IOTC-2021-WGFAD02-INF11

ICES Journal of Marine Science

ICES Journal of Marine Science (2021), https://doi.org/10.1093/icesjms/fsab175

Original Article

Surface habitat modification through industrial tuna fishery practices

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Dupaix, A., Capello, M., Lett, C., Andrello, M., Barrier, N., Viennois, G., and Dagorn, L. Surface habitat modification through industrial tuna fishery practices. – ICES Journal of Marine Science, 0: 1–14.

Received 12 May 2021; revised 13 August 2021; accepted 23 August 2021.

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 (FOBs) (Freon and Dagorn, 2000; Castro *et al.*, 2002). The first FOBs were all natural, mainly parts of trees (logs) floating out in the ocean. Taking advantage of the associative behaviour 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 FOBs (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 10300 active FADs recorded in September 2013 (Maufroy *et al.*, 2017). In the same period, the number of FAD deployments increased, with an estimation of 14000 deployments in 2013

(Gershman *et al.*, 2015) and this increase continued until 2018 (Katara *et al.,* 2018, Floch *et al.*, 2019). 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 Indian Ocean Tuna Commission (IOTC) 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 FOBs 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.,* 2021).

This study aims at determining the modifications of the surface habitat of tropical tuna related to the intensive deployment of FADs in the IO, 10 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) Global Positioning System (GPS) positions from tracking buoys deployed on FOBs by purse seine vessels (2014–2018).

Observer data were 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 ∼3600 to ∼11700 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 include the date, time, and location of the main activities of the vessel (e.g. fishing sets, installation or modification of FOBs, and searching for FOBs). For every activity occurring on a FOB, the type of operation (e.g. deployment, removal, and observation of a FOB) 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 (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 FOBs 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 FOBs 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, and 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; and 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 10000 mangrove polygons were randomly sampled from the 173051 polygons that compose the IO portion of the GMW 2016 shapefile (mean surface area of a polygon: 0.2 km^2). Secondly, 10000 river mouths locations were sampled out of the 18703 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 three-dimensional 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 1×10^{-9} m^2/s^3 [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 22657 observations of FOBs from 2006 to 2018, 19155 (84.5%) of which were FADs, 1666 (7.4%) were NLOGs and 1836 (8.1%) were ALOGs. The number of FOB observations increased after 2013, with more than 4000 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 1200 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

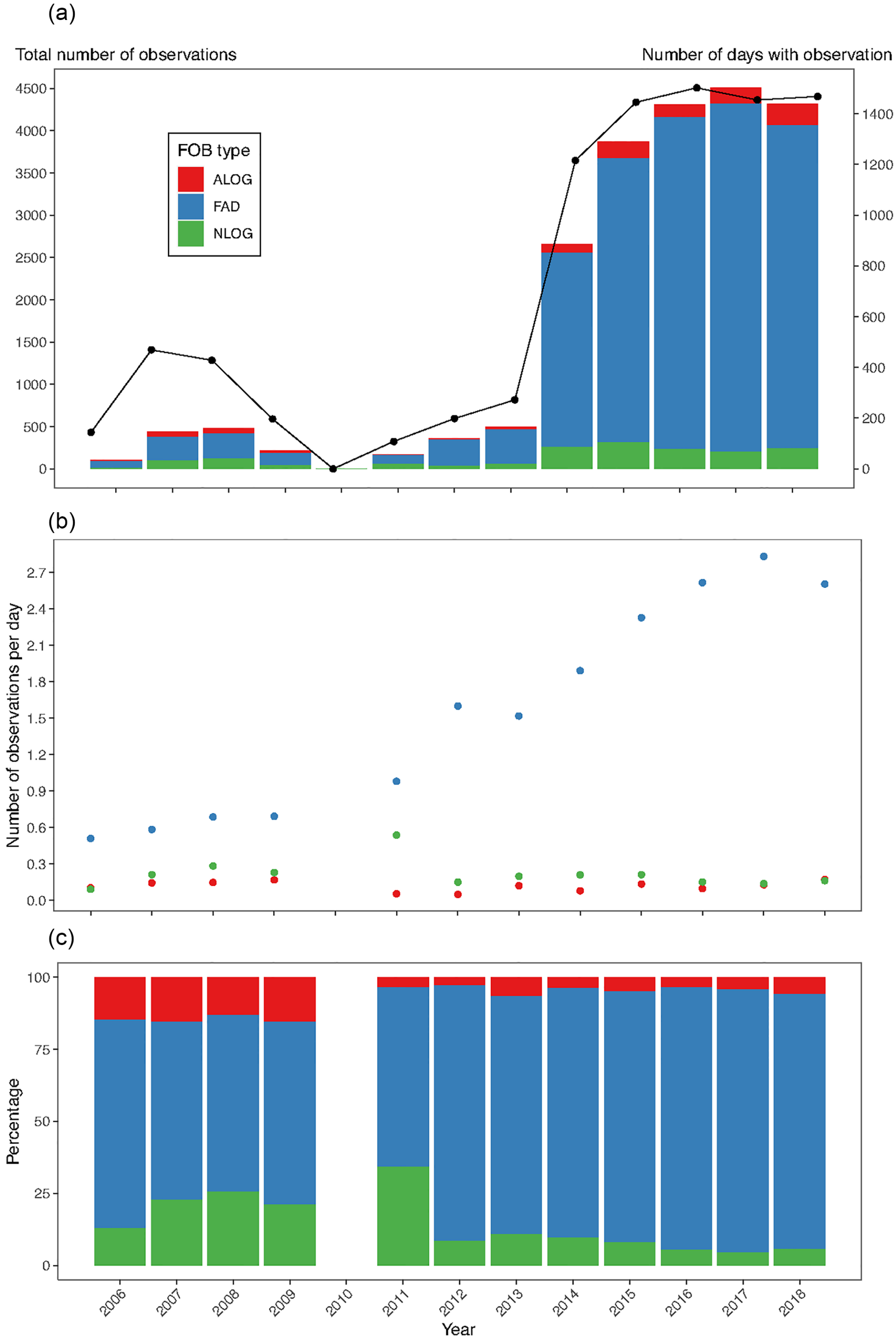

Figure 1. Change in the number of FOBs observed from 2006 to 2018 in the IO. (a) Number of FOBs observed over time, by FOB type, and number of days with observations per year (black line). (b) Number of observed FOBs, by FOB type, divided by the number of days of observation. (c) Proportion of each FOB 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).

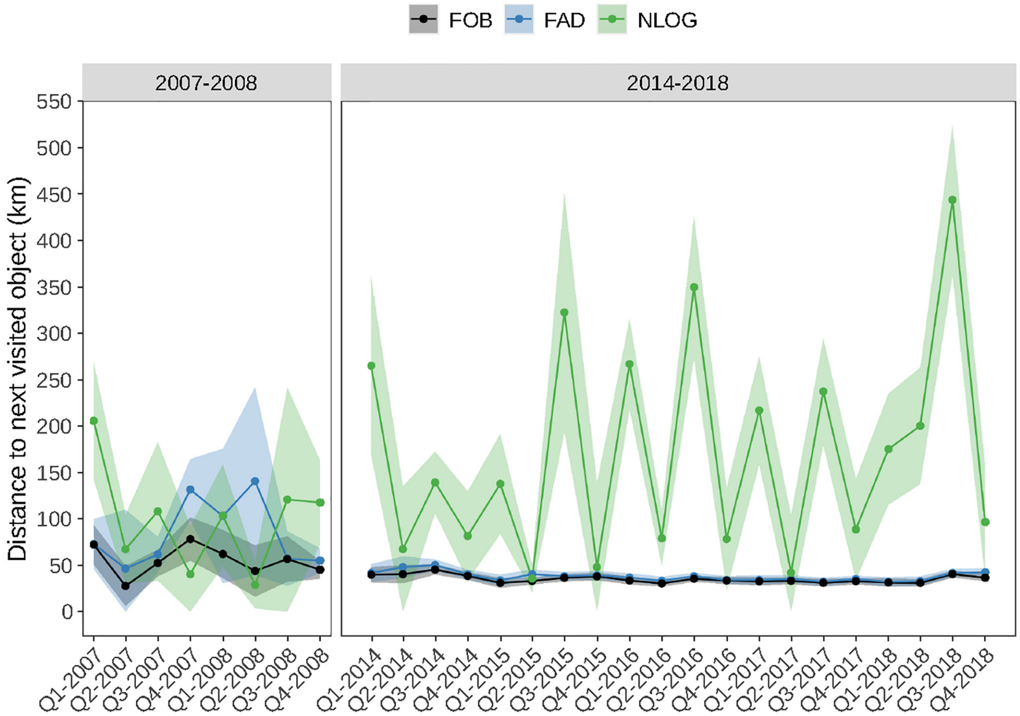

Figure 2. Quarterly median spatial distance between two consecutive encounters of FOBs for the two study periods (2007–2008 and 2014–2018). The distance was calculated between two consecutive encounters of any type of FOBs (FAD, ALOG, or NLOG; black line), between encounters of FADs only (blue line) and between encounters of NLOGs only (green line). The colored areas around the lines represent the SE.

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 $W = 1.3 \times 10^7$, $p = 2.0 \times 10^{-59}$ with NLOGs). The median distance between two consecutive NLOGs did not significantly differ between the two study periods ($W = 9.2 \times 10^4$, $p = 0.36$). However, the median distance between two consecutive FADs or between two FOBs of any type decreased ($W = 5.8 \times 10^6$, $p = 9.5 \times 10^{-23}$ and $W = 1.0 \times 10^7$, $p = 2.0 \times 10^{-20}$, respectively) after 2014. Finally, seasonal differences were observed in the distance between NLOGs, with larger distances in quarters 1 (December–February) and 3 (June–August) than in quarters 2 (March–May) and 4 (September–November) (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: $\chi^2 = 36.3$, $p = 2.5 \times 10^{-7}$). 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 North-West Seychelles, and 4.0 ($SD = 3.2$) in South-East 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: $W = 11$, $p = 1.5 \times 10^{-2}$; $W = 6$, $p = 1.9 \times 10^{-5}$; and $W = 10$, $p = 1.9 \times 10^{-3}$ in Somalia, North-West Seychelles, and South-East Seychelles, respectively. The maximum observed multiplication factor was 177, 56, and 48 in Somalia (1st quarter 2018), North-West Seychelles (2nd quarter 2017) and South-East 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).

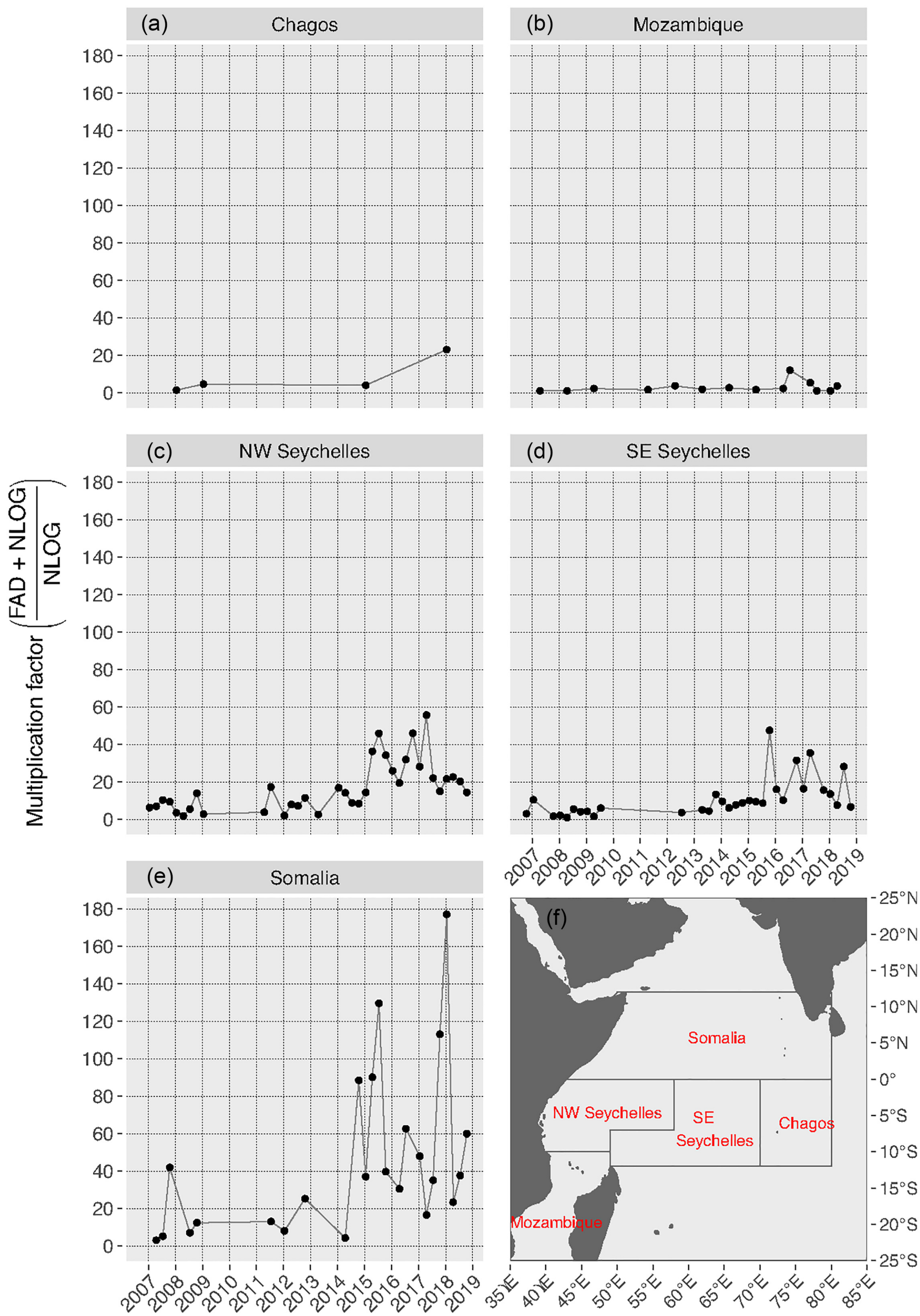

Figure 3. Quarterly multiplication factor in the different IOTC areas from 2007 to 2018: in Chagos (a), Mozambique Channel (b), North-West Seychelles (c), South-East Seychelles (d), and Somalia (e). Map of the IOTC areas as defined in Dagorn *et al.* (2013a) (f). The multiplication factor was calculated only for the quarters with observations of both NLOGs and FADs.

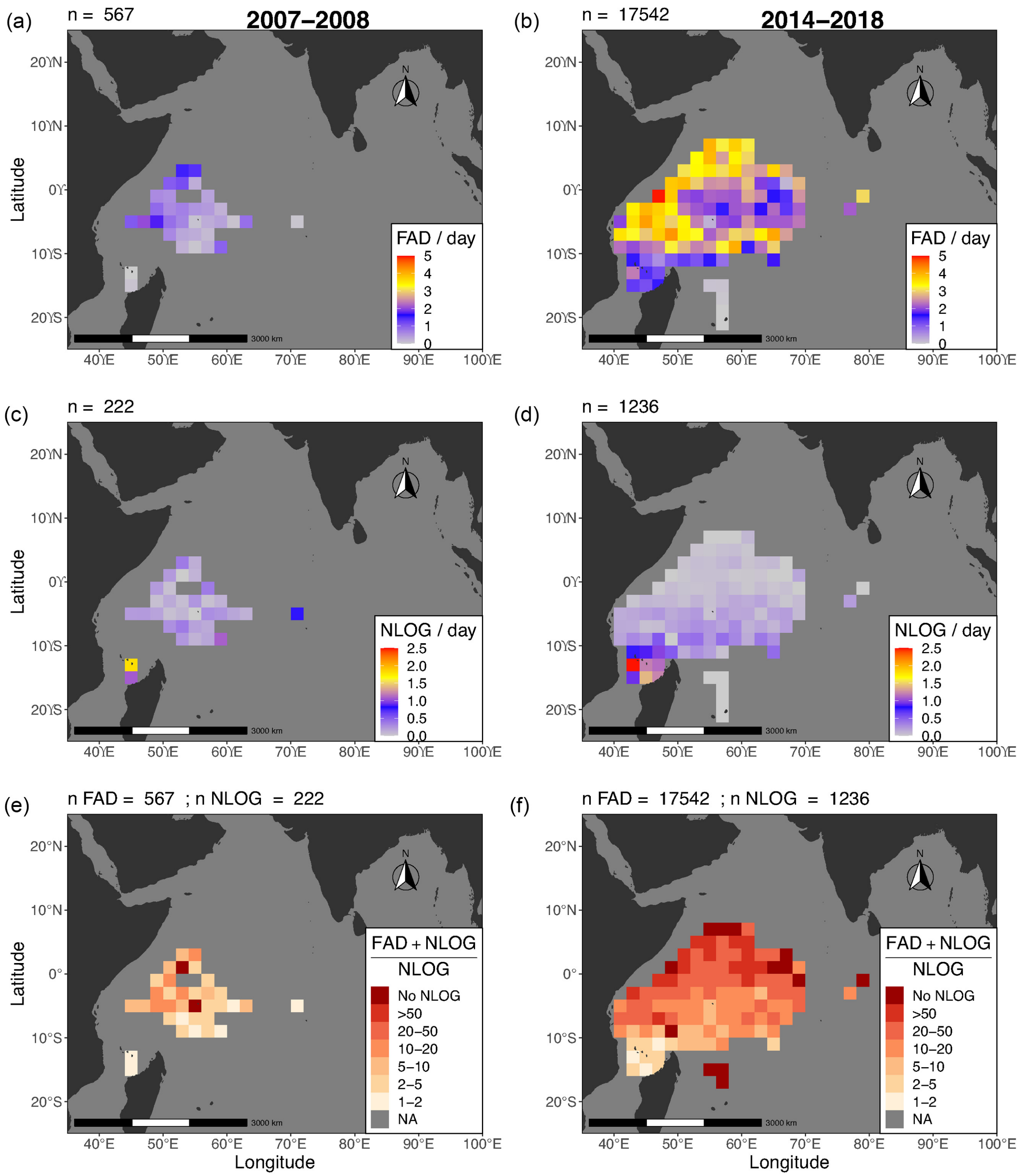

Figure 4. Spatial distribution of FOBs observed in the western IO for the two periods (2007–2008 and 2014–2018). (a–b) Number of FAD observations divided by the number of days of observations. (c–d) Number of NLOG observations divided by the number of days of observations. (e–f) multiplication factor (ratio of FADs + NLOGs over NLOGs). Dark grey: less than 10 days of observation per cell.

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 6136 different FOB trajectories, 5686 (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 (3.18×10^{-1} FAD/cell) was around ten times higher than the density of instrumented NLOGs (3.60×10^{-2} NLOG/cell). The distribution of buoy deployment

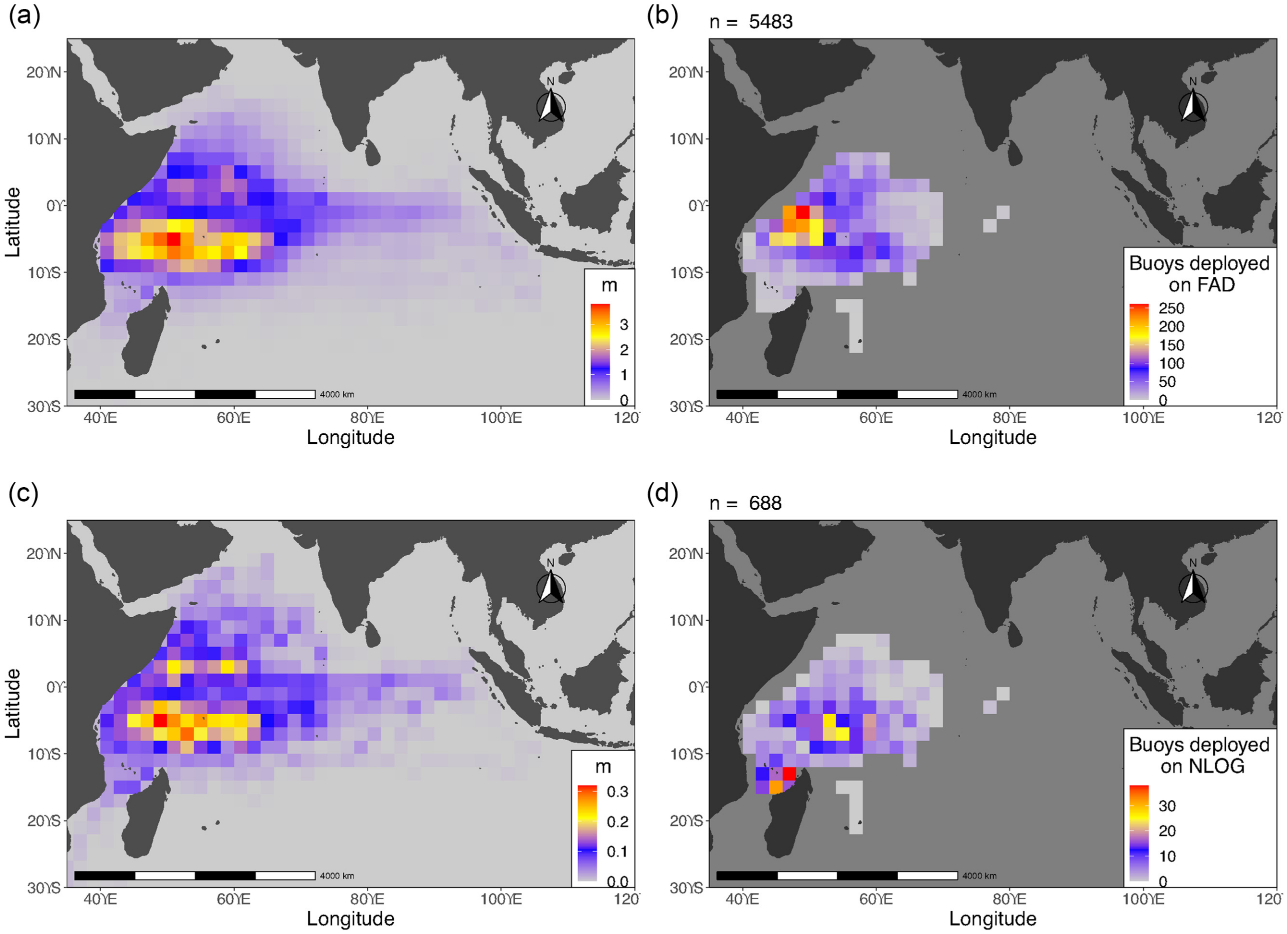

Figure 5. Spatial distribution of instrumented FOBs, from 2014 to 2018. Mean number of buoys associated with an object per day per cell (m), obtained from the GPS buoy trajectories dataset, for FADs (a) and NLOGs (c). Number of buoys deployment per cell, obtained from the observers' dataset, on FADs (b) and on NLOGs (d); n: total number of deployments. Dark grey: less than 10 days of observation per cell.

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 S8, with other forcing products in Supplementary Figure S9). Results were similar when considering inputs either from mangroves only or from rivers only (Supplementary Figure S11). 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 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 to 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

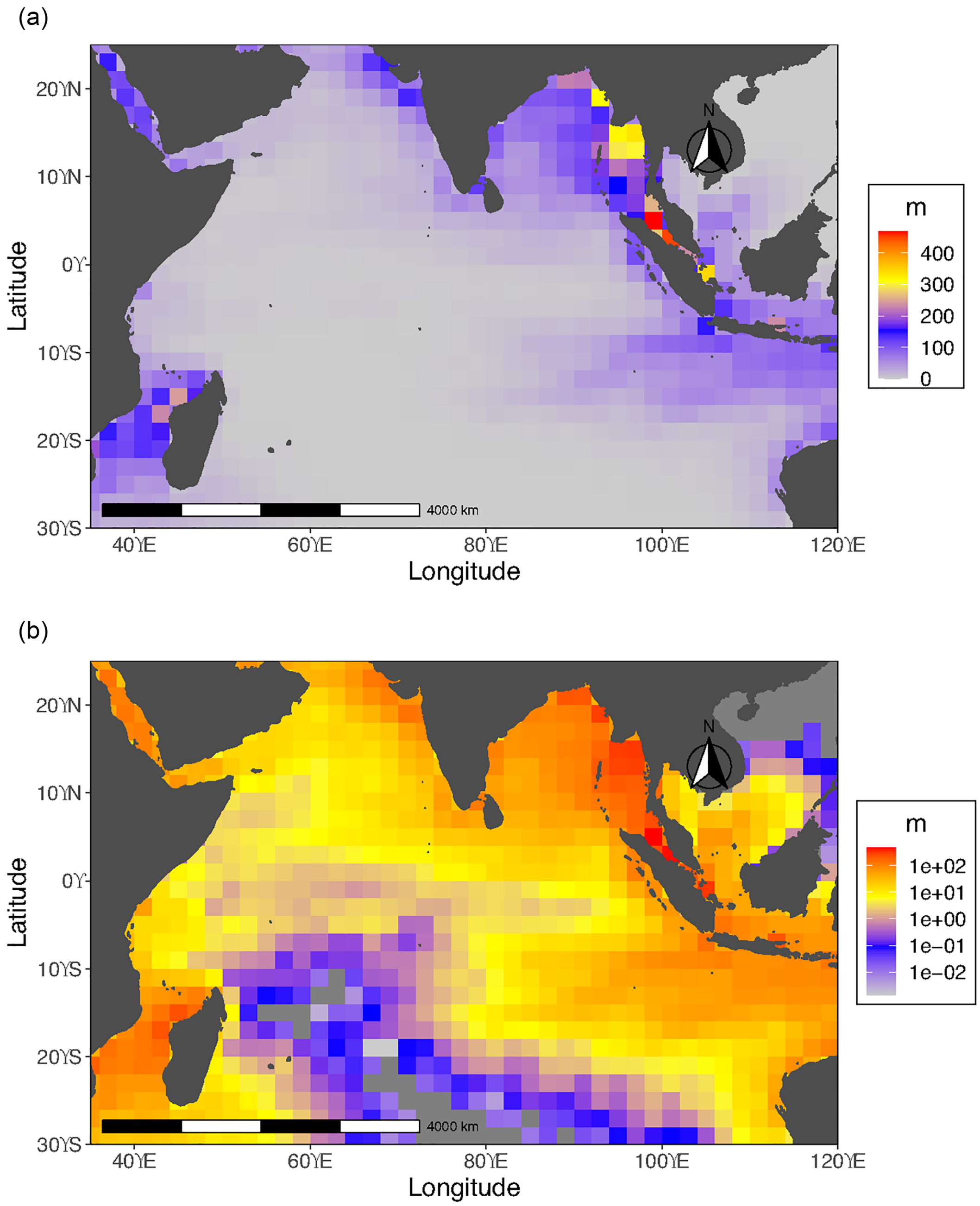

Figure 6. Putative spatial distribution of NLOGs obtained from simulated trajectories for the IO, in 2014. The mean number of simulated NLOG per cell is shown (m), aggregated over a transport time of 180 days, using forcing currents produced by NEMO at surface. Linear color scale (a) and log transformed color scale (b).

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 FOBs) 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 North-West Seychelles and South-East Seychelles, and multiplication factors have increased three to fourfold 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 FOBs 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 S1–S4). 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 provide access to every encountered FOB, 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 S5), this seasonal coverage precludes the balanced sampling of all regions. Buoy GPS data do 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 S5 and S6), 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 remain 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 a Marine Protected Area 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 S7). 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 S9). 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 1000 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 S8) 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 S10). 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 (Davies *et al.*, 2017; Curnick *et al.*, 2021). Mangrove and rivers are the two most likely sources of NLOGs (Caddy and Majkowski, 1996; Krajick, 2001; Thiel and Gutow, 2005). The NLOG distributions obtained from these two sources independently were consistent (Supplementary Figure S11) 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 IO. Densities of FOBs (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 FOBs 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 behavioural 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 behaviour 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 behavioural 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 behavioural 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 behaviour, 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 FOBs as they knew they were leaner than 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 FOBs 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 behaviour, e.g. the probability to associate to FOBs, changes with their condition.

Similar studies comparing FAD and NLOG distributions do not yet exist in other oceans. 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.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contributions

CL, MA, MC, and LD conceived the idea. AD performed the analysis. MC and LD provided advice on the analysis of the observer and GPS data. CL, GV, MA, and NB provided advice on the Ichthyop simulations. AD led the writing. All authors discussed the results, contributed to the writing, and gave final approval to the manuscript.

Funding

This study was supported by the Mediterranean Centre for Environment and Biodiversity Laboratory of Excellence (CeMEB LabEx), through the research project TREES@SEA (Floating objects in the open ocean: unveiling modifications of the pelagic habitat induced by global change).

Data availability statement

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

Acknowledgements

The observer data used were collected through the Data Collection Framework (Reg 2017/1004 and 2016/1251) funded by both IRD and the European Union and OCUP (Observateur Commun Unique et Permanent), an industry-funded program coordinated by ORTHONGEL since 2014. The authors sincerely thank IRD's Ob7–"Observatoire des Ecosystèmes Pélagiques Tropicaux Exploités"—in charge of the observer data collection, processing, management, and for sharing the data used in this study.

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Handling Editor: Manuel Hidalgo