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Abstract :

Natural floating objects (FOBs) have always been a major component of the habitat of pelagic species. Since the 1990s, the number of FOBs in the open ocean has increased greatly as a result of the introduction of fish aggregating devices (FADs) by the industrial tropical tuna purse seine vessels. These changes, and their potential impacts on the species that associate with FOBs, remain poorly understood. Using fisheries observer data, data from satellite-linked tracking buoys attached to FOBs and Lagrangian simulations, this study quantifies the temporal changes in the density and spatial distribution of FOBs due to the use of FADs in the Indian Ocean (IO) between 2006 and 2018. From 2012 to 2018, the entire western IO is impacted, with FADs representing more than 85% of the overall FOBs, natural FOBs less than 10%, and objects originating from pollution 5%. Results also suggest that both FADs and natural FOBs densities are lower in the eastern IO, but this initial investigation highlights the need for further studies. Our study confirms that FADs have greatly modified the density and spatial distribution of FOBs, which highlights the need to investigate potential consequences on the ecology of associated species.

Keywords : ecological trap, fish aggregating devices, Indian Ocean, Lagrangian simulations, pelagic habitat, purse seine fisheries, tropical tuna

INTRODUCTION

Studying the impact of human activities on natural ecosystems is a central issue in marine ecology and conservation (Halpern et al. 2008; Cigliano et al. 2015; Díaz et al. 2019). The majority of studies that address human-induced modifications of marine habitats are related to climate change, where most research focuses on shifts in biomass and distribution of marine species due to ocean acidification and warming (Dueri et al. 2014; Bryndum-Buchholz et al. 2019; Lotze et al. 2019). However, fisheries can also cause modifications of marine habitats, *e.g.* by altering the seabed (Neumann et al. 2016).

Many pelagic species, such as tropical tuna, are known to associate with floating objects (Freon and Dagorn 2000; Castro et al. 2002). The first floating objects were all natural, mainly parts of trees («logs») floating out in the ocean. Taking advantage of the associative behavior of pelagic species, tuna purse seine vessels began using fish aggregating devices (FADs), i.e. man-made objects, in the early 1990s (Davies et al. 2014). Throughout this paper we will refer to drifting Fish Aggregating Devices as "FADs", to natural floating objects (such as logs or parts of trees) as "NLOGs", to artificial drifting objects other than FADs (e.g. originating from human

pollution) as "ALOGs" and to any type of floating objects (FADs, NLOGs or ALOGs) as "FOBs".

The exact number of FADs is unknown, however a drastic increase has occurred since fishers

began using them three decades ago. In the Indian Ocean (IO), a fourfold increase in the

number of FADs was estimated between 2007 and 2013, with 10,300 active FADs recorded in

September 2013 (Maufroy et al. 2017). In the same period, the number of FAD deployments

increased, with an estimation of 14,000 deployments in 2013 (Gershman et al. 2015) and this

increase continued until 2018 (Floch et al. 2019, Katara et al. 2018). The increasing use of FADs

was observed mainly where purse seine fleets operate, i.e. in the western IO (Báez et al. 2020).

Consequently, the proportion of tuna captured around FOBs in the IO has increased, with

approximately 86% of tuna caught by purse seine fleets in 2018 originating from FOBs. Purse

seine catch on FOBs represents 40% of the total tuna catch in this ocean, all gears and fishing

modes included (IOTC 2020c, 2020d, 2020e). Purse seine fishing around FOBs, when compared

to targeting free-swimming schools, has the advantage of both reducing the search effort and

increasing the catchability of tuna (Dagorn et al. 2013a). However, this fishing mode also leads

to higher by-catch rates (Dagorn et al. 2013b; Davies et al. 2014) and increased catches of

small yellowfin (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*), which are currently

both subject to overfishing in the IO (IOTC 2020a; Merino et al. 2020). These direct impacts of

FAD fishing are regularly receiving research attention (*e.g.* Filmalter et al. 2013; Dagorn et al.

2013b, Wain et al. 2021) and are considered by Regional Fisheries Management Organizations

(RFMO) for developing and adopting conservation measures. For example, the IOTC (Indian

Ocean Tuna Commission) aimed at "[reducing] juvenile Bigeye tuna and Yellowfin tuna

mortalities from fishing effort on Fish Aggregating Devices" through a resolution limiting the

number of FADs to 500 per vessel per year in 2019 (IOTC 2019). Moreover, this fishing practice

also increases the number of floating objects at sea, which can modify the habitat of animals

which naturally associate with such structures (Dagorn et al. 2013a), with possible

consequences on their ecology. Furthermore, it also generates coastal and marine pollution

when FADs wash ashore (Imzilen et al. 2021). The indirect impacts of the presence of a large

number of FADs drifting in the ocean on marine species is yet to be fully assessed and

considered in fisheries management.

It has been hypothesized that high numbers of FADs could result in an "ecological trap" for

tropical tuna (Marsac et al. 2000; Hallier and Gaertner 2008). An ecological trap occurs when

individuals select poor-quality habitats when they are misled by cues that are no longer

correlated to habitat quality due to anthropogenic changes (Battin 2004; Gilroy and Sutherland 2007). This selection of poor-quality habitat then leads to a reduction in their fitness. It has been hypothesized that, by modifying the density and spatial distribution of FOBs, the massive deployment of FADs could retain or transport individuals in areas that are ecologically unsuitable for them (Marsac et al. 2000; Fonteneau et al. 2013). Moreover, this mechanism could lead to an export of tuna biomass out of large Marine Protected Areas, undermining their effectiveness (Boerder et al. 2017; Curnick et al. 2020).

This study aims at determining the modifications of the surface habitat of tropical tuna related to the intensive deployment of FADs in the IO, ten years after an initial short-term (2007-2008) assessment by Dagorn et al. (2013a) in the western IO. We consider that NLOGs constitute a natural feature of this habitat while FADs represent the major human-induced change (as in Dagorn et al. 2013a). Hence, we assess the increase in the number of FADs relative to the number of NLOGs, and the resulting modifications on FOBs distribution. In the present study, we aim at (i) quantifying the surface habitat changes in the western IO (the main fishing grounds of the purse seine fleet) over 2006-2018, due to the deployment of FADs by fishers,

and (ii) undertaking an initial evaluation in the eastern IO, beyond the main fishing grounds of the purse seine fleet.

METHODS

FOB data

FADs and NLOGs locations were obtained from (i) data recorded by scientific observers onboard purse seine vessels (2006-2018), and (ii) GPS positions from tracking buoys deployed on FOBs by purse seine vessels (2014-2018).

Observer data was collected on-board French purse seine vessels operating in the tropical western IO. The French fleet is one of the main purse seine fleets operating in the IO, after the Spanish and Seychellois fleets, and is responsible for about 15% of the total IO purse seine catch (IOTC, 2020b). Like the other purse seine fleets, the French fleet operates mainly in the western IO. Between 2006 and 2018, it was composed of 6 (in 2007) to 12 (in 2018) purse seine vessels, for a total carrying capacity increasing from ~3,600 to ~11,700 t. Supply vessels are also in use since 2016 (one since 2016 and a second one since 2018; Floch et al., 2019). Observer coverage of the fleet increased from 7% in 2013 to more than 25% in 2017 and 2018

(IOTC, 2020f). The observer data includes the date, time, and location of the main activities of the vessel (e.g. fishing sets, installation or modification of FOBs, searching for FOBs, etc.). For every activity occurring on a FOB, the type of operation (e.g. deployment, removal, observation of a FOB, etc.) and the type of object (FAD, NLOG, or ALOG) are reported. When the observed FOB is equipped with a satellite-linked tracking buoy, the type of operation on the buoy (deployment, removal, observation, etc.) and the buoy's unique identification number are also reported.

The GPS position dataset contains the unique identification number of the buoys, the date and time of the buoy's GPS positions and their associated geographical coordinates. The elapsed time between two positions recorded from the buoys can be remotely controlled by the vessels and ranged between 2 and 12 hours. To determine when a buoy was at sea and attached to a FOB, rather than onboard a vessel before deployment or following recovery, the dataset was filtered using the algorithm developed by Baidai et al. (2017).

FOB spatial distribution from observer data

We calculated the overall number and proportion of the different FOB types on an annual basis from the observer data between 2006 and 2018. We also report the number of

observation days during the same period. An observation day corresponds to a day where at least one activity was registered by an observer onboard a fishing vessel. The remaining analysis focused on two time periods when observer coverage was highest (2007-2008 and 2014-2018). The choice of these two periods also allowed us to compare our estimates to those obtained in a previous assessment (in Dagorn et al. 2013a). Only a portion of ALOGs originate from fisheries, and mainly from other fishing modes than purse seine fishing. Hence, as our study aimed at determining the impact of industrial FAD fisheries on the pelagic habitat, the rest of the analysis focused on the comparison between the spatial distributions of FADs and NLOGs.

As an estimate of the density of FOBs encountered by observers, we determined, for each study period, the median spatial Euclidean distance between the locations of two consecutive encounters of floating objects on a quarterly basis. Two consecutive FOB encounters were defined as two observations consecutive on the observer record and performed by the same vessel, during the same trip. This distance was calculated for all floating objects together (FADs, NLOGs and ALOGs), for FADs only and for NLOGs only. For each FOB type and each quarter, we also calculated the standard error SE of the distance, with: $SE = \frac{SD}{\sqrt{N}}$, where SD is

the standard deviation and N is the number of distances. For each of the two considered study periods (2007-2008 and 2014-2018), we performed Wilcoxon rank sum tests to determine if the distance was different depending on the FOB type. We also performed Wilcoxon tests to determine if, when considering one type of FOB, the distance differed between the two study periods. A FOB multiplication factor was also calculated, on a quarterly basis, for each study period. This factor was calculated as the ratio of the sum of observed FADs and NLOGs divided by the number of NLOGs, and was calculated for each macro-area used in Dagorn et al. (2013a): Somalia, South East Seychelles, North West Seychelles, Mozambique Channel, Chagos. Hence, a multiplication factor greater than 2 means that more FADs were observed than NLOGs. This calculation was performed for every quarter with at least one NLOG observation. For all calculations, the quarters used were defined according to the seasonality of purse seine fleet (Dagorn et al. 2013a): Q1, December to February; Q2, March to May; Q3, June to August; Q4, September to November. To test whether the multiplication factor significantly differed between macro-areas, we performed a Kruskal-Wallis test. Also, in order to assess a possible modification of the multiplication factor between the two study periods (2007-2008 and 2014-2018), we performed Wilcoxon tests.

In addition, the spatial distributions of observed FADs and NLOGs were assessed for each study period, considering the total number of observations of each FOB type per 2° square cell. This figure was then divided by the observation effort, which was the number of observation days in each cell. A vessel was considered to have spent a day in a cell when the first entry of the day, in the observer data, was located in this cell. Cells with too few data (*i.e.* less than 10 vessel days), were discarded (~ 0.3% of all data, with cells located at the border of the main fishing grounds). Spatial maps of the FOB multiplication factor were also constructed for each study period using the ratio of the sum of the number of observed FADs and NLOGs divided by the number of NLOGs for each 2° cell with at least one NLOG.

FOB spatial distribution from GPS data

In order to investigate the spatial distribution of FOBs beyond the industrial purse seine fishing grounds (*i.e.* where observer data are not collected), we also considered the data provided by the satellite-linked tracking buoys attached to FOBs. To achieve this, GPS positions of FOBs equipped with buoys were merged with the observer data, using the buoys unique identification number common to the two databases to determine the FOB type to which each buoy was attached. The trajectories obtained from the GPS data were reconstructed at a

regular 6-hours interval using the R package *trajectories* v. 0.2-1 (Moradi et al. 2018). For each

type of FOB considered in the study (FADs and NLOGs), spatial densities, expressed as the

mean number of reconstructed GPS positions per day, were estimated in 2° cells, between

2014 and 2018. Finally, the number of buoys deployed on each FOB type was also estimated

for the same time period.

Lagrangian simulations of NLOGs

Observations of NLOG by scientific observers onboard industrial purse seine vessels are

inherently limited to their fishing grounds (Western IO). To overcome this bias, these datasets

were complemented with Lagrangian simulations. The Lagrangian simulations assumed that

NLOGs are transported by ocean currents like water parcels, building on previous results

showing that FOBs drift similarly to oceanographic drifters in the IO (Imzilen et al. 2019) and

can therefore be simulated using Lagrangian models (Imzilen et al. 2016; Davies et al. 2017;

Phillips et al. 2019). We used the Lagrangian tool *Ichthyop* v.3.3. (Lett et al. 2008) to simulate

the drift of NLOGs.

NLOGs likely originate from multiple terrestrial sources, including mangrove forests and rivers (Thiel and Gutow 2005). Here, we explored the distribution of virtual NLOGs originating from both sources. Firstly, mangrove locations used as a potential NLOG source were obtained from the Global Mangrove Watch (GMW) 2016 (Lucas et al. 2014). A total of 10,000 mangrove polygons were randomly sampled from the 173,051 polygons that compose the IO portion of the GMW 2016 shapefile (mean surface area of a polygon: 0.2 km²). Secondly, 10,000 river mouths locations were sampled out of the 18,703 obtained from the HydroATLAS database v1.0 (Linke et al. 2019). For both mangroves and river mouths locations, particles were released at the center of the closest sea cell. One particle was released from each point every month from July 2013 to December 2014. To transport these particles, the surface currents obtained through the 3D hydrodynamic model NEMO were used (Madec 2016, spatial resolution: 1/12°; temporal resolution: 1 day). Particles were transported for 180 days, after which they were considered sunk and were removed from the simulations. The sensitivity of the obtained results to the drifting time was assessed, testing drifting times ranging from 30 to 360 days. As little variation of particles distribution were observed for times ranging from 180 to 360 days, the smallest value was used (180 days). Advection was simulated using a

Forward Euler integration scheme and a diffusion component was added using a dissipation rate of 1 x 10^{-9} m²/s³ (following Peliz et al. 2007). Similarly to the FOB GPS data, the particle trajectories obtained from the simulations were then used to generate standardized distribution maps of virtual NLOGs, where the total number of particles in each 2° cell during 2014 was divided by the number of days. As such, these maps represent the mean number of particles per simulation day in each 2° cell.

RESULTS

Modification of FOBs distribution from observer data

The observer data included 22,657 observations of FOBs from 2006 to 2018, 19,155 (84.5%) of which were FADs, 1,666 (7.4%) were NLOGs and 1,836 (8.1%) were ALOGs. The number of FOB observations increased after 2013, with more than 4,000 observations per year since 2015 (Figure 1A). This increase was due to both better coverage of the French purse seine fleet (from less than 500 days during the initial years of the study period to more than 1,200 days since 2014, Figure 1A) and a higher number of FADs per day (Figure 1B). The number of observations of FADs per day increased over the years from a minimum of 0.51 observations

per day in 2006 to a maximum of 2.83 in 2017 (Figure 1B). Conversely, the number of

observations per day of both NLOGs (minimum value = 0.09 in 2006 and maximum

value = 0.54 in 2011) and ALOGs (minimum value = 0.05 in 2012 and maximum value = 0.17 in

2018) remained stable over the study period. Similarly, the percentage of observed FADs

increased in time with a clear transition occurring in 2012 (Figure 1C), from 63% during 2006-

2011 to 89% in 2012-2018. The percentage of NLOGs simultaneously decreased from 24% in

2006-2011 to only 6% in 2012-2018 (Figure 1C).

The median distance between two consecutive FOB encounters, during 2007-2008, showed

no major difference between FADs and NLOGs (70 km and 74 km respectively; $W = 5.2 \times 10^4$, p

= 0.84). During this period, the median distance between two consecutive FOBs of any type

was significantly lower than when considering only FADs or only NLOGs: median distance of

56 km ($W = 2.2 \times 10^5$, $p = 2.4 \times 10^{-3}$ with FADs and $W = 9.4 \times 10^4$, $p = 2.3 \times 10^{-2}$ with NLOGs). During

2014-2018, the distance between two consecutive FADs became significantly lower than

between two consecutive NLOGs (37 km and 89 km respectively; $W = 1.1 \times 10^7$, $p = 3.0 \times 10^{-49}$).

The median distance between two consecutive FOBs of any type stayed lower than when

considering only one FOB type ($W = 1.6 \times 10^8$, $p = 5.3 \times 10^{-9}$ with FADs and $W = 1.3 \times 10^7$, p =

$2.0x10^{-59}$ with NLOGs). The median distance between two consecutive NLOGs did not significantly differ between the two study periods (W = $9.2x10^4$, p = 0.36). However, the median distance between two consecutive FADs or between two FOBs of any type decreased (W = $5.8x10^6$, p = $9.5x10^{-23}$ and W = $1.0x10^7$, p = $2.0x10^{-20}$ respectively) after 2014. Finally, seasonal differences were observed in the distance between NLOGs, with larger distances in quarters 1 (Dec-Feb) and 3 (Jun-Aug) than in quarters 2 (Mar-May) and 4 (Sept-Nov) (Figure 2).

The FOB multiplication factor (the ratio of the sum of observed FADs and NLOGs divided by the number of NLOGs) differed significantly between macro-areas (Kruskal-Wallis test: χ^2 = 36.3, p = $2.5x10^{-7}$). It also seemed to increase through time in every macro-area (Figure 3), except in the Chagos region, where a lack of observations precluded a conclusive analysis (Figure 3A). The Mozambique Channel was the region with the lowest multiplication factor values: 1.1 in 2007-2008 (hence 10 times more NLOGs than FADs); the factor increased to 3.7 (sd = 3.7) in 2014-2018, but this increase was not significant (Wilcoxon test: W = 10, p = 0.4). A higher number of FADs than NLOGs (multiplication factor > 2) was already evident in the first study period in the other regions (mean multiplication factor in 2007-2008: 13.9 (sd = 16.1) in Somalia, 7.2 (sd = 3.9) in NW Seychelles and 4.0 (sd = 3.2) in SE Seychelles).

However, the multiplication factor increased further in recent years: mean values in 2014-2018 of 62.0 (sd = 46.5), 25.1 (sd = 13.0) and 16.0 (sd = 11.8); Wilcoxon tests: W = 11, p = 1.5×10^{-2}; W = 6, p = 1.9×10^{-5}; and W = 10, p = 1.9×10^{-3} in Somalia, NW Seychelles and SE Seychelles respectively. The maximum observed multiplication factor was 177, 56 and 48 in Somalia (1st quarter 2018), NW Seychelles (2nd quarter 2017) and SE Seychelles (4th quarter 2015), respectively.

The maps of FOB spatial distributions obtained from observer data confirmed a clear increase in the number of FADs between the two study periods while maintaining similar spatial patterns (Figure 4). In 2007-2008, FADs were mainly present in the western part of the study area, close to the border of the Somalian Exclusive Economic Zone (EEZ) (Figure 4A). In 2014-2018, the number of FADs per day of observation was much higher, with FADs present in nearly the entire sampled area but still with higher numbers close to the border of the Somalian EEZ (Figure 4B). In both study periods, NLOGs were observed mainly in the Mozambique Channel (Figure 4C-D). In 2014-2018, less than 20% of NLOG observations occurred North of 5°S (Figure 4D). Overall, there were more FADs than NLOGs everywhere in the sampled area except in some parts of the northern Mozambique Channel (Figure 4E-F).

Modification of FOBs spatial distribution from GPS data

Matching the unique buoy identification number between the observer and buoy databases allowed for the identification of FOB type for 6,136 different FOB trajectories, 5,686 (92.7%) of which were FADs, and 450 (7.3%) were NLOGs. Higher densities were found around the Seychelles and close to the Somalian EEZ, both for FADs (Figure 5A) and buoy-equipped NLOGs (Figure 5C). The average density of buoys associated to FADs (3.18 x 10^{-1} FAD/cell) was around ten times higher than the density of instrumented NLOGs (3.60 x 10^{-2} NLOG/cell). The distribution of buoy deployment obtained from the observer data was slightly different for NLOGs and FADs, with the majority of buoys associated with FADs being deployed west of the Seychelles (Figure 5B) and a high proportion of deployment on NLOGs around the Seychelles and in the Mozambique Channel (Figure 5D). The main difference was observed in the Mozambique Channel, where buoy deployments were essentially conducted on NLOGs only.

Simulated trajectories

Figure 6 shows the distribution of virtual NLOGs obtained from the Lagrangian trajectories starting from mangrove areas and river mouths and transported for 180 days (results for other

lifetime values with NEMO at surface in Supplementary Figure 8, with other forcing products in Supplementary Figure 9). Results were similar when considering inputs either from mangroves only or from rivers only (Supplementary Figure 11). The highest numbers of simulated NLOGs were observed in the Mozambique Channel, in the Bay of Bengal and in the eastern part of the Arabian Sea. Only small densities of simulated objects were found offshore (between 5°N and 10°S), with densities one to two orders of magnitude smaller than in the Bay of Bengal or in the Mozambique Channel (Figure 6B).

DISCUSSION

Modification of the FOB distribution in the western IO

Our results show that FAD numbers in the IO have increased between 2007 and 2017, which is in agreement with previous studies (Morgan 2011; MRAG 2017; Maufroy et al. 2017). Assessing the recent evolution of FAD numbers in the IO is important, as the latest assessment was based on data from 2007 to 2013 (Maufroy et al. 2017). Resolutions adopted by the Indian Ocean Tuna Commission (IOTC) limited the number of active buoys associated with FADs to 350 per vessel in 2017 and then to 300 per vessel in 2019, with an annual maximum number

of 500 FADs deployed per vessel (IOTC 2017, 2019). It is still too early to assess the impact of such resolutions, but it would be important to determine if the stabilization of the number of FADs observed in our study from 2017 to 2018 persists in the near future.

This study also reveals a significant increase in the proportion of FADs compared to other FOB types in the western IO, increasing from 60-70% of the observations between 2006 and 2010 to more than 85% in recent years (2014-2018). A very limited number of studies compared the numbers and distributions of NLOGs and FADs. Phillips et al. (2019), using data from 2016 and 2017 and Lagrangian simulations, showed an increase in FOB densities induced by FAD deployments in the western Pacific Ocean as well as a modification of the areas where the highest FOB densities are observed. In the western IO, Dagorn et al. (2013a), using data from 2007 and 2008, found that FADs did not create new FOB areas (*i.e.* they were not present in areas that were previously free of floating objects) as both types of FOBs were found everywhere. The number of FOBs, however, at least doubled in all fishing grounds used by the purse seine fleet, and was multiplied by 20 or 40 in some areas (*e.g.* Somalia area). Ten years after this study, and under the hypothesis that the number of NLOGs remained stable, we found that even the Mozambique Channel, where NLOG were still more numerous than FADs

at the time, has shown an increase in the proportion of FADs, with FADs multiplying the number of FOBs by ~3.7 in 2014-2018. Somalia is still the most impacted area, ahead of NW Seychelles and SE Seychelles, and multiplication factors have increased three to four-fold between 2007-2008 and 2014-2018 in the entire western IO. Therefore, our study does not only confirm Dagorn et al.'s (2013a) results for 2007-2008, but with the number of NLOGs remaining stable, it also shows that the number of FOBs has increased even more since then, with the Mozambique Channel even being impacted. This trend is shown by the reduction of the mean distance between two consecutive FAD encounters in 2014-2018 relative to that of 2007-2008, with FOBs now found closer to each other. In recent years, the fishing strategy of the French purse seine vessels rapidly evolved from fishing mainly on floating objects encountered at random (i.e. not equipped with their own tracking buoys, Snouck-Hurgronje et al. 2018) to deploying a higher number of buoy-equipped FADs and fishing mainly on their own objects (Marsac et al. 2017). Indeed, the proportion of FADs deployed by the French fleet that were equipped with echosounder buoys went from 0% up until 2009 to 100% after 2014 (Marsac et al. 2017). This shift in fishing strategy could artificially increase the observed number of FADs in our data. However, when assessing the same metrics discussed above using

observations of randomly encountered objects only (objects which do not belong to the vessel or its fishing company), the results showed similar trends (Supplementary Figures 1-4). The only difference was that the increase in the number of FADs in recent years was less drastic (Figure 1B).

In the western IO, the FAD distribution obtained from GPS data (Figure 5A) showed broad agreement with that obtained from observer data (Figure 4B), with slight differences mainly observed in the north of the fishing grounds. These differences can be explained by the sampling schemes specific to each dataset. The observer data provides access to every encountered floating object, but only in the areas where fishing vessels with onboard observers are present. Because some regions are only fished at a given time of the year (*e.g.* the Mozambique Channel from March to May, Supplementary Figure 5), this seasonal coverage precludes the balanced sampling of all regions. Buoy GPS data does not suffer such bias as it is independent of the trajectories of fishing vessels. However, it is also important to note that only a subset of NLOG and FAD trajectories could be identified in the GPS database, as cross referencing the unique buoy identifiers in the observer data reduced the number of exploitable trajectories. Furthermore, only the data from the French buoys were available for

this study. Three major purse seine fleets operate in the western IO (French, Seychellois and Spanish). Despite these fleets historically showing different fishing strategies in relation to FADs (Guillotreau et al. 2011; Marsac et al. 2017; Maufroy et al. 2017; Snouck-Hurgronje et al. 2018), recent studies highlighted high spatial correlations between the deployment locations of FADs exploited by these fleets in recent years (Katara et al. 2018). Although the total number of FADs cannot be calculated from the available data, the spatial patterns of FADs obtained from the GPS buoys can be considered reliable. In the study by Katara et al. (2018), lower correlations were found in the first half of the year. The difference observed in the second half of the year explains why, when considering the spatial distributions of FADs by quarter (Supplementary Figures 5 and 6), results from the two datasets showed more similarity in quarters 1 and 4 than in quarters 2 and 3. The spatial distribution of NLOGs obtained from the observer data (Figure 4C-D) differed in general terms with that obtained from the GPS positions of buoys (Figure 5C). Here, it is important to note that the purse seine vessels generally do not instrument (with satellite-linked buoys) all the NLOGs that they encounter. This is particularly true in locations were the NLOG abundance is high, like the Mozambique Channel, thus introducing a possible bias between the real number of NLOGs

and the number of NLOGs equipped with a buoy. Furthermore, buoys cannot be deployed on

NLOGs that do not pass through the fishing grounds, which may further bias results obtained

using satellite-linked buoy data. As such, observer data still remains the most reliable data

source to assess FAD and NLOG relative distributions in the western IO.

Modification of the FOB distribution in the eastern IO

As tuna purse seine fishing grounds are mostly located in the western IO, the impact of FAD

deployment on the eastern IO cannot be studied using observer data. Furthermore,

comparing NLOG and FAD spatial distributions in the eastern IO using GPS data from satellite-

linked buoys was not possible either, as explained above.

To obtain a more accurate prediction of the NLOG distribution in the eastern IO, we performed

a Lagrangian simulation of NLOG trajectories. Contrary to the GPS-based distributions, the

NLOG distribution obtained from the simulation (Figure 6) were in agreement with those

obtained from the observer data in the western IO (Figure 4C-D). They also indicate high

numbers of NLOGs in the East of the Arabian Sea and in the Bay of Bengal. Van der Stocken et

al. (2019) simulated the dispersal of mangrove propagules and also observed high densities of

particles in the Mozambique Channel, in the eastern Arabian Sea and the Bay of Bengal. Other studies simulating the dispersal of plastic waste from rivers into the ocean also obtained similar areas with high densities (Lebreton et al. 2012; Van Sebille et al. 2015; Viatte et al. 2020).

In our study, NLOG distributions obtained from Lagrangian simulations and FADs distributions obtained from GPS buoy data show that FAD deployments probably have a low impact in the Bay of Bengal and in the eastern Arabian Sea. FADs seem to be in very low densities in these regions, whereas NLOGs occur in high densities. The results obtained here also suggest low densities of both FADs and NLOGs in the equatorial eastern IO. However, it is not possible to assess the impact of FAD deployments in this area with certainty for two reasons. Firstly, buoy data could lead to an underestimation of FAD densities in the equatorial eastern IO, as buoys can be deactivated by fishers when they leave the fishing grounds (e.g. they enter an MPA or drift too far from the fished area). However, we are confident that this bias is limited in its extent, as, in our data, less than 2% of all equipped FADs were deactivated in the eastern IO (see Supplementary Figure 7). Secondly, lagrangian simulations do not allow for quantitative comparisons with actual data.

Robustness of Lagrangian simulations

The assessment of the NLOG distribution in the eastern IO relies on Lagrangian simulations.

The impact of the current product used on the simulated distributions was tested (Supplementary Figure 9). It showed little influence on the relative distribution of simulated NLOGs, in line with results obtained previously (Amemou et al. 2020).

Previous modeling studies pointed at particle lifetime as a key parameter influencing the distributions obtained from simulations, particularly in studies conducted at large spatial scales (Pineda et al. 2007; Huret et al. 2010; Van der Stocken et al. 2019), including in the IO (Stelfox et al. 2020; Crochelet et al. 2020). Particle lifetime is often uncertain, as is the case in our study due to very limited knowledge on the lifetime of NLOGs. Reported estimations of NLOG lifetimes vary between half a day to more than 1,000 days (Thiel and Gutow 2005). However, the spatial distributions of NLOGs and the areas with highest putative NLOG densities obtained for different lifetimes (from 60 to 360 days, Supplementary Figure 8) were very similar. A large proportion of particles beached (i.e. they entered a cell classified as land in the current product) before the end of their lifetime, which could possibly explain the minor impact of the lifetime duration (Supplementary Figure 10). Previous studies also found

particles accumulation in the southern IO, which was not observed here (Van Sebille et al.

2015; Viatte et al. 2020). However, these studies focused on plastic debris or microplastics,

using a much larger drifting time than ours, varying from 20 to 50 years. Hence, while our

study suggests that the influence of drifting time on the distribution of simulated NLOGs may

be low, if NLOGs were to drift for several years before sinking, new accumulation areas could

be formed.

Other important parameters which might influence the distributions calculated from the

Lagrangian simulations are the location of NLOG inputs in the ocean and the magnitude and

seasonality of this input. Some studies simulating FAD trajectories showed that these

parameters could strongly influence the resulting FAD distributions (Curnick et al. 2021; Davies

et al. 2017). Mangrove and rivers are the two most likely sources of NLOGs (Thiel and Gutow

2005; Caddy and Majkowski 1996; Krajick 2001). The NLOG distributions obtained from these

two sources independently were consistent (Supplementary Figure 11) and are in line with

previously obtained results in the IO (Lebreton et al. 2012; Van Sebille et al. 2015; Viatte et al.

2020). The timing of the particle releases can also have an influence on the simulation results

(Siegel et al. 2003; Curnick et al, 2021). Seasonal variability in the input of NLOGs from rivers

has been reported (Caddy and Majkowski 1996, Hinojosa et al. 2011) and there may also be a seasonal pattern in the drift of NLOGs away from mangroves and out into the open ocean. Other important drivers of NLOGs release could be storms, which are also seasonal, or extreme once-off events like tsunamis. Doong et al. (2011) estimated that in Taiwan, the Morakot typhoon was responsible for the release of more than three million trees, of which less than 50% washed up on the Taiwanese coast. Studying the effects of the magnitude, location and seasonality of input of NLOG into the ocean is therefore an important area for further research.

Possible consequences of the pelagic habitat modifications on tropical tuna and associated species

Demonstrating habitat changes due to human activities is the first step in the investigation of the ecological trap hypothesis (Marsac et al. 2000; Gilroy and Sutherland 2007). Our study clearly highlights that FADs significantly modify the "floating object component" of the habitat of pelagic species. In the western IO, this change is more pronounced in 2014-2018 than in 2007-2008 (Dagorn et al. 2013a). Our study shows that, depending on the currents, FADs generally leave the western fishing grounds and drift towards the east of the Indian Ocean.

Densities of floating objects (natural or artificial) seem to remain low, suggesting a lesser impact in the Eastern IO, but further observations are clearly needed. Because this area is not used by purse seine vessels, scientists cannot use observer data to assess the extent to which FADs modify the eastern IO. Considering both sides of the IO, our results confirm those of Dagorn et al. (2013a): the first condition for an ecological trap (namely a rapid habitat modification) seems verified. However, considering the current state of knowledge, the consequences on the ecology of species which naturally associate with floating objects cannot be directly deduced (Dagorn et al. 2013a).

An increase in FOB density (due to the addition of FADs) could potentially have positive or negative consequences on the ecology of species that naturally associate with them. Some evidence has shown that FADs act as meeting points for a small pelagic species (*Selar crumenophthalmus*, Soria et al. 2009), helping fish to form schools or increase the size of their schools. In such cases, increased numbers of FOBs could have a positive influence for associated species. However, a behavioral model developed by Sempo et al. (2013) suggests that increasing FOB densities would modify fish distribution among FOBs. Fish would either be scattered among FOBs or aggregate around a single FOB, depending on the level of sociality

displayed by the species and on the FOB density. An increase in FOB density could also impact

the time fish spend associated with FOBs, decreasing the propensity to leave an area (Kleiber

and Hampton 1994, Robert et al. 2014b).

Recently, Pérez et al. (2020) used empirical data in arrays of anchored FADs and demonstrated

that a decrease in inter-FAD distances affects the associative behavior of tuna by increasing

the amount of time they spend associated with FADs. Currently, there are no scientific results

to indicate that the associative behaviour to anchored or drifting FADs results from different

behavioral processes (Dagorn et al. 2010). Tunas seem to orient themselves towards anchored

and drifting FADs from similar distances (Girard et al. 2004 ; Moreno et al. 2007), and

association times are similar for both FAD types (Robert et al. 2012 ; Dagorn et al. 2007 ;

Tollotti et al. 2020). It is therefore coherent, following Pérez et al. (2020), to consider that an

increase in drifting FAD densities increases the time spent by tuna associated to FADs. It is

noteworthy to remember that a behavioral change induced by an habitat modification could

be both beneficial or deleterious for the associated species.

The indicator-log hypothesis posits that natural FOBs are located in productive areas and are

therefore used by fish to find such areas or stay there (Dagorn et al. 2013b). Under this

hypothesis, and under the assumption that the physiological state of tuna does not influence their associative behavior, FADs would trap tuna and other pelagic species in poorer areas and an increase in their density would enhance this trap.

The residence time around FOBs is highly variable among species, with some species (such as the oceanic triggerfish, *Canthidermis maculata*, or the rainbow runner, *Elagatis bipinnulata*) associating with FADs for up to two to three months at a time (Tolotti et al. 2020; Forget et al. 2020). FADs could therefore have an impact on large scale movements, *e.g.* modify migration patterns or facilitate dispersal of species with low movement capabilities. Moreover, past studies highlighted differences in fish plumpness, growth rate and stomach fullness between tuna caught at FADs and in free swimming schools (Marsac et al. 2000; Hallier and Gaertner 2008; Robert et al. 2014a). It is important to note that such differences in body conditions were also noticed several decades ago when Japanese fishermen, in order to catch tuna for the katsuwobushi (dried tuna), were targeting skipjack associated to floating objects as they knew they were leaner that fish in free-swimming schools. While most studies concluded that tuna are in poorer physiological conditions when associated with FOBs, it is not known if this poorer condition is the result or the cause of their association (Dagorn et al. 2013b; Robert et

al. 2014a). In order to assess the impacts of FADs, which increase the number of floating objects in the ocean, on tuna and the other associated species, future studies should investigate how these changes could affect their physiological conditions. It will also be necessary to investigate if their associative behavior, e.g. the probability to associate to floating objects, changes with their condition.

Similar studies comparing FAD and NLOG distributions do not yet exist in other oceans. Regional Fisheries Management Organizations (RFMOs) set limits on the number of FADs to be used by purse seine vessels, with the primary objective of limiting the catches of small yellowfin and bigeye tuna as well as other bycatch species. Even if some RFMOs are starting to consider other possible impacts that do not directly concern catches (e.g. induced marine pollution by the Western and Central Pacific Commission; Hanich et al. 2019), they are often of lower priority. However, the extent of the modification of the surface habitat by the deployment of FADs, and the increasing trend observed over the last decade, strongly suggest the need for increased awareness among RFMOs for including these considerations in FAD management plans. We recommend that similar studies be conducted in the other oceans in

order to obtain a global view of the modification of the surface habitat induced by FADs and

continue to alert RFMOs of this potential issue.

AUTHOR CONTRIBUTIONS

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DATA AVAILABILITY STATEMENT

Observer data and GPS positions are available upon request to the IRD's Ob7 - "Observatoire des Ecosystèmes Pélagiques Tropicaux Exploités". The Global Mangrove Watch (GMW) dataset, used to determine mangrove locations is available at https://data.unep-wcmc.org/datasets/45 (last accessed May the 10th 2021).

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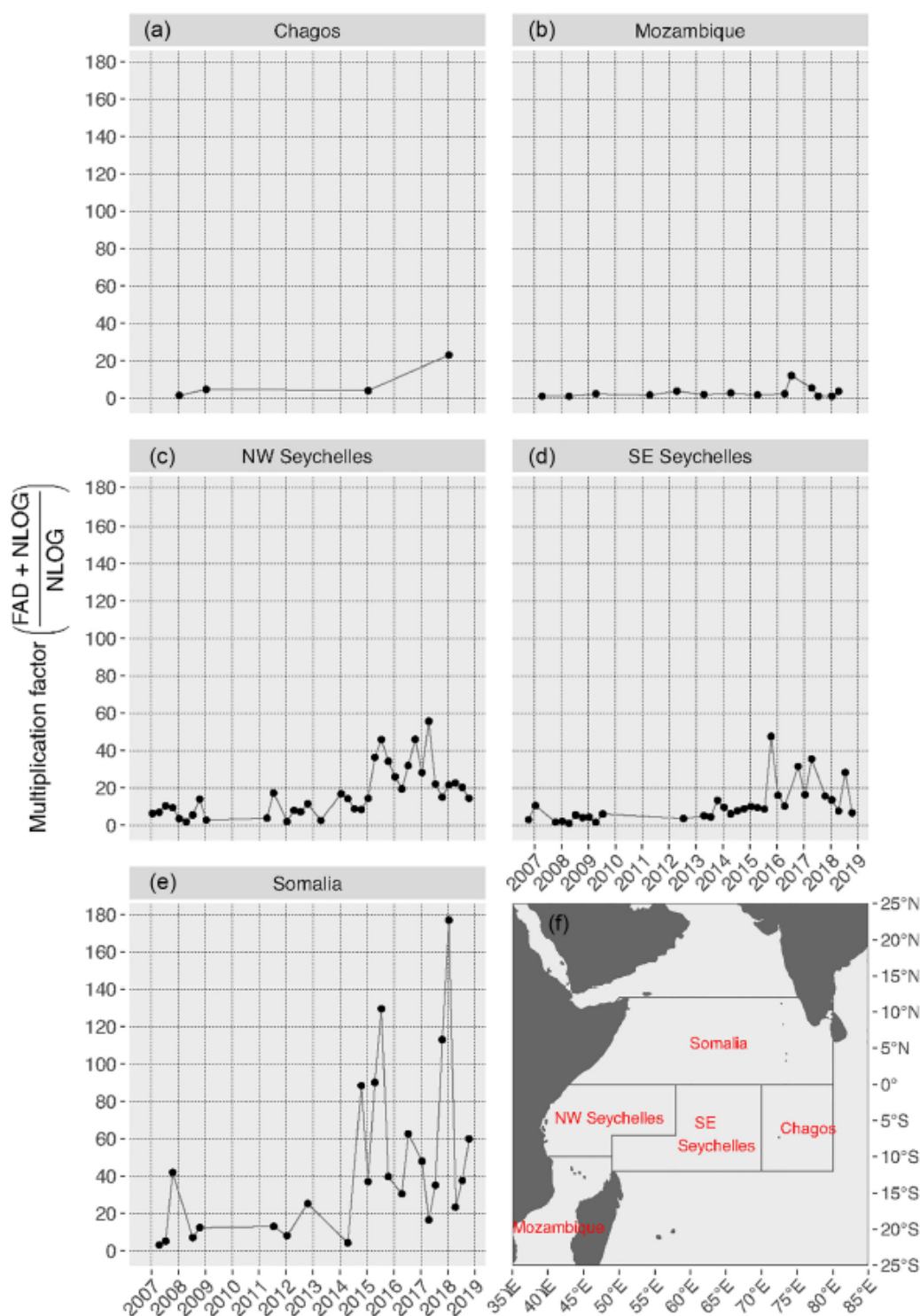
Figure 1: Change in the number of floating objects (FOBs) observed from 2006 to 2018 in the Indian Ocean. (A) Number of FOBs observed over time, by FOB type, and number of days with observations per year (black line). (B) Number of observed FOBs, by FOB type, divided by the number of days of observation. (C) Proportion of each FOB type per year. FAD (in blue): Fish Aggregating Device; NLOG (in green): Natural floating object; ALOG (in red): artificial log resulting from human activity (other than FADs).
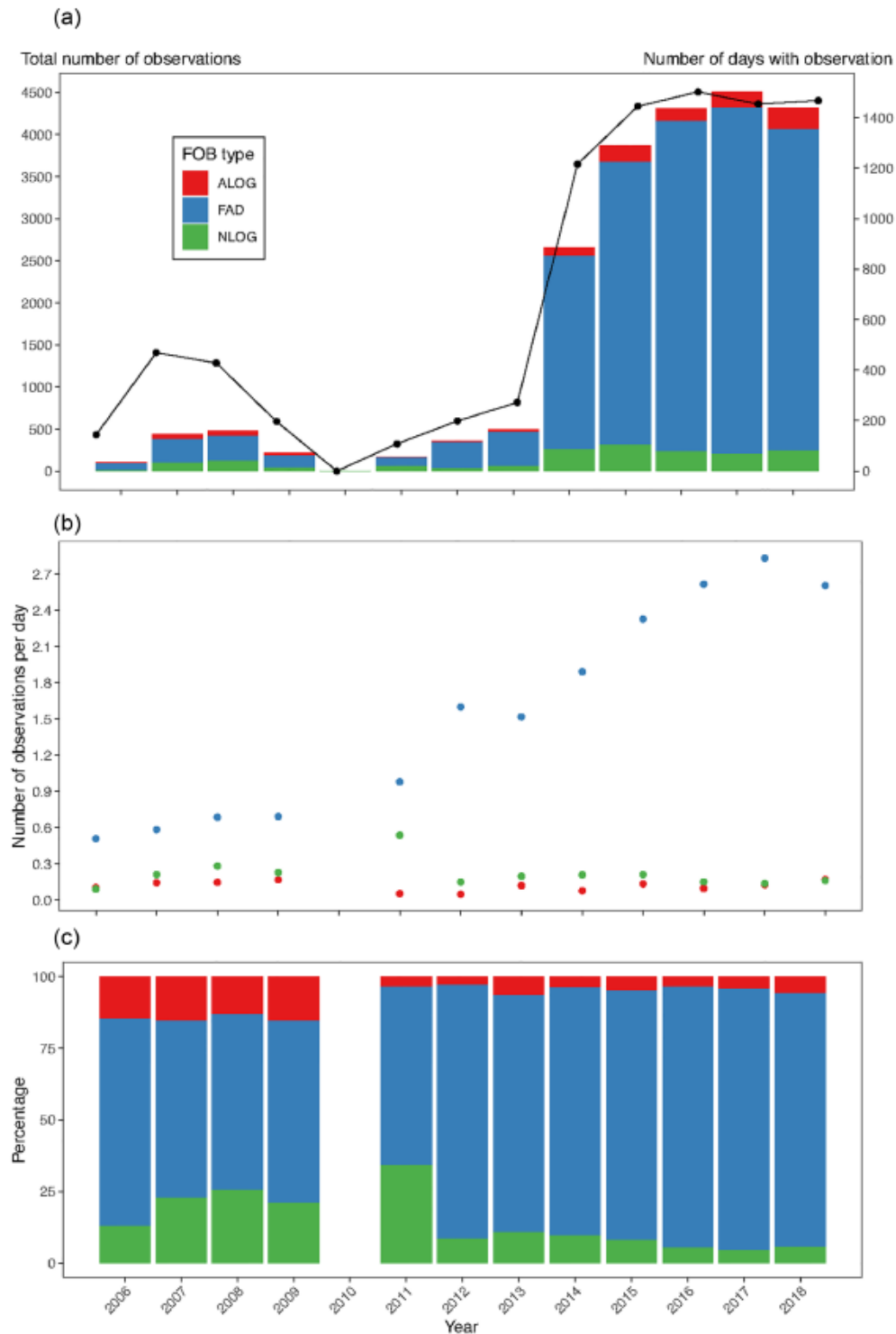
Figure 2: Quarterly median spatial distance between two consecutive encounters of FOBs for the two study periods (2007-2008 and 2014-2018). The distance was calculated between two consecutive encounters of any type of FOBs (FAD, ALOG or NLOG; black line), between encounters of FADs only (blue line) and between encounters of NLOGs only (green line). The colored areas around the lines represent the standard error.
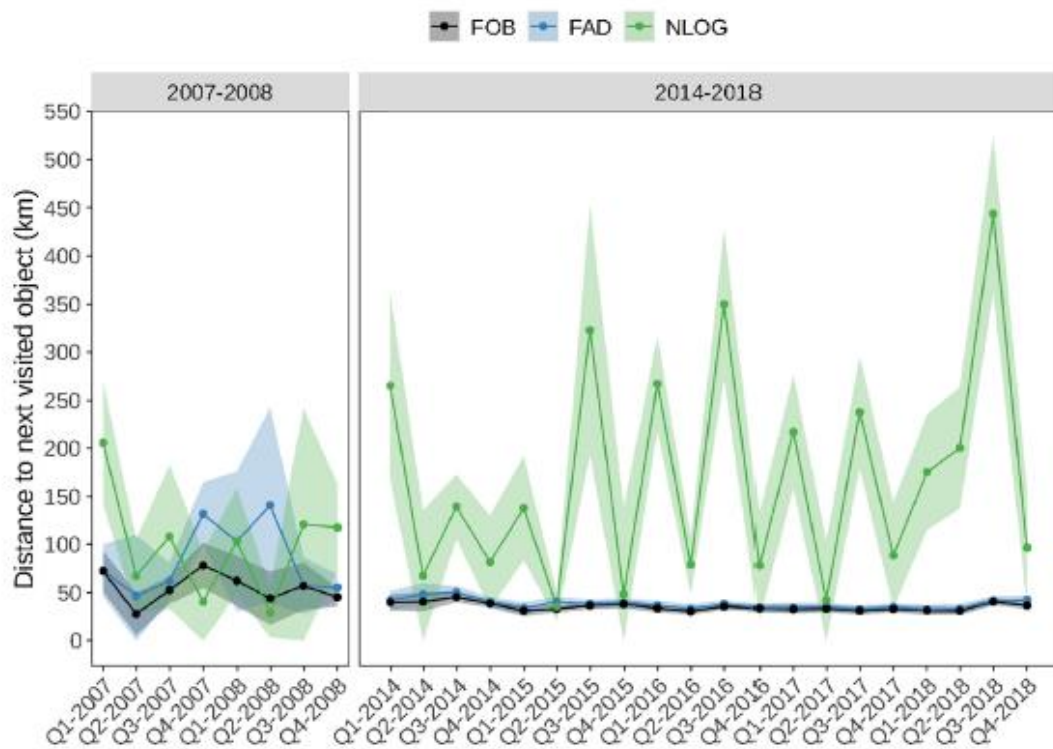
Figure 3: Quarterly multiplication factor in the different IOTC (Indian Ocean Tuna Commission) areas from 2007 to 2018: in Chagos (A), Mozambique Channel (B), North-West Seychelles (C), South-East Seychelles (D) and Somalia (E). Map of the IOTC areas as defined in Dagorn et al. (2013a) (F). The multiplication factor was calculated only for the quarters with observations of both NLOGs and FADs.

Figure 4: Spatial distribution of floating objects observed in the western Indian Ocean for the two periods (2007-2008 and 2014-2018). (A-B) Number of FAD observations divided by the number of days of observations. **(C-D)** Number of NLOG observations divided by the number of days of observations. **(E-F)** multiplication factor (ratio of FADs + NLOGs over NLOGs). Dark grey: less than 10 days of observation per cell.
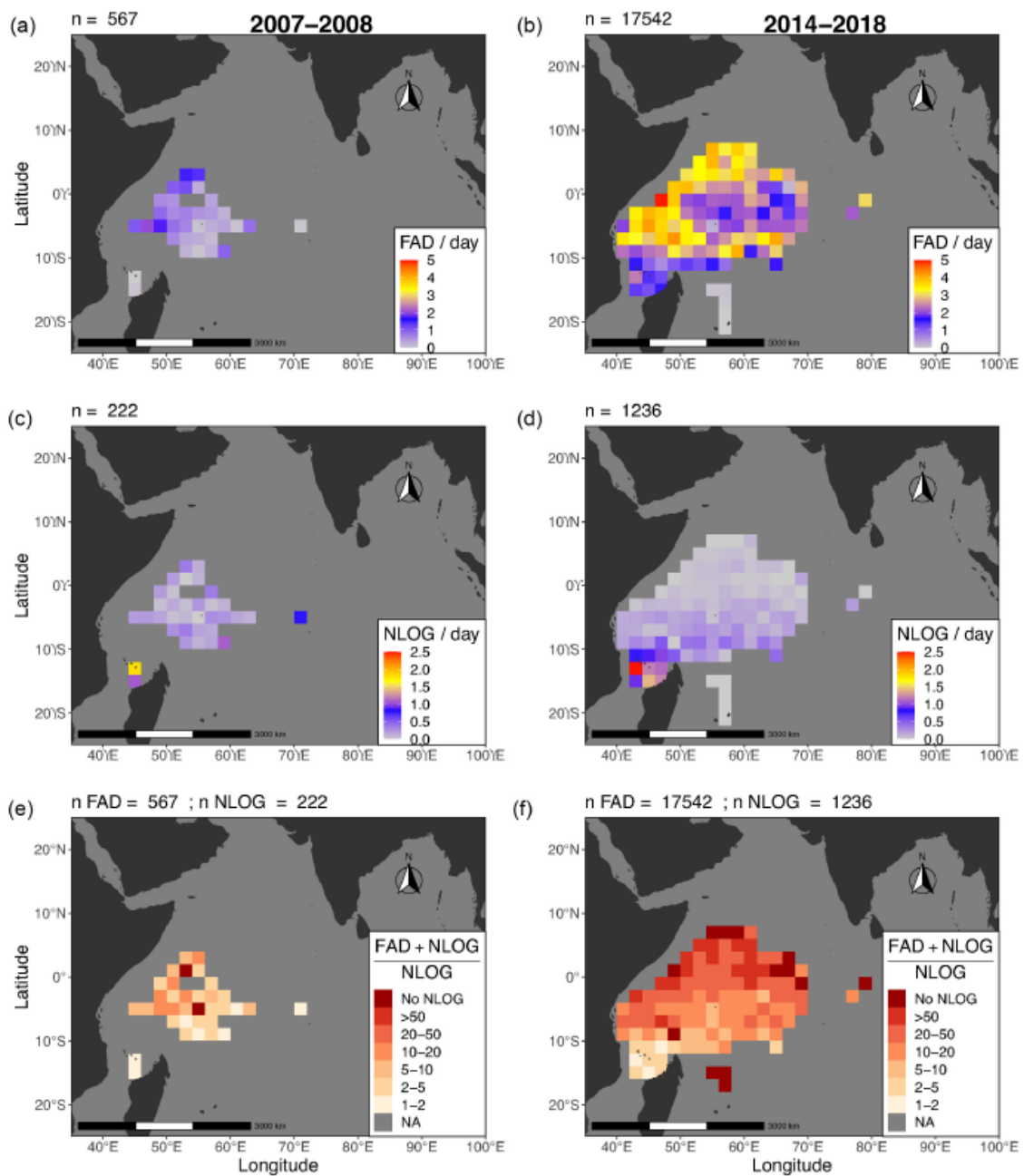
Figure 5: Spatial distribution of instrumented floating objects, from 2014 to 2018. Mean number of buoys associated with an object per day per cell (m), obtained from the GPS buoy trajectories dataset, for FADs **(A)** and NLOGs **(C)**. Number of buoys deployment per cell, obtained from the observers' dataset, on FADs **(B)** and on NLOGs **(D)**; n: total number of deployments. Dark grey: less than 10 days of observation per cell.
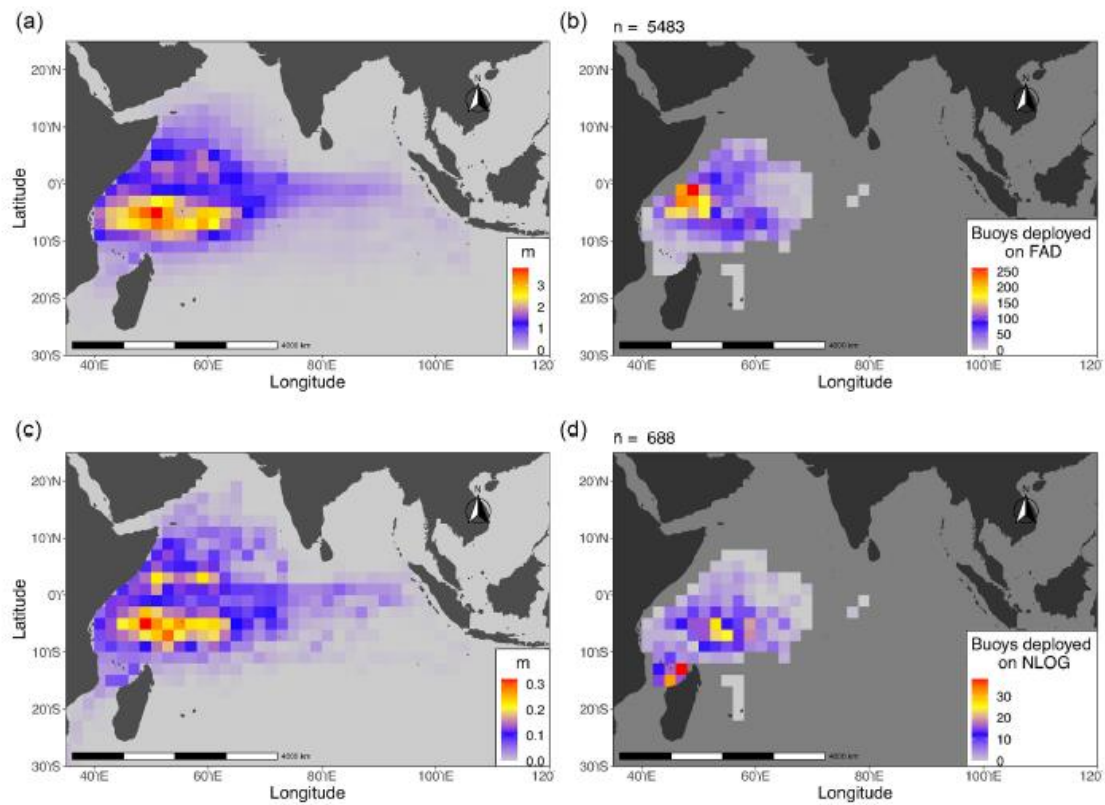
Figure 6: Putative spatial distribution of NLOGs obtained from simulated trajectories for the Indian Ocean, in 2014. The mean number of simulated NLOG per cell is shown (m), aggregated over a transport time of 180 days, using forcing currents produced by NEMO at surface. Linear color scale (A) and log transformed color scale (B).