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A review of mobulid ray interactions with fisheries for tuna and tuna-like species in the Indian Ocean

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Introduction

Manta and devil rays (*Mobula* spp.) are threatened globally, primarily from fishing pressure, with all Indian Ocean species reported to be in decline (Bizzarro *et al.*, 2009; Marshall *et al.*, 2018; Marshall, Barreto, Bigman, Carlson, D. Fernando, Fordham, Francis, Herman, Jabado, Liu, Pardo, Rigby, Romanov and Walls, 2019; Marshall, Barreto, Bigman, Carlson, D. Fernando, Fordham, Francis, Herman, Jabado, Liu, Pardo, Rigby, Romanov, Smith, *et al.*, 2019; Marshall, Barreto, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Pacoureau, *et al.*, 2019; Marshall, Barreto, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Rigby, *et al.*, 2019). Mobulids are large, mobile marine animals that can cover vast areas of ocean (Jaine *et al.*, 2014; Thorrold *et al.*, 2014). To be able to effectively mitigate the impacts of fishing, we need to understand their spatial and temporal ecology, including the factors governing their distribution, and how they interact with fisheries. While there has been a global increase in research and data on mobulid rays in recent years, our knowledge of their ecology and distribution in the Indian Ocean and interactions with pelagic tuna and tuna-like fisheries is still relatively limited and there remain key gaps in our understanding of their oceanic habitats and interactions with the physical environment (Stewart *et al.*, 2018). This study represents the first attempt to explore mobulid interactions across many of the major tuna fleets operating in the Indian Ocean based on a newly collated observer dataset managed by the IOTC. This study aims to review the available observer information to identify spatial and temporal hotspots and analyse trends in interactions with the different fisheries in operation across the Indian Ocean to support the conservation and management of these species.

Background

Following a fairly recent taxonomic revision, the family Mobulidae now comprises eight nominal species (previously 11) under a single recognised genus (previously 2); *Mobula* (White *et al.*, 2018). Under the current classification, a total of six species are found in the Indian Ocean; *Mobula birostris* (oceanic manta ray), *Mobula alfredi* (reef manta ray), *Mobula mobular* (spinetail/giant devil ray), *Mobula tarapacana* (sicklefin devil ray), *Mobula thurstoni* (bentfin devil ray), and *Mobula kuhlii* (shortfin pygmy devil ray) (Lawson *et al.*, 2017). This includes *M. japanica* and *M. eregoodootenkee* which are now considered junior synonyms of *M. mobula* and *M. kuhlii* respectively (White *et al.*, 2018).

Biological characteristics

Mobulids (manta and devil rays) are medium to large batoid fishes, reaching wingspans of up to seven metres and occupying primarily pelagic, offshore marine habitats (Couturier et al., 2012) and have life history characteristics that make them exceptionally susceptible to overexploitation (Croll *et al.*, 2016). These rays are slow growing, with long maturation times and presumed high longevity, although much of this information is lacking, particularly at the species level (Stewart *et al.*, 2018). The fecundity of mobulids is extremely low. Usually only one pup is produced per litter, and the gestation period is long, potentially between one and three years (Couturier *et al.*, 2012; Marshall, Barreto, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Rigby, *et al.*, 2019). Although variable across species, most annual fecundities are ~0.5 pups per year, particularly for larger species (Dulvy, Pardo, *et al.*, 2014). As a result, the estimated maximum rate of intrinsic population increase (r_{max}) for large mobulids (0.116 $year^{-1}$) is among the lowest of all elasmobranchs, and is actually quite close to marine mammals (median r_{max} of 0.07 $year^{-1}$) (Dulvy, Pardo, *et al.*, 2014; Croll *et al.*, 2016; Lawson *et al.*, 2017). These biological characteristics are likely to vary among species and geographically due to variable environmental conditions. For more broadly distributed species such as *M. mobular, M. thurstoni, M. tarapacana,* and *M. birostris,* regional differences may be more relevant (Stewart *et al.*, 2018).

Due to these extremely conservative, K-selected, life history characteristics, mobulids are not considered to be able to support sustainable targeted fisheries of any type. Moreover, estimates of mobulid extinction risk suggest that populations are unlikely to withstand current levels of fishing mortality and that their ability to recover from fishing impacts is also likely to be low (Dulvy, Fowler, *et al.*, 2014). *Mobula birostris and M. alfredi* are currently both considered vulnerable*, M. mobular, M. tarapacana* and *M. thurstoni* are classed as endangered and *M. kuhlii* is classified as data deficient according to the IUCN Red List of Threatened Species (Bizzarro *et al.*, 2009; Marshall *et al.*, 2018; Marshall, Barreto, Bigman, Carlson, D. Fernando, Fordham, Francis, Herman, Jabado, Liu, Pardo, Rigby, Romanov and Walls, 2019; Marshall, Barreto, Bigman, Carlson, D. Fernando, Fordham, Francis, Herman, Jabado, Liu, Pardo, Rigby, Romanov, Smith, *et al.*, 2019; Marshall, Barreto, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Pacoureau, *et al.*, 2019; Marshall, Barreto, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Rigby, *et al.*, 2019).

Ecology and Distribution

While mobulid species have many common biological characteristics, their ecologies nevertheless appear to be species-specific, and sometimes region-specific (Couturier *et al.*, 2012). Manta and devil rays are found circumglobally in tropical, subtropical and temperate waters ranging from 40° N to 40° S, although the majority of species have a tropical to subtropical distribution, preferring warm water temperatures of 20–26° C (Couturier *et al.*, 2012; Hacohen-Domené *et* *al.*, 2017; Lawson *et al.*, 2017). They are regarded as pelagic or epipelagic species, and are encountered across broad geographic ranges, in both shallow inshore environments and deeper offshore waters (Anderson, Adam and Goes, 2011; Tremblay-Boyer and Brouwer, 2016). Movement studies suggest that mobulids are highly mobile and able to undertake long-distance migrations with examples of individual *M. alfredi* travelling approximately 2,500 km in just a few months (Jaine *et al.*, 2014). Studies of *M. tarapacana* in the central North Atlantic Ocean confirm that this species is also capable of travelling large distances through the oligotrophic open ocean while diving to depths of up to 2,000m (Thorrold *et al.*, 2014). Nevertheless, much more limited movement patterns have been observed in other studies, e.g., *M. mobular* in the eastern Pacific (Croll *et al.*, 2012). While individuals are often solitary or travelling in small groups, most species have also been observed gathering in schools ranging in size from a few to hundreds of individuals (Anderson, Adam and Goes, 2011; Couturier *et al.*, 2012). Large seasonal aggregations are known to occur at different locations throughout their ranges (Couturier *et al.*, 2012; Graham *et al.*, 2012; Jaine *et al.*, 2014; Hacohen-Domené *et al.*, 2017), however, the drivers for this behaviour, common to both manta and devil rays, are still poorly understood and remain elusive. The main explanation for these aggregations is thought to be the confluence of an optimal set of determining environmental factors which affect primary productivity (Couturier *et al.*, 2012). Manta and devil rays are generally passive filter-feeding planktivores feeding almost exclusively on zooplankton, although they may also exhibit some piscivorous behaviour consuming some fish and crustaceans, so have most commonly been reported foraging in productive waters (Graham *et al.*, 2012; Hacohen-Domené *et al.*, 2017). While foraging is thought to be the main driver behind aggregations (Anderson, Adam and Goes, 2011), manta rays also aggregate by reefs at 'cleaning stations' where parasites and dead tissue may be removed by small fish, or congregate inshore for courtship and breeding during specific periods (Marshall, Dudgeon and Bennett, 2011; Rohner *et al.*, 2013) and substantial site fidelity has been observed (Dewar *et al.*, 2008; Marshall, Dudgeon and Bennett, 2011).

Associations have been documented linked to coastal areas and continental shelves (Alfaro-Cordova *et al.*, 2017; Hacohen-Domené *et al.*, 2017), seamount and islands (Anderson, Adam and Goes, 2011), upwelling zones, lower sea surface height (Lezama-Ochoa, M. Hall, *et al.*, 2019), shallow mixed layers or cold sides of thermal fronts (Graham *et al.*, 2012), sea state, moon illumination (Jaine *et al.*, 2012), current patterns (Barr and Abelson, 2019), ENSO-related climate phenomena (Beale *et al.*, 2019) and high primary productivity (Lezama-Ochoa, M. A. Hall, *et al.*, 2019). It has been suggested that these environmental conditions affect both the spatial distribution of plankton as well as the effectiveness of cleaning by the cleaner wrasse which in turn influence the behaviour of mobulid rays (Barr and Abelson, 2019). Although there has been an increasing amount of research into mobulid rays and their distribution in recent years, particularly for mantas, our understanding about their oceanic habitat and relationships with the environment is still relatively limited (Lawson *et al.*, 2017; Lezama-Ochoa, M. Hall, *et al.*, 2019).

Fisheries interactions

The particular life history characteristics of mobulid rays mean that these species are likely to have a poor ability to withstand even low levels of fishing mortality, however, they are either directly targeted or form valuable bycatch in small-scale fisheries and are accidentally caught as bycatch in industrial fisheries, where they are mostly discarded. The magnitude of these interactions (particularly as bycatch) is poorly documented although there is anecdotal evidence of an unprecedented decline in the landings of mobulid rays in some coastal countries of the Indian Ocean.

The attraction of mobulids to productive habitats and distribution in coastal, epipelagic areas makes them vulnerable to capture by an array of fishing gear. Manta and devil rays are threatened globally throughout their range by surface gill net, longline, purse seine and directed harpoon fisheries in which they are caught as a targeted species or as incidental catch (White *et al.*, 2006; Shahid *et al.*, 2018). Mobulids are often fished and traded under one general category, leading to a dearth of species-specific fisheries information and it is highly likely that reported landings only represent a fraction of total fishing-related mortality due to incomplete catch data (Ward-Paige, Davis and Worm, 2013; Croll *et al.*, 2016).

Targeted fisheries

Artisanal fisheries have targeted mobulids for decades for meat (consumed locally), cartilage (exported as filler for shark fin soup), and skin (exported for leather) (White *et al.*, 2006; Croll *et al.*, 2016), however, mobulid byproducts have increasingly been considered as valuable commodities in international trade markets. The dried gill rakers (brachial filter plates) are particularly sought after and are used in Asian dried seafood and traditional Chinese medicine medicinal products, where they have increased demand so dramatically that directed targeted fisheries have emerged or expanded for nearly all mobulid species (Couturier *et al.*, 2012; Lawson *et al.*, 2017; O'Malley *et al.*, 2017).

Targeted mobulid fisheries generally use gear types such as gill nets, harpoons, hook and line and gaffs (Couturier *et al.*, 2012; Croll *et al.*, 2016; Lezama-Ochoa, M. Hall, *et al.*, 2019) and all mobulid species present within a fishing area tend to be exploited (Couturier *et al.*, 2012). A number of fisheries targeting mobulids across the Indian Ocean have been identified, the majority of which are characterised as artisanal (Croll *et al.*, 2016). Sri Lanka has several harpoon fisheries for mobulid rays (Fernando and Stevens, 2011). In parts of Indonesia, harpoons are used to catch whales and sharks, as well as mobulid rays, the targeting of which increased following the development of the international market in branchial filter plates (Dewar, 2002). In northeast India, there are seasonal harpoon fisheries for devil rays in Andhra Pradesh and Lakshadweep Islands (Couturier *et al.*, 2012). Harpooning is also commonly used in southern Mozambique to catch mantas as well as *M. kuhlii* which are consumed locally (Couturier *et al.*, 2012), while in Oman *M. khulii* and *M. thurstoni* have also been confirmed in artisanal fisheries landings (Henderson and Reeve, 2011). There have also been cases of more opportunistic fishing of mobulids documented, whereby fishers change their strategy when target species are scarce and intentionally fish for mobulids or where mobulids caught unintentionally as bycatch are retained (White *et al.*, 2006; Dharmadi and Fahmi, 2014; Alfaro-Cordova *et al.*, 2017).

Nevertheless, over the past decade there has been significant progress made in reducing targeted fishing pressure on manta and devil rays. There is anecdotal evidence that successful conservation campaigns may be reducing demand for gill plates in conjunction with stronger government policies on wildlife trade in China (Lawson *et al.*, 2017). In addition, countries with some of the largest export markets for mobulid gill rakers have now banned the capture, retention and sale of mobulid rays, and these species continue to be further protected national and internationally each year. All mobulid species have now been added to Appendix II of the Convention on International Trade in Endangered Species, an intergovernmental agreement which closely controls the international trade of listed species (CITES, 2016), and are now protected under Appendices I and II of the Convention on Migratory Species, which requires member countries to enact legislation protecting the species within their territorial waters (CMS, 2017). In the Indian Ocean, Resolution 19/03 *On the conservation of mobulid rays caught in association with IOTC fisheries* was introduced in 2019, banning the retention of mobulids by any fishery, other than those for subsistence, throughout the IOTC Area of Competence. Nevertheless, enforcement still remains a key issue.

Bycatch fisheries

While international commitments and national fisheries regulations have sought to prevent the retention and landing of mobulid rays, the vast majority of mobulid captures are actually a result of unintentional bycatch (Croll et al., 2016). This is a result of the high degree of distributional overlap of mobulids with tuna and tuna-like fisheries, due to the similarity in their distributions across epipelagic tropical habitats in regions of high productivity (Shahid et al., 2018). Incidental catches are therefore thought to be a key source of mortality for mobulids which are taken as bycatch during large-scale commercial fishing operations, small-scale fishing operations as well as in passive shark protection nets (Couturier et al., 2012). Mobulids are caught in virtually every fishing gear type (Stewart et al., 2018), but the fishing gears with the highest reported mobulid bycatch rates are gillnets and purse seines (Croll et al., 2016; Alfaro-Cordova et al., 2017; Fernando, 2018; Shahid et al., 2018). Given that handling practices may be detrimental to the survival of some discards and the limited information on post-release survival which, based on anecdotal evidence, may be very low (Francis and Jones, 2017), bycatch is thought to be an important source of mortality for mobulids and is important to monitor.

Purse seines

Given their broad spatial distribution, intensity of effort, and reported bycatch, commercial tuna purse seine fisheries are thought to pose one of the most significant threats to mobulids globally (Ward-Paige, Davis and Worm, 2013; Croll et al., 2016; Stewart et al., 2018). Existing data indicate that bycatch mortality may be large (Hall and Roman, 2013). Romanov (2002) estimated that between 253 and 539 mobulids were caught by purse seiners in the western Indian Ocean each year (1985-1994), while more recent estimates of 1936 mobulids per year (1981-2008) (Croll et al., 2016), or 183[2] individuals per year between 2003 and 2009 (Amande *et al.*, 2012). Mobulid interactions with FAD sets are extremely low, while sets on free schools have higher but still very sporadic mobulid catch rates (Romanov, 2002; Hall and Roman, 2013).

Gillnets

Drifting gillnet fisheries also pose a significant threat to mobulids, particularly given the scale of the fisheries in the Indian Ocean (32% of captures of target tuna and tuna-like species 2016-2018)[3]. Although some targeted fisheries for mobulids exist in Sri Lanka, the vast majority of mobulids captured there are reported by fishers to have been retained bycatch from the gillnet fisheries targeting skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*) and billfish (Fernando, 2018). The mobulid catches of these fisheries are particularly large, with estimated total landings exceeding 56,000 individuals in 2011, primarily driven by the market for gill rakers (Fernando and Stevens, 2011). Similarly in Indonesia, the drifting gillnet fisheries targeting skipjack have recorded substantial bycatch of mobulid rays. A survey of four landing sites between 2001 and 2005 resulted in estimates of an annual mobulid catch of 4110 individuals (544 t), with fishery-wide bycatch likely to be significantly greater (White *et al.*, 2006). Mobulids are also caught in pelagic gillnets targeting tuna and tuna like species off the Pakistani coast where they are generally retained and utilised for dried meat, fishmeal and oil extraction, while some are released alive (Moazzam, 2018; Shahid *et al.*, 2018).

Longline

There is often no information on mobulid catches in the literature on bycatch in Indian Ocean longline fisheries (e.g. Huang and Liu, 2010) or the information is limited due to small sample

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[2] Calculated based on an average weight of 285kg or 300cm for an unidentified mobulid (Notarbartolo-Di-Sciara, 1988)

[3] Dataset: IOTC-2019-WPTT21-DATA03-NC

sizes (Coelho, Lino and Santos, 2011), however, it is noted that bycatch rates in the western and central Pacific bycatch rates (individuals per set) were reported as ~1 for *M. birostris* , ~1 for *M. mobular* and~3 for *M. tarapacana* which were similar to, slightly lower than and slightly higher than the purse seine CPUEs respectively (Tremblay-Boyer and Brouwer, 2016).

METHODS

Data

While data on mobulids are limited globally, they are particularly poor for the Indian Ocean and many interactions are simply not reported. Given the incredibly limited amount of data available for this study, a data mining and collation exercise was necessary to form the basis of the analysis.

While a very small amount of information on mobulids is available in the discards dataset held by the IOTC Secretariat, it is generally unclear whether the data have been raised to the level of the fleet or what corresponding level of effort they are associated with (e.g. number of sets, hooks, vessel days etc). There is also no spatial information provided with the discard data. Therefore, this study focussed on fisheries data from the IOTC Regional Observer Scheme regional database. This database has only recently been developed, and so observer data from CPCs are still in the process of being extracted, collated, cleaned and entered into the database (IOTC, 2019b). All observer data in the ROS database held by the IOTC Secretariat as of October 2019 were downloaded from the IOTC WPEB webpage for analysis[4], including information from the purse seine fleets of EU-France, EU-Spain, Rep. of Korea, Mauritius, Seychelles and the longline fleets of EU-France, Japan and Sri Lanka (Table 3). This study is the first use of bycatch data from this database and therefore there were number of issues associated with the dataset that first had to be resolved before the analysis could be completed. Therefore several revisions were later provided, but remaining in the same format and level of aggregation as the published dataset.

While the majority of data submitted to the IOTC have now been included in the database (62 % of trips), due to the rare-event nature of mobulid interactions and the importance of maximising the quantity of data available for the study, further data mining was undertaken to supplement the dataset. Individual observer trip reports were reviewed[5] and assessed in terms of expected input time and value added to the study. Based on this, all electronically submitted datasets were input, wherever possible, as well as a number of non-electronic datasets which were in a consistent enough format to enable some level of automated and time-efficient data entry. This

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[4] https://iotc.org/sites/default/files/documents/2019/08/IOTC-2019-WPEB15-DATA12_Rev1_-_ROSAll_0.zip

[5] As per a confidentiality agreement consistent with IOTC Res. 12/02

resulted in the addition of observer data from a further eight longline fleets: Australia, Taiwan,China, EU-Portugal, EU-UK, Indonesia, Rep. of Korea, South Africa and Sri Lanka (

Table 3). An additional dataset for the gillnet fleet of Pakistan was also provided by WWF-Pakistan for use in the analysis. The information for Pakistan and EU-France (Reunion) contains data collected by crew and the data from Australia is based on electronic monitoring rather than human observers in recent years. While these do not adhere to the strict definition of onboard, human, totally impartial observers as outlined in IOTC Res. 11/04, obtaining a more complete and comprehensive dataset was considered to be the priority at this stage and so all of these data were included in the analyses. This resulted in a more comprehensive final dataset which included over 1512 trips from 16 fleets (

Table 3). Observer datasets not included in the analysis were those limited predominantly by the format and extent of reporting to IOTC[6]. These included China LL (no spatial data provided), some years for EU,Spain PS and LL (non-standard formats were provided), France OT PS (non-standard format), EU,Italy (non-standard format), certain trips for Indonesia (excluded where there was no clear link between set and catch information), Kenya LL (non-standard format and unclear species definitions for rays), Madagascar (non-standard format), Mauritius LL (rays not distinguished between mobulids and others), Mozambique (non-standard format), some years for South Africa LL (non-standard formats) and Tanzania (no spatial or bycatch information).

As expected in meta-analyses which use multiple datasets collected by different programmes, a substantial amount of data-cleaning was required to synthesise the datasets. Species code lists and classifications were aligned, as were tables of fate (discarded/retained) and condition of bycatch (varying degrees of life exhibited on release). In general, information was aggregated to the coarsest resolution available in order to unify the dataset. Data were cleaned and filtered for errors such as missing spatial information, inverted latitude and longitudes and captures taken inland, resulting in the removal of some records. Although it would have been interesting to explore trends in purse catches by free school and associated sets separately, given that mobulids are found in environmental conditions that are favoured by free schooling tunas and do not show associative behaviour with floating objects (Romanov, 2002; Hall and Roman, 2013), published observer data was provided in the form of aggregate totals for purse seine fisheries so these could not be distinguished in the analyses. The majority of data were reported at a spatial resolution of 1° x 1° (91 % of records), but in some instances only 5° x 5° resolution data were provided for certain longline fleets. Given the focus on spatial patterns in the analysis and as the

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[6] IOTC-2019-SC22-07

cast majority of data were reported at a scale of 1° x 1° or finer, this was used as the standard scale for most analyses, where the midpoint of 5° x 5° datasets were used where necessary.

Catch conversions

Observer data were reported in units of both weight and numbers of individuals so a series of conversions were used to estimate total numbers and total weight across all fleets for the different species. For mobulids, the disc width – total weight relationship provided by Notarbartolo-Di-Sciara (1988) for *M. Japanica* (now known as *M. mobular*) was used to estimate the weight of an individual (Equation 1), based on its common length (Table 1). Reliable data were not available for the other species observers in the dataset (*M. birostris, M. alfredi* and *M. kuhlii*), however, as all mobulid species are morphologically similar, this relationship was also used for the other species. Common lengths reported in Fishbase.org were used (Table 1) and for species for which none was reported, an approximation of 2/3 the maximum length was used.

Equation 1. $W_{(kg)} = 4.29 \times 10^{-10} (_{DW(mm)})^{3.4}$

All reported catches of mobulid species were included in the dataset, including aggregate grouping of unidentified "*Mobula spp.*", unidentified mantas and unidentified devil rays. Further groupings at a higher level of aggregation were removed from the dataset (e.g. AG18 which covered all rays, including mobulids as well as pelagic sting rays).

Target species definition

Target species were defined in

Table 2. These are a core group of market species that are generally the target of IOTC fisheries. Captures of the first five species are considered to be most reliably reported and therefore provide some of the most accurate datasets. The nominal captures of these species have been commonly used as anchor points from which to estimate bycatch, effort or for other extrapolation purposes. Three species of neritic tunas were also added as they are often targeted by the smaller scale fisheries and the gillnet fisheries.

Catch rates

Datasets submitted in line with the original IOTC reporting guidelines for observer data[7] did not provide set level effort data and so the ROS database estimates this for purse seine fisheries. For longline fleets, sets may span more than one grid cell and so estimation requires a greater number of assumptions and is even less accurate so this was not attempted here. To overcome the problem of the lack of reported spatial effort information, a ratio of mobulid bycatch to target catches was instead used as a measure of the mobulid catch rate, i.e., target catches were used

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[7] IOTC Observer manual v.1, 2010.

as a proxy for effort. This has the advantage of enabling direct comparisons across different gear types and data reporting methods. It uses the reported information directly rather than relying on estimates based on assumptions and is therefore more accurate. It can also be used in conjunction with other datasets that do not include effort information, eg, nominal catches for purposes such as extrapolation. While BPUE catch rates assume that catches of mobulids are proportional to effort, catch ratios assume that mobulid catches are proportional to target catches. While neither of these assumptions are likely to be completely true, a catch ratio was the preferred unit of measurement in this study for the reasons described.

To calculate the ratio, discards were included in addition to retained catches for all species. Comparing mobulids catches with only retained target catches may be useful for potential scaling to overall nominal catches (which do not include discards) and may be more accurately reported. However, discard reporting should be more accurate for observer datasets, compared with logbooks, and including discarded catches is more likely to better reflect the true ratio of mobulid to target catches. As the discarding of target species is low, this nevertheless makes little difference to the overall ratios.

Target and mobulid catches were summed for each {flag, gear, year, month and grid cell} combination. All combined {flag, gear, year, month and grid cell} records which contained neither target catches nor mobulid catches were removed from the analysis. Catch ratios were based on the number of individuals of mobulids and catch weight of target species as this was considered to be the most accurate ratio given that the vast majority of data were reported in this way.

Ratios were calculated as:

$$R = \frac{N_r + N_d}{W_r + W_d}$$

Where R is the catch ratio, N_r is the number of mobulids retained, N_d is the number of mobulids discarded, W_r is the weight of target species retained and W_d is the weight of target species discarded, all by {year, fleet, gear type, month and grid cell}.

There were two cases where records with reported mobulid catches had zero target catches for the corresponding record resulting in infinite ratios which were removed from the analysis. Two fleets also had to be excluded from all analyses involving ratios (Seychelles and EU, France purse seine fleets) as the observer data on target catches was incomplete. This resulted in a reduction in records from 8115 to 6093 as a substantial proportion of the data came from these two fisheries. A Kruskall-Wallis rank sum test was used to test for significance in the difference in catch rates among gear types.

Environmental variables

Environmental datasets were downloaded from the MODIS-Aqua satellite data from the NASA ocean data portal.[8] Monthly chlorophyll-*a* (Chl-*a*) and sea surface temperature (SST) data were downloaded at a resolution of 9km. Clouds were masked out of these images. Red colours generally represent high chlorophyll concentrations, however, suspended matter other than phytoplankton (e.g. detritus) can increase the uncertainty of the chlorophyll estimate, an artefact that is particularly common in coastal regions (Moore, Campbell and Dowell, 2009; Zheng and DiGiacomo, 2017). Catches of mobulids were overlain with the SST and Chl-*a* maps during 2017 and 2018 to include periods during which hotspots have occurred. Data were downloaded by month for the entire year to evaluate seasonal variability in the environmental variables and mobulid interactions. Mobulids were plotted as point locations for visualisation, however, these were not precise locations as the data were reported by grid cell (usually 1° by 1°) and so the central point of this was taken and then jittered to better illustrate the total number of interactions by area. Catches were explored by species and gear type and the total proportion of manta and devil ray interactions (excluding the unidentified Mobula spp. category) for purse seine and longline fisheries was compared using a z-test.

Random Forest

A random forest regression model was used to identify spatio-temporal patterns in mobulid catch rates across fleets, a method that has proved useful in similar large-scale bycatch analyses (Oliver *et al.*, 2015). Random Forests are a non-parametric method requiring no assumption of statistical distributions which are capable of handling data with highly correlated and nonlinear factors and have been shown to perform well in bycatch research, reducing the biases associated with rare event species and low observer coverage (Pons *et al.*, 2008; Carretta, Moore and Forney, 2017, 2019; Stock *et al.*, 2019). Random forests are an ensemble method, which build regression trees from multiple bootstrap samples, using about 2/3 of the original data set each time, and averaging across them to produce a prediction that does not overfit the data and reduces the bias and variance of the model (Breiman, 2001). The remaining third of the data (the out-of-bag (OOB) data) can then be used as a natural 'test' set for validation whereby, for each observation, the

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[8] NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group; (2018): MODIS-Aqua Ocean Color Data, NASA OB.DAAC. doi: 10.5067/AQUA/MODIS/L3M/CHL/2018. Accessed on 19/03/2020.
NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group; (2017): MODIS-Aqua Ocean Color Data, NASA OB.DAAC. doi: 10.5067/AQUA/MODIS/L3M/CHL/2017. Accessed on 16/04/2020.

trees that did not use that data point can be used to form the prediction and thereby determine the OOB error.

The number of mobulid interactions was used as the response variable against the predictors: weight of target catch, flag, gear (factor), year (factor), month (factor), latitude and longitude. Random forests already include interactions between covariates and treat continuous covariates as nonlinear so latitude and longitude were included to estimate a spatial effect (Breiman, 2001; Stock *et al.*, 2019). Five hundred trees (ntree=500) were grown which was sufficient to stabilise the OOB error and the number of predictor variables to be randomly used at each node was trialled to find the number that minimised the OOB error (mtry=4). The importance of predictors was determined by comparing the percentage increase in mean square error (MSE) when variables are randomly permuted and the marginal effects of variables were examined though partial dependence plots. Analyses were performed using the 'randomForest' package in R.

Results

A total of 614 mobulids were reported for all fleets throughout the observation period. Mobulids were observed in most parts of the western Indian Ocean, with notable absences across the centre and southeast (Figure 1). The total catches of mobulid and target species observed in this study, compared with the total Indian Ocean catches of target species over the study period are summarised in Table 4. On average, the observer coverage across fleets included in the study dataset was 2.2% and as a proportion of total catches of target species reported across the entire Indian Ocean, this was 0.2%.

Reporting of mobulids has generally increased over this time, although fewer were reported in 2019 due to the time lag in the submission of recorded data to the IOTC. The increase in reporting of observer data including mobulid catches can be seen in Figure 2 in which higher catches are apparent beginning in 2011 and increasing until 2018, however when viewed as catch rates in terms of a mobulid:target catch ratio, there is no trend apparent over time (Figure 3).

Spatial pattens

In terms of spatial patterns, the highest number of mobulids observed across all years and fleets were located in the areas southwest of Madagascar, east of Chagos and the Maldives, and along the Pakistani coastline with lower numbers reported across the northwest equatorial region and the Australian coastline (Figure 4). In comparison, target catches from the same dataset were highest across the northwest equatorial region where the purse seine fishery is focussed, and along the Pakistani coastline. Catches recorded in weight were more evenly distributed whereas catches in numbers were more heavily concentrated in this region, as these are predominantly purse seine fishing ground where higher numbers of smaller individuals are captured (Figure 5).

When spatial patterns were viewed in terms of catch rates (number of mobulids per 100t of target species) one of the main differences was the relatively higher catch rates in coastal areas including off the west coast of Australia, along the east coast of South Africa and off the southwest coast of Indonesia (Figure 6). Another notable difference was the low catch rates in the northwest equatorial region purse seine fishing grounds, however, this is partly due to the exclusion of the French and Seychellois purse seine fisheries from all catch ratios due to their lack of reporting of total catches of target species in observer data.

Trends by gear

There were also notable differences in the spatial distribution of catches by gear type. Only one gillnet fishery was represented in the dataset and so observations from this fishery were centred in a very localised area along the Pakistani coastline and overall catches reported were relatively low. Data for the longline fleets covered most of the ocean, with highest catches east of the Maldives/Chagos region and southwest of Madagascar. Datasets for the purse seine fleets were located in the northwest equatorial region south of the Pakistani gillnet fishery, resulting in relatively little spatial overlap among gear types. Mobulild catches by the purse seine fleet were fairly evenly distributed across the range, with a notable gap in the middle so that catches formed a doughnut shape in the region (Figure 7). The gillnet fishery had the highest proportion of {grid, year, month, flag, gear} records with positive mobulid catches (8.7 %), followed by the purse seine fisheries (5 %), with the longline fisheries having the lowest proportion of positive records (2.1 %). However, when looking at the catch rate (numbers of mobulids per 100 tonnes target catch) for positive records only, the rates were highest for the longline fleet, followed by gillnets and lowest for purse seine fisheries (Figure 8), although there was also substantial variation within gear types. This suggests that purse seine fisheries may interact with mobulids more frequently at a lower level, while longline fleets appear to have less frequent interactions but when they do, catch rates are greater. The gillnet fishery has both more frequent interactions and also higher catch rates than the purse seine fisheries. The overall mean catch ratios observed were highest for the longline (17.26) and gillnet fisheries (11.17) followed by the purse seine fishery (0.43), and the Kruskal-Wallis test indicated that these differences were significant ($H = 68.858$, $df = 2$, $p < 0.01$). Nevertheless, these catch rates do not include the French and Seychellois purse seine fleets which reported greater numbers of mobulids than the other purse seine fleets (Table 5).

Trends by fleet

Figure 9 shows the distribution of mobulid catches by fleet over the observation time period (annual catches provided in Table 5). These within-fleet distributions indicate that, in addition to the patchy nature of interactions across the entire dataset, the catches of mobulids by individuals fleets have also been intermittent and patchy, both temporally and spatially, with highly variable numbers of mobulids reported by fleets throughout the time period. The absolute values here are not so important due to the varying level of effort reported among fleets and between years for each fleet but give an overview of the dataset.

The positive encounter rate varied widely across all fleets. Within the longline fleet, this ranged from 31.9% positive mobulid {flag, gear, year, month, grid cell} records for the Portuguese fleet to 0.2% for the Taiwanese fleet. There was similar variation observed within the purse seine fleet with 13.6% of records including mobulids for the Seychelles fleet (4.1% for France PS) while only 0.7% of records for the Korean purse seine fleet included mobulids. Of the positive records, there was still considerable variability in catch rates among fleets even within gears, with particularly high catch rates for the Sri Lankan fleet (Figure 10 and Table 6).

Seasonal patterns

Some seasonal patterns were also present in the dataset, with higher prevalence of catches between May and July across most regions, with another peak in January in the purse seine fishing grounds (Figure 11 and Figure 12a). This was apparent in terms of both total numbers as well as catch rates of mobulids (Figure 12). The trend appears to be predominantly driven by the longline fleets (Figure 13a), but was also apparent in the catch rates for the purse seine fleet (without PS-SYC and PS-EU.FRA), though the gillnet fleet shows no such trend (Figure 13b).

Environmental variables

Mobulid points of capture were overlain onto maps of sea surface temperature and Chl-*a* concentration by month for 2017 and 2018, the years with the highest observed effort. This time period coincides with a positive Indian Ocean dipole which began in 2017 and continued through 2018, creating warm temperature anomalies across the western Indian Ocean (Marsac and Demarcq, 2019).

The signature upwelling in the Arabian Sea and along the Somali coastline during the southwest monsoon is highlighted by the cooler sea surface temperatures from June to September 2018 (Figure 14). A this time of year the cooler, upwelled water deflects off the coast resulting in a large offshore phytoplankton bloom (Figures 15 & 16). There is also a notably cooler trend in this region in Jan-Feb 2018 during the northeast monsoon. There were some mobulid catches associated with the southwest monsoon upwelling, particularly from July - August 2017 and July – September 2018, and also catches in the region during the northeast monsoon bloom in January.

A further band of high producitvity just north of a curl driven upwelling event, known as the Seychelles-Chagos thermocline ridge, which peaks during the southwest monsoon was particularly noticeable in March 2018 and visible in both SST and Chl-*a* maps, with corresponding catches of mobulids along it. At the same time in the southern Indian Ocean, cooler waters extended northwards with the onset of the austral winter with a coresponding increase in productivity in the area extending northeastwards form the Aghulas Current convergence zone at the southern end of the Mozambique Channel. High catches of mobulids were observed associated with this high productivity area between May and July 2018.

In June 2017 there were particularly high catches of mobulids just south of India coinciding with and area of high productivity at this time (Figure 15) which was also elevated in that year relative to typical conditions (Marsac and Demarcq, 2019).

The centre of the south Indian Ocean subtropical gyre was notable as a large area of low chlorophyll concentration with almost no mobulids caught in the region throughout the time period. Despite these observations, there were still many spatio-temporal observations of mobulid interactions that did not fit these trends where individuals were caught in locations of very low chlorophyll concentration.

Random Forest

The explanatory variables included in the random forest model accounted for 47 % of the variation in the observer data, which is not particularly high but a substantial improvement in explanatory power from large scale elasmobranch analyses conducted at a global scale (Oliver *et al.*, 2015). The most influential variable included in the model was the vessel flag (Figure 17), with Sri Lanka, Portugal, South Africa and Pakistan having the greatest effect on model predictions (Figure 18b). Month of the year was the second most important predictor variable with June being associated with the highest mobulids catches (Figure 18d). The weight of target catches was also influential with greater mobulid catches associated with greater target catches until an asymptote is reached beyond which the level of target catches does not influence mobulid bycatch (Figure 18g). At very low levels of target catch weight, mobulid bycatch increased, presumably because of two data points where mobulid catches occurred with no corresponding target catch. Higher catches were predicted in 2011, however, there was no trend indicated (Figure 18c). Longitude was a more important explanatory variable than latitude, with higher mobulid catches predicted in the western and northern Indian Ocean (Figures 18e & 18f). The relationship between the two corresponds fairly closely to the locations where observed mobulid captures were highest (Figure 18h). The variable with least explanatory power was gear type. Gillnets were associated with higher mobulid catches, however the marginal differences among gear types were small (Figure 18a).

Species – specific information

Of the 614 individual interactions reported between 2007 and 2019, approximately half were identified to species level while the remainder were reported as unidentified mobulids, unidentified mantas, or unidentified devil rays. Of the interactions that were reported to species level, the majority were *M. mobular,* the spinetail mobula or giant devil ray (81 %), followed by *M. birostris*, the giant manta ray (17 %), with markedly fewer *M. alfredi*, the reef manta ray, and *M. kuhlii*, the Shortfin pygmy devil ray (both <1 %) (Table 7).

There were no discernable patterns apparent in the spatial distribution of captures by species (Figure 19). Unidentified devil rays were reported predominantly in the major purse seine fishing grounds in the north west Indian Ocean, whereas the unidentified manta rays were mostly located in the south west, close to the South African coastline. Nevertheless, catches of both the manta *M. birostris* and the devil ray *M. mobular* were widely distributed across the ocean. For the less reported *M. alfredi* these were observed in the western region and the single *M. kuhlii* was observer in the east, off the Indonesian coast.

There were substantial differences in the species reported among fleets. For Sri Lanka and Mauritius, *M. mobular* was the only species recorded, while for Australia only *M. birostris* were recorded (explaining the higher catch weights in this area), Figure 4b. For the Pakistani gillnet fleet captures were all reported as unidentified, while other fleets generally reported different species captures. Nevertheless, most fleets reported a substantial proportion as some sort of species aggregate (Figure 20).

In terms of gear type, as Pakistan represented the only gillnet fleet, these were all unidentified to species level. Both purse seine and longline fleets reported substantial captures of *M. mobular, M. birostris* and some *M. alfredi,* however, in terms of unidentified captures, these were almost all mantas for the longline fleet and devil rays for the purse seine fleet (Figure 21). The results from statistical tests indicated that the proportion of interactions with manta rays was significantly higher for longine fleets and the proportion of interactions with devil rays was significantly higher for purse seine fleets ($z = 6.14$, $df = 1$, $p < 0.01$).

While there was an increase in overall interactions in January and later in middle of the year, there were no clear trend in species interactions throughout the course of the year, with most spread relatively evenly throughout the year (Figure 22 and Figure 23) and across gear types (Figure 24).

Similarly, although the reporting of mobulid interactions increased over time (Figure 25a) and the proportion of completely unidentified mobulid interactions has decreased, while there was no clear trend in species reported over time (Figure 24b).

Status of measured variables: fate, condition and length

The vast majority of reported mobulid catches were discarded (93 %), while very few were retained (Pakistani gillnet fleet, Sri Lankan and French longline fleets and Seychelles purse seine fleet) and for others the fate was not recorded (Figure 26). Of those discarded, 15 % were discarded dead and 35 % were released alive while the status was unknown for the remaining 50 %. Of those released alive, the condition was unknown for the majority of individuals (70 %), while 17.5 % were reported as healthy and active, 11 % as injured and distressed and 1.5 % as dying.

No manta rays were reported as retained; those discarded were either devil rays or unknown species (Figure 27). While some mobulids were retained by each gear type, these only formed a substantial proportion of total mobulid captures for the gillnet fleet which retained 42 % of captures (31 % discarded and 27 % unknown), whereas for the purse seine and longline fleets almost all mobulids were discarded (Figure 28).

The majority of individuals discarded across all species were released alive, where the condition was known. The highest rates of live releases were reported for *M. birostris* and *M. mobular* and devil rays (>50 %) and *M. mobular* was the only species for which individuals were reported to have been released alive in an active, healthy state (Figure 29). Least is known about the ultimate fate of captures by the longline fisheries (Figure 30). For the purse seine fisheries, the majority were released alive, although the condition was unknown. A substantial proportion were also reported as dead, but the number of individuals where the condition was unknown was low. For the gillnet fishery, of those discarded, half were reported to have been released alive.

Disc lengths were reported for 177 individuals by the French, Spanish and Seychellois purse seine fleets and the French longline fleet (one individual). Of the 33 *M. birostris* measured, 73 % were juveniles. Two *M. alfredi* were measured, one 310 cm and the other 510 cm, so both likely to be mature (Table 1). Of the 81 *M. mobular* measured, 35.8 % were juveniles, 29.6 % were adults while the remainder were in the range of lengths at maturity (200 – 240 cm) (Marshall, Barreto, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Rigby, *et al.*, 2019). All other rays measured were identified only as devil rays. The mean length of these 77 individuals was 237 cm, which is within the range of maturity the largest species, *M. mobular,* so it is likely that the majority were mature. The gillnet fleet reported predominantly small individuals ranging from 14 – 80 kg (under 210 cm) with the exception of 3 larger individuals. The species were unidentified however.

Discussion

Across all gear types, catches were fairly patchy and intermittent in nature, characteristic of their sparse, fragmented populations (Marshall et al., 2018). There were often no interactions observed at all (and some particularly noticeable absences such as a trip by Taiwan,China longline fleet which reported not a single discard during the entire trip), sometimes very low numbers of mobulids caught (e.g. single individuals per trip), and at other times there were close to one hundred individuals caught in a single trip, a feature which appears characteristic of mobulid interactions with fisheries (Alfaro-Cordova *et al.*, 2017; Ruiz *et al.*, 2018; Lezama-Ochoa, M. Hall, *et al.*, 2019).

Of particular note were the high catches by the Sri Lankan longline fleet in 2017 and the Portuguese longline fleet in 2018. Neither of these was during a single set, but rather both were single trips in which many of the catches were mobulids. The Portuguese fleet undertook a trip between April and August 2018 during which particularly high interactions with unidentified manta rays were reported. While there were no more than 6 individuals recorded per set, mantas were present in many of the sets and so a high total (115 individuals) was reported across the entire trip. Similarly, a short trip which took place by the Sri Lankan longline fleet from mid-June to early July 2017 reported extremely high catches (89 individuals) of mobulid rays, all of which were identified as *M. japonica*, the spinetail mobula or giant devil ray, now *M. mobular*. Interactions were reported for the majority of sets, with up to 22 *M. mobular* individuals caught in a single set. However, a trip that took place just prior to that (mid-May to early June) reported not a single interaction with a mobulid ray. This trip took place in the same region but slightly further northwest. This suggests that some kind of temporal-spatial effect is influencing the abundance of rays in an area or influencing their catchability, leading to their presence in an area for a period of time that coincides roughly with the length of a fishing trip rather than just a fishing set, i.e., on the order of months rather than days. However, with only two trips reported in a single year from the entire Sri Lankan fishery, and a single trip reported per year by the Portuguese longline fleet few conclusions can be drawn, though it would be interesting to explore these patterns further once more data become available. It is also worth noting that in both trips the majority of rays were discarded alive (>85 % discarded alive by the Portuguese fleet and >78 % by the Sri Lankan fleet).

Populations of all mobulid species present in the Indian Ocean are most likely in decline (Bizzarro et al., 2009; Dharmadi and Fahmi, 2014; Lewis et al., 2015; IOTC, 2018a; Marshall et al., 2018; Marshall, Barreto, Bigman, Carlson, D. Fernando, Fordham, Francis, Herman, Jabado, Liu, Pardo, Rigby, Romanov and Walls, 2019; Marshall, Barreto, Bigman, Carlson, D. Fernando, Fordham, Francis, Herman, Jabado, Liu, Pardo, Rigby, Romanov, Smith, et al., 2019; Marshall, Barreto, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Pacoureau, et al., 2019; Marshall, Barreto, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Rigby, et al., 2019), however, no indications of population decline were apparent from this study in which catch rates fluctuated around 4 individuals per 100 t of target species captures between 2009 and 2019. This may be reflective of the low coverage of fishing effort, the limited historical information prior to 2009 or the limited information available at species level where trends may be more evident.

While a number of reviews highlight the importance of interactions of the purse seine and gillnet fisheries with mobulids, observations from the current study suggest that the longline fleets should also be given due attention as they may also have a significant role to play in the mortality of these species. Given the filter-feeding nature of mobulids, the potentially high rates of hooking by longliners is fairly surprising. Preliminary findings from the Portuguese observer programme suggest that the majority of mobulids are hooked (sometimes in the mouth while often a hook may have caught the wing, mouth flaps or other body part) while line entanglements are rarer (Coelho, pers. comm.). Direct hookings to the mouth might potentially be more prevalent for the more piscivorous species such as *M. tarapacana.* This study has shown that longline fleets can interact with mobulids at a large scale and suggests that catch rates of the longline fishery may possibly be higher than for the purse seine fishery. However, these results are based only on three purse seine fleets (EU, Spain, Rep. of Korea and Mauritius) for limited time periods and should be re-evaluated once information on target captures is available from the French and Seychelles purse seine fleets.

The relatively high catch rates of the gillnet fisheries are also evident from the observer dataset (Table 6). Given the importance of the gillnet fleet and small-scale longline fisheries in the Indian Ocean in terms of the scale of catches, it is crucial to obtain more information from these fisheries for a fuller understanding of the population-level impacts.

The suggestion that gillnet and longline fisheries may have higher catch rates and are potentially a source of greater mobulid mortality than purse seine fisheries in the Indian Ocean is somewhat in agreement with estimates of total mobulid interactions calculated by Garcia and Herrera (2018). Their analysis was based on different data sources from the current study including catch rates for longline and gillnet fleets derived from the literature (White *et al.*, 2006; Varghese, Vijayakumaran and Gulati, 2013), catch rates for the purse seine fleets based on fine scale Spanish observer data and information on total target captures and effort taken from IOTC nominal catch and catch-and-effort datasets. They predicted that mobulids interact predominantly with the gillnet fisheries (>99 %) followed by longline (0.3 %) and purse seine (0.1 %) fleets to a much lesser extent, although estimates were not calculated for a number of longline fleets which may have contributed to the relatively low predictions for this fishery. No extrapolations or predictions of total ocean-basin catches were made from the current study given the very low observer coverage represented in the dataset (<1 %) and the rare and patchy nature of the data, however, the scale of catches by fishery should be taken into consideration as well as the catch ratio. While bycatch rates are important, even fisheries with very low bycatch rates can have a significant impact if they operate on a very large industrial scale. The longline fishery was only responsible for 7 % of target species captures in 2018 while the purse seine fishery took a much larger proportion of catch at 37 %, and so even while the catch rates might be fairly low the overall impact may still be substantial. The gillnet fleets were responsible for 30 % of target species captures in 2018, which, combined with the high catch rates, suggests that this fishery may have the greatest impact on mobulid mortality in the Indian Ocean. Nevertheless, gear type was the least influential explanatory variable in results from the random forest model, suggesting that the greater variation in catch rates by flag may outweigh the effect of gear type in importance. In some cases the two may also be confounded as a number of flags used only a single gear type.

Results suggest that the spatial distribution of mobulids in the Indian Ocean may be determined by a suite of environmental variables corresponding to particular oceanographic water masses and features such as upwelling, convergence zones and high primary productivity with the main hotspots linked to seasonal or permanent productive areas. High correspondence with these features indicates that foraging behaviour may be driving the main aggregations observed in this dataset.

In general, higher catches were observed during the southwest monsoon, with results from the random forest model predicting the highest catches in June. This corresponds to findings for catches of *M. birostris* by the gillnet fleets of Sri Lanka and Indonesia which during this season (Fernando and Stevens, 2011; Dharmadi and Fahmi, 2014). At this time of year, there is notably increased productivity in certain regions due to upwelling events and increased mixing, allowing cooler, nutrient rich waters rise towards the surface and stimulate primary productivity. Mobulids catches corresponding to these areas of seasonal higher productivity (0.4 - 0.5 mg.m^{-3}) have been observed in the Arabian Sea, south of the Mozambique Channel, in the coastal areas off South Africa, Australia, Indonesia and south of India, although sea surface chlorophyll around India was elevated relative to normal for the area at that time (Marsac and Demarcq, 2019) so this may not be typical. This suggests that much of the seasonal distribution of mobulids is primarily related to temporal variations in chlorophyll concentration. Mobulid interactions were also observed within a range of warm water temperatures from approximately 20 - 30° C, consistent with other global observations (Couturier et al., 2012).

Interestingly, the spatial pattern of all mobulid interactions (across all years and seasons) in the Arabian Sea is that of a doughnut with an absence of interactions in the centre (Figure 1). There is a complicated seasonal gyre system in this area with two gyres developing during the southwest monsoon phase, exporting primary productivity along their paths of motion, one of which is known as the Great Whirl (Beal and Donohue, 2013). Marsac and Demarcq (2019) noted that drifting objects are often temporarily trapped in the anticyclonic Great Whirl along with a large biomass of associated juvenile tuna. Mobulids have been observed to only rarely be caught by purse sine sets on drifting objects (Romanov, 2002; Hall and Roman, 2013) and the notable absence of mobulids in this region corresponds with this finding. They have also been potentially linked to a preference for cyclonic eddies and lower sea surface height; in this study they were notably absent from anticyclonic eddies (Lezama-Ochoa, M. A. Hall, *et al.*, 2019).

Despite the association with chlorophyll blooms, mobulids were not observed in areas with the highest levels of chlorophyll. In the Pacific, the presence of M. mobular was predicted in waters with chlorophyll concentrations between 0.5 – 1 mg.m3 (Lezama-Ochoa, M. A. Hall, et al., 2019) whereas in this study associations seemed apparent at lower levels of 0.4 - 0.5 mg.m3. It is possible that this is simply a reflection of the small dataset and limited coverage of some of the productive coastal areas located in EEZs unavailable to the observed fleets such as the Somali EEZ, and due to the piracy that took place in the region overlapping with the time period of the study (Chassot et al., 2010).

Results should be interpreted with caution given that the data are necessarily biased towards fisheries and fleets that have submitted data to be analysed, the level of observer coverage of these fisheries and the fisheries-dependent distribution of the observed effort. Separating potential trends in mobulid distributions with those of fishing behaviour is also difficult. Some observed seasonality in mobulid catches (e.g. in Indonesia) has been attributed to factors such as calmer weather conditions making fishing trips more common during the southwest monsoon rather than necessarily indicating an increased abundance at that time (Dharmadi and Fahmi, 2014). Nevertheless, the results provide a preliminary overview of the potential environmental characteristics of their seasonally preferred habitats and the importance of interactions across the main gear types. It is important that trends are also be explored through fisheries-independent studies such as pop-up archival satellite tagging (ideally from scientific cruises to achieve true independence in the tagging location) to improve understanding of areas of significance and the reasons for these further.

Better definition of the overlap between mobulid distributions and fisheries is important for the identification of priority areas in which to minimize bycatch (Lawson *et al.*, 2017), and Stewart et al., (2018) have suggested that setting fishing gear above the thermocline depth could reduce bycatch rates of *M. birostris,* given the strong associations with the thermocline in this species. However, the finding that mobulids are closely associated with areas of high productivity where many freely aggregating schools of tuna are found and the overlap in depth of the thermocline with many fishing gears suggests that this may be difficult without restricting commercial fishing operations and setting gear at shallower depths is likely to introduce bycatch problems for other species groups.

Therefore, concurrent research is also needed into other bycatch mitigation strategies. For gillnet fisheries potential mitigation strategies include the avoidance of setting in areas where rays can actually be seen as present and schooling prior to setting and a reduction in soak times of nets to potentially reduce the period of entanglement and increase probability of survival (Hutchinson, M., Poisson, F. and Swimmer, 2017). Other proposed mitigation methods have focused on gear modifications to gillnets including the use of various coloured light-emitting diodes in or near the ultraviolet range in a particular optical range that deters mobulid rays while not impacting the catch of target species, a concept currently being trialled in Pakistan and Indonesia (Fernando, 2018; Stewart *et al.*, 2018). Gear modifications have also been explored for longline fisheries; Piovano and Gilman (2017) recorded significantly higher standardised ray catch rates on narrower J-shaped hooks than on wider circle hooks, thought to be due to the smaller minimum width of the J-shaped hooks. However, although the data included some observations of *M. birostris* results were predominantly based on sting ray observations. A key recommendation for purse seine fleets has been to avoid setting on ray-associated tuna schools, and for all fisheries best practices for returning rays to the ocean should be adopted (Poisson F., Vernet A. L., Séret B., 2012; Francis and Jones, 2017). However, bycatch mitigation methods have not been explored extensively for mobulids and more work in this area is required (Stewart *et al.*, 2018). The IOTC WPEB has agreed that mitigation methods should be thoroughly investigated and developed for all fisheries with mobulid bycatch (IOTC, 2018b).

The species observed most frequently was *M. mobular* followed by *M. birostris* and, to a lesser extent, *M. alfredi* and *M. kuhlii.* The high observed catches of *M. mobular* are consistent with the high reported catches of the species from the Sri Lankan fish markets in 2011 (Fernando and Stevens, 2011). White et al., (2006) also reported that the highest mobulids catches in the Indonesian gillnet fisheries were of *M. mobular.* Catches of *M. tarapacana* were also reported in relatively high numbers as the second most frequently caught species in both surveys and *M. thurstoni* were also recorded at lower levels, however, not a single individual of either species was identified in the observer datasets used in the present study. This may be reflective of the low level of species identification by many fleets and the difficulty observers may have in distinguishing between some species of devil ray.

Results suggest that there may be a trend in species groups interactions by gear type given the higher percentage of devil ray interactions with purse seine fisheries and higher percentage of manta ray interactions with longline fisheries (Figure 20). This may indicate a trend towards interactions with larger individuals for longlines and smaller for purse seine, however, as the majority of purse seine interactions with mobulids are with sets on free schools, rather than on associated sets, there is no clear reason to expect a size distinction and it may instead be reflective of the differing species distributions. Given the high proportion of aggregate species groupings in the dataset, improving species identification skills of observers is a clear priority for the Regional Observer Scheme. Updating the IOTC *Species identification guide for sharks and rays in the Indian Ocean*[9] with recent taxonomic changes and the continued translation and distribution in relevant languages (currently available in English, French, Urdu and Persian) is important and the implementation of species identification training as part of the Regional Observer Scheme Pilot Project training programme in key fisheries should also result in improvements to the quality of the dataset. Another possibility might be to use an alternative system whereby characteristics, rather than species, are identified and later used to determine the species based on a classification tree, as has proved successful for the IATTC (Lezama-Ochoa, M. Hall, *et al.*, 2019).

No manta rays were reported as retained by any fleet; discards comprised either devil rays or unknown species. This may be due to the greater awareness of the threats to mantas than devil rays and corresponding protective restrictions that have been put in place on manta rays ahead of devil rays in a number of countries as highlighted by Lawson et al., (2017), or it may be due to factors such as the greater size of mantas making them more difficult to handle, manoeuvre, preserve and transport if retained or the increased likelihood of damaging fishing gear, both of

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[9] https://www.iotc.org/science/species-identification-cards

which have been reported in Sri Lanka (Fernando and Stevens, 2011). Although *M. mobular* reaches a similar size to *M. alfredi* so this would also apply to large individuals of that species. Nevertheless, provided adequate enforcement is in place at the national level this distinction should not be a phenomenon in future following the regional ban on the retention of mobulids[10].

Many mobulids were released alive following capture with a smaller proportion discarded dead, however, the number of rays released for which the condition was unknown was higher than either and so no attempt was made to determine the likely mortality rate from the fisheries in this study.

Many rays that are released alive may still die due to the weak condition they may be in following poor handling practices (Poisson *et al.*, 2014; Mozzam pers. comm). There has only been one tagging study specifically evaluating the post release mortality of mobulid rays which took place in the New Zealand purse seine fishery, exclusively tagging *M. mobular* (Francis and Jones, 2017). In this experiment only three out of seven rays survived and notably all tagged rays were reported to have swum away vigorously when released showing that improved data collection on the condition of releases by observers is not necessarily a good indicator of survival. This highlights the importance of further tagging experiments, for the gillnet and longline fisheries as well as the purse seine fisheries, alongside routine data collection (Francis and Jones, 2017). While best practice handling and release guidelines have been developed for purse seine, longline and gillnet fisheries now (Poisson F., Vernet A. L., Séret B., 2012; Francis, 2014; Hutchinson, M., Poisson, F. and Swimmer, 2017; Jones and Francis, 2017; WCPFC, 2017; Carlson, John; Horn, Calusa; Creager, 2019; Martin, 2020), there needs to be further research into the efficacy of these methods through the collection of data on specific handling practices combined with satellite tagging studies across different gear types, species and sizes to review and determine which methods optimise survival (IOTC, 2018b). Nevertheless, the results from this study are in line with others that suggest the at-haulback mortality rates for mobulids appear to be relatively low (Coelho, Lino and Santos, 2011; Clavareau *et al.*, 2020) and so improved handling methods may prove successful in reducing mortality.

One of the aims of this study was to generate some specific recommendations regarding areas for data improvements to enhance monitoring and understanding of the fishery impacts to more appropriately be able to mitigate the threats to manta and devil rays. In addition to those recommendations already detailed above including species identification, some further suggestions are outlined here starting with the most efficient, lowest resource utilising activities.

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[10] IOTC Resolution 19/03 *On the conservation of mobulid rays in IOTC fisheries*

While substantial work has already been undertaken to collate and standardise the historical observer datasets that were used in this study, this work needs to be finalised to make the most of the datasets that have already been submitted to IOTC by CPCs (Table 3) and should be supported by CPCs. Improving the reporting of future datasets by submitting information on time to enable researchers to perform timely analyses, submitting data in the correct electronic format to prevent transcription errors from occurring and reporting data of good quality, at the required level of resolution, without crucial gaps (e.g. unique identifiers to link sets and trips) is important. Increasing the level of observer coverage or introducing this for key fleets is also critical and is currently being supported by the ROS Pilot Project capacity building programme (IOTC, 2019b). This is particularly necessary when exploring trends in interactions with rare event species. Standardising the reporting of future data should be prioritised by observer programmes in the region. Data should be reported based on the requirements agreed in 2019 (IOTC, 2019a) in terms of both the data fields and format of reporting with consistent use of categories and codes. For particular tagging projects, a standardised tagging card should be produced (Bach *et al.*, 2018) containing standardised information on release methods through coordination with other tRFMOs so that datasets can be pooled.

This study presents the first analysis of mobulid interactions with tuna and tuna-like fisheries in the Indian Ocean at a regional scale presenting information from a wide range of different fleets in the most comprehensive analysis of mobulid bycatch so far in an area which has been notoriously data poor. Through the use of fisheries-dependent information this study advances our understanding of spatial and temporal dynamics in the mobulid bycatch of fisheries for tuna and tuna-like species in the Indian Ocean. Despite the many caveats and biases associated with the dataset, it provides a valuable source of information for these fisheries at an ocean basin level, the scale at which a highly mobile species like these need to be assessed and managed.

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Tables

Table 1. Mobulid species occurring in the Indian Ocean

Code	Common name	Latin name (previously)	Maximum length (cm)[11]	Common length (cm)	Length at maturity (cm)
RMB	Giant oceanic manta ray	*Mobula (Manta) birostris*	910	450	400[12]
RMA	Alfred manta (reef manta ray)	*Mobula (Manta) alfredi*	500	-	270-350[13]
RMM (RMJ)	Spinetail/giant devil ray	*Mobula mobular*[14]	520 (310)	(225)	200-240[15]
RMT	Chilean devilray (sicklefin devilray)	*Mobula tarapacana*	305	250	198-250[16]
RMO	Smoothtail mobula (Bentfin devilray)	*Mobula thurstoni*	220	150	150-163[17]
RMK (RME)	Shortfin pygmy devil ray	*Mobula kuhlii*[18]	120	-	115-119[19]
MAN/AG30	Mantas, devil rays nei	*Mobula (Mobula and Manta)*	-	-	
MNT/AG70	Manta rays	*M.birostris and M.alfredi (Manta spp.)*	-	-	
RMV/AG71	Devil rays	*All others not included in MNT (Mobula spp.)*	-	-	

Table 2. List of target species and common weights used for conversions

Gear	Species	Common weight used in this study (kg)	Method and reference
All	Albacore	14.2	Catch-and-effort data provided by Taiwan,China (2005-2017 reported in both numbers and weight used to calculate average weight (IOTC-2019-WPTmT07-DATA04-CELL)
All	Swordfish	60	Common weight at capture from IOTC Species Executive Summary Supporting Information
LL	Yellowfin tuna	45	IOTC Species Executive Summary Supporting Information (2005-2018)
PS	Yellowfin tuna	8.8	Weighted average of log school and unassociated catch mean weights
All	Skipjack tuna	3.0	IOTC Species Executive Summary Supporting Information
LL	Bigeye tuna	50	IOTC Species Executive Summary Supporting Information (2005-2018)
PS	Bigeye tuna	4.6	Weighted average of log school and unassociated catch mean weights

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[11] Lengths taken from Fishbase.org

[12] Marshall et al., 2018

[13] Marshall, Barreto, Carlson et al 2019

[14] Including the junior synonym *Mobula japanica*

[15] Marshall, Barreto, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Rigby and Romanov, 2019

[16] Marshall, Barreto, Bigman, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Pardo, Rigby, Romanov and Walls, 2019.

[17] Marshall, Barreto, Bigman, Carlson, Fernando, Fordham, Francis, Herman, Jabado, Liu, Pardo, Rigby, Romanov, Smith et al., 2019.

[18] Including the junior synonym *Mobula eregoodootenkee*

[19] Bizzarro et al., 2009.

All	Kawakawa	1.09	Average length at capture IOTC Species Executive Summary Supporting Information (40cm) L-W relationship from Fishbase.org
All	Narrow-barred Spanish mackerel	4.5	Average length at capture IOTC Species Executive Summary Supporting Information (85cm) L-W relationship from Fishbase.org
All	Longtail tuna	2.6	Average length at capture IOTC Species Executive Summary Supporting Information (60cm) L-W relationship from Fishbase.org

Table 3. Observer data included in this study (total of >1512 trips)

CPC	Gear	Years	Number of trips	Source	% fleet coverage[20]
Australia	LL	2010	2	Collated from individual word.docx and excel.xlxs	7.84
		2011	1		
		2012	3		
		2014	6		
		2015	11		
		2016	28		
		2017	0		
Taiwan,China	LL	2013	19	Collated from individual .pdf documents	2.27
		2014	18		
		2015	26		
		2016	18		
		2017	20		
		2018	5		
EU,France	LL	2009	4	ROS database	14.59
		2010	6		
		2011	42		
		2012	85		
		2013	82		
		2014	75		
		2015	86		
		2016	50		
		2017	61		
		2018	46		
EU,FRA	PS	2005	1	ROS database	23.19
		2006	8		
		2007	11		
		2008	13		
		2009	3		
		2011	3		
		2012	7		
		2013	10		
		2014	41		
		2015	49		
		2016	56		
		2017	56		
		2018	60		
EU,ESP	PS	2015 - 2016	1	ROS database	3.92
		2016	15		

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[20] Average last 5 years from IOTC-2019-SC22-07

EU,PRT	LL	2011 2012 2013 2014 2015 2016 2017 2018	1 1 1 1 1 1 1 1	Collated from .pdf and excel.xlxs docs	9.94
EU,UK	LL	2018	2	Collated from excel.xlxs docs	1.55
Indonesia	LL	2014 2016 2017 2017-2018	5 4 2 1	Collated from excel.xlxs docs	0.46
Japan	LL	2012 2013 2014 2015 2016	10 8 12 12 9	ROS database	-
Korea	LL	2012 2013 2014 2015 2016 2017	2 2 1 3 3 1	Collated from word.docs	3.63
Korea	PS	2013 2014 2015 2016	1 2 1 2	ROS database	13.58
Mauritius	PS	2015 2016 2017	5 8 4	ROS database	23.59
Pakistan	GN	2013 2014 2015 2016 2017	-	Collated from excel.xlxs docs provided by WWF-Pakistan	-
Seychelles	PS	2014 2015 2016 2017 2018 2019	7 66 63 91 83 44	ROS database	30.31
South Africa	LL	2016 2017	5 8	Collated from .docs and .pdf documents	-
Sri Lanka	LL	2017 2018 2019	2 4 3	ROS database and collated from excel.xlxs docs	0.08

Table 4. Catches of mobulids and target species by year throughout the study period. Columns highlighted in light grey are based on observer data used in this study and columns highlighted in dark grey are the total catches of target for the fleets included in this study and all fleets operating in the Indian Ocean based as reported by IOTC in 2019[21]

Year	Mobulids (no.)	Target catch (no.)	Mobulids (kg)	Target catch (kg)	Total Indian Ocean target catches for fleets included study (t)	Observer coverage of fleets in study (%)	Total Indian Ocean target catches for all fleets (t)	Percentage of total IO target catch represented in this study
2005	0	74	0	222	106,957	0.0002%	1,563,890	0.0000%
2006	0	196	0	1,231	98,558	0.0012%	1,561,432	0.0001%
2007	7	2,574	5,868	12,109	69,535	0.0174%	1,355,361	0.0009%
2008	0	3,202	0	17,311	74,909	0.0231%	1,306,024	0.0013%
2009	4	2,793	606	47,609	56,940	0.0836%	1,287,589	0.0037%
2010	1	1,718	1,131	81,988	455	18.0085%	1,290,415	0.0064%
2011	22	6,932	11,165	290,597	44,093	0.6591%	1,331,644	0.0218%
2012	20	28,568	6,643	920,626	51,634	1.7830%	1,414,703	0.0651%
2013	56	282,263	9,141	2,584,834	170,606	1.5151%	1,487,960	0.1737%
2014	46	430,660	11,904	3,999,341	305,101	1.3108%	1,461,306	0.2737%
2015	65	546,680	12,845	4,294,573	286,340	1.4998%	1,424,507	0.3015%
2016	60	3,696,091	15,958	18,303,196	513,341	3.5655%	1,500,252	1.2200%
2017	156	861,751	21,857	5,308,636	365,835	1.4511%	1,529,151	0.3472%
2018	175	93,736	69,141	1,631,962	304,301	0.5363%	1,657,809	0.0984%
2019	2	3,224	1,203	40,376	N/A	N/A	N/A	N/A
Total	**614**	**5 960 463**	**167 463**	**37 534 609**	**2,448,604**		**20,172,042**	

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[21] IOTC-2019-WPTT21-DATA03-NC: https://www.iotc.org/WPTT/21/Data/03-NC

Table 5. Total number of mobulids observed by fleet and year. Blank cells indicate years in which no observer data were used in this study.

FLEET	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
GN-PAK									3	15	12	8	7		
LL-AUS						1	1	0		4	0	0	0		
LL-EU.FRA					1	0	5	2	1	2	0	5	8	20	
LL-EU.PRT							15	16	47	1	0	0	7	115	
LL-EU.UK													0		
LL-IDN										2		0	0	0	
LL-JPN								1	1	3	0	1			
LL-KOR								0	0	0	3	1	0		
LL-LKA													89	3	0
LL-TWN,CHN									0	0	0	0	5	1	
LL-ZAF[22]												2	4		
PS-EU.ESP												4			
PS-EU.FRA	0	0	7	0	3		1	1	4	17	32	20	8	18	
PS-KOR									0	1	0	0			
PS-MUS											4	3	0		
PS-SYC										1	13	16	28	18	2

Table 6. Catch rates (number of mobulids per 100 tonnes of target species) by fleet.

	Gillnet	Longline	Purse seine
Sri Lanka		107.28	
South Africa		28.22	
EU, Portugal		21.71	
Pakistan	5.94		
Australia		2.97	
Indonesia		2.47	
EU, France		1.87	not calculated[23]
Rep. Korea		0.88	0.02
South Africa-Japan[24]		0.55	
Japan		0.20	
Taiwan, China		0.11	
Mauritius			0.08
EU, Spain			0.04
EU, UK		0.00	
Seychelles			not calculated

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[22] Including all captures reported by ZAF observers on JPN-flagged vessels

[23] Incomplete target species captures provided by PS-EU.France and PS-Seychelles

[24] For the purposes of this table the South African chartered Japanese flagged vessels were kept separate rather than combined with the rest of the South African fleet due to differences in operations

Table 7. Annual interactions by species

Year	*Mobula* spp.	Manta rays	Devil rays	*M. mobular*	*M. birostris*	*M. alfredi*	*M. kuhlii*	Total
2007				2	5			7
2009				3		1		4
2010					1			1
2011	15			1	6			22
2012	14		1	3	2			20
2013	3	1	1	48	3			56
2014	15		8	12	9	1	1	46
2015	15		28	17	5			65
2016	13		15	21	11			60
2017	14	2	21	113	6			156
2018	2	115	9	41	7	1		175
2019			1		1			2
Total	91	118	84	261	56	3	1	614

Figures

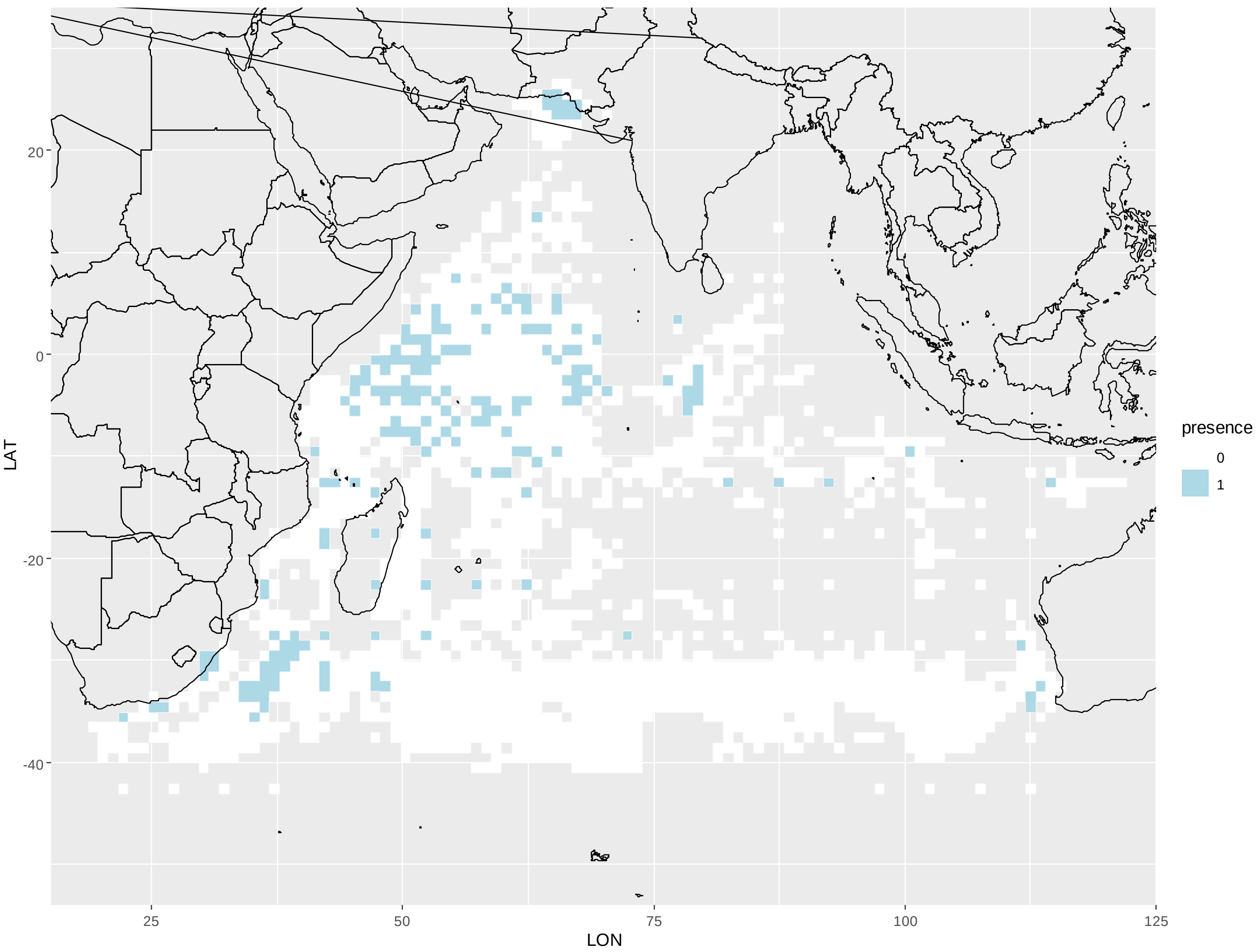


Figure 1. Presence and absence of reported mobulids across all fleets and years (2007-2019). NB for the few fleets that reported at a resolution of 5x5 degrees, the central grid cell was plotted in order to combine all data onto a single map for visualisation purposes (resulting in a few data points that appear to be on land when plotted).

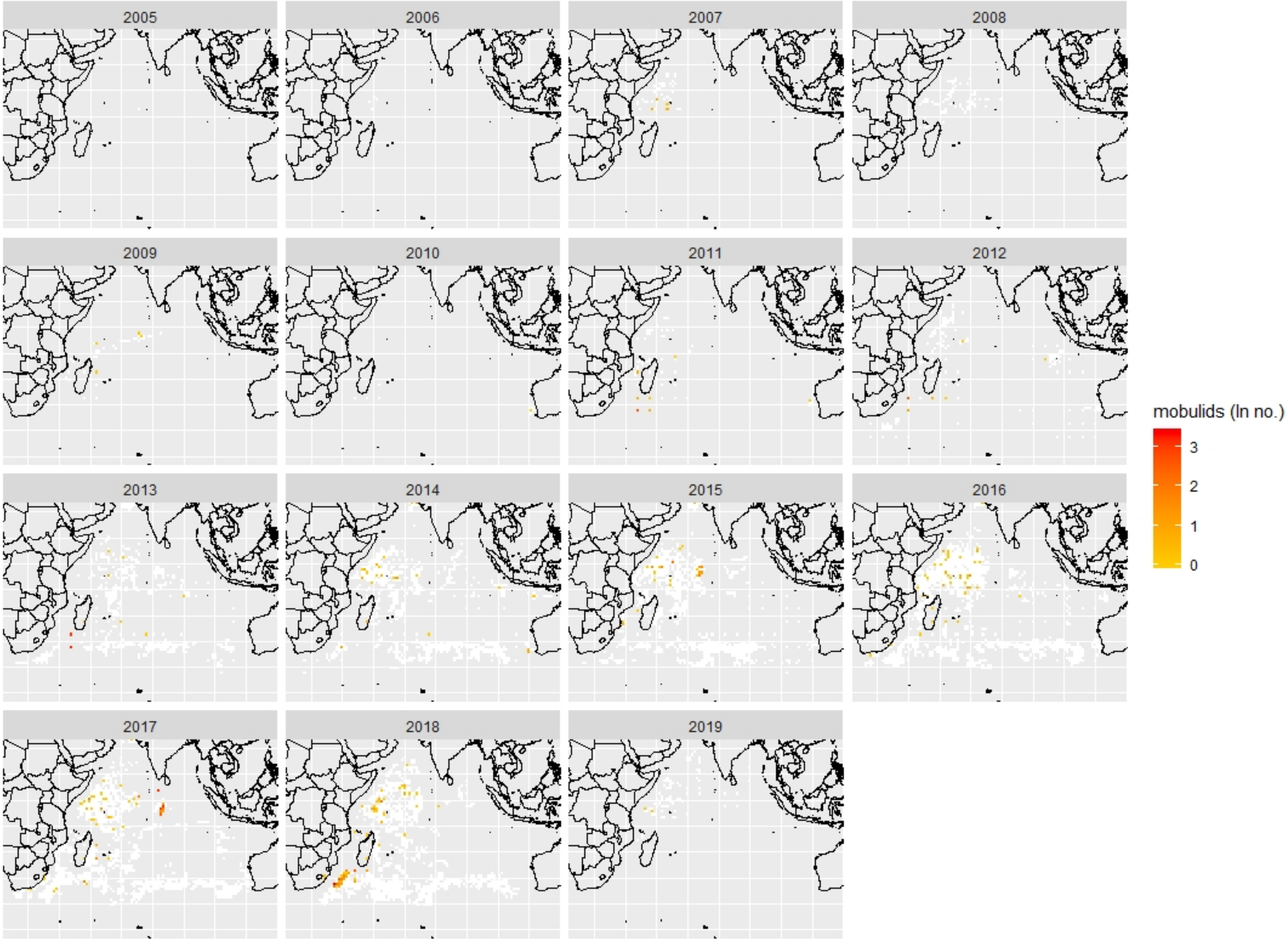


Figure 2. Number of mobulid captures observed by year across all fleets (log scale).

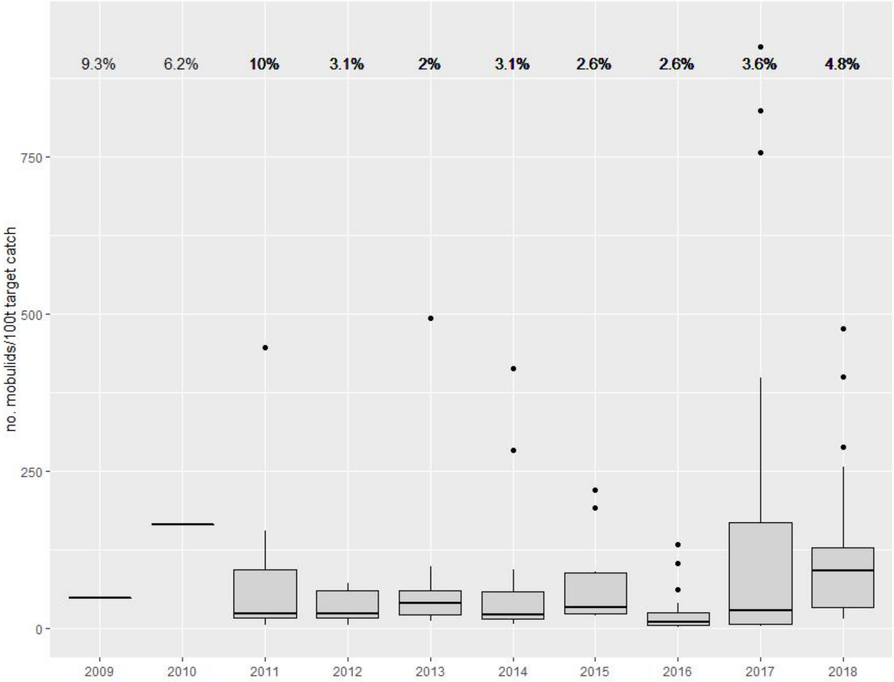
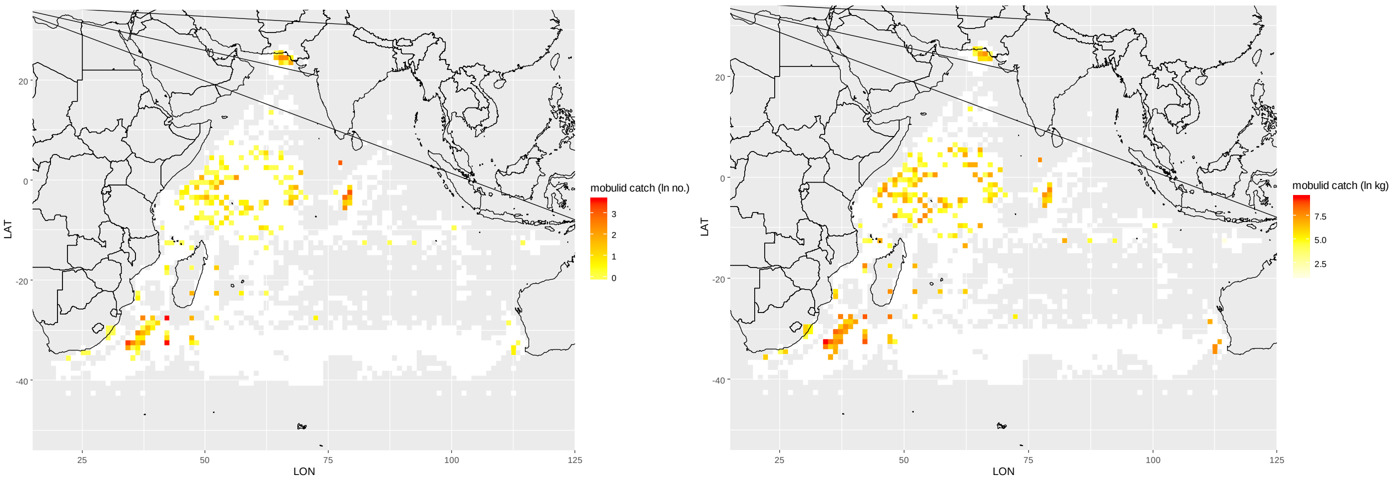
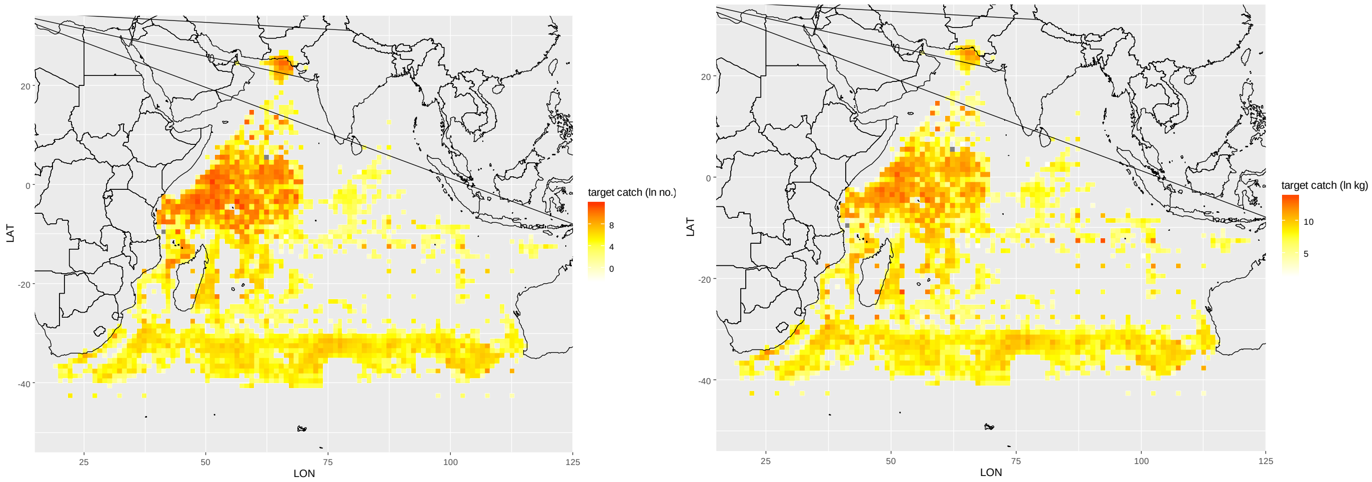


Figure 3. Positive catch rates (numbers of mobulids per 100 tonnes target catch) and percentage of positive mobulid catches by year per {fleet, month, grid cell combination}. Five outliers removed from 2017 and one from 2015. EU.FRA-PS and EU.SYC-PS not included in plot.



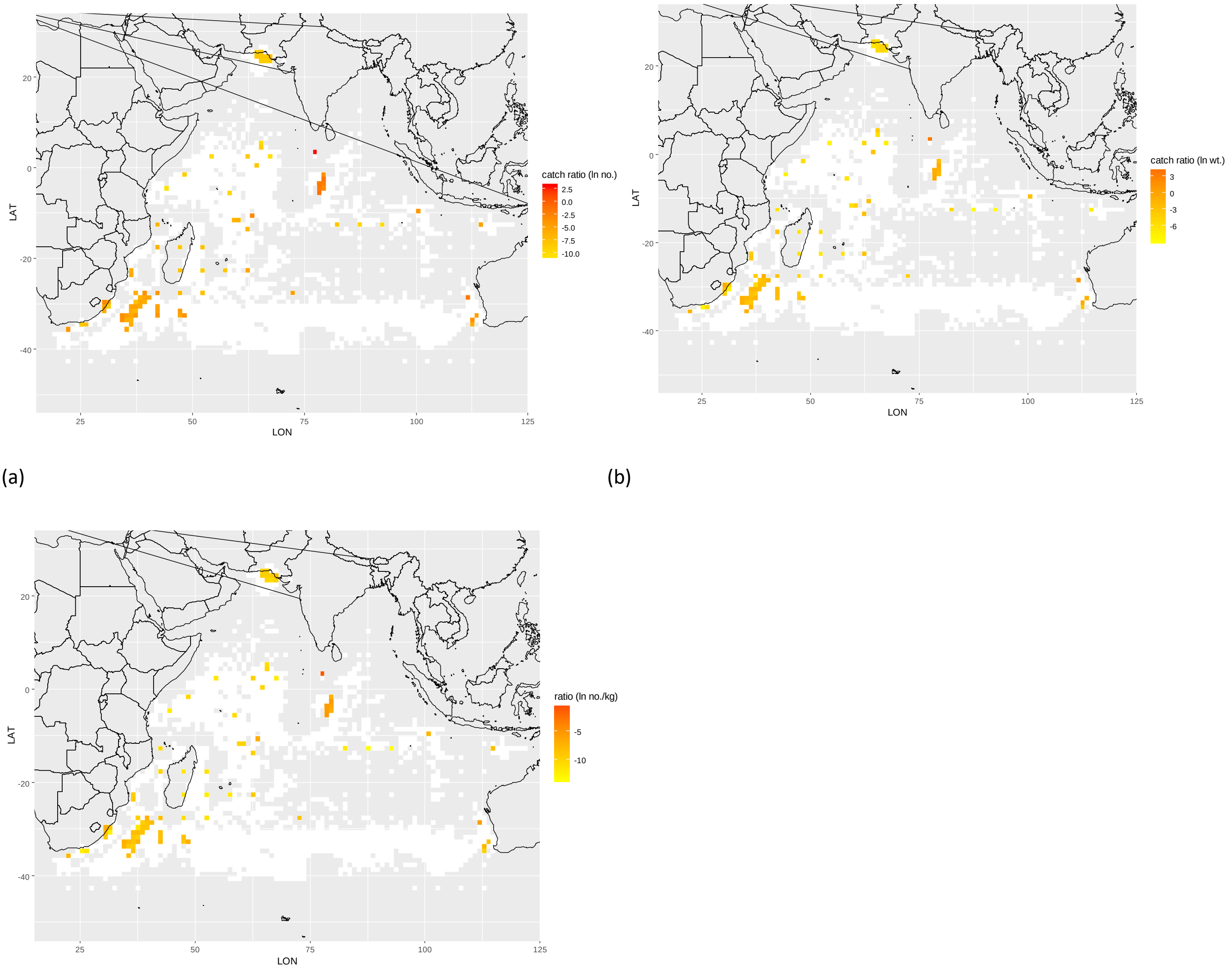
(a) (b)

Figure 4. Reported total numbers (a) and weight (b) of mobulids (log scale)



(a) (b)

Figure 5.Reported total catches of target species (a) numbers, (b) weight (log scale)



(a)

(b)

(c)

Figure 6. Catch rates of mobulids in numbers of individuals (a), and weights (b), and individuals per kg (c) on a log scale. EU.FRA-PS and SYC-PS excluded.

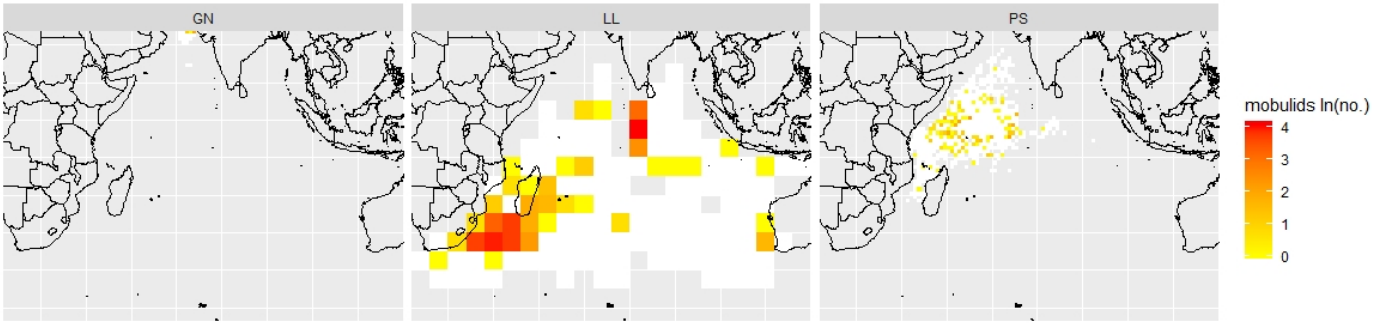


Figure 7. Number of mobulids reported by gear type across all fleets (log scale) at a resolution of 1x1 degree grid cells for surface fisheries and 5x5 for longline fisheries across all years

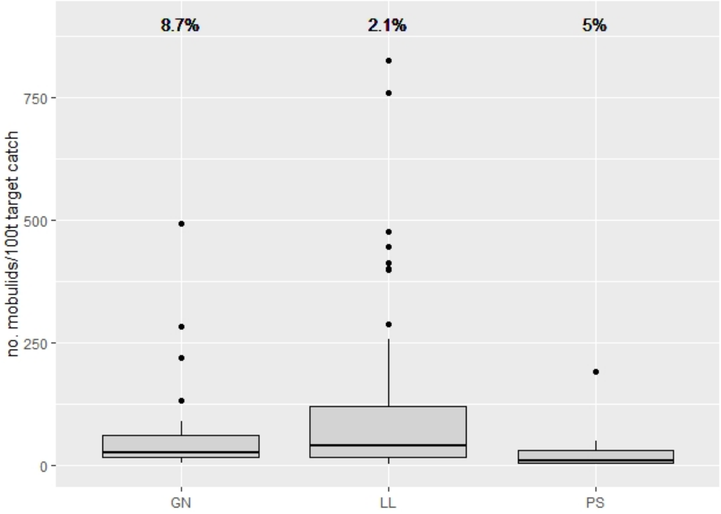


Figure 8. Positive catch rates (numbers of mobulids per 100 tonnes target catch) and percentage of positive mobulid catches by gear per {year, fleet, month, grid cell combination}. Five outliers removed from LKA-LL 2017, one from PAK-GN and one from ZAF-LL. EU.FRA-PS and EU.SYC-PS not included in plot.

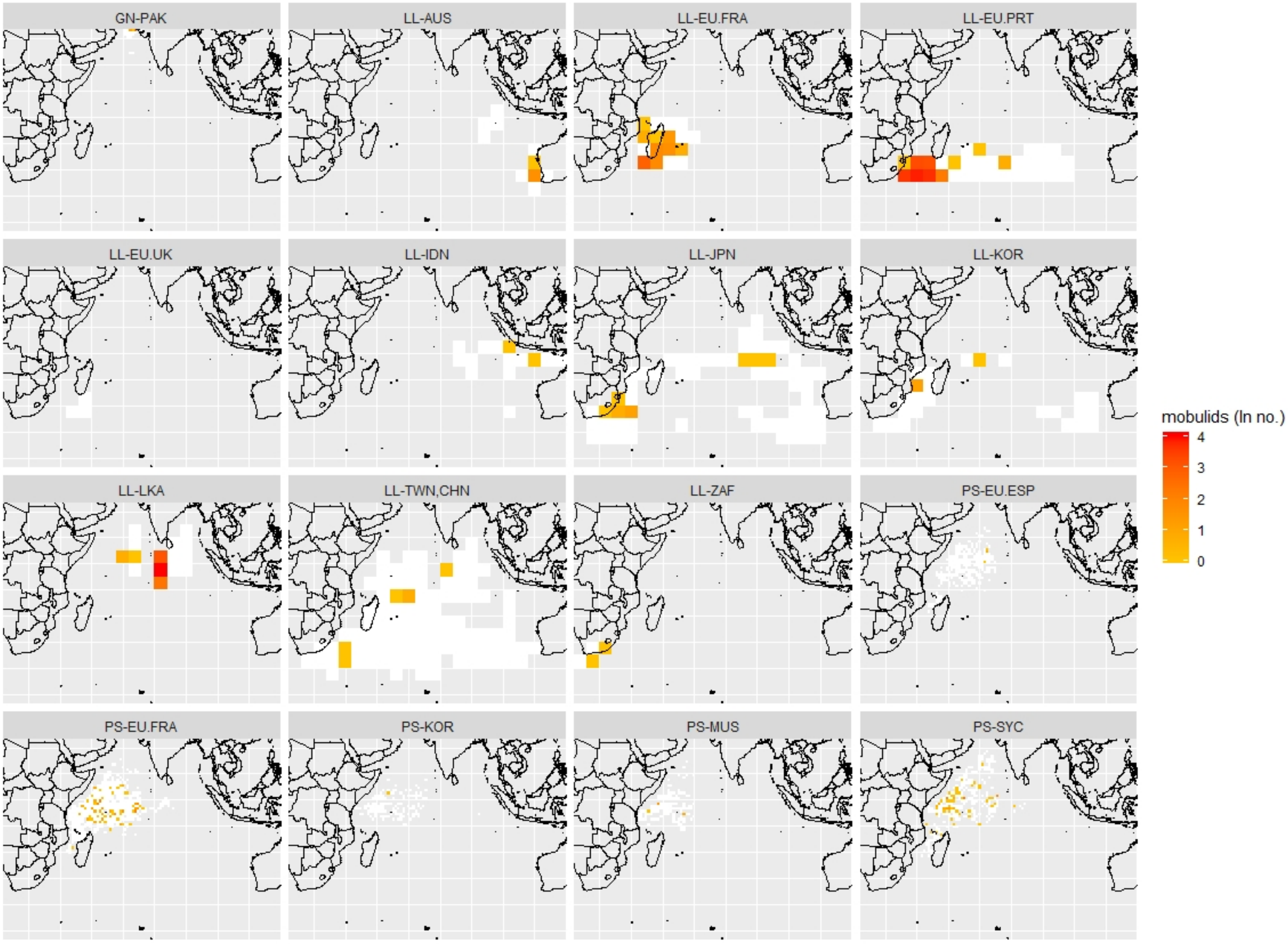


Figure 9. Number of mobulids reported by fleet (log scale) at a resolution of 1x1 degree grid cells for surface fisheries and 5x5 for longline fisheries across all years

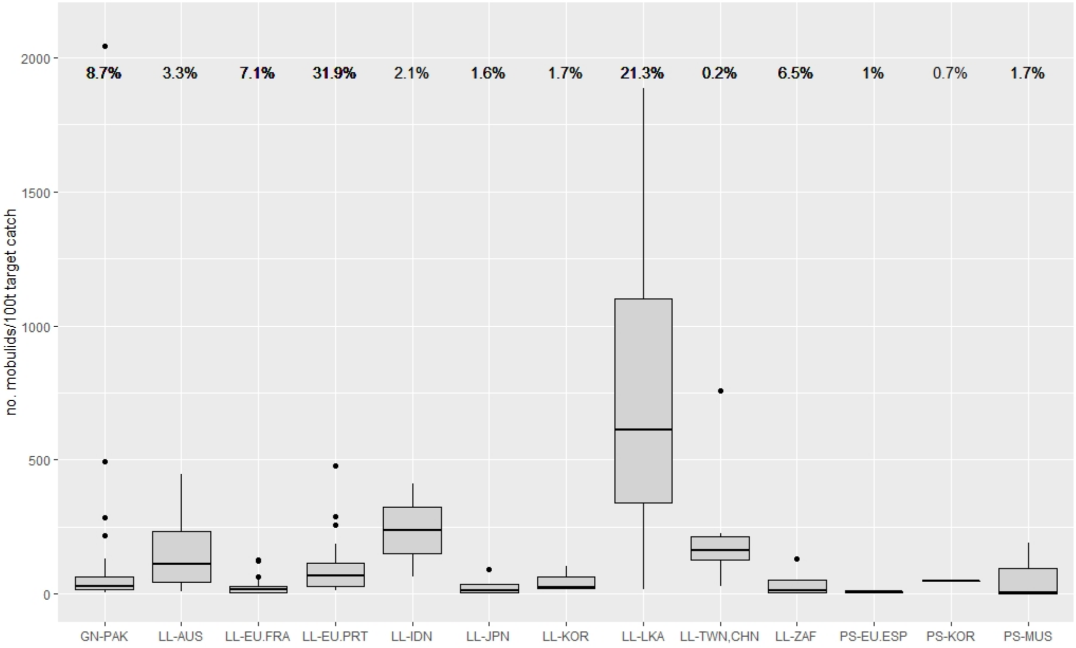


Figure 10. Positive catch rates (numbers of mobulids per 100 tonnes target catch) and percentage of positive mobulid catches by fleet per {year, month, grid cell combination}. Two outliers removed for LL-LKA and one for LL-ZAF. Two infinite values removed (EU.PRT and ZAF) EU.FRA-PS and EU.SYC-PS removed from the plot.

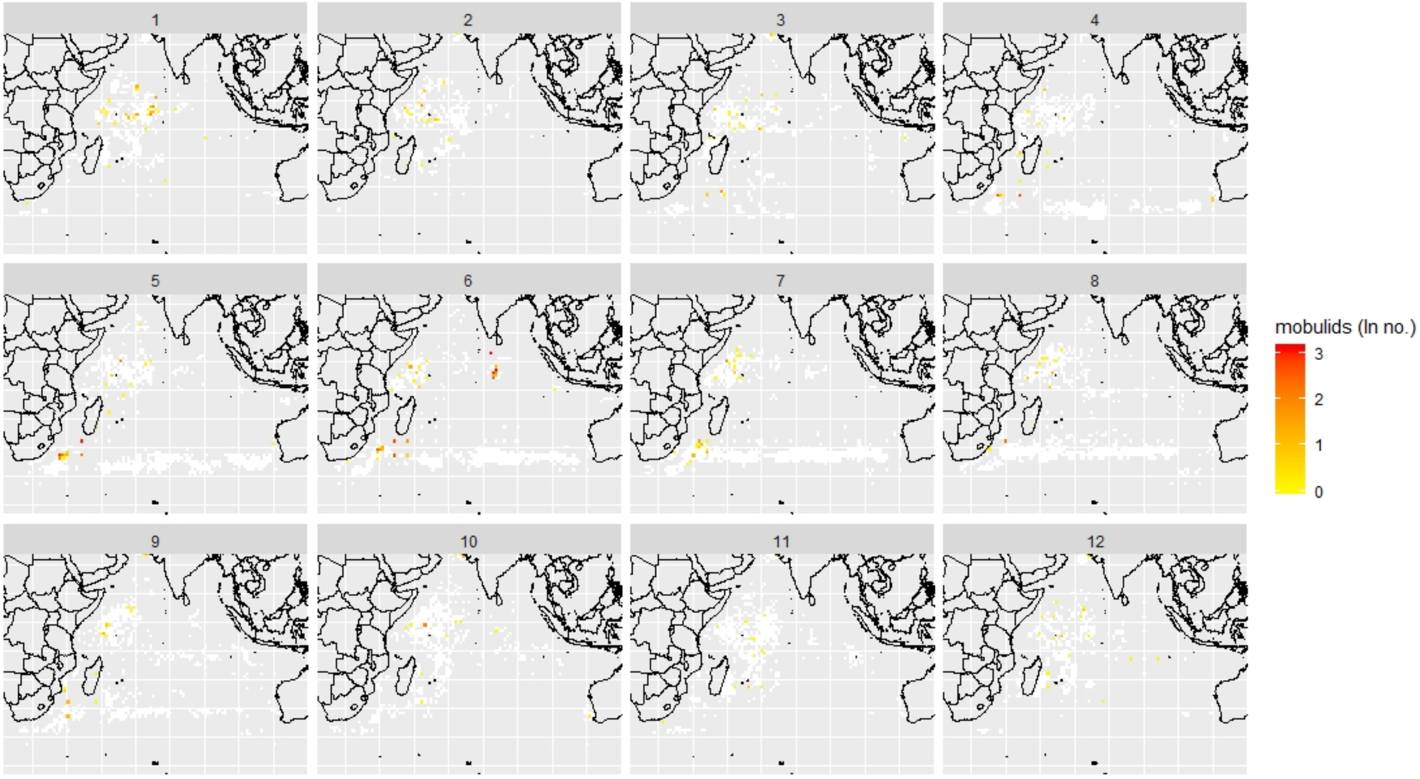


Figure 11. Mobulid catches by season (log scale) across all fleets and years.

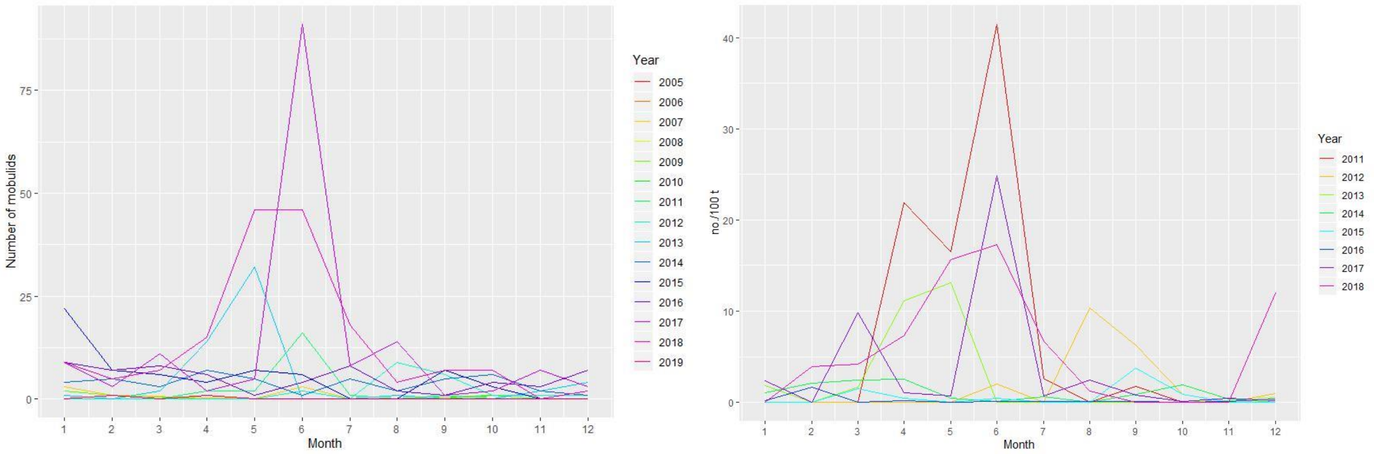


Figure 12. Seasonal mobulid interactions in numbers (a) and seasonal catch ratios (PS-SYC and PS-FRA excluded with years 2005-2010 and 2019 with very few resulting data points) (b)

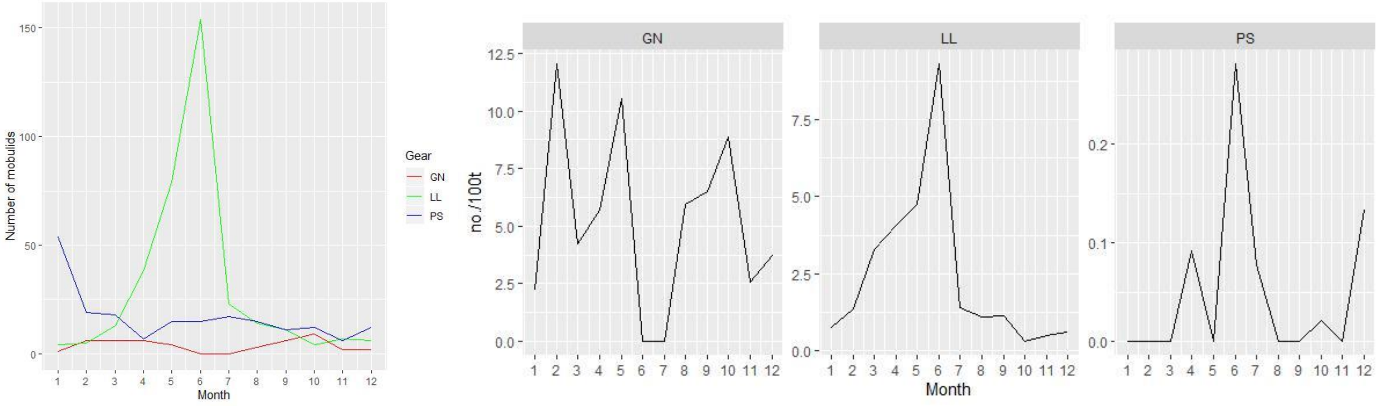
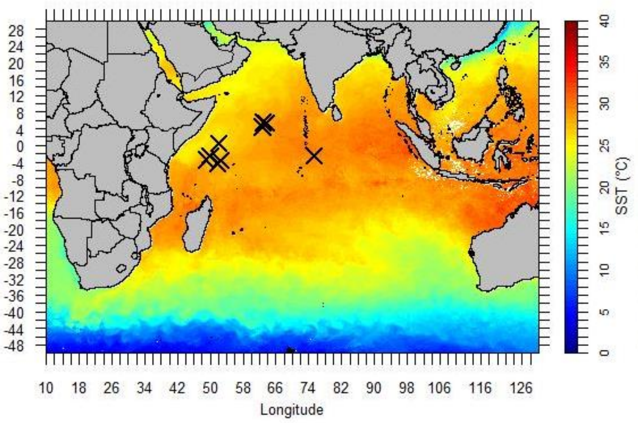


Figure 13. Seasonal mobulid catches in (a) numbers by gear type, and (b) as catch ratios (numbers per 100 tonnes target catch). NB PS-SYC and PS-EU.FRA not included in catch ratios.



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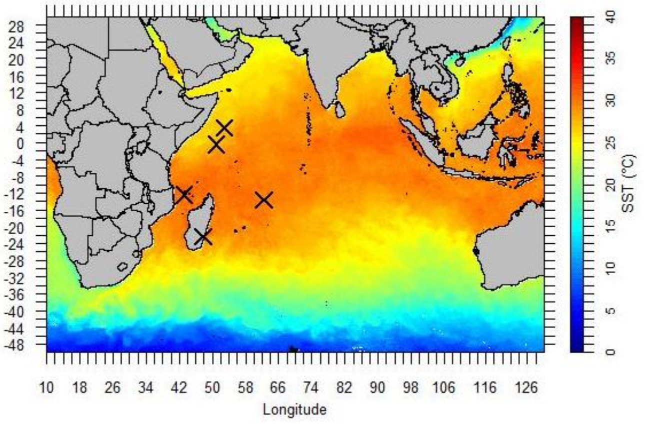
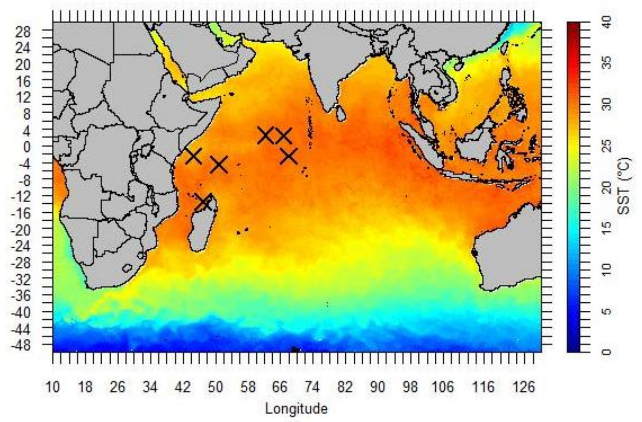
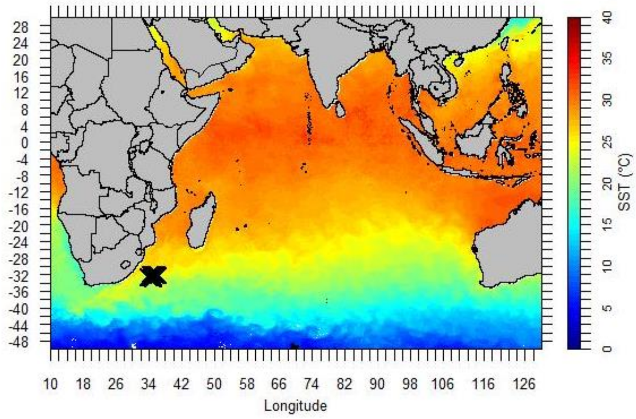


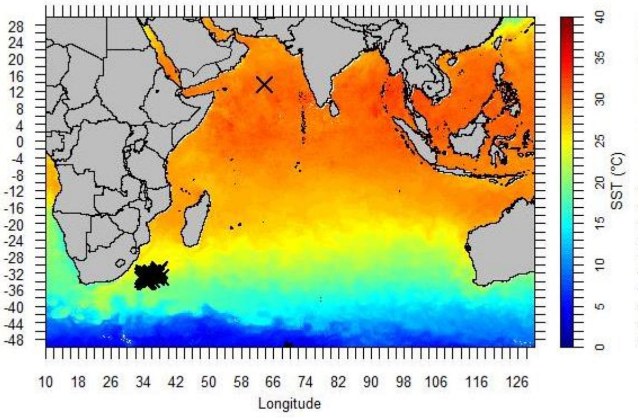
n = 5 Feb 2018



5 n = 7 Mar 2018



8 n = 15 Apr 2018



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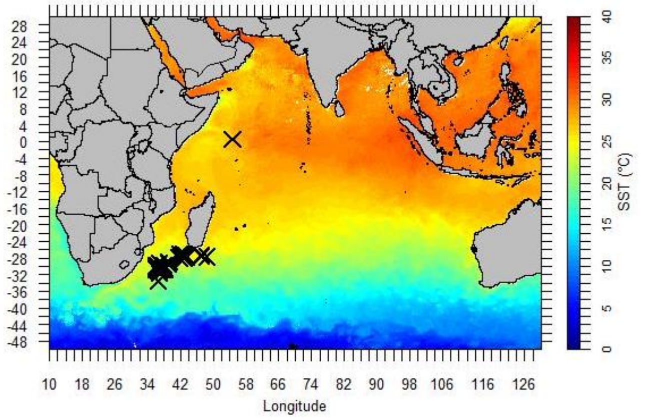
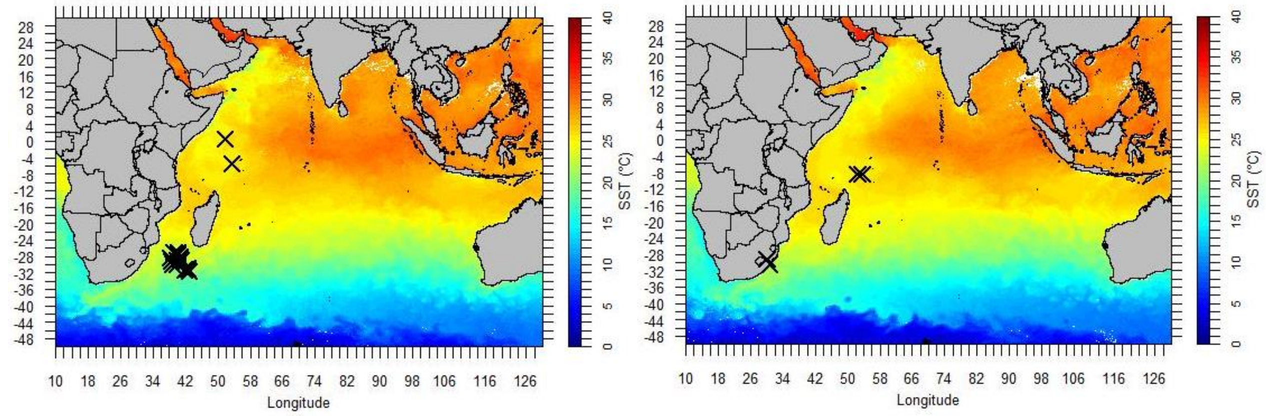


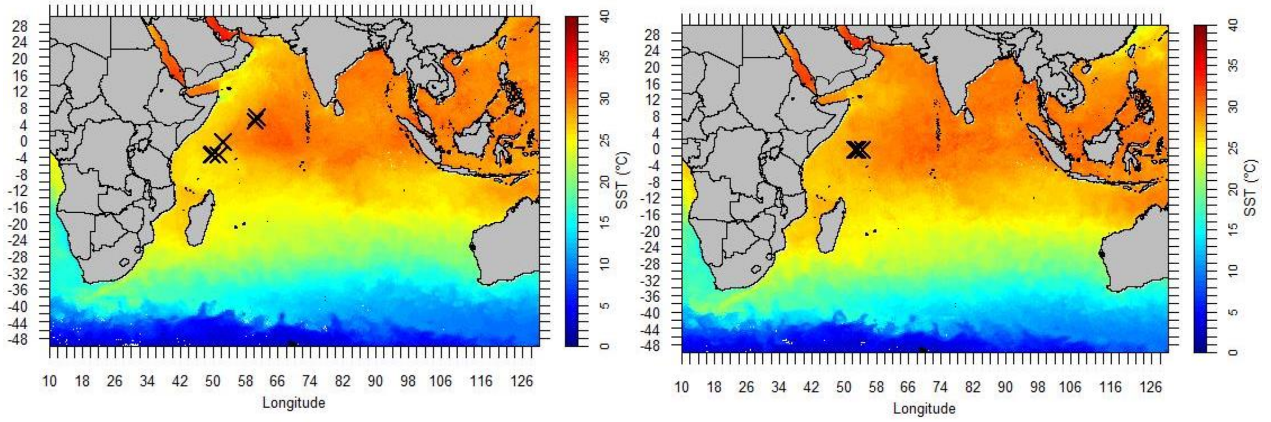
n = 46 Jun 2018



9

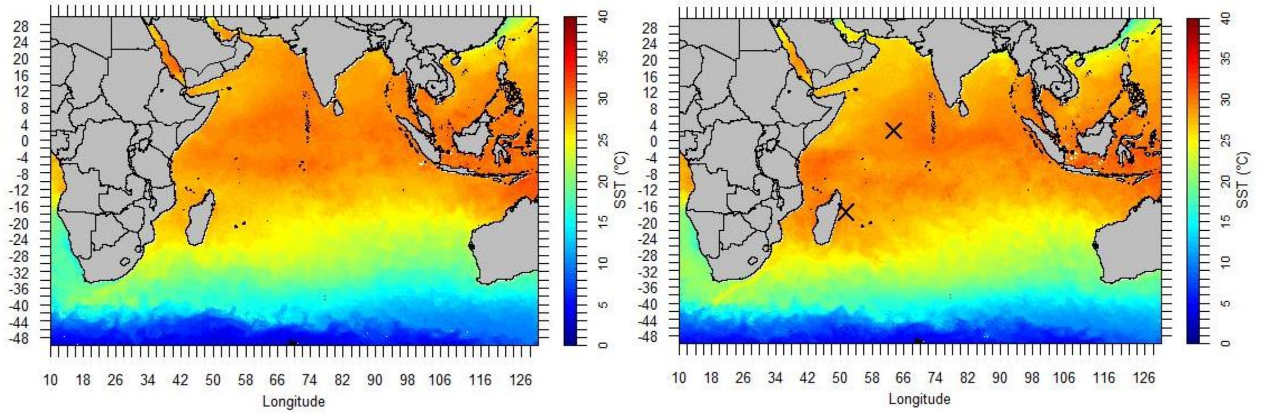
n = 18 Jul 2018

n = 4 Aug 2018



n = 7 Sep 2018

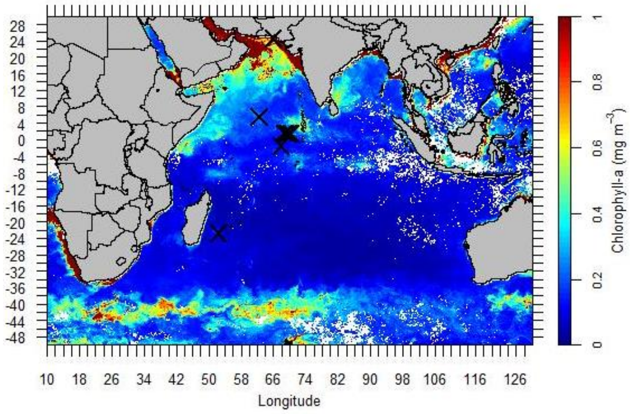
n = 7 Oct 2018



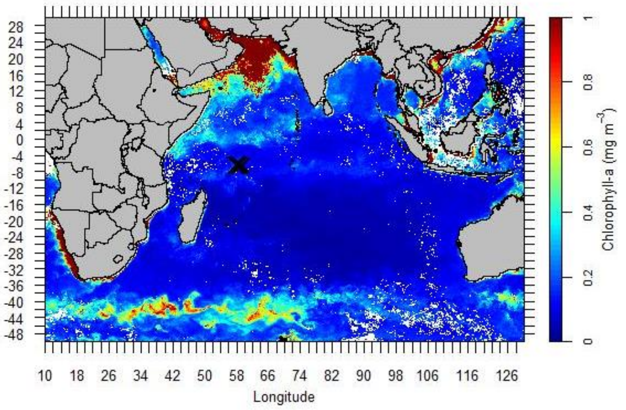
n = 0 Nov 2018

n = 2 Dec 2018

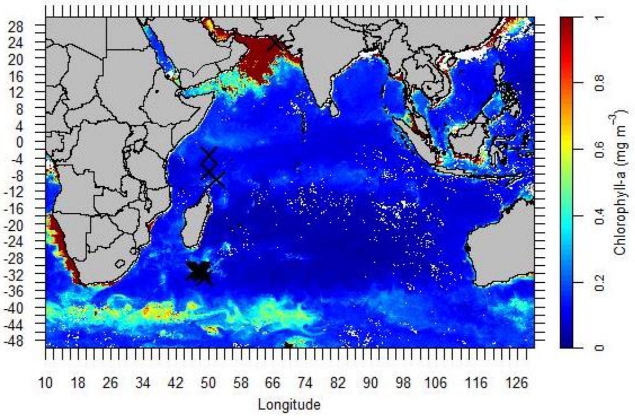
Figure 14. Mobulid catches (black crosses) and sea surface temperature by month, 2018.



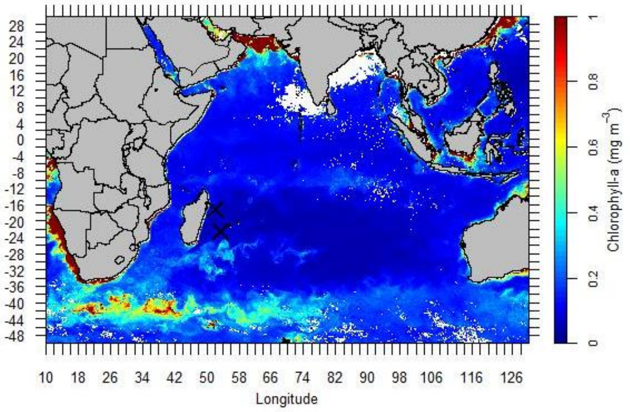
n = 9 Jan 2017



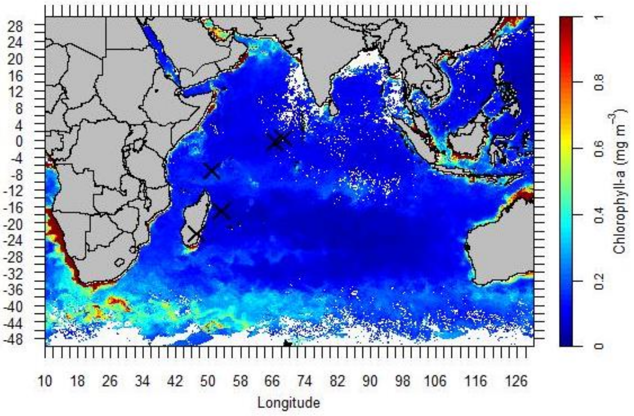
n = 3 Feb 2017



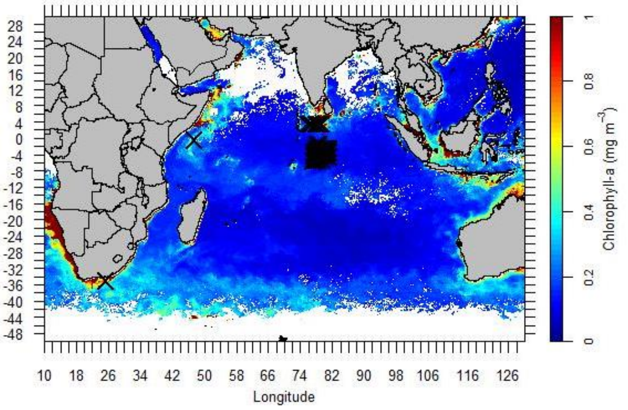
n = 11 Mar 2017



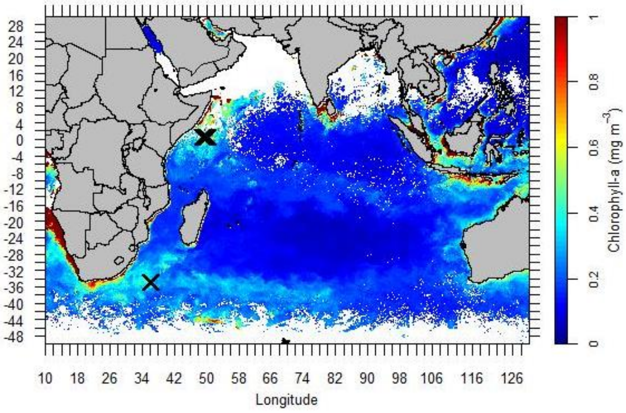
n = 2 Apr 2017



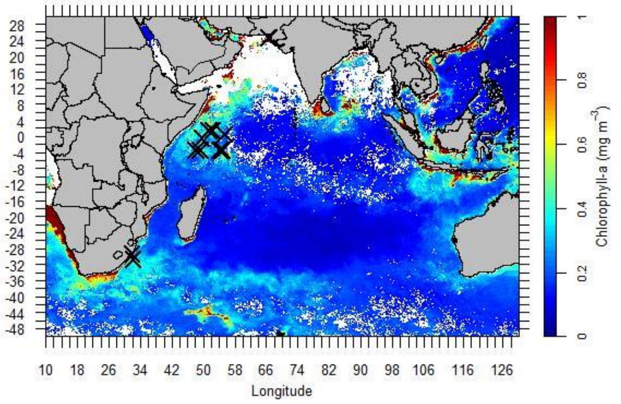
n = 5 May 2017



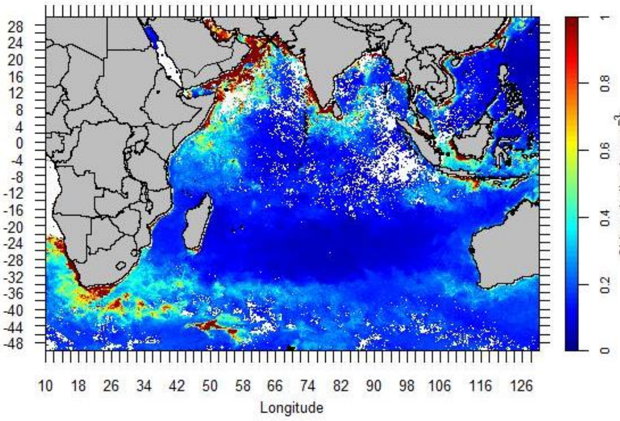
n = 91 Jun 2017



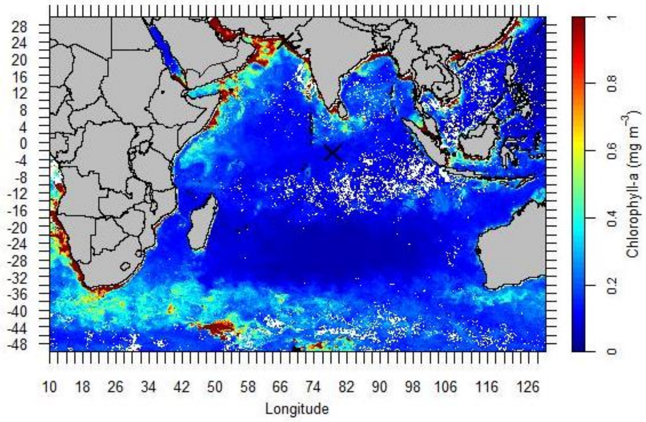
n = 8 Jul 2017



n = 14 Aug 2017



n = 1 Sep 2017



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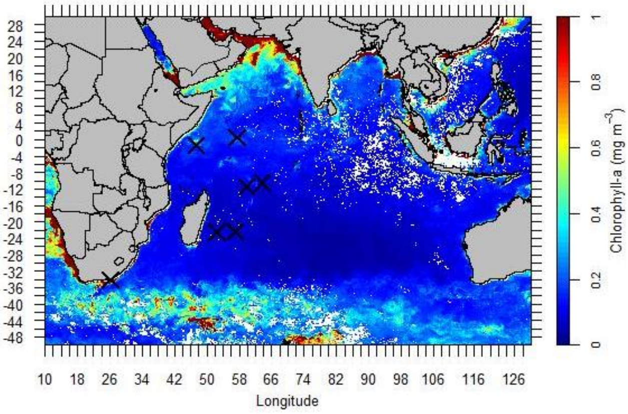
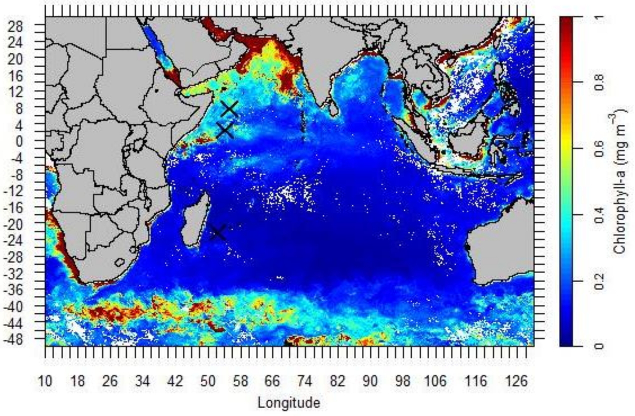
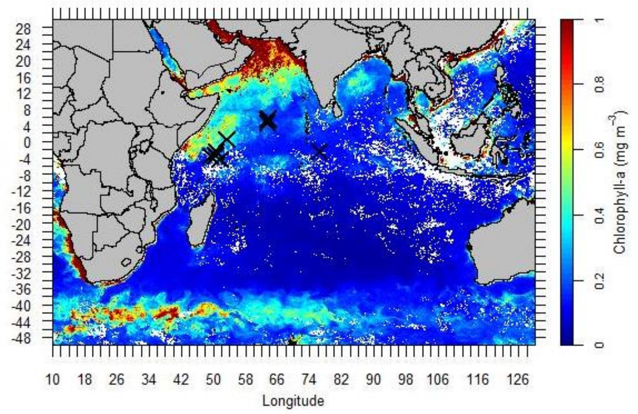


n = 7 Nov 2017

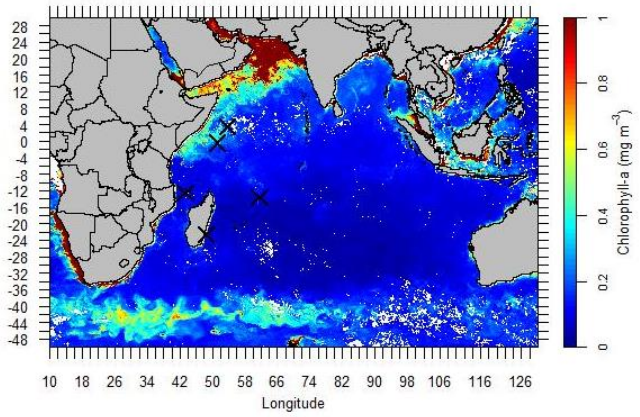


n = 3 Dec 2017

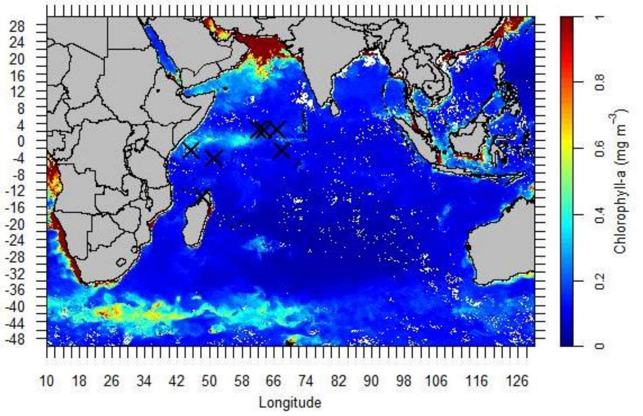
Figure 15. Mobulid catches (black crosses) and Chl-a concentration by month, 2017.



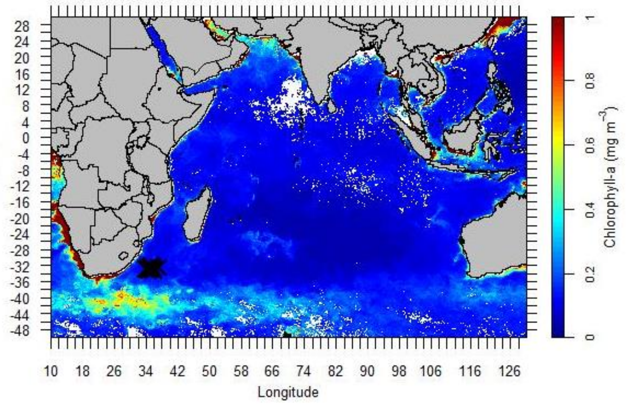
n = 9 Jan 2018



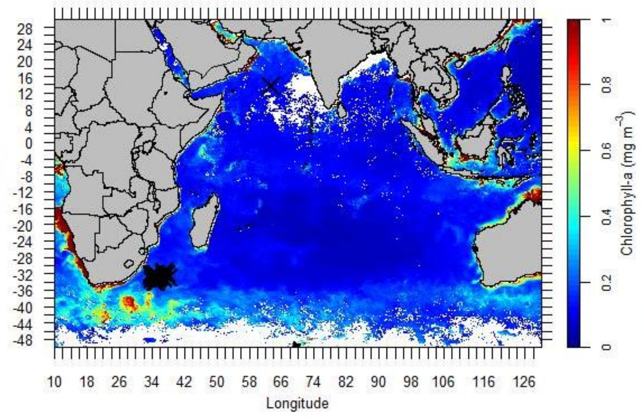
n = 5 Feb 2018



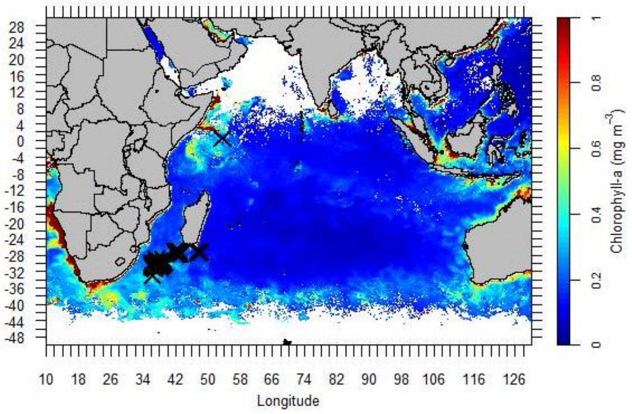
n = 7 Mar 2018



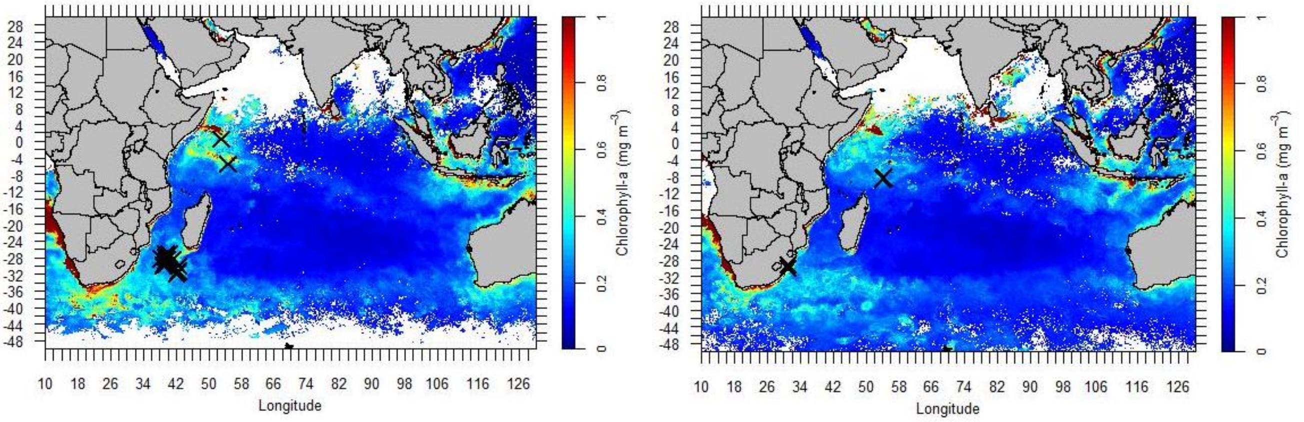
n = 15 Apr 2018



n = 46 May 2018

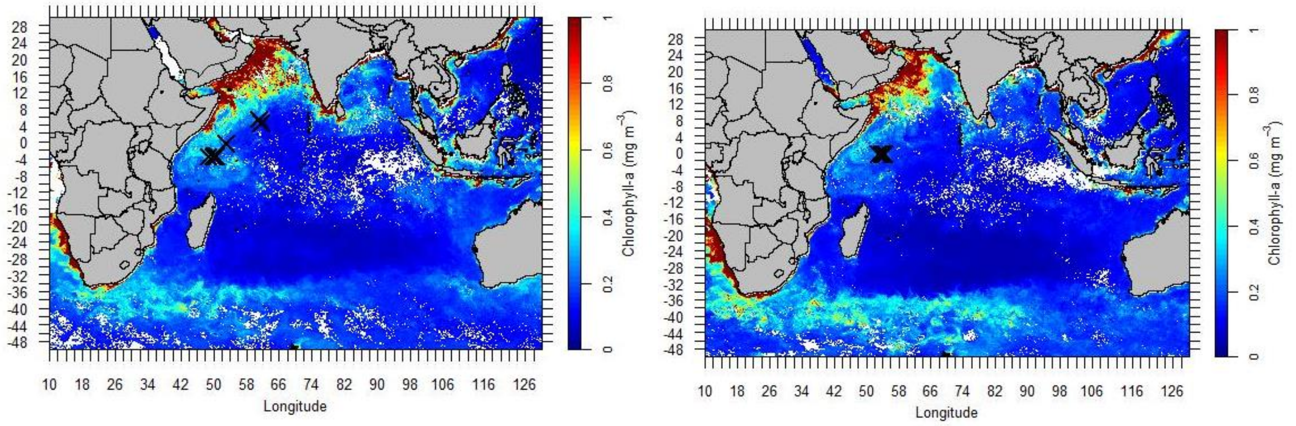


n = 46 Jun 2018



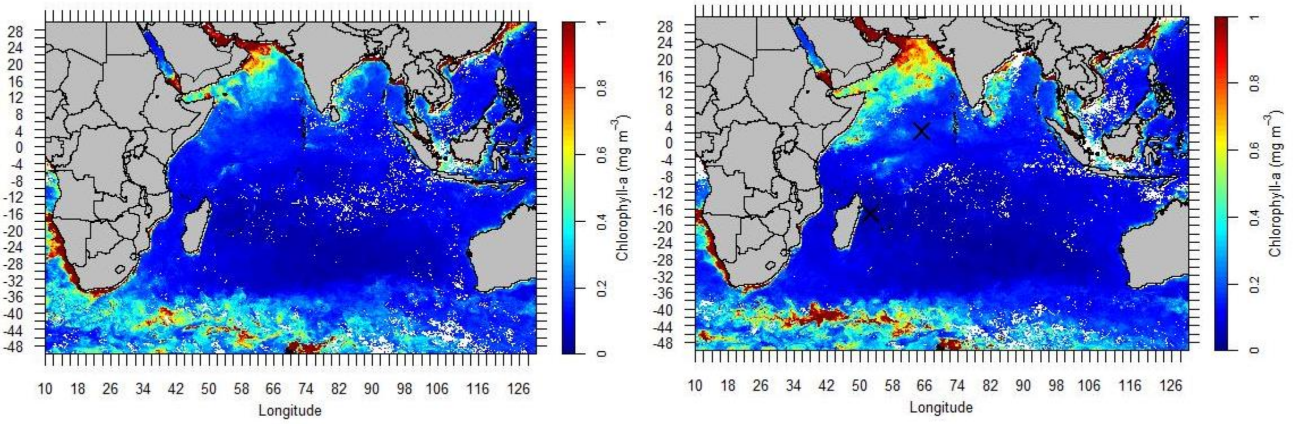
n = 18 Jul 2018

n = 4 Aug 2018



n = 7 Sep 2018

n = 7 Oct 2018



n = 0 Nov 2018

n = 2 Dec 2018

Figure 16. Mobulid catches (black crosses) and Chl-a concentration by month, 2018.

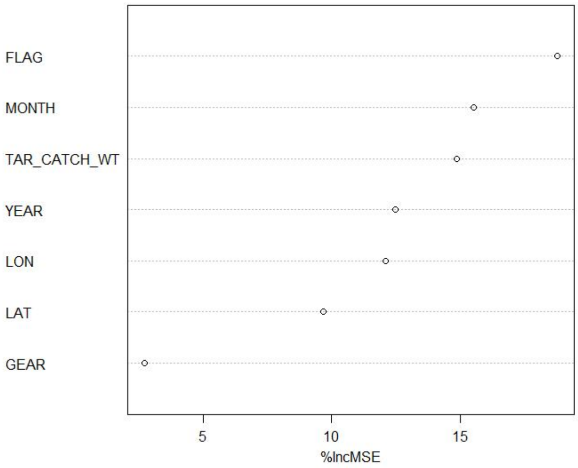
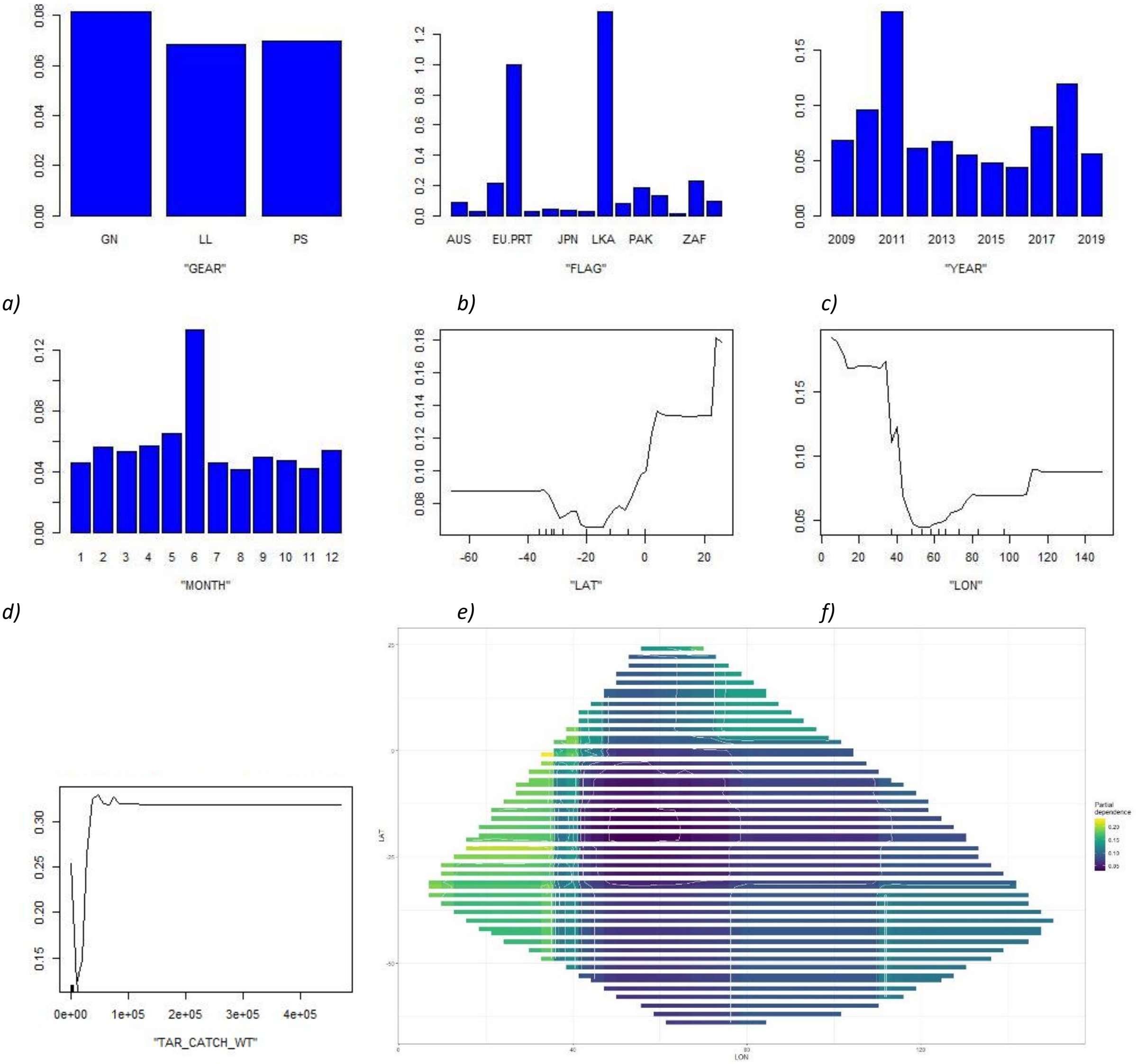


Figure 17. Importance of explanatory variables used in the random forest model



a)

b)

c)

d)

e)

f)

g)

h)

Figure 18. Partial dependence plots showing the marginal effects of all variables included in the random forest model on predicted mobulid captures: (a) gear (b) flag (c) year (d) month (e) latitude (f) longitude (g) weight of target catch and (h) latitude and longitude plotted together.

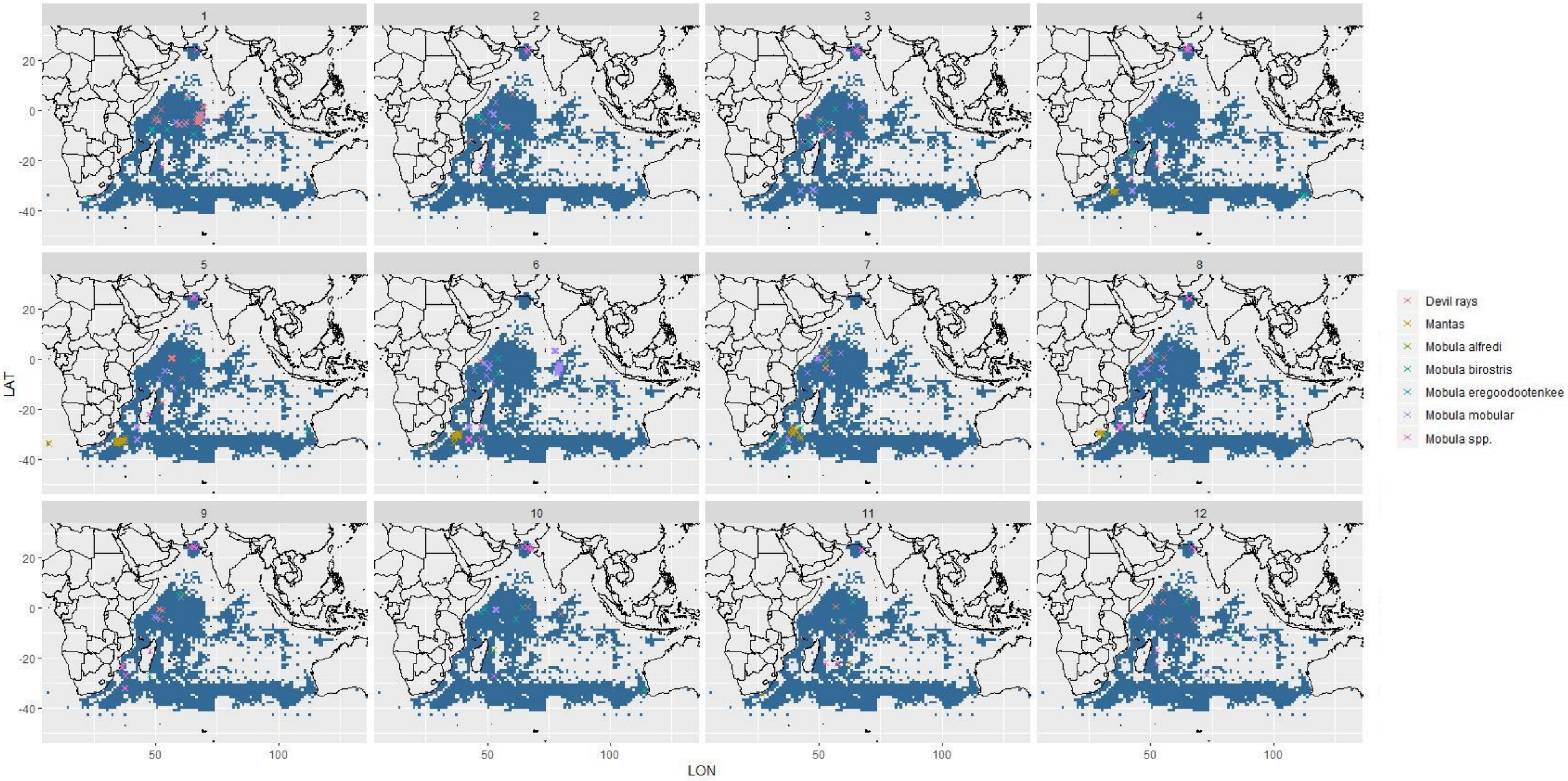


Figure 19. Distribution of captures by species for all years where blue cells represent the area observed and yellow crosses indicate mobulid captures (jittered)

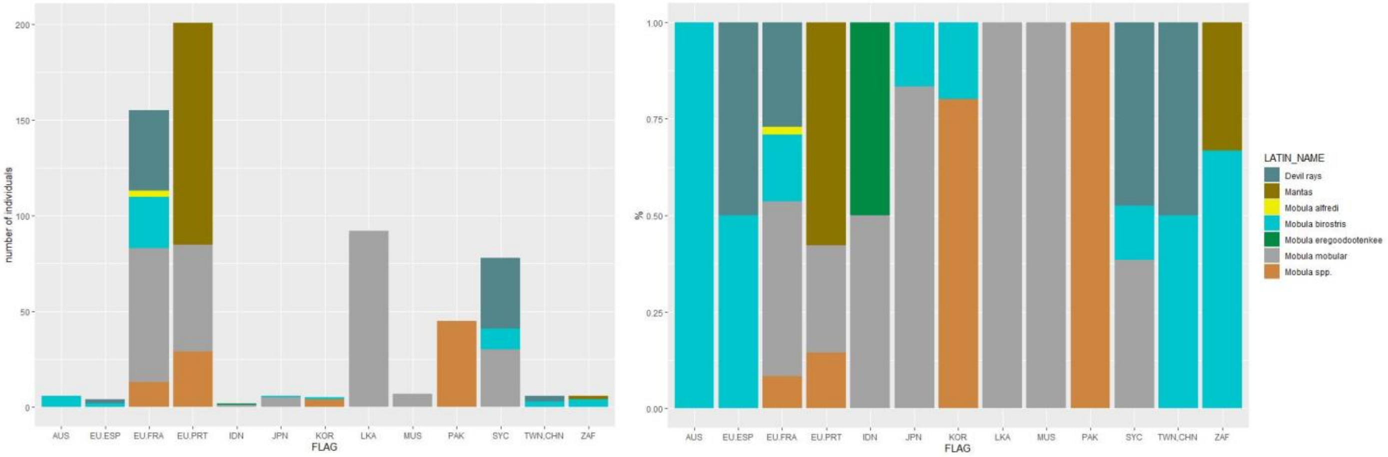


Figure 20. Species interactions by fleet (a) numbers and (b) proportions

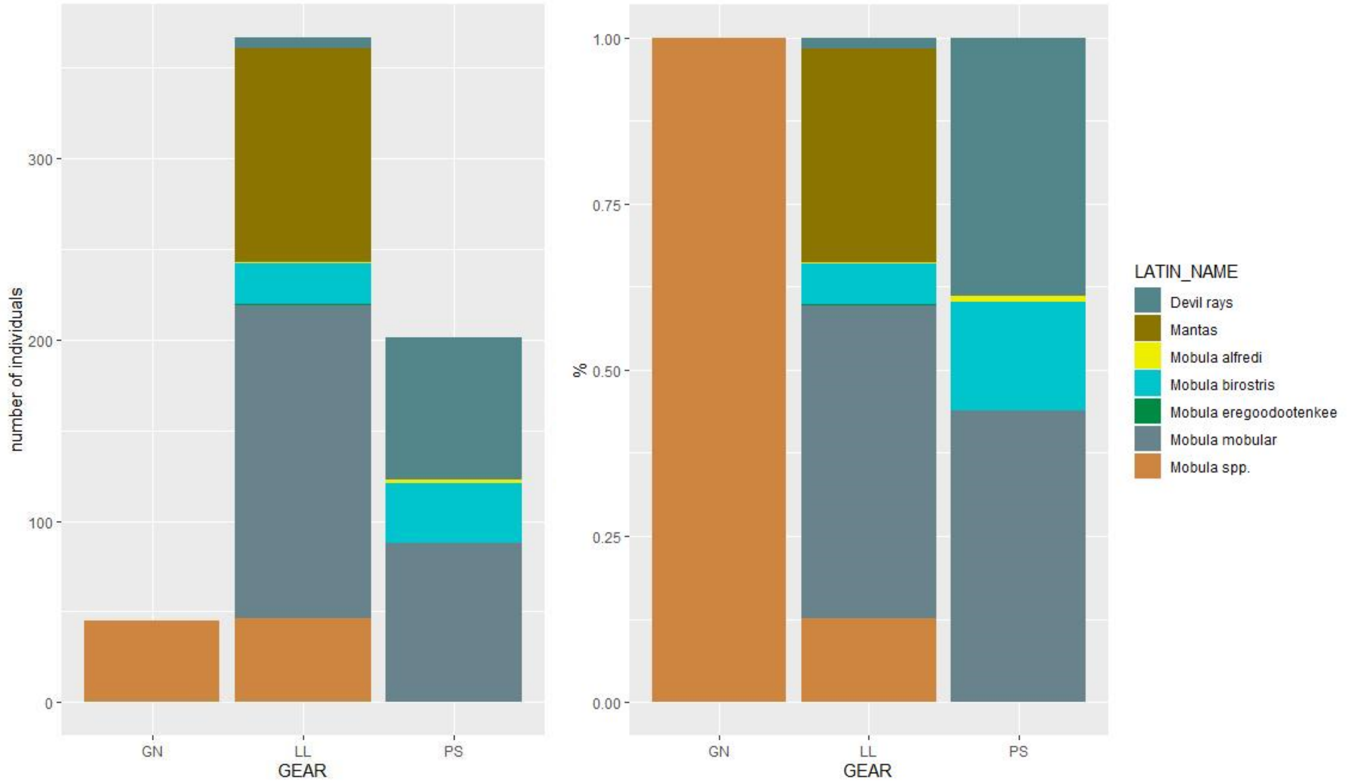


Figure 21. Species interactions by gear type

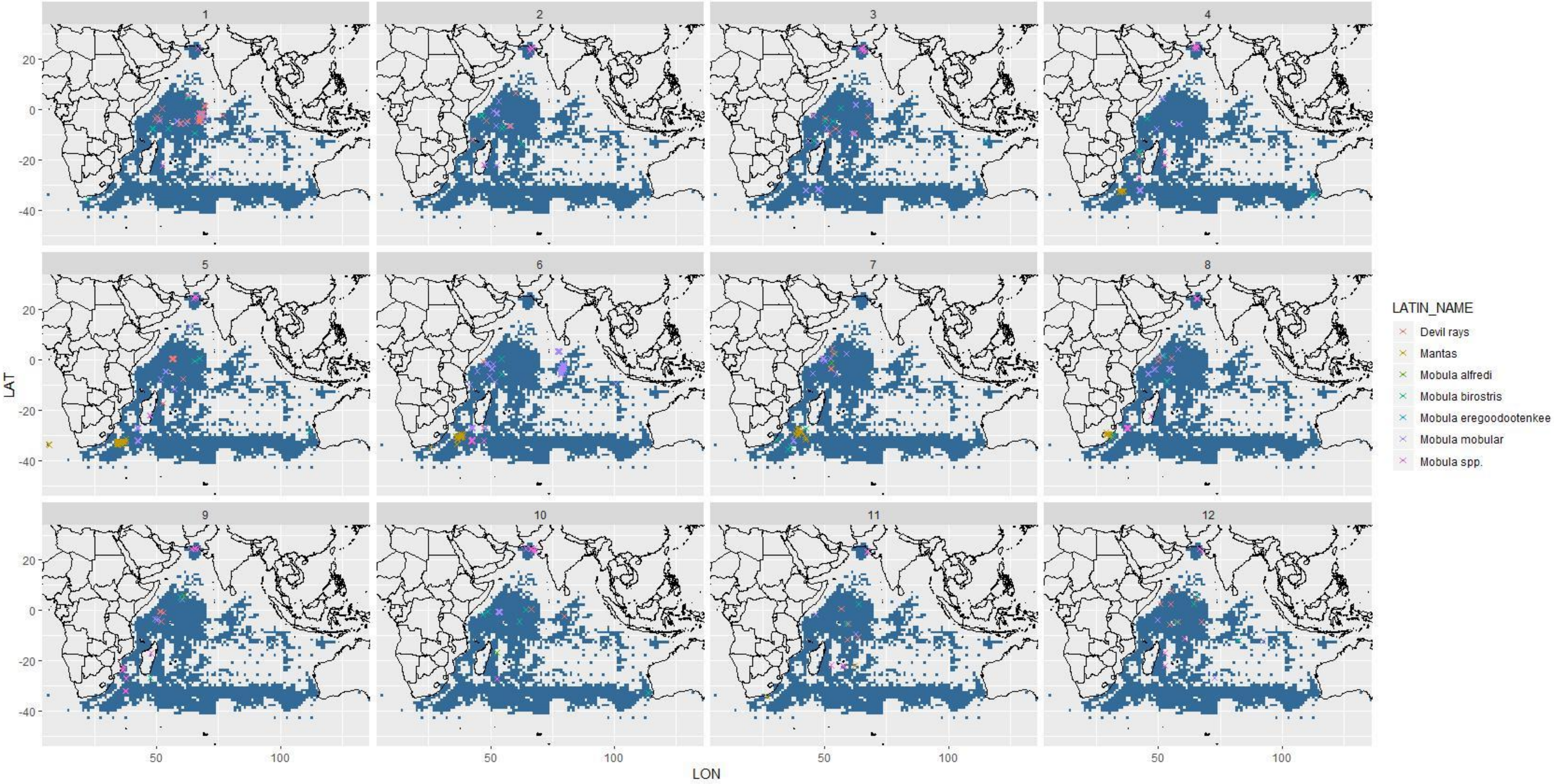


Figure 22. Species interactions by month

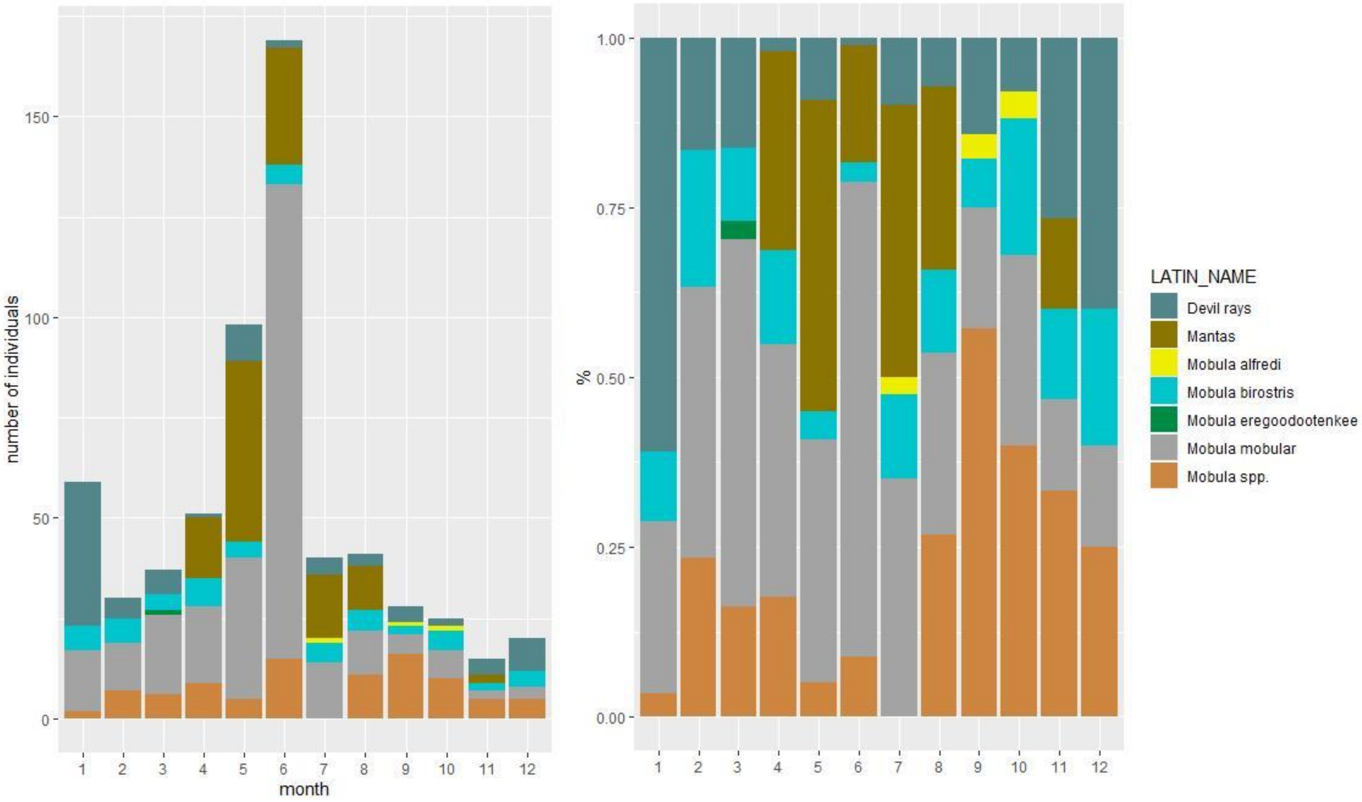


Figure 23. Species interactions by month (a) numbers (b) proportions

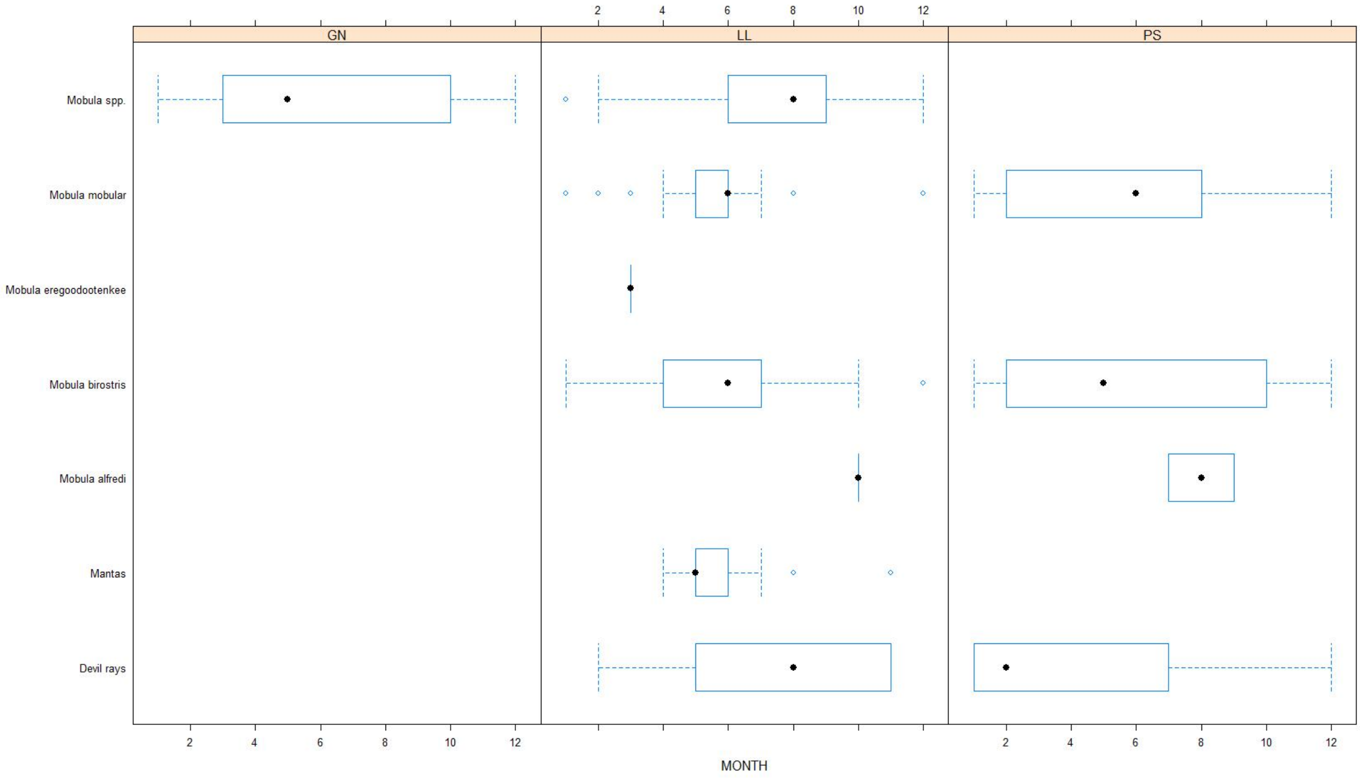


Figure 24. Species interactions by month and gear

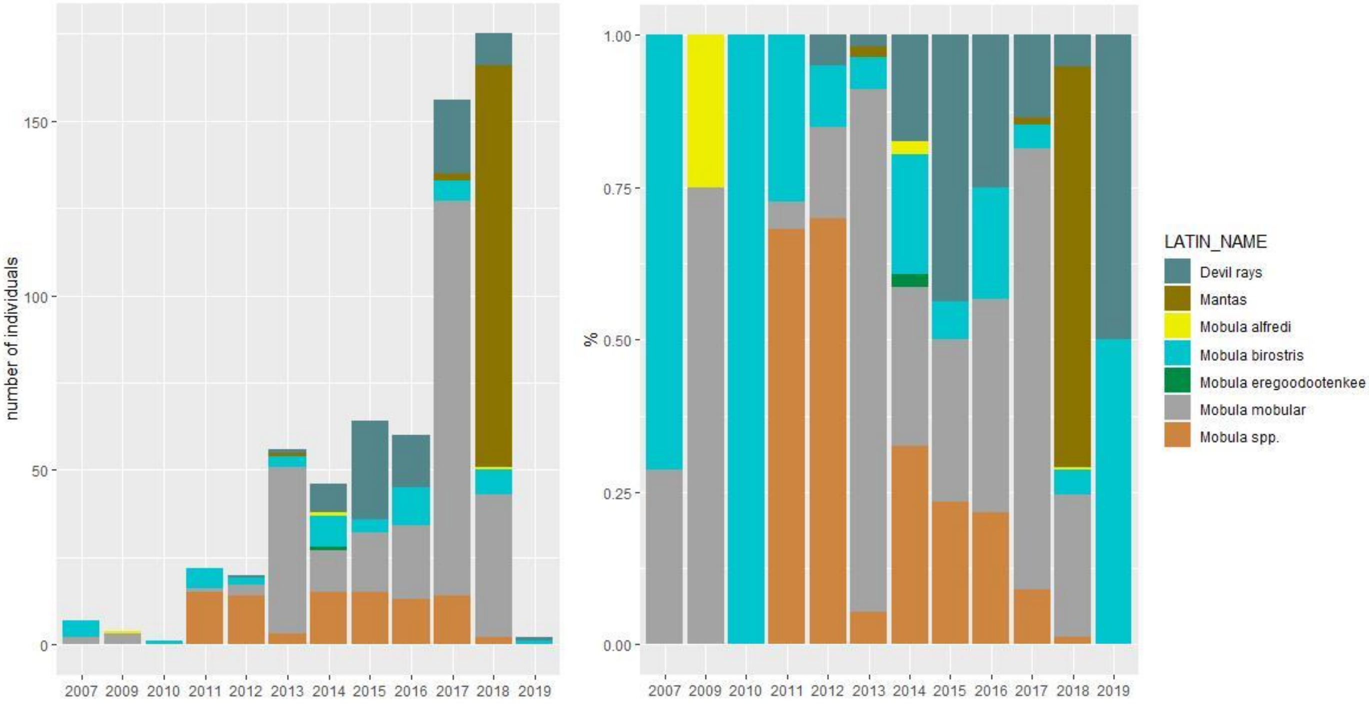


Figure 25. Species interactions by year (a) numbers (b) proportions

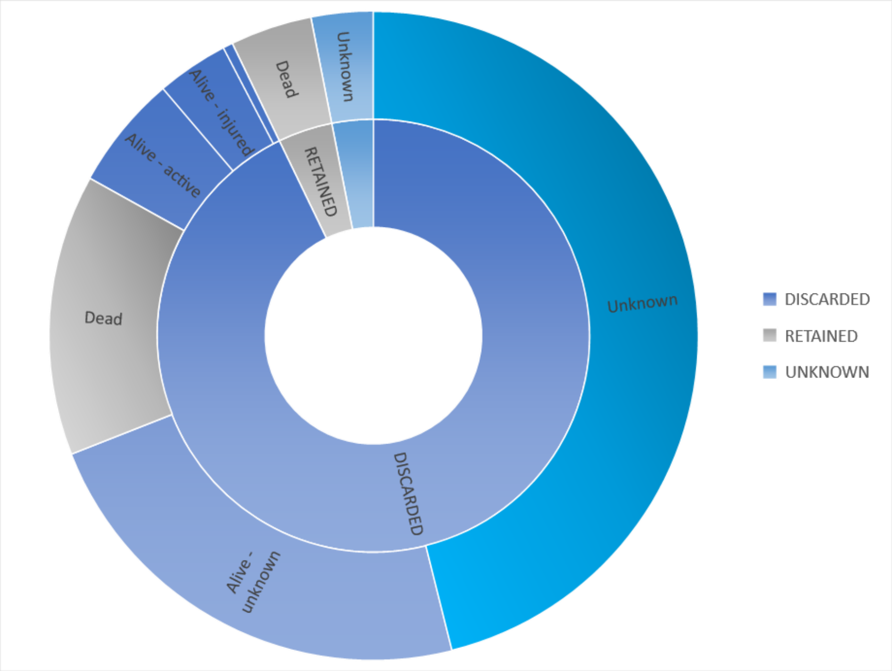


Figure 26. Fate and condition of interactions

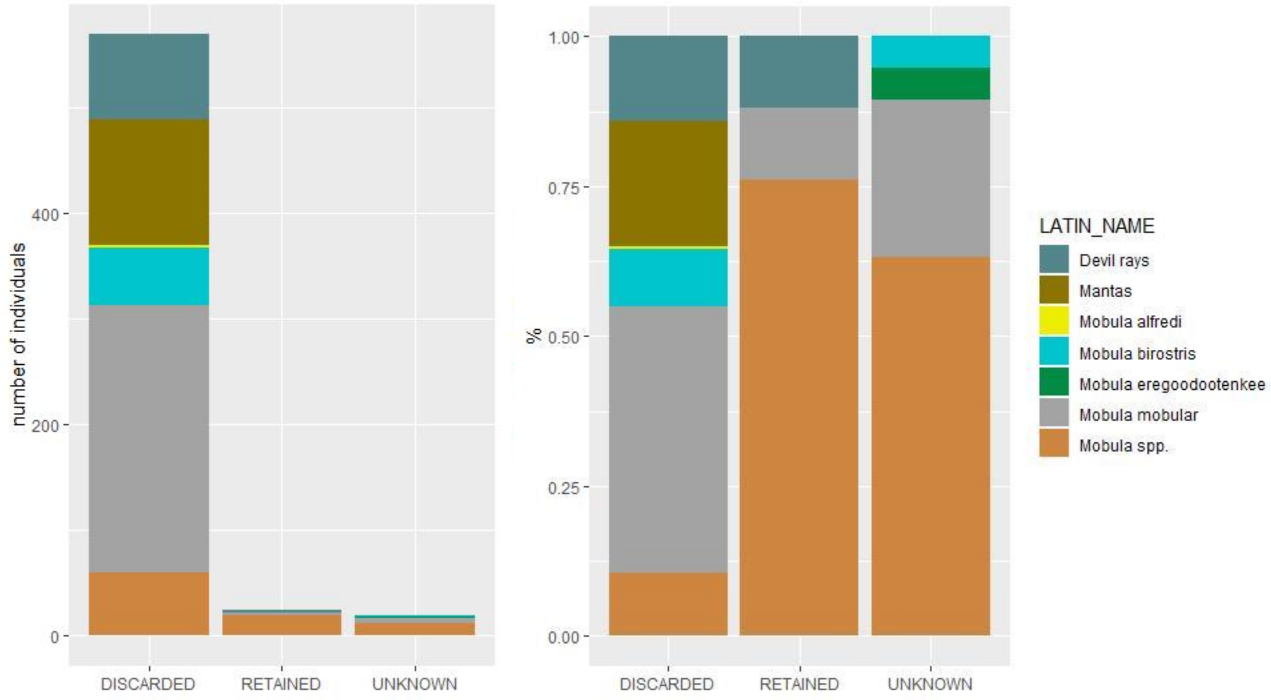


Figure 27. Fate of interactions by species (a) numbers (b) proportions

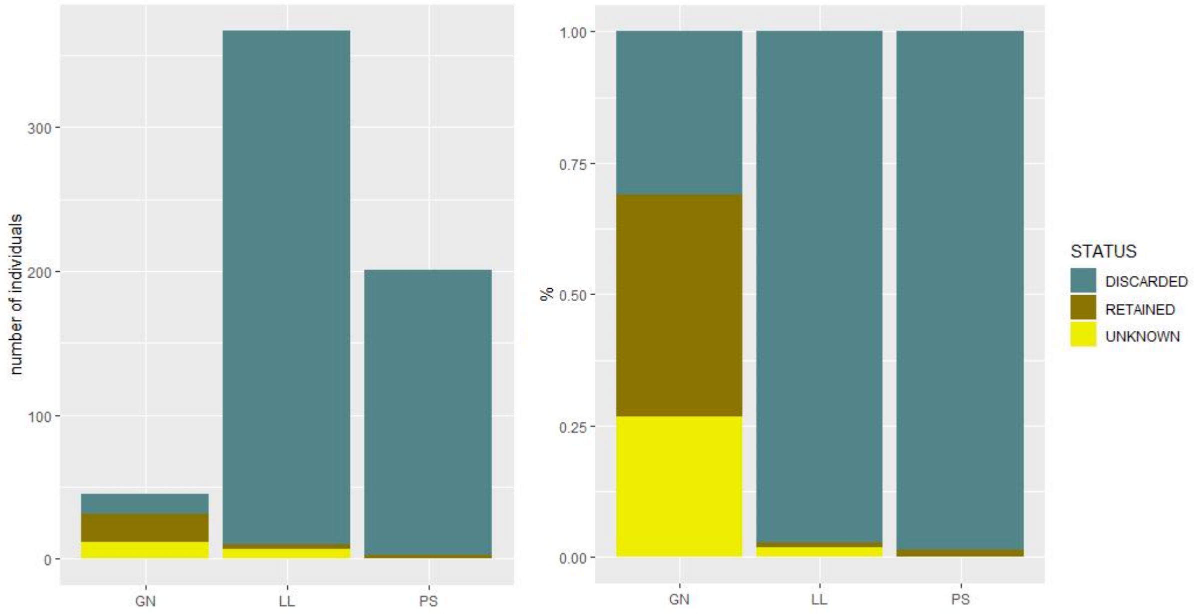


Figure 28. Fate of mobulids by gear type

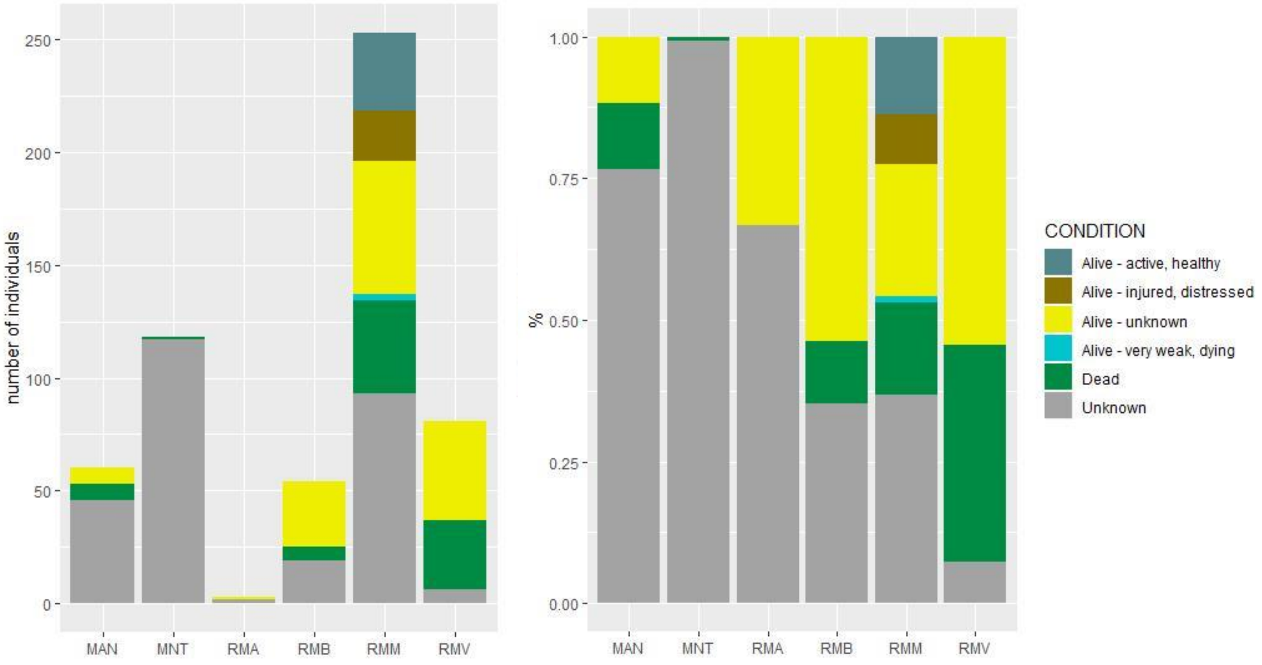


Figure 29. Condition of mobulid discards. MAN = all mobulid species, MNT = manta rays, RMA = M. alfredi, RMB = M.birostris, RME = M. eregoodootenkee, RMM = M.mobular and RMV = devil rays.

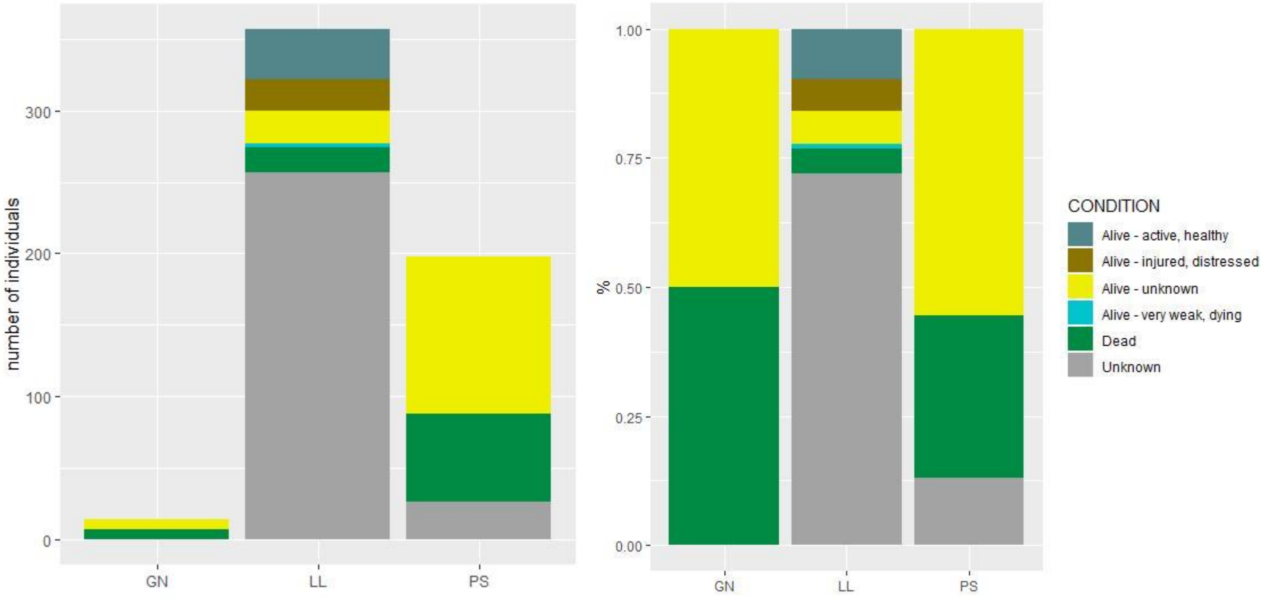


Figure 30. Condition of discards by gear type