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Original Research Article

Elasmobranch bycatch distributions and mortality: Insights from the European tropical tuna purse-seine fishery

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ABSTRACT

Despite bycatch of elasmobranch (sharks and rays) being a major concern in most fisheries worldwide, there is a lack of knowledge on their spatio-temporal species distribution, biology (life stage and sex-ratios), as well as their at-haulback mortality rate. Observer data from the French and Spanish tropical purse-seine tuna fisheries operating in the eastern Atlantic and western Indian Oceans between 2005 and 2017 were analysed to investigate elasmobranch bycatch. Data included 24 elasmobranchs species and distribution patterns of catch per unit of effort (CPUE) by species and sex-ratio were found to vary with life stages, areas, seasons and fishing modes. In general, higher catches were found in FAD-associated sets (>40%) than free tuna school sets (<17%) although this can vary depending on the species. For the large majority of species, a high proportion of juveniles were caught (30.7−100%), apparent at-haulback mortality rates was high (24.3−63.9%) and finally sex ratios was unbalanced (13.3−66.7% of females). Areas and seasons identified from these different components should be of interest for the monitoring and management of elasmobranch bycatches.
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1. Introduction

Marine diversity is impacted by various anthropogenic activities, with fishery considered as one of the main threats (Dulvy et al., 2003). In the case of elasmobranchs (e.g. sharks and rays), specific life history traits (slow growth, late sexual maturity and low fecundity) lead to high vulnerability to fishing pressure (Frisk et al., 2001). Many elasmobranchs are now classified as vulnerable, near threatened or endangered by the International Union for the Conservation of Nature (IUCN; www.redlist.org), and included in Appendix II of the Convention on International Trade in Endangered Species (CITES; www.cites.org).

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Certain life-stages and sex could be affected differently by fisheries depending on their spatio-temporal distribution, behaviour and the amount of time spent on fishing grounds. Fishing effort and the type of fishing gear may also influence interaction with elasmobranch. For instance, juveniles have high nutrient needs, which often leads them to occupy specific areas that would particularly favour their development compared to areas occupied by adults that have different needs (Heupel and Simpfendorfer, 2002). These areas may overlap areas of high fishing effort (Coelho et al., 2018), as highlighted by the high number of juvenile silky shark *Carcharhinus falciformis* (FAL) caught as bycatch in the longline fishery in the western and central Pacific Ocean (Hutchinson et al., 2013). In addition, population analysis has shown that high juvenile mortality has a significant impact on population growth and status (Hutchinson et al., 2013). Male and females may also occupy specific areas/habitat at certain periods of the year, and the study of the sex-ratio is of critical importance to determine potential breeding or mating areas (Coelho et al., 2018; Joung et al., 2017). For example, spatial segregation between male and female blue shark *Prionace glauca* (BSH) has been observed with an unbalanced sex-ratio varying with seasons (Castro and Mejuto, 1995; Coelho et al., 2018; Hazin et al., 1994). Likewise, the Mauritanian coast is known to be a mating area for blackchin guitarfish *Glaucostegus cemiculus* (GLC), marbled stingray *Dasyatis marmorata* (RDQ), milk shark *Rhizoprionodon acutus* (RHA) and Atlantic weasel shark *Paragaleus pectoralis* (PAP) (Valadou et al., 2006). It thus important to assess species sex-ratio in fishing zones (Coelho et al., 2018).

The tropical tuna purse-seine fishery targets the three main topical tuna species: skipjack *Katsuwonus pelamis* (SKJ), yellowfin *Thunnus albacares* (YFT) and bigeye tuna *Thunnus obesus* (BET), but also catch unintentionally non-target species and under-sized tunas that we will call hereafter bycatch (Amandè et al., 2012). The total discards amount represents 1–5% of the total tonnage, and small and damaged tunas represent 90–95% of the bycatch (Hall and Roman, 2013). Bycatch rates vary depending on the fishing modes, with sets on tuna schools associated with drifting Fish Aggregating Devices (FAD) generally producing higher bycatch levels than sets on free-swimming tuna schools (FSC) (Dagorn et al., 2013). In the eastern Atlantic and western Indian oceans, the European tropical tuna purse-seine fishery (France and Spain) is the main surface fishing fleet (70% of the purse-seine tuna captured) that is operating in the tropical region since 1960s and 1980s respectively. These fisheries exhibit high seasonal variability which may also lead to varying bycatch rates per species, life stages and sex-ratios. In particular, the main fishing zones are the Gabonese to Angolan coastal zones between April and September in the Atlantic Ocean, and the Mozambique Channel between April and May in the Indian ocean (Escalle et al., 2017).

Despite the importance of having good knowledge on the spatial and temporal species distribution of elasmobranch species, life history stages (juveniles *vs* adults), sex-ratio and at-hauling mortality rates, very little information is available (Amandè et al., 2010; Croll et al., 2016; Escalle, 2016a; Hutchinson et al., 2013; Poisson et al., 2014, 2016; Ruiz et al., 2018). The aim of this study is to provide and analyse these critical components for elasmobranch bycatch species in the European tropical tuna purse-seine fishery in the eastern Atlantic and western Indian oceans using data collected by scientific observers onboard fishing vessels between 2005 and 2017.

2. Material and methods

2.1. Data

Scientific observer data collection was supported by EU-funded Data Collection Framework (EU DCF, regulation [CE] 199/2008) for both France and Spain since 2005 and industry-funded observer programs such as OCUP (Observateur Commun Unique et Permanent) coordinated by ORTHONGEL (ORganisation française des producteurs de THON conGELé et surgelé). The coverage rate over the period considered was about 23% of all fishing sets in the Atlantic Ocean (100% since 2014) and 12% in the Indian Ocean (50% since 2014) (Escalle et al., 2017). For each fishing set, information on latitude/longitude and time/date was recorded, and elasmobranch bycatches were identified to the species level when possible and taxonomic group otherwise. In this study, only data recorded at the species level were considered (98% of individuals). The status upon release was also recorded (released alive or dead, i.e. at-haulback mortality), based on visual assessment, which may be different to the actual survival of the individual after release. Individuals are released as quickly as possible following the best practices adopted by the European purse-seine fleet to increase survival rate (Poisson et al., 2012). Given the objective of releasing individuals as soon as they were observed, only a fraction could be measured (total length [TL] for sharks and disk width [DW] for rays) and sexed by the observer (59.8% of the total number of individuals caught were used to investigate the spatial-temporal distribution of the sex-ratio at different life stages, see Table S1). We discriminated juvenile and adult life stages based on the size-at-maturity (L_{50}) for each species available from Fishbase (fishbase.org, Table S2). The percentage of females and males was also calculated for species presenting a sufficient number of individuals sampled (i.e. >120 recorded individuals according to histograms of abundance distributions) for which sex information was available. The regions analysed represent the main fishing grounds of European (French and Spanish) purse-seine vessels operating in the tropical eastern Atlantic and western Indian Oceans (see Figures S1 and S2).

2.2. Analyses

Catch per unit effort (CPUE) was computed for each 1° grid cell, per EEZ, and using the number of individuals for a particular species caught divided by the number of fishing sets. Seasonal variability in distribution of CPUE as a function of life-stages was also considered. Therefore, sex-ratio was analysed by ocean, Exclusive Economic Zone (EEZ) and 1° grid cell, as

well as by life stage and fishing mode. Then, seasons were defined by quarter in the Atlantic Ocean (season 1: January–March, season 2: April–June, season 3: July–September, and season 4: October–December), and by monsoon in the Indian Ocean (season 1: December–March, season 2: April–May, season 3: June–September, season 4: October–November) as defined by Escalle et al. (2015). Finally, elasmobranch assemblages were also studied using complementary biodiversity indices: i) species richness per unit effort (RPUE), computed in the same way as CPUE, using the number of elasmobranch species caught; ii) unbiased Simpson's diversity, also known as Probability of Interspecific Encounter (PIE) (Hurlbert, 1971); and iii) Simpson's evenness (Smith and Wilson, 1996) indices. In contrast to species richness, Simpson's diversity has been shown to be relatively stable to sample size variation (i.e. number of sets) (Lande, 1996), as confirmed in preliminary analyses on the data set. The results of diversity indices are presented in the supplementary materials.

The equality of relative proportions of the different species according to seasons, oceans and fishing modes were tested using a test of equal proportions (H0: proportions are equal). The distributions of diversity index values were compared for these same modalities with boxplots and, due to residuals distribution properties, with a non-parametric analysis of variance (i.e. Kurskal Wallis test, H0: distributions of ranked values are equal among modalities). In case of rejection of H0, pairwise modality comparisons were performed to identify more precisely the differences with the non-parametric post-hoc test of Siegel and Castellan (1988). All analyses were performed using the R software (R Development Core Team, 2019).

3. Results

3.1. General description

Between 2005 and 2017, 11,612 and 9538 fishing sets were monitored by scientific observers in the Atlantic and Indian oceans respectively. Among 24 species identified whatever ocean considered, a total of 18 elasmobranch species were present in the Atlantic Ocean and 15 in the Indian Ocean (10 species found in both oceans). We focused our study on 7 sharks and 3 ray species (which number of individuals > 120 individuals caught in both oceans according to histograms of abundance distributions, Figs. 1 and 2 and S3): blue shark *Prionace glauca* (BSH), great hammerhead *Sphyrna mokarran* (SPK), oceanic whitetip shark *Carcharhinus longimanus* (OCS), scalloped hammerhead *Sphyrna lewini* (SPL), FAL, shortfin mako *Isurus oxyrinchus* (SMA), smooth hammerhead *Sphyrna zygaena* (SPZ), devil fish *Mobula mobular* (RMM), giant manta *Manta birostris* (RMB) and pelagic stingray *Pteroplatytrygon violacea* (PLS) (Table S1).

Elasmobranchs were present in 3240 sets in the Atlantic Ocean, and 4472 sets in the Indian Ocean (27.9% and 46.9% of observed sets respectively). A total of 55,127 individuals were caught, with 32,987 (59.8%) of these individuals measured. In both oceans, the majority of the elasmobranchs were FAL (14,722 individuals, representing 77.6% of the total number of elasmobranchs in the Atlantic, and 31,332 individuals representing 92.9% of the total in the Indian Ocean; see Table S3). The second most abundant species caught was SPL in the Atlantic Ocean (6.9% of the total number of elasmobranchs; 1491 individuals) and OCS in the Indian Ocean (2.1%; 706 individuals) (Table S3).

In general, the occurrence of elasmobranchs was higher in FAD sets. In addition, a significant proportion of FAL is caught under FADs, it represents 95.9% of the abundance of elasmobranchs captured in the Indian Ocean and 71.1% in the Atlantic Ocean, which differs significantly from other species (Chi2 = 24.932, ddl = 8, p = 0,001). In the Atlantic Ocean 39.5% of FAD sets (2159 sets) had elasmobranchs compared with 17.6% (1081) for FSC sets. Similarly, 67.8% of the FAD sets (4004) captured elasmobranch in the Indian Ocean compared with 12.9% in FSC sets (468).

3.2. Spatial and temporal distribution

The spatio-temporal distribution of the fishing effort and elasmobranch bycatch varied with season, fishing mode, and area. In the Atlantic Ocean, seasons 2 and 3 (April to September) presented the highest proportions of sets with elasmobranch bycatch for both fishing modes (respectively 46.9% and 50.2% of FAD sets, and 26.6% and 25.7% of FSC sets; see Table S4). These proportions are significantly different between seasons (FAD: Chi2 = 9.71, ddl = 3, p = 0.02; FSC: chi2 = 10.91, ddl = 3, p = 0.02). During these seasons, fishing effort was very localised, with most bycatch of elasmobranchs found off the coast of Gabon, Angola, Senegal and Mauritania (Figures S2 and S3). In the Indian Ocean, however, no clear seasonal variability could be detected (Figures S2 and S3), with more than 67% of FAD sets and <20% of the FSC presenting elasmobranch bycatches year-round (Table S4).

In the Atlantic Ocean, the highest CPUE of shark bycatch was found off the coast of Gabon, especially in quarters 2 and 3 (Figs. 3 and 4). Five species (SPL, SPZ, BSH, FAL and SMA) among the ten species selected contributed to 37.3–89.1% of the total number of individuals caught in the Atlantic Ocean within this area. The coasts of Angola and Mauritania also presented high proportions of elasmobranch in the catches, including two species of ray (RMM and RMB). However, these levels remained lower than off the coast of Gabon. In the Indian Ocean, the highest CPUE of elasmobranchs was found in the Seychelles EEZ. Four species (BSH, OCS, FAL and SMA) accounted for 24.5%–45.7% of the total number of individuals caught in the Indian Ocean. Compared with the Atlantic Ocean, the spatial distribution of elasmobranch bycatch in the Indian Ocean is more homogeneous (Figures S1 and S2).

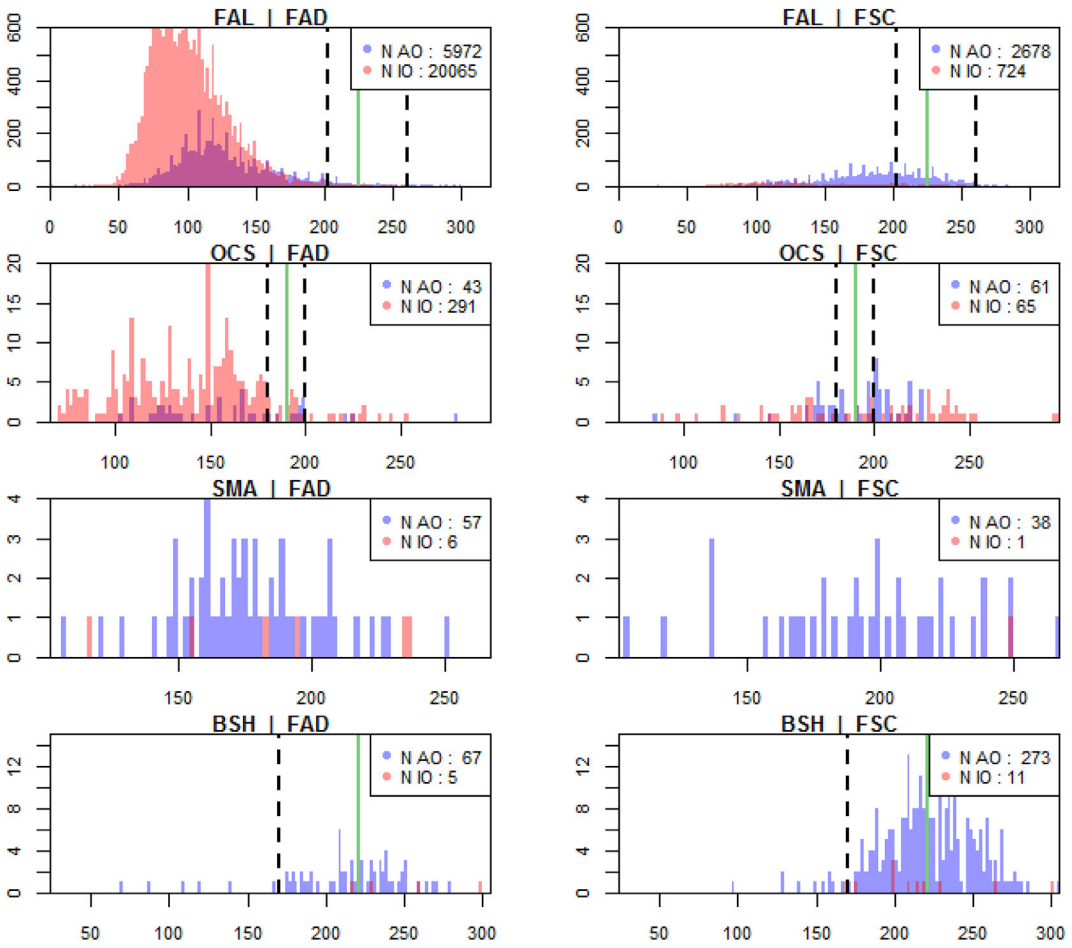

Fig. 1. Size distribution of *Carcharhinus falciformis* (FAL), *Carcharhinus longimanus* (OCS), *Isurus oxyrinchus* (SMA) and *Prionace glauca* (BSH) in Fish Aggregating Devices (FAD) sets versus Free school (FSC) sets in the Atlantic Ocean (AO; blue distribution) and in the Indian Ocean (IO; red distribution). N AO and N IO correspond to the number of individuals caught in the Atlantic and Indian Oceans, respectively. The green line corresponds to L50 sexual maturity length and black dashed line corresponds to the range of first and last length of sexual maturity. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.3. Juveniles and adults

Among the ten species considered in this study, over 53.8% of the individuals caught were measured in the Atlantic Ocean, with 1476 individuals (12.8%) classified as adults and 10,045 as juveniles (87.2%). In the Indian Ocean, 63.7% of individuals were measured, with 272 adults (1.3%) and 21,194 juveniles (98.7%) (Table S1).

Six species in the Atlantic Ocean (SMA, SPK, SPL, SPZ, RMB and FAL) and five species in the Indian Ocean (SMA, FAL, OCS, RMB and PLS) presented more than 70% of juveniles (Table S5). For most species, smaller individuals were found under FADs compared with FSC sets in both oceans (Figs. 1 and 2 and S3). Moreover, for the same species, individuals appear smaller in the Indian Ocean than in the Atlantic Ocean (Figs. 1 and 2 and S3). Generally, while fewer adults were found, their distribution was more localised than the juvenile one (Figs. 3 and 4). In the Atlantic Ocean for instance, adult FAL were localised off the coast of Gabon and Angola for both fishing modes (Fig. 3). Juveniles caught in FSC sets were more localised than adults (Fig. 3), while juveniles caught in FAD sets were distributed across the whole spatial range of the fishery. SPK and SPL were mostly found off the coast of Gabon and Mauritania during the second and third seasons (April to September) for both life stages (Fig. 4). FAL, SPL and SPZ presented higher percentages of juveniles in the Atlantic Ocean near the coasts (Fig. 5 and S4). For OCS, catches of juveniles appeared to be localised near the Somalian coast in the Indian Ocean (Figure S5).

3.4. Sex-ratio

For most species considered, over 65% and 55% of the individuals caught were sexed in the Atlantic and Indian Oceans respectively (Table S1).

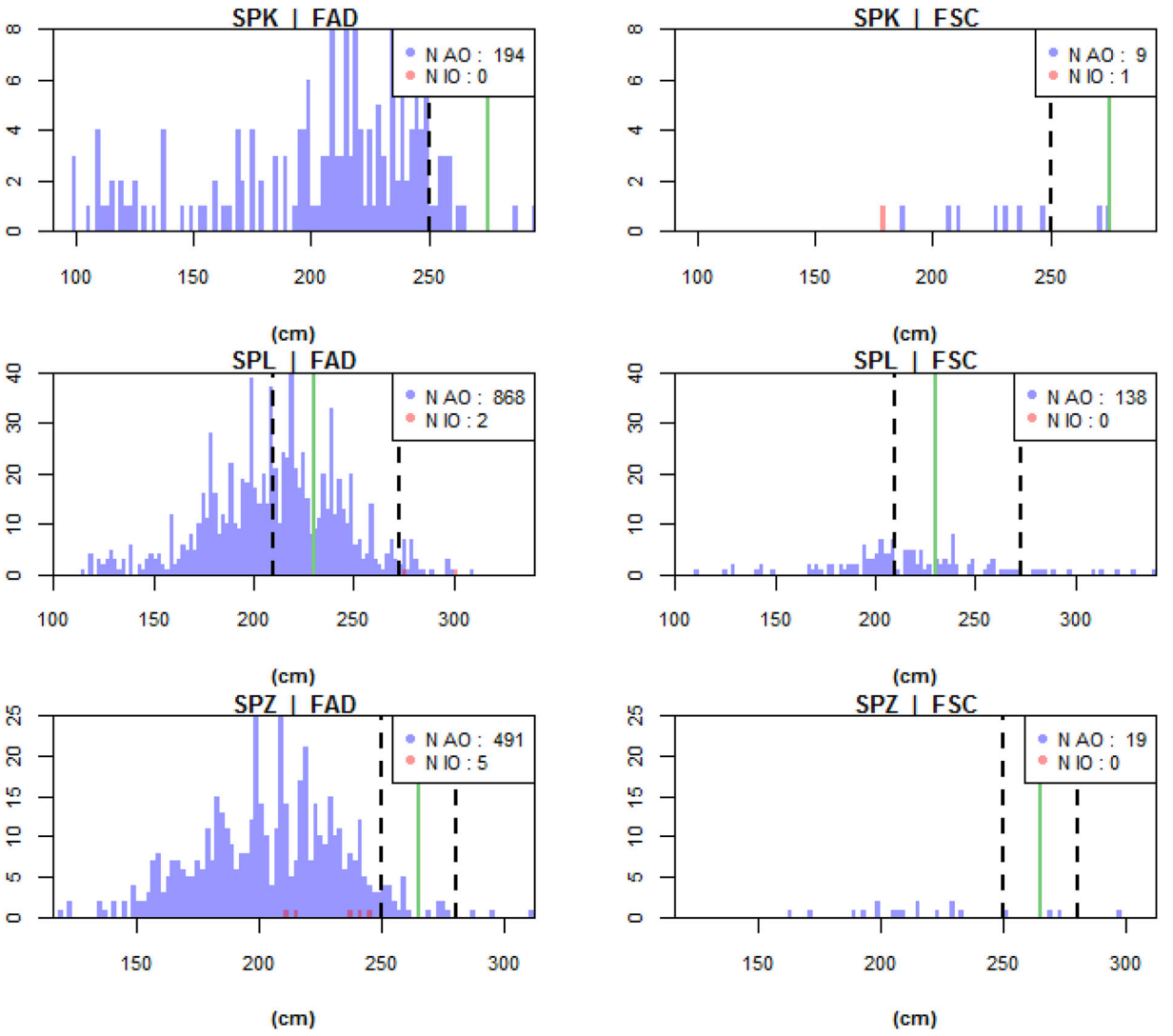

Fig. 2. Size distribution of the *Sphyrna mokarran* (SPK), *Sphyrna lewini* (SPL) and *Sphyrna zygaena* (SPZ) in Fish Aggregating Devices (FAD) sets versus Free school (FSC) sets in the Atlantic Ocean (AO; blue distribution) and in the Indian Ocean (IO; red distribution). N AO and N IO correspond to the number of individuals caught in the Atlantic and Indian Oceans, respectively. The green line corresponds to L50 sexual maturity length and black dashed line corresponds to the range of first and last length of sexual maturity. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

In the Atlantic Ocean, the percentage of females ranged between 13.3% and 66.7%, with the BSH (13.3%) and the SPK (41.4%) presenting the lowest proportion of females (Table S5). In contrast, SMA, SPZ and RMM presented a percentage of females higher than 60% (respectively 61.8%, 63.8% and 66.7%; Table S5). For 8 species (out of 10 species), the percentage of females was higher under FAD than FSC (Table 1). The difference in the percentage of females between fishing modes ranged from 1.1 for FAL to 27.6 for BSH. RMM and SPK was the only species to show a greater percentage of females under FSC.

In the Indian Ocean, the sex-ratio appeared to be more balanced than in the Atlantic Ocean, with the percentage of females ranging between 35.3% and 57.7% (Table S5). For 4 species out of the 7 present in this ocean, the percentage of females was higher under FAD than FSC (Table 1). The difference in the percentage of females between fishing modes ranged from 1.5 for OCS to 50 for SMA. BSH, PLS and SMA were the three species showing a greater percentage of females under FSC (Table 1).

Adult SPL and FAL females were mostly caught near the Gabonese and Angolan coasts (Figs. 6 and 7). The opposite trend was observed for BSH, with mostly males in these areas (Figure S6). Irrespective of life stage, the lowest percentages of females were found in BSH caught (Table S5).

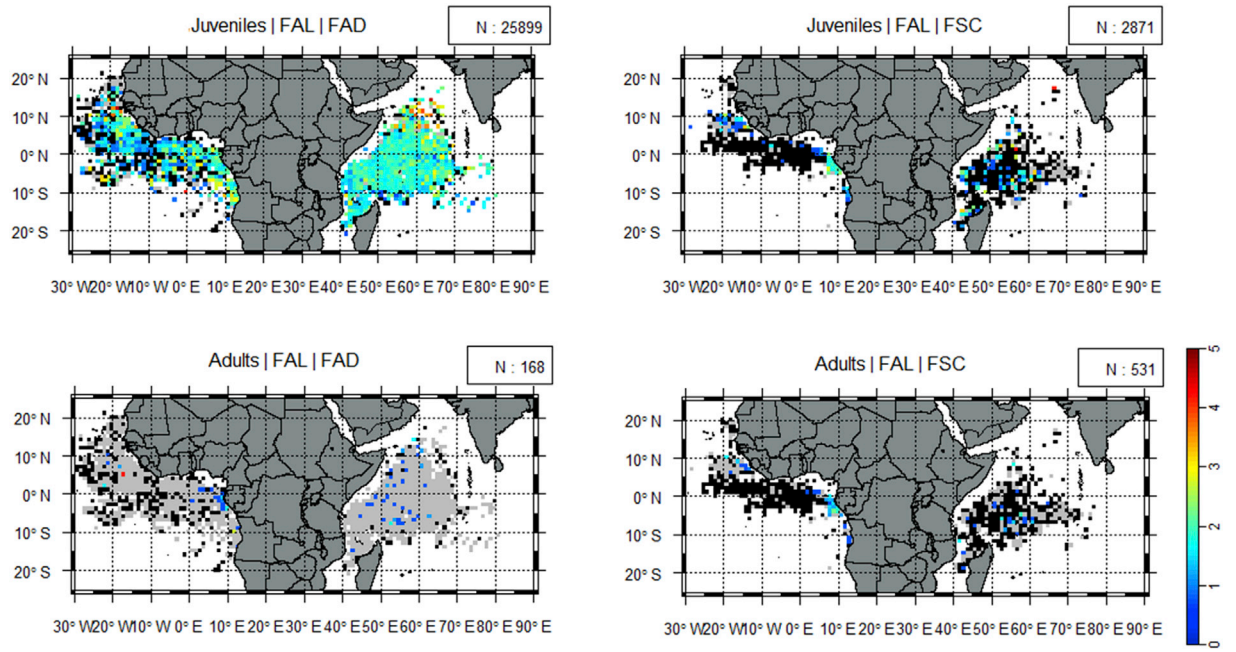

Fig. 3. Distribution of logarithmic CPUE of *Carcharhinus falciformis* (FAL) in function of life stage and fishing mode per 1° square. Black squares correspond to sets without elasmobranch caught, grey squares correspond to sets having caught other elasmobranch species, and finally the color gradient corresponds to CPUE values (number of individuals per set). N corresponds to the total number of individuals caught. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

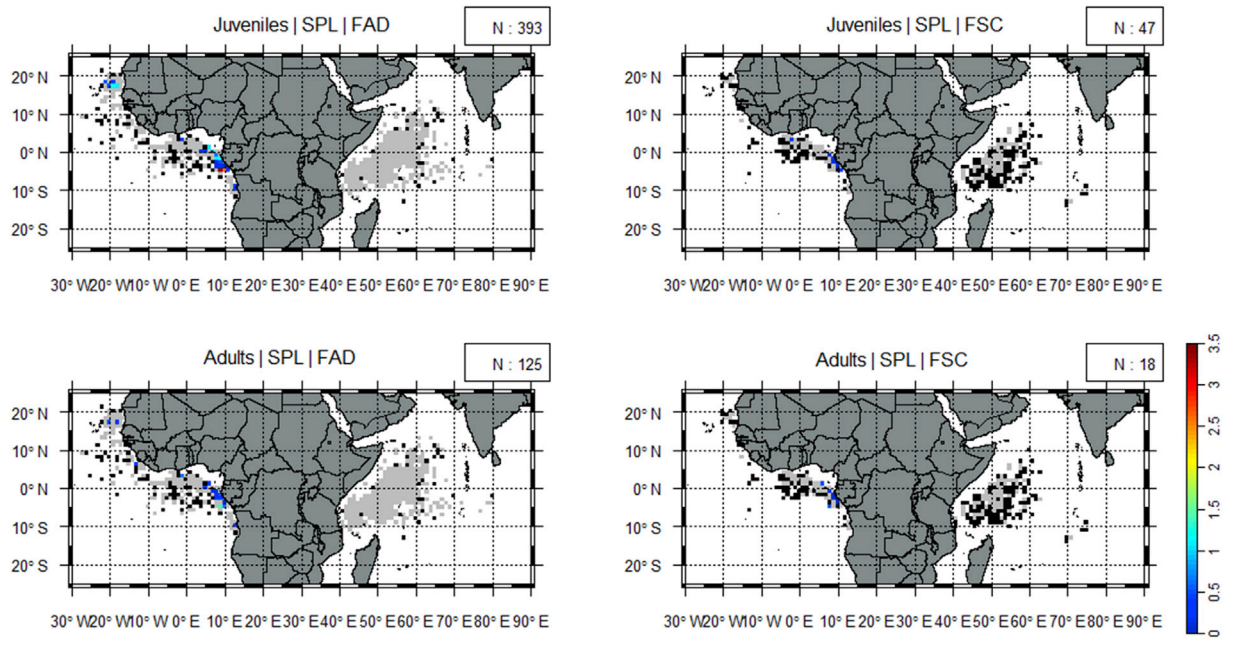

Fig. 4. CPUE distribution of *Sphyrna lewini* (SPL) as a function of life stage and fishing mode during the third quarter (i.e. seasons including highest caught value) per 1° square. Black squares correspond to sets without elasmobranch caught, grey squares correspond to sets having caught other elasmobranch species, and finally the color gradient corresponds to CPUE values (number of individuals per set). N corresponds to the number of individuals caught. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

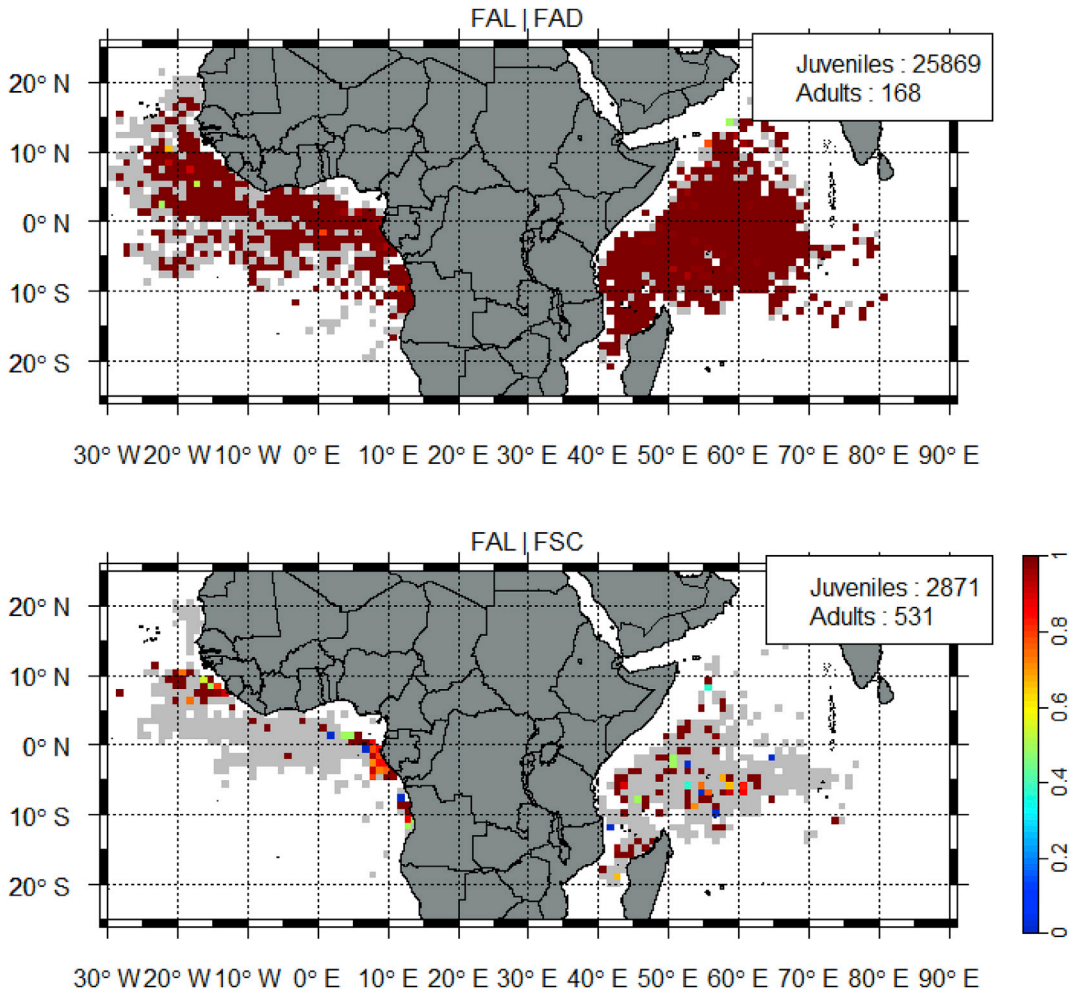

Fig. 5. Juvenile percentage of *Carcharhinus falciformis* (FAL) as a function of fishing mode per 1° square. Color gradient corresponds to the juvenile percentage (0 = 0% juvenile, 1 = 100% juvenile), grey cells correspond to fishing effort distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.5. Apparent mortality rates

Apparent at-haulback mortality rates ranged from 33.2% to 60.4% in the Atlantic Ocean, and from 30.7% to 63.9% in the Indian Ocean (Table S5). Species with the highest at-haulback mortality were SPZ (60.4%) in the Atlantic Ocean and PLS (63.9%) in the Indian Ocean (Table S5). For the majority of species, higher at-haulback mortality rates were found in FAD sets compared with FSC sets in both oceans (Table 1).

Concerning at-haulback mortality by EEZ, higher values were observed in the Atlantic Ocean in the Cape Verde and Mauritanian EEZs for FAL, RMB, RMM, SPZ and SPK (>80%). In the Indian Ocean, higher at-haulback mortality was observed in international waters for BSH (83.3%) and PLS (69.4%).

4. Discussion

4.1. Environmental and spatial effects

The distribution of fishing effort and elasmobranch catches varied with the season and across fishing grounds, with fishing sets and levels of CPUE being more localised in specific areas within the eastern Atlantic Ocean than the western Indian Ocean. It has been suggested that primary productivity may influence the distribution of large pelagic species, including those of elasmobranch species (Escalle et al., 2016a; Fonteneau and Marcille, 1988; Lezama-Ochoa et al., 2016; Lopez et al., 2017a, 2017b). However, sightings are dependent on the intensity of the fishing effort, which itself undergoes seasonal variation across the fishing areas. For this reason, an ecological study per set of the distribution of these species is beyond the scope of

Table 1
Percentage of juveniles and females and apparent mortality rates by fishing modes (FAD = Fish Aggregating Devices; FSC = Free swimming school) in the Atlantic and Indian Oceans.

Common name	Atlantic Ocean						Indian Ocean					
	FAD			FSC			FAD			FSC		
	% juvenile	% female	Mortality rate	% juvenile	% female	Mortality rate	% juvenile	% female	Mortality rate	% juvenile	% female	Mortality rate
Prionace glauca (BSH)	51.5	35.6	27.5	50.6	8.0	36.5	40.0	33.3	70.6	70.0	37.5	44.4
Mobula mobular (RMM)	32.0	49.2	62.6	27.0	52.9	29.9	50.0	66.7	29.7	20.0	50.0	31.4
Manta birostris (RMB)	92.7	70.4	56.2	96.4	61.1	22.6	76.7	46.7	32.6	83.3	26.3	18.5
Sphyrna mokarran (SPK)	98.8	40.0	58.4	88.9	71.4	70.0	–	–	–	–	–	–
Carcharhinus longimanus (OCS)	76.7	64.9	68.2	39.3	51.7	25.3	92.4	57.4	27.2	42.9	55.9	27.3
Pteroplatytrygon violaeca (PLS)	34.1	61.0	34.1	41.3	40.0	32.6	73.6	34.5	65.6	73.2	42.9	61.7
Sphyrna lewini (SPL)	71.6	58.2	45.8	65.2	56.4	41.7	0.0	0.0	33.3	–	–	–
Isurus oxyrinchus (SMA)	100	68.5	62.3	100	51.4	56.1	100.0	50.0	57.1	100.0	100.0	75.0
Carcharhinus falciformis (FAL)	97.9	51.6	54.3	81.9	50.5	48.2	99.7	52.2	60.5	92.2	44.1	46.3
Sphyrna zygaena (SPZ)	98.1	64.2	60.6	84.2	52.6	52.0	–	–	–	–	–	–

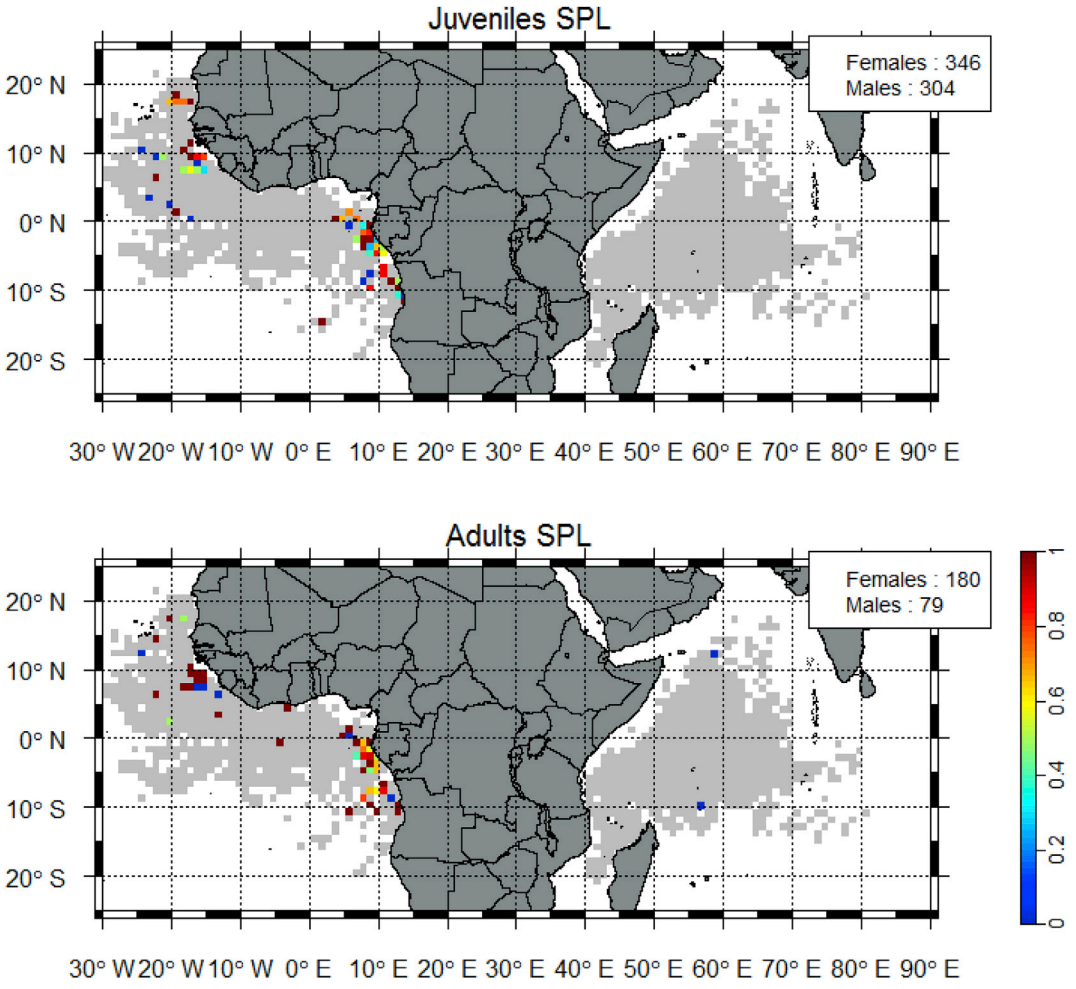

Fig. 6. Sex-ratio distribution of *Sphyrna lewini* (SPL) as a function life stage per 1° square. Color gradient corresponds to the percentage of females (0 = 0% and 1 = 100%), grey cells correspond to fishing effort distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

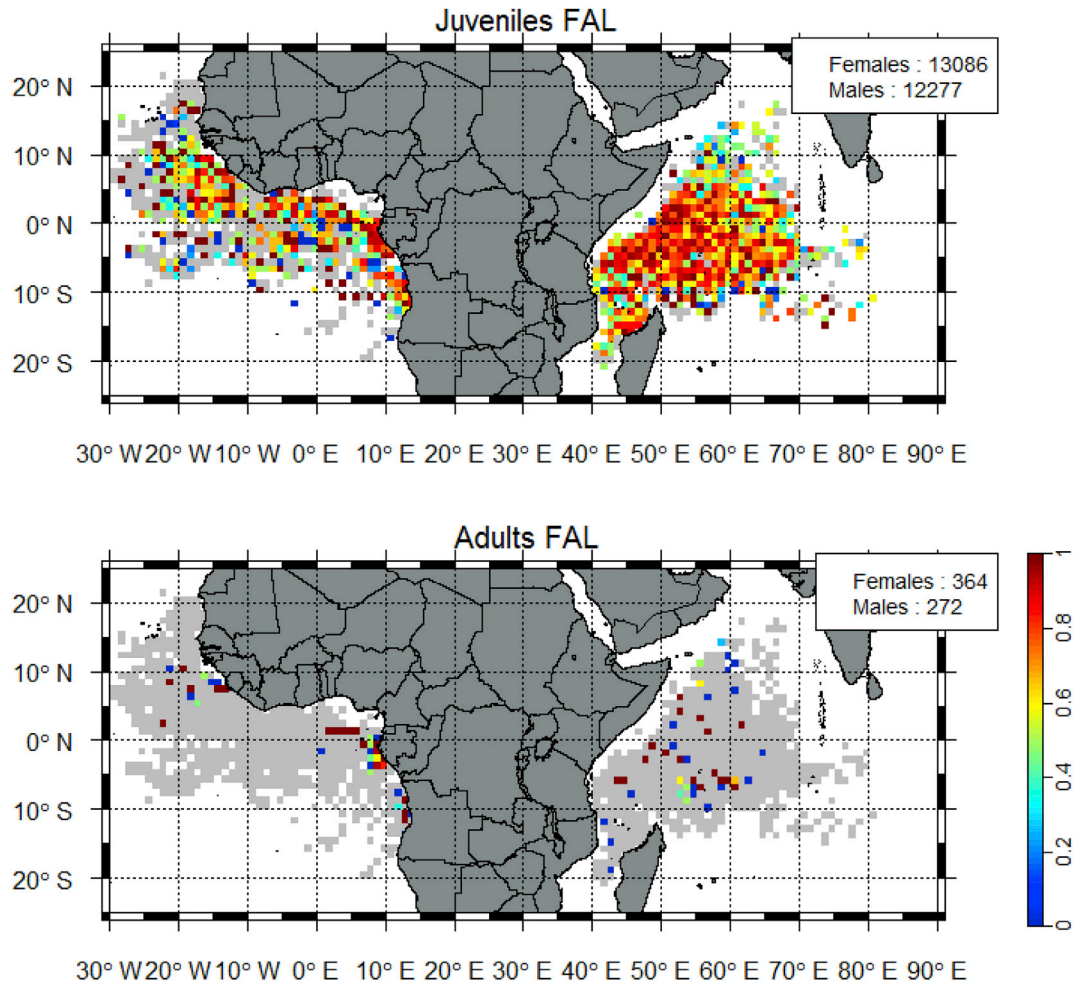

Fig. 7. Sex-ratio distribution of *Carcharhinus falciformis* (FAL) as a function of life stage per square of 1°. Color gradient corresponds to the percentage of females (0 = 0% and 1 = 100%), grey cells correspond to fishing effort distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

this study. The aim of this work was to identify spatial strata where the tuna purse-seine fishery and bycatch of elasmobranchs co-occur across seasons for interest in management and conservation of these species in the tropical eastern Atlantic and western Indian Oceans. To focus on the spatial distribution, analyses were conducted by aggregating years. In this study, the main areas of higher catches, expressed as CPUE, of elasmobranchs in the Atlantic Ocean were off the coasts of Gabon, Angola, Senegal and Mauritania, mainly between July and September (season 3). This corresponds to seasonal peaks in productivity in those areas, due to coastal upwelling and terrigenous river discharges off Mauritania, Senegal, Gabon, Congo and Angola. In addition, the thermal domes of Guinea and Angola reinforce the high productivity of this environment, and this leads to higher tuna catch rates (Fonteneau and Marcille, 1988; McGlade et al., 2002). It should also be specified that these four coasts are exposed to greater fishing effort than other Atlantic EEZs, based on fishing agreements with the respective countries. The higher numbers of individuals per unit of effort caught were during the second and third quarters, and varied according to the species as well. Hammerhead shark species were principally observed near the Atlantic coast, in the Gabon and Angola EEZs. These species are known to be coastal, which corroborates other studies where the distribution of pregnant females, for example, was limited to the coast of south-west Mexico (Bejarano-Álvarez et al., 2011). In the Indian Ocean, the fishing effort is distributed mostly in the open-ocean areas, and elasmobranch catches appeared to be higher also when CPUE is considered. However, no clear seasonal variability could be detected. Moreover, tropical tuna purse seine fishery is a surface fishing. Thus, minimum oxygen layer depth is not accurate for our study related to this fishery. It would has been appropriate for fishing strategy dealing with broader depth range. More generally, environmental variables available at the spatio-temporal scale of our study (e.g. Sea Surface Temperature (SST) and Eddy Kinetic Energy, chlorophyll-a concentration, depth, slope and distance to land) have been shown in previous studies to poorly explain patterns in this fishery and oceans,

for elasmobranch such as whale shark *Rhincodon typus* (with less than 6% of deviance in GAM, Escalle et al., 2016a), or even for the entire bycatch community (Lezama-Ochoa et al., 2015, 2018).

4.2. Fishing mode effect

The distribution of elasmobranch bycatches varies with the fishing mode (FAD vs free schools). The proportion of FAD sets having at least one elasmobranch caught was higher (39.3% and 67.8% in the Atlantic and Indian oceans, respectively) than for free school sets (17.5% and 12.8%) in both oceans. This result is consistent with greater diversity in predators such as tunas, sharks or marine mammals observed associated with FADs (Fonteneau, 1993). In addition, FADs whether natural or artificial, drift according to currents and winds, and tend to aggregate in convergence areas (Fonteneau, 1993; Maufroy et al., 2015). Moreover, natural floating objects are often located in productive areas, as stipulated by the indicator-log hypothesis (Hall, 1992). Fréon and Dagorn (2000) added that after a while, the nutrient-rich waters generate plankton blooms and as previously observed, it has been suggested that primary productivity may influence the distribution of large pelagic species such as tunas or elasmobranchs. In addition, Escalle et al., (2016b) showed that a reduction in sets on whale sharks and whales (which are specific, sometimes incidental, fishing modes) would lead to a reduction in shark bycatch. Similar patterns would probably be observed in case of FAD sets reduction.

4.3. High occurrence of juveniles

Among the 10 species considered, *Carcharhinus falciformis* catch rates appeared to be much higher than the other elasmobranchs, which extends and confirms the results of Amandè et al. (2010). In addition, this species contributed to the majority of juveniles bycatch (i.e. 93.1% and 99.5% in the Atlantic and Indian oceans respectively). This predominance of juveniles in *Carcharhinus falciformis* confirms observations made for purse-seine fishery in all oceans (e.g. Filmalter et al., 2013; Hutchinson et al., 2013), as well as for *Prionace glauca* caught by the longline fishery in the Atlantic and Indian oceans (Coelho et al., 2018). However, this distribution, including by life stage, was relatively scarce or absent for the other species in the literature. In the present study, bycatches per life-stages were investigated for different species of elasmobranchs and highlighted the general trend across species to have a high majority of juveniles captured by the purse-seine fishery on FADs (30.7−100% of juveniles in the Atlantic Ocean, and 36−100% in the Indian Ocean). This study also provides new information on the relative distribution of juveniles and adults for the main elasmobranch species caught by purse-seiners in both oceans. The proportion of juveniles is higher near the Gabonese and Angolan coasts in the Atlantic Ocean for *Carcharhinus falciformis, Isurus oxyrinchus, Sphyrna mokarran, Sphryna lewini* and *Sphyrna zygaena*. Temperature and nutrient intake could explain the proximity of juveniles to the coast (Coelho et al., 2018). Finally, for some species, including *Carcharhinus falciformis*, size distribution analysis indicated that a high proportion of the number of juveniles were captured.

4.4. Sex-ratio

Most elasmobranch species exhibited highly unbalanced sex-ratios, such as *Prionace glauca*, with a male dominance (13.4% of females in the Atlantic Ocean and 36.4% in the Indian Ocean; Table S5). This situation may be of particular concern with regard to this species if this low female percentage is representative of the *Prionace glauca* population at the scale of both oceans. In addition, males and females may be segregated in different areas depending on the season, which has previously been shown in the Pacific Ocean (Hazin et al., 1994). By contrast, *Manta birostris* has a higher percentage of females in the Atlantic Ocean (66.7%; Table S5). In most areas, the percentage of females of many species was higher, but with a more localised distribution. For instance, in the Mauritanian EEZ, *Carcharhinus falciformis*, *Manta birostris*, *Sphyrna lewini* and *Sphyrna zygaena* have a high percentage of females (>70% of females). This area is known to be a mating area for blackchin guitarfish, marbled stingray, milk shark and Atlantic weasel shark, and a nursery area for blackchin guitarfish, as well as a feeding area for Lusitanian cownose ray, *Rhinoptera marginata* (Valadou et al., 2006). The Mauritanian coasts may also be suitable as mating and nursery areas for other elasmobranch species such as *Carcharhinus falciformis*, *Manta birostris*, *Sphyrna lewini* and *Sphyrna zygaena*.

4.5. Mortality

Apparent at-haulback mortality rates varied between 33.2% (*Pteroplatytrygon violacea*) and 60.4% (*Sphyrna zygaena*) in the Atlantic Ocean, and between 24.3% (*Manta birostris*) and 63.9% (*Pteroplatytrygon violacea*) in the Indian Ocean. However, this corresponds to the status at the time of release, which likely underestimates the actual mortality considering there might be post-release mortality. For instance, post-release mortality studies using electronic tagging and blood chemistry analysis estimated the actual fishing mortality of *Carcharhinus falciformis* caught by the purse-seine fishery in the Western and Central Pacific Ocean, and the Indian Ocean at about 80% (Hutchinson et al., 2013; Poisson et al., 2014). These authors found that most *Carcharhinus falciformis* (and probably other shark species), being compressed in the brailer with a few tonnes of fish during brailing operations, have very high apparent mortality rates due to physical compression and anoxic conditions during this process. By contrast, Hutchinson et al. (2013) found that *Carcharhinus falciformis* meshed in the net and brought onboard during the hauling process have lower at-haulback mortality rates (18%). Nevertheless, in the current study, the at-haulback

mortality rate for *Carcharhinus falciformis* was 51.7% in the Atlantic Ocean, and 60% in the Indian Ocean. More specifically, for all species considered, the individuals caught in FAD sets had a higher at-haulback mortality rate (50.2% and 57.9% in the Atlantic and Indian oceans, respectively) compared with FSC sets (37.5% and 39.4%). This may be due to more juveniles being caught in FAD (92.6% and 99.4%) than FSC sets (74.9% and 84.4%). Juveniles are more vulnerable than adults and may have different swimming capacity and behaviour. In addition, mortality rates varied depending on the area considered. For instance, very high apparent mortality rates were detected in the Mauritania EEZ (>80%) for *Carcharhinus falciformis*, *Manta birostris* and *Mobula mobular*. This may well be linked to the high dominance of juveniles in this area, which may be a nursery area, as suggested previously.

5. Conclusion

Areas and seasons identified with relatively high bycatch rates of elasmobranchs are known to present high primary productivity. This factor is a main driver of the distribution of both targeted tunas and non-targeted species of tropical purse-seine fisheries. Relatively high values of elasmobranch catch rates were observed for all species 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 for the monitoring and management of elasmobranch bycatches.

Moreover, most species showed a high proportion of juveniles caught by purse-seiners, with individuals caught under FADs being generally smaller than in FSC sets. For some species, including*Carcharhinus falciformis*, the high number of juveniles caught should also be noted, and might be concerning for population status. Once brought on board, elasmobranchs are released alive, when possible, by the crew and following best practices methods. Nevertheless, high apparent mortality rates have been recorded, which is also accompanied by unbalanced sex-ratios dominated by males for some species, such as *Prionace glauca*. Some areas, such as Mauritania and Gabon, could potentially constitute breeding and nursery areas for several species. Further studies should therefore be performed to confirm these conclusions and their potential importance for the conservation of elasmobranch populations.

To our knowledge previous studies were dedicated to single species such as *Rhincodon typus* (Capietto et al., 2014; Escalle et al., 2016a,b, 2019), *Carcharhinus falciformis* (Poisson et al., 2014; Lopez et al., 2020), *Prionace glauca* (Coelho et al., 2018) or to the entire bycatch community (not only elasmobranchs, without focused on this group of particular concerns) by mean of multivariate analyses and diversity indices (Lezama-Ochoa et al., 2015, 2018, Escalle et al., 2019). In addition, until now no studies have investigated the spatio-temporal distributions of sex-ratio, life-stage and apparent at haulback mortality of all elasmobranch species found as bycatch in purse seine fishery. Thus, our study is descriptive as a first and necessary step, and innovative as the first to investigate these essential features for the entire elasmobranchs bycatch group.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01211.

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