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ELASMOBRANCHES BYCATCH IN THE FRENCH TROPICAL PURSE-SEINE FISHERY OF THE EASTERN ATLANTIC OCEAN: SPATIO-TEMPORAL DISTRIBUTIONS, LIFE STAGES, SEX-RATIO AND MORTALITY RATES

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SUMMARY

Marine megafauna, especially sharks and rays, are caught as bycatch by the tropical tuna purse-seine fishery. We studied their spatio-temporal distribution patterns by species and by the diversity of assemblages, as well as by differentiating juveniles and adults in the eastern Atlantic Ocean. We also investigated sex-ratios and mortality rates at release. Data were collected by scientific observers onboard French purse-seiners between 2005 and 2017. Among the 18 species of elasmobranches caught, 85.4% of the individuals were silky sharks. Distributions of catch per unit of effort (CPUE) by species, sex-ratios and diversity indices varied with life stages, areas, seasons and fishing modes (fish aggregating device vs. free-swimming tuna school sets). These differences appear to be linked to specific environmental conditions occurring in some areas and seasons. Higher elasmobranches catch rates in FAD sets (40%) compared to FSC sets (17%) were detected. Overall, this study highlights high elasmobranches bycatch rates, high mortality rates for most species (12.76─56.93%; average 45.8%), and high proportion of juveniles caught for the large majority of species (21.27─100%; average 87.4%).

RÉSUMÉ

La mégafaune marine, en particulier les requins et les raies, sont capturés comme des prises accidentelles par la pêcherie de senneurs ciblant les thonidés tropicaux. Nous avons étudié leur répartition spatio-temporelle, par espèce et par la diversité des assemblages, ainsi qu'en différenciant les juvéniles et les adultes dans l'océan Atlantique oriental. Nous avons également étudié les sex-ratios et les taux de mortalité à la remise à l'eau. Les données ont été recueillies par des observateurs scientifiques embarqués à bord de senneurs français entre 2005 et 2017. Parmi les 18 espèces d'élasmobranches capturés, 85,4 % des spécimens étaient des requins soyeux. Les distributions de la capture par unité d'effort (CPUE) par espèce, sex-ratio et indices de diversité variaient en fonction du cycle vital, des zones et des modes de pêche (dispositif de concentration des poissons par opposition à opérations sur bancs libres). Ces différences semblent être liées à des conditions environnementales spécifiques qui se produisent dans certaines régions et saisons. Des taux de capture supérieurs d'élasmobranches dans les opérations sous DCP (40%) par rapport aux opérations sur bancs libres (17%) ont été détectés. Dans l'ensemble, cette étude met en évidence les forts taux de prise accessoire d'élasmobranches, les taux élevés de mortalité pour la plupart des espèces (12,76–56,93% ; moyenne 45,8%), et la forte proportion de juvéniles capturés pour la grande majorité des espèces (21,27 –100%, moyenne 87,4%).

RESUMEN

La mega fauna marina, especialmente los tiburones y rayas, es capturada de forma fortuita por las pesquerías de cerco tropical. Se estudian sus patrones de distribución espacio temporal por especies y por la diversidad de sus asociaciones, así como mediante una diferenciación entre adultos y juveniles en el océano Atlántico oriental. También se ha investigado la

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proporción de sexos y las tasas de mortalidad tras la liberación. Los datos fueron recopilados por observadores científicos a bordo de cerqueros franceses entre 2005 y 2017. Entre las 18 especies de elasmobranquios capturadas, el 85,4% de los ejemplares capturados fueron tiburón jaquetón. La distribución de la captura por unidad de esfuerzo (CPUE) por especies, proporciones de sexos e índices de diversidad variaban en función de las fases del ciclo vital, las zonas, las temporadas y los modos de pesca (lances sobre dispositivos de concentración de peces frente a lances sobre bancos libres de túnidos). Estas diferencias parecen estar vinculadas con condiciones medioambientales específicas que se producen en algunas zonas y temporadas. Se detectaron tasas más elevadas de capturas de elasmobranquios en lances con DCP (40%) que en lances sobre bancos libres (17%). En general, en este estudio se resalta elevadas tasas de captura fortuita de elasmobranquios, tasas de mortalidad elevadas para la mayoría de las especies (12,76–56,93%; promedio 45.8%), y una elevada proporción de juveniles capturada para la mayoría de las especies (21,27–100%; promedio 87,4%).

KEYWORDS

Bycatch, elasmobranches, juveniles, sex-ratio,
mortality, FAD, free school, tropical tuna purse-seine

1. Introduction

Marine diversity is impacted by several anthropogenic activities, with fishing activities considered as one of the main threat (Dulvy *et al*., 2003). The tuna purse-seine fishery (PSF) generates relative high bycatch rates, i.e., catches of non-target species or of under-sized individuals from target species. Two main fishing modes can be identified: sets on free-swimming tuna schools (FSC) and sets associated to Fish Aggregating Devices (FAD). The latter generates a higher proportion of bycatch, including vulnerable species such as sharks and marine turtles (Dagorn *et al*., 2013).

In this study, we focused on elasmobranch bycatches in the French tropical tuna purse-seine fishery in the Atlantic Ocean between 2005 and 2017. Many elasmobranch species are classified as Vulnerable or Endangered by the International Union for Conservation of Nature (IUCN) and are included in Appendix II of the Convention of Trade in Endangered Species (CITES). They are particularly vulnerable to overfishing mainly due to late maturity and low fecundity (Frisk *et al*., 2001). Juveniles are more vulnerable than adults and have a high nutrient need, which often leads them to occupy areas productive areas (Heupel and Simpfendorfer, 2002). However, fishing effort may potentially be important in areas with high abundance of juveniles. Globally, despite the importance of the juvenile compartment for many species, very little information on their spatial and temporal distribution is available (Croll *et al*., 2015; Escalle, 2016), especially for rays with very limited data availability (Croll *et al*., 2015). Indeed, in the western and central Indian Ocean, high numbers of juvenile silky sharks (*Carcharhinus falciformis*) are caught as bycatch by longliners, and population analysis has shown that high juvenile mortality has a significant impact on demographic growth (Hutchinson *et al*., 2013). Likewise, the study of sex-ratios is of critical importance (Joung *et al*., 2017; Coelho *et al*., 2017).

The aim of this study is to analyze the spatio-temporal distribution of elasmobranches captured by the French tropical tuna purse-seine fishery for both fishing modes. Analyses will focus on i) the spatio-temporal distribution of each species, juveniles and adults separately, as well as the distribution of the diversity of elasmobranch assemblages, ii) the sex-ratio of each species, iii) the impact of the fishery on elasmobranches in terms of mortality rates.

2. Methods

We used data on elasmobranch bycatches collected by scientific observers aboard French purse-seiners. A subset of these data was considered to assess size distributions (total length TL for sharks, and WD disk width for rays) and sex-ratios (when available). This subset corresponds to 63% of all individuals captured (9,807 individuals measured among the 15,555 caught). Discrimination between juveniles and adults was then carried out based on measured TL and size at maturity (L50) of each species using information available in Fishbase (fishbase.org).

Seventeen elasmobranches species have been observed. However, 11 species were analyzed in more detail (> 57 individuals caught), seven sharks and four rays: blue shark (*Prionace glauca*), great hammerhead (*Sphyrna mokaran*), oceanic whitetip shark (*Carcharhinus longimanus*), scalloped hammerhead (*Shyrna lewini*), silky shark (*Carcharhinus falciformis*), shortfin makos (*Isurus oxyrinchus*), smooth hammerhead (*Sphyrna zygaena*), devil fish (*Mobula mobular*), giant manta (*Manta birostris*), pelagic stingray (*Pteroplatytrygon violacea*) and spinetail mobula (*Mobula japanica*) (**Table 1**).

Catches Per Unit of Effort (CPUE) were computed for each 1° grid cell, using the number of individuals caught divided by the number of sets. CPUE were then plotted as map at a 1° grid cell resolution.

Seasonal variability was also considered using quarters (Escalle, 2016). Elasmobranch assemblages were also studied using complementary diversity indices: i) species Richness Per Unit of Effort (RPUE) computed such as CPUE from the number of elasmobranch species caught, ii) unbiased Simpson's diversity, also known as Probability of Interspecific Encounter (Hurlbert, 1971) and iii) Simpson's equitability (Smith and Wilson, 1996). Contrarily to species richness, Simpson’s diversity has been shown being relatively stable to sample size variation (here number of sets) (Lande, 1996). Thus the initial value of this index was considered (i.e. not adjusted by number of sets).

Indices were computed as follows:

- Simpson diversity: $(N/N\text{-}1) \times 1\text{-}D$
  with D = , with Ni : number of individuals for each species i; N : total number of individual of elasmobranch within a set; N_{sp} : species number.

- Species Richness Per Unit of Effort: $RPUE = N_{sp} / N_{set}$
  with N_{set} : sets number.

- Simpson’s equitability: $E = 1\text{-}D / (1\text{-}1/ N_{sp})$

Apparent mortality rates were calculated for each of the 11 species selected, and computed in each of the 14 Exclusive Economic Zones (EEZ) based on the status of individuals at release assessed by scientific observers. Status include being released alive at sea, released dead at sea and found dead in the net.

The percentage of females and males was also calculated for each of the 11 species selected among individuals that were measured (Number of female or male / Number of female + number of male).

3. Results

3.1 General description

Between 2005 and 2017, 8673 fishing sets were monitored by scientific observers in the Atlantic Ocean. 2308 sets had at least one species of the seventeen elasmobranch species captured as bycatch (i.e. 26.6%). Among the 15,555 individuals captured, 71% were silky sharks (i.e. 11,048 individuals). The remaining individuals were 929 Scalloped hammerheads (6.0%), 532 Smooth hammerheads (3.4%), 472 Blue sharks (3.0%), 250 Pelagic stingrays (1.6%), 202 Great hammerheads (1.3%), 94 Spinetail mobulas (0.6%), 78 Oceanic whitetip sharks (0.5%), 62 Giant mantas (0.4%), 61 Shortfin makos (0.34%) and 57 Devil rays (0.4%) (**Table 1**).

A percentage of 40.22% FAD sets had at least one elasmobranch (1,451 out of 3607 sets) and 16.92% for FSC sets (857 out of 5,066 sets). Half of the species showed higher bycatch rates under FADs (the 3 Sphyrnidae species, the Silky shark and the Giant manta ray).

3.2 Spatial and temporal distribution

The spatial and temporal distribution of the fishing effort and elasmobranches bycatch varied with season, fishing modes, and areas. The first and second quarters had the highest proportions of elasmobranch bycatches (51–53% of FAD sets and 26–28% of FSC sets, respectively; **Table 2**). During these quarters, the fishing effort was very localized, and elasmobranch bycatches were mostly found on the coasts of Gabon, Angola, Senegal and Mauritania (**Figures 1 and 2**).

In the Gabonese EEZ, high proportions of individuals were observed for the 11 species compared to the other EEZ. Specifically, 5 species (Blue shark, Scalloped hammerhead, Smooth hammerhead, Silky shark and Shortfin mako) presented 45 to 88% of the total number of individuals caught in the eastern Atlantic Ocean localized in the Gabonese EEZ (**Table 3**). The second EEZ with the highest proportion of elasmobranch catches was the Angolan EEZ. However, the proportion of individuals captured appeared lower than in the Gabonese EEZ, with only one value greater than 45% of individuals captured in this EEZ (55.3% for the Spinetail mobula; **Table 3**).

3.3 Mortality rates

Mortality rates of the 11 species were higher for FAD sets (51.0% of the individuals captured died) compared to FSC sets (40%). Mortality rates ranged from 12.76% to 56.93%, with an average of 45.8% (**Table 4**). The species with the highest mortality rate is for the Great hammerhead shark with 57.0% and the lowest is the Spinetail mobula with 12.76% (**Table 4**). In the Gabonese EEZ, 6 species have mortality rates higher than 30%. However, the highest mortality rates are observed in Mauritania EEZ, specifically for captures of Smooth hammerhead sharks (86.58%) and the Giant mantas (84.20%, **Table 4**).

3.4 Life stages

Among the 11 studied species, more than 60% of the individuals caught were measured, with 1,139 individuals classified as adults and 7864 as juveniles. For most of species, a majority of juveniles were caught: 100.0% for the Shortfin mako, 99.8% for the Smooth hammerhead, 99.0% for the Great hammerhead, 98.0% for the Giant manta, 92.8% for the Silky shark, 70.2% for the Scalloped hammerhead, 59.3% for the Oceanic whitetip shark, 49.4% for the Blue shark, 39.1% for the Spinetail mobula, 32.2% for the Pelagic stingray and 21.3% for the Devil ray. In addition, most species had smaller individuals caught under FADs than in FSC sets (**Table 4, Figures 3 and 4**). Generally, distributions of adults were more spatially localised than juvenile distributions (**Figure 3**).

For all species combined, catches of juveniles represent 71.1% of all individuals captured under FAD compared to 34.7% in FSC sets. Similar proportions were found by species, which validates that these proportion are not influenced by abundant species.

3.5 Sex ratio

For most species considered, more than 60% of the individuals caught were sexed (**Table 4**). However, it varied according to species, with only 32% of the Pelagic stingray and Spinetail mobula were sexed. Blue sharks and Great hammerheads presented lower proportions of females (respectively 11.0% and 38.0%, **Table 4**). On the contrary Silky sharks, Pelagic stingrays, Devil rays and Scalloped hammerhead sharks had a sex-ratio around 50.0%. Finally, Oceanic whitetip sharks, Smooth hammerheads, Shortfin makos and Giant mantas showed sex-ratios biased towards females, respectively 61.0%, 62.0%, 65.3 and 66.7% (**Table 4**).

3.6 Diversity of elasmobranch assemblages

In one set, it is rare to find more than 1 or 2 elasmobranch species (up to 4 in some cases). Species Richness per Unit of Effort (RPUE) was significantly higher in the third quarter in FAD sets (Figure 5, $Chi^2 = 84.13$, df = 7, p = $1.98e^{-15}$). This corresponds mainly to the Gabon and Angola areas (**Figure 5**). For Simpson's equitability (correlated with Simpson's diversity which was thus not retained for the rest of the analyses), the level of dominance did not vary due to the high dominance of the silky shark (median close to 0; **Figures 6 and 7**). However, highest values of Simpson's equitability were observed under FADs in the third quarter ($Chi^2 = 60.68$, df = 7, p = $1.103e^{-10}$). Indirectly, this is due to higher RPUE. RPUE and Simpson’s equitability appeared high in similar areas and seasons (**Figures 7**): second and third quarter in Gabon and third and fourth quarters in Angola.

4. Discussion

This study based on observer data of the French tropical tuna purse-seine fishery focused on elasmobranches spatio-temporal distribution patterns in the Atlantic Ocean between 2005 and 2017. The Silky shark highly dominated the elasmobranch catches, as previously noted on this ocean (Amandè *et al*., 2010) and presented a majority of juveniles (i.e. 93%). This majority of juveniles is well known for Silky sharks captured by the purse-seine fishery in all oceans (e.g. Filmalter *et al*., 2013, Hutchinson *et al*., 2013), as well as for Blue sharks captured by the longline fishery in the Atlantic and Indian Oceans (Coelho *et al*., 2017), but this information is relatively scarce or absent for the other species. In our study, a high majority of juveniles was also observed for most of studied species, with a minimum of 60% of individuals for a given species being juveniles. In addition, our study also brings new information on the relative distribution of juveniles and adults of the 11 species of elasmobranches the most captured as bycatch of the purse seine fishery in the eastern Atlantic Ocean.

In the eastern Atlantic Ocean, the distribution on fishing effort, elasmobranch catches, as well as diversity indices vary depending on the season and the type of tuna school targeted. Firstly, primary productivity has been suggested to influence the distribution of target species and thus of the fishing effort, but also that of elasmobranch species (Escalle, 2016; Fonteneau *et al*., 1988; Lezama-Ochoa *et al*., 2016). We have found that fishing effort and elasmobranch catches were mainly localised in the coastal areas of Gabon, Angola, Senegal and Mauritania, mainly from June to August. This corresponds to seasonal peaks in productivity due to coastal upwellings and terrigenous rivers discharge off Mauritania, Senegal, Gabon, Congo and Angola. In addition, the thermal domes of Guinea and Angola reinforce the productivity of this environment and leads to higher tuna catch rates (Fonteneau, 1988). Secondly, the distribution of elasmobranch bycatches also varies with fishing mode. Indeed, the proportion of FAD sets having at least one elasmobranch captured was higher (40%) than free school sets (16%). This is an expected result, as it is common to observe many predators such as tuna, sharks or marine mammals associated to FADs (Fonteneau, 1993). However, FADs, whether they are natural or artificial, drift according to currents and winds and tend to aggregate in some areas (Fonteneau, 1993; Maufroy *et al*., 2016), which may also explain the spatial heterogeneity of the elasmobranch catches at the scale of the eastern Atlantic Ocean.

Apparent mortality rates were calculated for individuals with known fate and varied between 13% (Pelagic stingray) and 57% (Great hammerhead shark). However, this corresponds to the fate at the time of release and may underestimate the actual mortality on the longer term. For instance, post-release mortality rates using electronic tagging and blood chemistry analysis has been estimated at 80% for silky sharks captured by the purse-seine fishery in the Western and Central Pacific Ocean and the Indian Ocean (Hutchinson *et al*., 2015; Poisson *et al*., 2014), while the apparent mortality for this species was 46.60% in this study dedicated to the eastern Atlantic Ocean. In particular these authors found that most silky sharks (and likely other shark species) that spend time in the sack and that are brought onboard during brailing have very high mortality rates. This is due to compressed and anoxic conditions during these processes. To the contrary, Hutchinson *et al*. (2015) found that Silky sharks meshed in the net and brought onboard during the hauling process have lower mortality rates (18%). Nevertheless, it was found that individuals captured in FAD sets had higher mortality rates (51%) compared to FSC sets (40%). This may be due to the fact that more juveniles are caught on FAD (71% of individuals) compared to FSC sets (35%). Indeed, juveniles are more vulnerable than adults and may have different swimming capacity and behaviour than adults. In addition, mortality rates varied depending on the area (i.e. EEZ) considered. For instance, very high mortality rates were detected in the Mauritanian EEZ (80%). This may also be linked to the high dominance of juveniles in this area, which may potentially act as a nursery area.

Finally, we found that some species had very unbalanced sex-ratios, such as the Blue shark, with a high dominance of males (89%), which has already been shown in the Pacific Ocean by Hazin *et al*. (1994). This situation may be particularly preoccupying if low female ratio is representative of the Blue shark population at the scale of the ocean. However, males and females may be segregating in different areas depending on the season, as it has been found in the Pacific Ocean based on longline fishery data (Hazin *et al*., 1994).

5. Conclusion

Areas and seasons identified with relatively high catches of elasmobranches are known to present high primary productivity. This environmental condition appears to influence the distribution of tunas, targeted species of the purse-seine fishery and therefore also fishing effort, and then elasmobranch bycatch distributions. Relatively high values of elasmobranch CPUE were observed for all species combined off Gabon during the second and third quarters of the year, and Angola during the last two quarters. These areas and seasons could therefore be of particular interest in monitoring and management of elasmobranches bycatches.

Moreover, most species showed a large majority of juveniles caught for the purse-seiners. Individuals caught under FADs were generally smaller than in FSC sets. For some species, including the Silky shark, the high number of newborn individuals captured should be noted. This high proportion of juveniles and newborn is preoccupying. Once brought onboard, elasmobranches are released alive when possible. High mortality rates have however been recorded, which is also accompanied with unbalanced sex-ratios toward males for some species.

Further investigations on the distribution of sex-ratios could allow identification of potential breeding areas, and other key areas in the conservation of elasmobranches populations.

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Table 1. Percentage of elasmobranches caught, measured and sexed in Atlantic Ocean. Percentage of individuals measured = Number of individuals measured / Number of individuals caught, percentage of individuals sexed = Number of individuals sexed / Number of individuals measured.

FAO code Common name Scientific name	*Number of individuals caught*	*% Individuals caught*	*% Individuals measured*	*% individuals sexed*
BSH Blue shark *Prionace glauca*	472	3.03	75.00	91.30
FAL Silky shark *Carcharhinus falciformis*	11078	71.02	62.00	83.90
OCS Oceanic whitetip shark *Carcharhinus longimanus*	78	0.50	75.60	91.50
SPL Scalloped hammerhead *Sphyrna lewini*	929	5.97	82.00	88.30
SPZ Smooth hammerhead *Sphyrna zygaena*	532	3.42	78.50	95.69
SPK Great hammerhead *Sphyrna mokarran*	202	1.29	96.00	79.40
SMA Shortfin mako *Isurus oxyrinchus*	61	0.39	86.88	92.45
PLS Pelagic stingray *Pteroplatytrygon violacea*	250	1.61	82.80	31.40
RMB Giant manta *Manta birostris*	62	0.40	82.00	64.70
RMJ Spinetail mobula *Mobula japanica*	94	0.60	68.00	21.00
RMM Debil fish *Mobula mobular*	57	0.36	82.45	85.11

Table 2. Percentage of sets by quarter and fishing mode.

Quarters	*% sets under FAD with elasmobranches caught*	*% sets on FSC with elasmobranches caught*
1	22.33	3.87
2	50.67	28.47
3	53.46	25.82
4	32.87	12.70

Table 3. Percentage of individuals caught in Gabonese EEZ, Angolan EEZ and higher proportion of individuals caught for each species. GAB = Gabon, INT = international, CPV = Cape Verde, AGO = Angola.

Common name	*% in Gabon EEZ*	*% in Angola EEZ*	*Highest % individuals caught - EEZ*
Blue shark	87.92	1.91	87.92-GAB
Silky shark	56.36	13.05	56.36 – GAB
Oceanic whitetip shark	23.07	5.13	35.89 – INT
Scalloped hammerhead	63.62	11.94	63.62 - GAB
Smooth hammerhead	50.75	9.96	50.75 - GAB
Great hammerhead	31.18	2.97	44.55 - CPV
Shortfin mako	45.90	22.75	45.90 - GAB
Pelagic stingray	4.00	40.80	40.80 - AGO
Giant manta	3.22	3.22	8.71 - INT
Spinetail mobula	9.57	55.32	55.32 - AGO
Devil fish	14.03	33.33	33.33 - AGO

Table 4. Mortality rates, percentage of females and percentage of juveniles.

Common name	% juvenile	% female	Death rate
Blue shark	49.40	11.00	32.84
Silky shark	92.97	50.00	46.60
Oceanic whitetip shark	59.32	61.00	38.40
Scalloped hammerhead	70.28	56.90	41.66
Smooth hammerhead	99.75	62.00	54.69
Great hammerhead	98.97	38.00	56.93
Shortfin mako	100.00	65.30	49.18
Pelagic stingray	32.21	52.30	30.00
Giant manta	98.00	66.67	43.53
Spinetail mobula	39.06	71.40	12.76
Devil fish	21.27	47.50	28.07

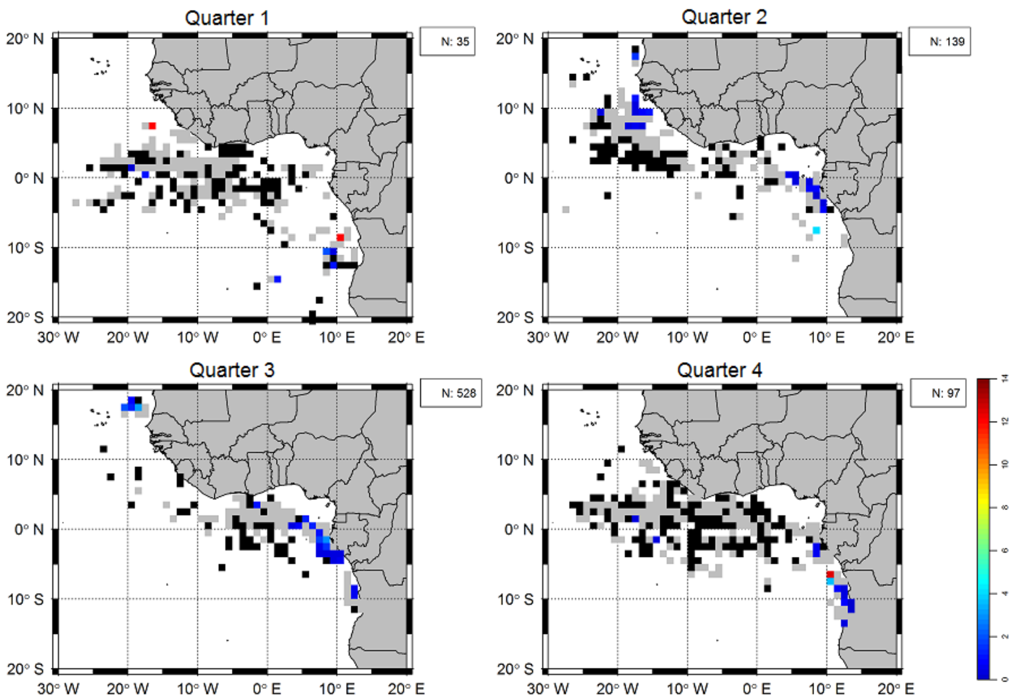

Figure 1. Quarterly distribution of Catches per Unit of Effort (CPUE) of the Scalloped hammerhead under FADs, per square of 1. Black squares correspond to sets without elasmobranches caught, grey squares correspond to sets having caught other elasmobranch species and finally the colour gradient corresponds to CPUE values (Number of individuals per set). N corresponds to the number of individuals caught.

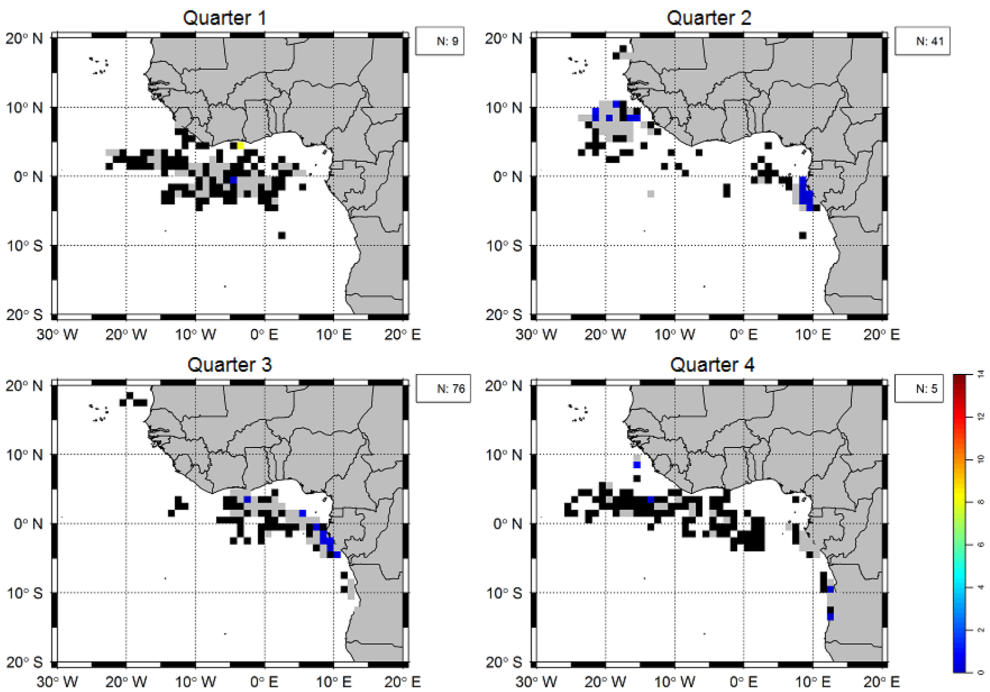

Figure 2. Quarterly distribution of Catches per Unit of Effort (CPUE) of the Scalloped hammerhead in free-swimming tuna school sets (FSC), per square of 1° in FSC sets. per square of 1. Black squares correspond to sets without elasmobranches caught, grey squares correspond to sets having caught other elasmobranch species and finally the colour gradient corresponds to CPUE values (Number of individuals per set). N corresponds to the number of individuals caught.

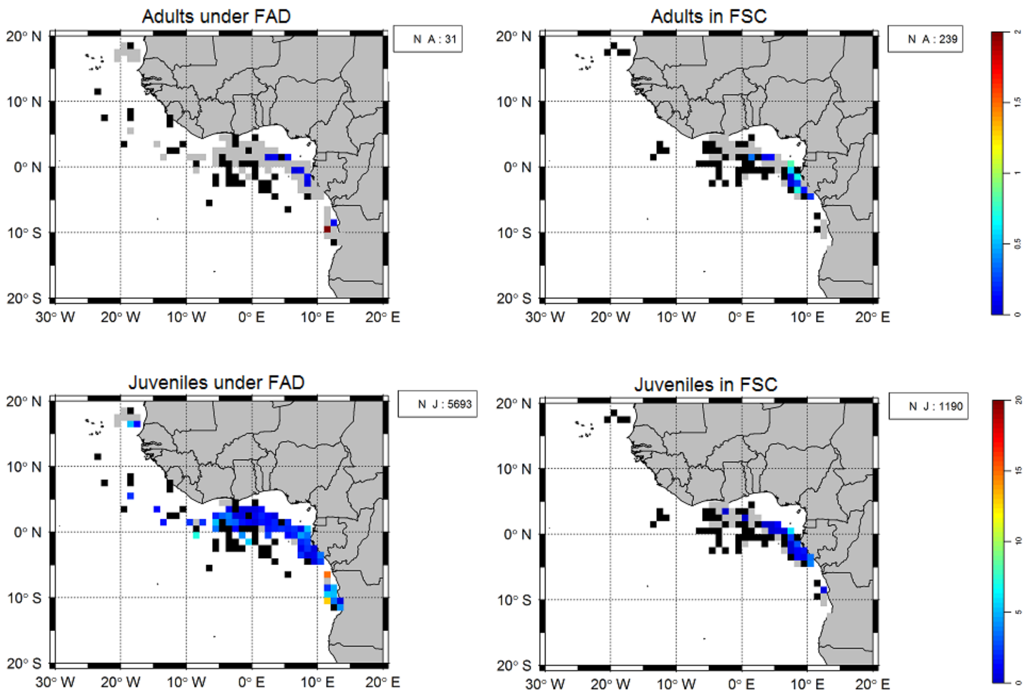

Figure 3. Distribution of Catches per Unit of Effort (CPUE) of Silky shark per square of 1° during the third quarter by fishing mode and life stage. Black squares correspond to sets without elasmobranches caught, grey squares correspond to the capture other elasmobranches than the species concerned and finally the colour gradient corresponds to CPUE values (Number of individuals per set). N A is the number of adult individuals caught and N J is the number of juveniles.

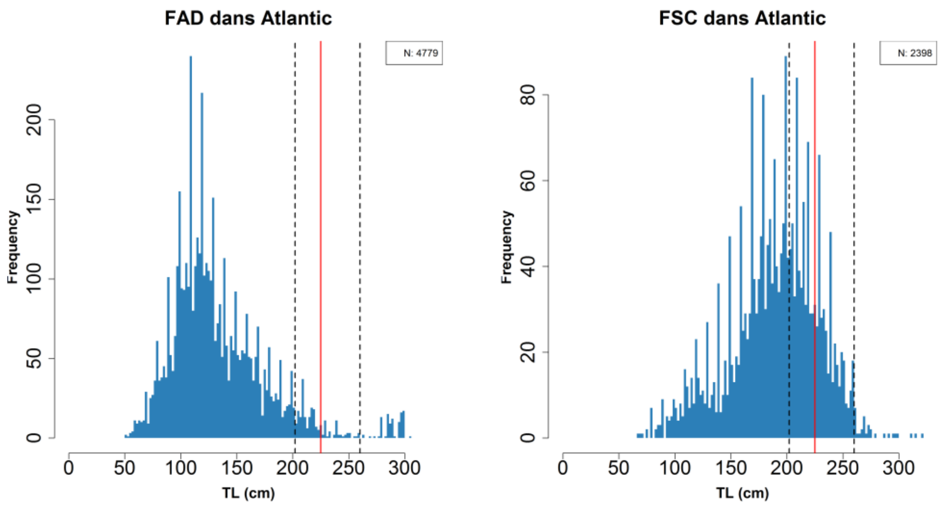

Figure 4. Size distribution of the Silky shark in FAD versus FSC sets. N corresponds to individuals caught number. The red line corresponds to L50 sexual maturity length and black dashed line corresponds to the range of first and last length of sexual maturity

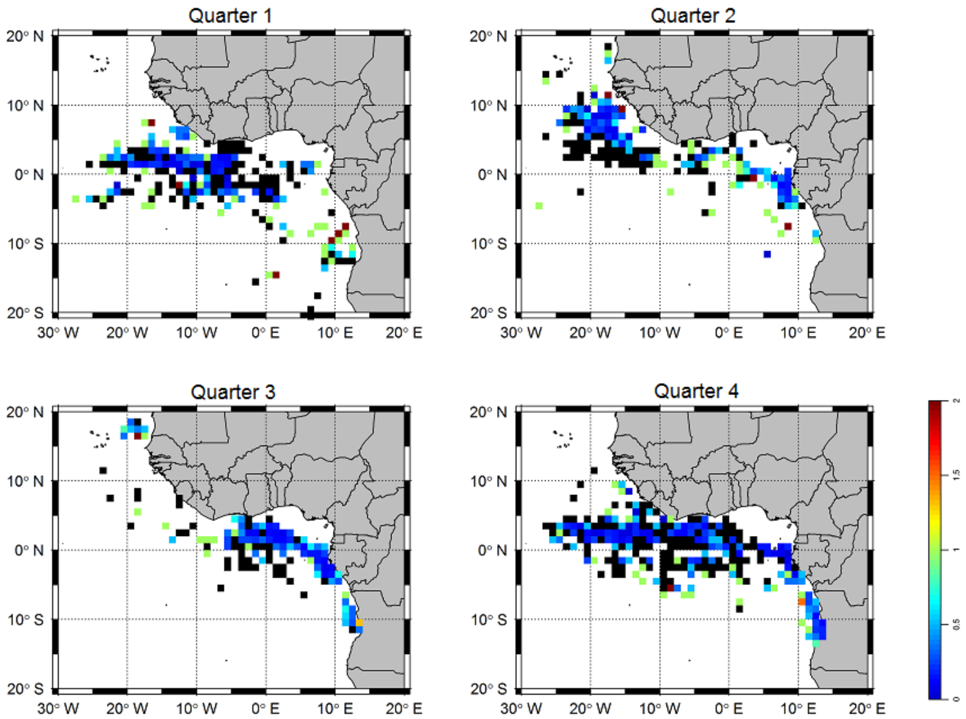

Figure 5. Quarterly distribution of the species Richness per Unit of Effort (RPUE) of elasmobranches by 1 ° square under FADs. Black correspond to RPUE = 0 and the colour gradient correspond to the values of RPUE.

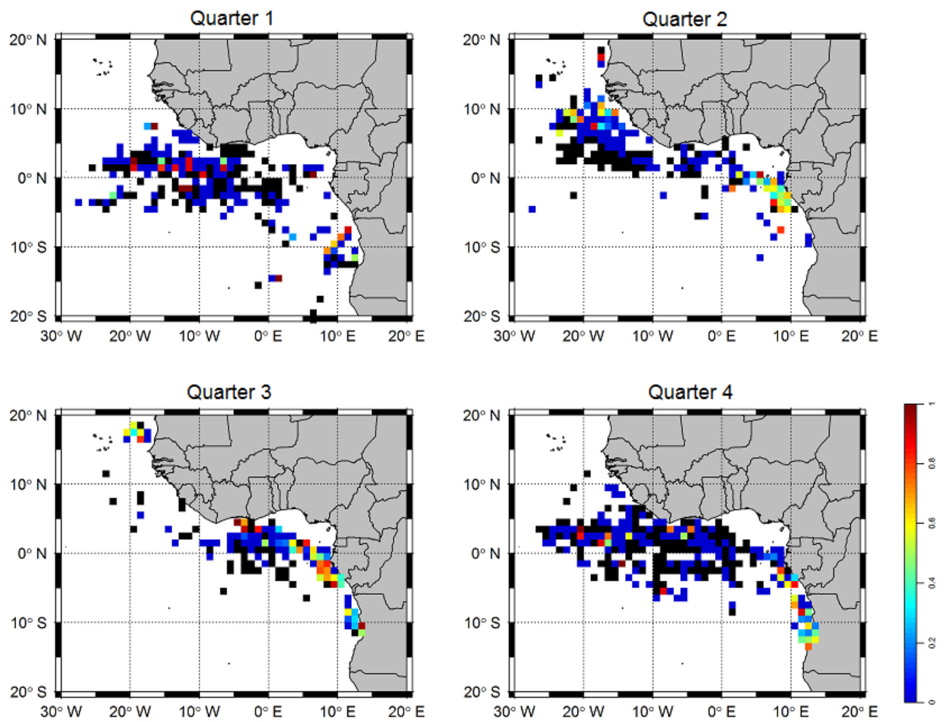

Figure 6. Quarterly distribution of Simpson's equitability of elasmobranches by 1 ° square under FADs. Black squares correspond to Simpson's equitability = 0 and the colour gradient correspond to the values of Simpson's equitability.

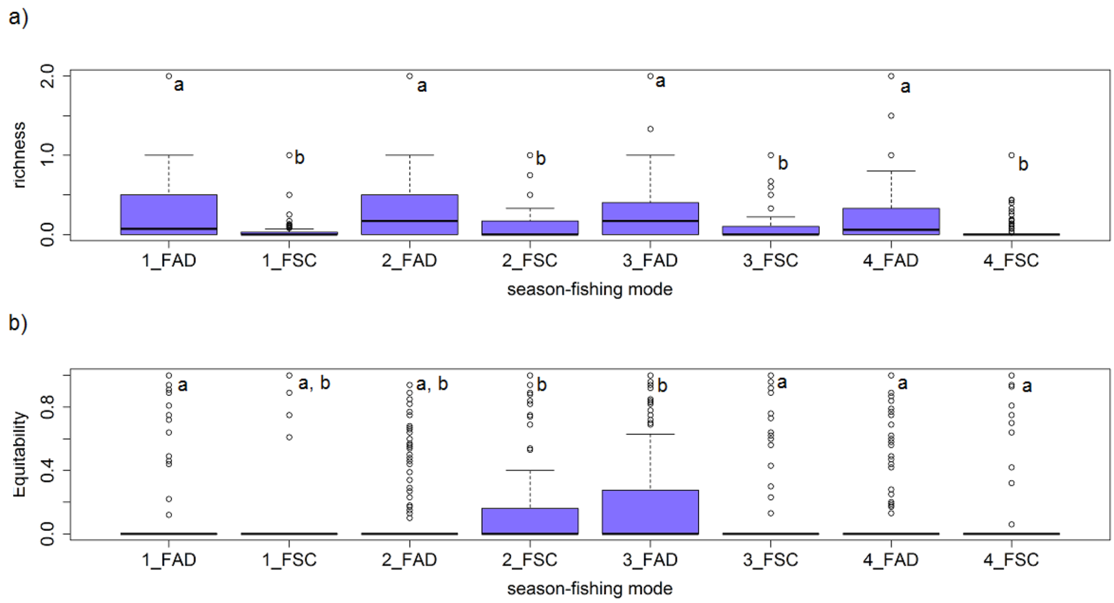

Figure 7. a) Species richness per unit of effort boxplot, b) Simpson's equitability boxplot, as a function of the quarter and fishing mode. On axis x: factor of interaction between season – fishing mode. Letters correspond to the groups formed with the post hoc test of Siegel and Castellan (1988).