fisheries management so that it is truly beneficial to the organisms (Hughes et al. 2016, Mesnildrey et al., 2013, Vandeperre et al. 2011). There is strong evidence stating that sharks have site fidelity at some sites (Byrne et al. 2019). Our results follow this direction, indeed, at some locations, sharks of the same species were present over multiple years such as at the MPAs at the sites of: Long reef where the broadbill were present in 2012, 2017, 2018 a fishing effort of 1, then the silky shark on the island of Chagos in 2012, 2015 and 2016 with a fishing effort of 0, but also in Perth canyon where the copper shark was seen in 2017 and 2018 which has a fishing effort of fishing 1.

These environments are therefore part of the areas that can be considered as a current refuge with no fishing pressure for the animals. Indeed, the Chagos Archipelago is the largest marine protected area with a no-take zone in the world, i.e., an area where no extractive activities are allowed and where sharks are not subject to fishing pressure (Sheppard et al., 2012). Palau was the world's first shark sanctuary established in 2009, which banned shark fishing in its entire 630,000 square kilometer exclusive economic zone (EEZ) (Friedlander et al. 2014). But, despite strong fishing pressure on some sites, we still see fidelity with notably Shark bay where the dusky shark and the grey shark appeared in 2017, 2018 and 2019 which is a non-protected site with a fishing effort of 2, as well as Ascension Island where the blue shark and the silky shark appeared in 2017 and 2018 which is not a protected area with a fishing effort of 2, then on the island of New Caledonia, the whitetip shark was seen in 2012 and 2016 and the whitetip shark in 2012 and 2016, which is not an MPA either, with a fishing effort of 2, and also Ningaloo, where the dusky shark was detected in 2018 and 2019, which is an MPA, but with a fishing effort of 2. These results demonstrate the importance of these environments and the importance of setting up fisheries management. Scientists have highlighted low-cost opportunities to decrease bycatch, especially on pelagic longlines, experienced by sharks with the use of thinner ropes that sharks could cut when biting, changes in hook depth (outside of sharks' preferred depths), the type of hook that would not allow sharks to latch on, and more recently, the development of gear with electrical signals that would allow sharks to avoid fishing vessels (Godin et al. 2013).

CONCLUSION ET PERSPECTIVES

This study reflects the enormous impact of fishing on shark populations and the value of implementing management in all these areas identified as critical habitats. High seas fishing activity is now synchronized with thermal fronts, imposing even more striking pressures on elasmobranchs (Queiroz et al. 2016). Too many of these important sites considered as potential refuges and nurseries are in critical need of management. There is ample evidence that strong and effective management allows populations to rebound (Hilborn et al. 2020). It is important to note that in some locations, changes are taking place. In particular, the archipelago of Palau has since January 1, 2020, banned strict resource extraction in 80% of its area. (Palau National Marine Sanctuary Goes Into Effect, 2020). The island of Malpelo is improving its sanctuary laws and received the Global Ocean Refuge (GLORES) award in 2017. This award recognizes this sanctuary as an exemplary management sanctuary. The island of Ascension is in the process of establishing one of the largest marine protected areas, which will be operational in the year 2020.

While research on critical habitats for pelagic shark species is still in its beginning stages, it is becoming increasingly clear that the various life stages rely on an extremely limited and diminishing number of habitats.

There are controversial views on which life stages should be protected. Some scientists express the view that the simple presence of juveniles does not justify habitat protection (Heupel et al. 2007). While others report that protection should focus more on areas used by juveniles rather than those used by young-of-the-year (Kinney & Simpfendorfer, 2009). We would argue that there is no one stage less important than another. Indeed, if effective management is to be achieved, it is essential to link the conservation of early life stages with management strategies that encompass older individuals residing outside the nurseries.

In the oceans, the least protected ecosystems on our planet, sharks are an evolutionary marvel on the brink of extinction. All sites identified as critical habitats should be given immediate protection, protection commensurate with their immense shark conservation value.

17

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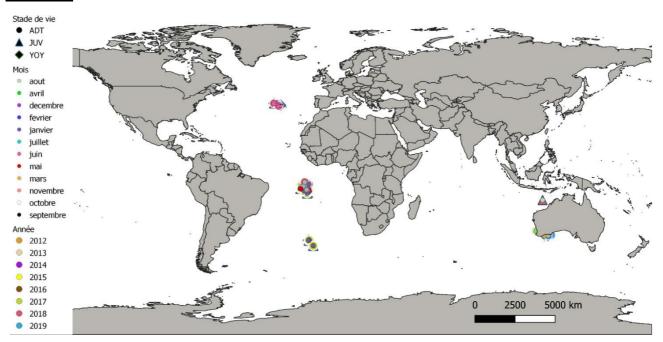
24

ANNEXES

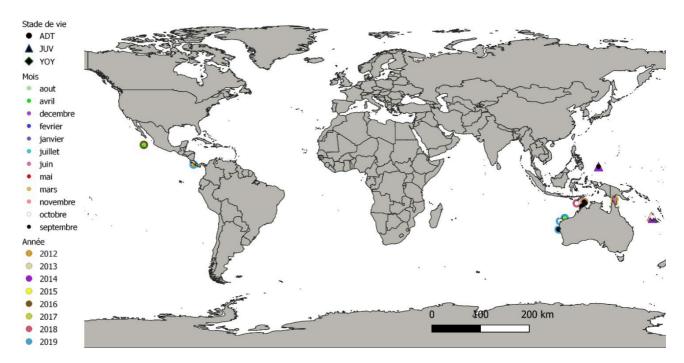
<u>Annexe 1 : Taille utilisée pour l'identification des différents stades</u> <u>de vie de chaque espèce.</u>

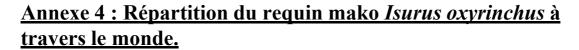
Espèces	Taille maximum pour les jeunes de l'annéeTaille maximum pour le juvéniles	
Requin cuivre	68,1 cm	168,7 cm
Requin obscur	83, 2 cm	212,7 cm
Grand requin marteau	60,5 cm	157,5 cm
Requin gris Sandbar	60,0 cm	103,2 cm
Requin marteau halicorne	54,0 cm	139,4 cm
Requin à pointe blanche	70,2 cm	152, 5 cm

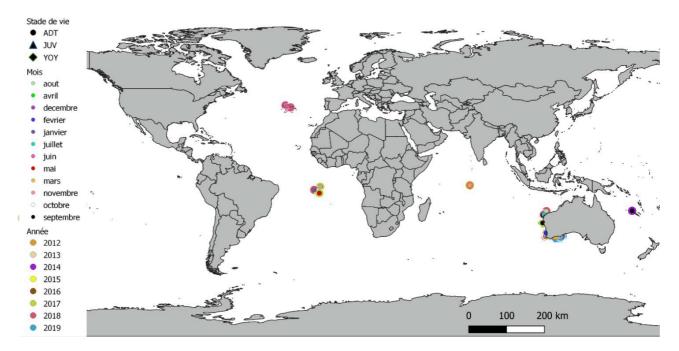
<u>Annexe 2 : Répartition du requin bleu *Prionace glauca* à travers le monde.</u>



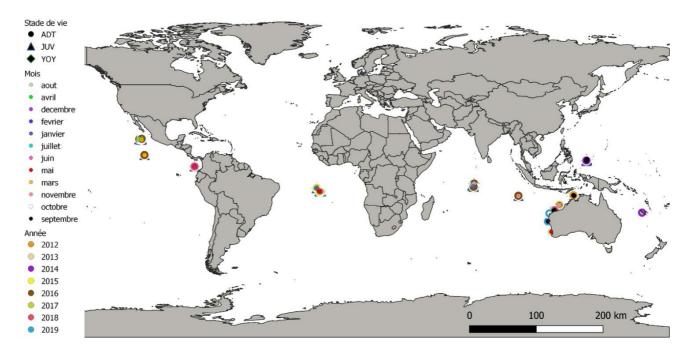
Annexe 3 : Répartition du requin bordé *Carcharhinus limbatus* à travers le monde.

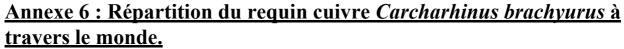


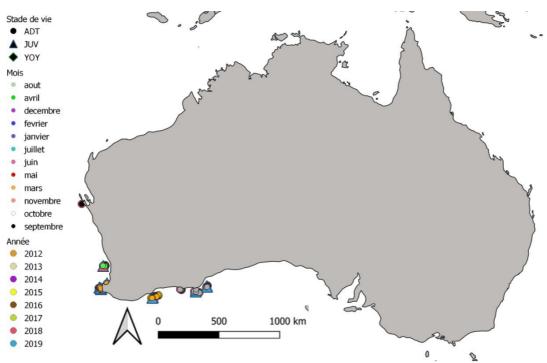




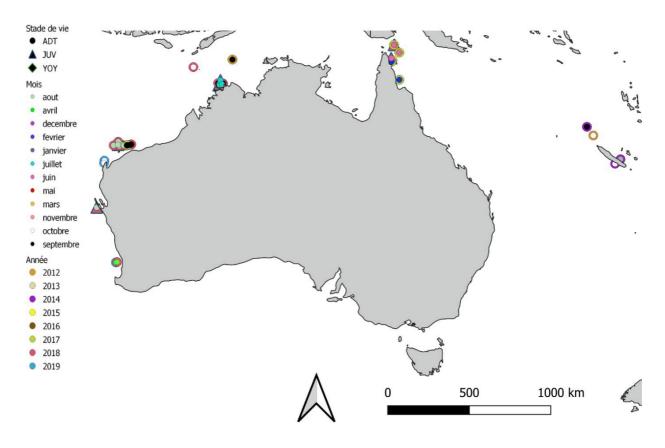
Annexe 5 : Répartition du requin soyeux *Carcharhinus falciformis* à travers le monde.



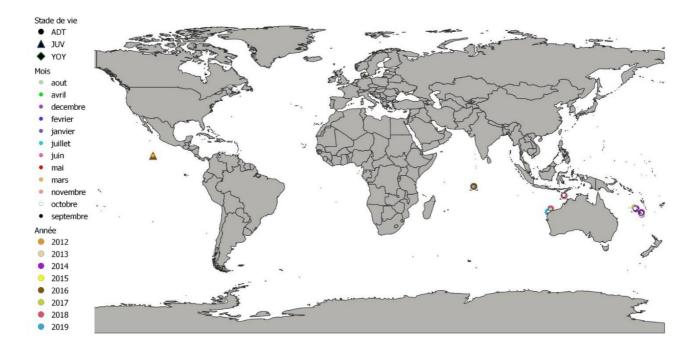




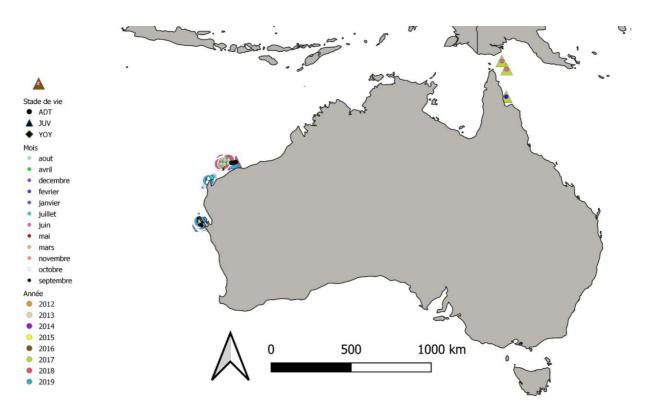
Annexe 7 : Répartition du grand requin marteau *Sphyrna mokarran* à travers le monde.



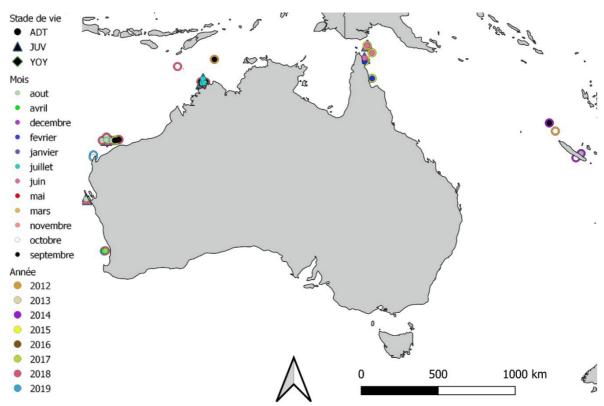
Annexe 8 : Répartition du requin à pointe blanche *Carcharhinus albimarginatus* à travers le monde.



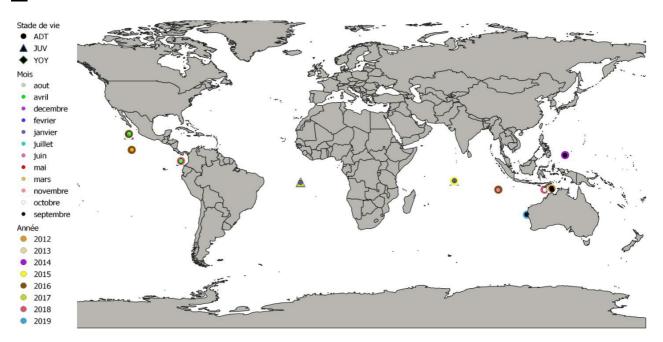
Annexe 9 : Répartition du requin gris *Carcharhinus plumbeus* à travers le monde.



Annexe 10 : Répartition du requin obscur *Carcharhinus obscurus* à travers le monde.



<u>Annexe 11 : Répartition du requin halicorne *Sphyrna lewini* à travers le monde.</u>



Annexe 12 : Pourcentages des jeunes de l'année et des juvéniles/adultes observés pas site ainsi que la protection.

	% YOY	% de juveniles/	
Localisation		adults	Protection
Ascension	1%	99%	Not AMP
Azores	36%	64%	Not AMP
Bremer	9%	91%	AMP
Chagos	8%	92%	AMP
Clipperton	0%	100%	AMP
Cocos	0%	100%	AMP
FNQ	0%	100%	Not AMP
Gracetown	0%	100%	AMP
Malpelo	4%	96%	AMP
Montebellos	0%	100%	AMP
New Caledonia	0%	100%	Noy AMP
Ningaloo	0%	100%	AMP
Ashmore reef	0%	100%	AMP
Long Reef	10%	90%	AMP
Palau	8%	92%	Sharks sanctuary
Perth Canyon	0%	100%	AMP
Pilbara	3%	97%	Not AMP
Recherche	8%	92%	AMP
Revillagigedo	0%	100%	AMP
Rowley Shoals	0%	100%	AMP
Shark Bay	0%	100%	AMP
Timor	2%	98%	AMP
Tristan	21%	79%	Not AMP
Tristan - Gough	0%	100%	AMP