Can drifting objects drive the movements of a vulnerable pelagic shark?

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Abstract

1. Juvenile silky sharks (*Carcharhinus falciformis*) regularly associate with floating objects yet the reasons driving this behaviour remain uncertain. Understanding the proportion of time that silky sharks spend associated with floating objects is essential for assessing the impacts of the extensive use of fish aggregating devices (FADs) in the tropical tuna purse-seine fisheries, including increased probability of incidental capture and the potential of an ecological trap.

2. Previous studies provided insight into the amount of time that silky sharks spent at an individual FAD but were unable to assess neither the time spent between two associations nor the proportion of time spent associated/unassociated.

3. The percentage of time that juvenile silky sharks spend unassociated with floating objects was estimated through the analysis of horizontal movements of 26 silky sharks monitored with pop-up archival tags. Under the assumption that a high association rate with drifting FADs would align the trajectories of tracked sharks with ocean surface currents, a novel methodology is proposed, based on the comparison of shark trajectories with simulated trajectories of passively drifting particles derived using a Lagrangian model.

4. Results revealed that silky shark trajectories were divergent from surface currents, and thus unassociated with FADs, for at least 30% of their time. The potential of the methodology and the results are discussed in the context of increasing FAD densities in the Indian Ocean.

KEYWORDS

bycatch, fish aggregating devices, Lagrangian drift model, pop-up satellite archival telemetry, silky shark, vulnerability

1 | INTRODUCTION

The silky shark (*Carcharhinus falciformis*) is a pelagic shark with a circumglobal distribution in tropical and sub-tropical waters. Despite this wide range, little is known about its population sizes or trends in abundance (Bonfil, 2009). Owing to life-history traits common to many large top predators, such as low fecundity and late maturation, this species is particularly vulnerable to fisheries (Branstetter, 1987;

Oshitani, Nakano, & Tanaka, 2003) and is considered Near Threatened globally (Camhi, Valenti, Fordham, Fowler, & Gibson, 2009). Silky sharks are primarily caught in longline fisheries (Gilman et al., 2008) and to a lesser extent by tropical tuna purse-seine fisheries using fish aggregating devices (FADs) (Dagorn, Holland, Restrepo, & Moreno, 2013). FADs are typically floating rafts that are deployed by fishers in order to increase their access to schools of tropical tuna, which regularly associate with floating objects. These FADs can drift

with the currents for several months and their positions are remotely tracked in real-time using GPS. During their drifts, large aggregations of tropical tuna form around the FADs, along with several other pelagic species, including the silky shark. Tropical tuna purse-seine fisheries have two direct impacts on silky sharks: incidental bycatch, mainly when vessels set nets around floating objects (Dagorn, Holland, et al., 2013) and shark entanglement in FAD nets (Filmalter, Capello, Deneubourg, Cowley, & Dagorn, 2013). A third possible impact involves the possibility of an ecological trap, i.e. the risk that sharks become trapped within arrays of drifting FADs (an anthropogenic alteration to the natural habitat) for long periods of time, potentially modifying their movements and negatively impacting their biology (Marsac, Fonteneau, & Ménard, 2000).

Silky sharks constitute 90% of the elasmobranch bycatch caught within tropical tuna purse-seine fisheries (Dagorn, Holland, et al., 2013; Gilman, 2011). The similarity between the diel associative behaviour of silky sharks and tunas (association with FADs during daytime with excursions at night) explains why they are frequently caught when purse seiners set on floating objects (Forget et al., 2015). To reduce the fishing mortality of silky sharks, different mitigation methods have been proposed, e.g. targeting bigger schools of tunas to reduce bycatch proportions (Dagorn et al., 2012) or implementing better release practices (Eddy, Brill, & Bernal, 2016; Hutchinson, Itano, Muir, & Holland, 2015; Poisson, Filmalter, Vernet, & Dagorn, 2014; Poisson, Seret, Vernet, & Goujon, 2014). Despite these measures, the increased number of sets on FADs (Marsac, Fonteneau, Lucas, Báez, & Floch, 2017) results in an increased number of silky sharks being incidentally caught by the purse-seine fisheries. Conversely, the evaluation of the extent of shark entanglement in the underwater nets of the FADs (Filmalter et al., 2013) has resulted in three of the four tuna Regional Fisheries Management Organizations responsible for the conservation and management of tunas, adopting resolutions on the use of non-entangling FADs (Murua et al., 2016). Finally, the consequences of anthropogenic habitat changes induced by increasing numbers of artificial floating objects (Dagorn, Bez, Fauvel, & Walker, 2013; Maufroy et al., 2017; Moreno, Dagorn, Sancho, & Itano, 2007) remain largely unknown.

The total number of FADs deployed by purse-seine fishing vessels represents the key variable determining the extent of the impacts of FAD fisheries. Some Regional Fisheries Management Organizations have set maximum limits controlling the number of FADs per vessel (e.g. 350 for the Indian Ocean) (IOTC, 2017). However, assessing the efficacy of such limits remains a point of debate due to limited knowledge on the relationships between the number of FADs and per-vessel catch (tunas and bycatch, including the silky shark) and the risk of an ecological trap. A critical variable in assessing such impacts is the proportion of time that these species spend in association with floating objects and how this could change as a function of local FAD density and environmental conditions. Species spending a small proportion of time associated with floating objects are assumed to be less vulnerable to fishing, and would have a lower probability of becoming trapped in an array of drifting objects. Recent behavioural studies

using acoustic telemetry methods highlighted the strong associative behaviour of juvenile silky sharks with floating objects, and estimated the average continuous residence times of 15 days and maximum observed continuous associations with the same FAD of 30 days (Filmalter, Cowley, Forget, & Dagorn, 2015). However, these field studies could not measure the time that tagged sharks spent between two floating object associations (absence times). Estimating this variable is critical for assessing the vulnerability of this species to FAD fisheries.

To date, two experimental designs have been utilized to estimate absence times. The first consisted of instrumenting all FADs within an array with acoustic receivers, and detecting fish equipped with coded acoustic tags within the array. Several field studies conducted on tunas at anchored FADs adopted this approach to measure the time spent at FADs and the time between two FAD associations. (Dagorn, Holland, & Itano, 2007; Robert, Dagorn, Filmalter, Deneubourg, Itano, & Holland, 2013; Rodriguez-Tress et al., 2017). Using this method Capello et al. (2016) estimated that yellowfin tuna (*Thunnus albacares*) spent 72% of their time associated with FADs in the array of anchored FADs around Oahu (Hawaii, USA), which is considered to be a high association rate. However, this approach is near impossible to replicate with drifting FADs due to the difficulty in locating all drifting objects within an area and the fact that arrays of drifting objects do not maintain their integrity for extended periods of time (e.g. floating objects do not always drift in parallel).

The second method consists of using the vertical behaviour of certain species to identify their association status. Some species, such as bigeye tuna (*T. obesus*) and in certain areas yellowfin tuna, exhibit different vertical behaviours during periods of association with a floating object and when they are free-swimming. The analysis of time series of vertical behaviour data of fish equipped with archival tags allowed the associative dynamics of these animals to be reconstructed (Phillips et al., 2017; Schaefer & Fuller, 2010). These studies estimated that bigeye and yellowfin tuna spend an average of 83 and 77% of their time respectively, in an unassociated state. Although the simple comparison of yellowfin tuna behaviour reported by Capello et al. (2016) and Phillips et al. (2017) highlights a need to conduct paired tests to distinguish between the two methods, this divergence could reveal that the same species can exhibit highly variable association rates. This emphasizes the need for further investigation into the effects of different variables (e.g. density of floating objects, biotic and abiotic environmental conditions) on association rates.

As silky sharks have not been found to display different vertical behaviour during associated and unassociated phases,, and are less commonly encountered within arrays of anchored FADs, neither of the methods described above have been successfully applied to this species for estimating association rates.

In this study, a novel approach for estimating the proportion of time silky sharks spend associated with floating objects is proposed. Recently, Imzilen et al. (2019) showed that FADs drifted identically to oceanographic drifters, i.e. followed the ocean near-surface currents. This result was used to hypothesize that a strong association rate in

silky sharks would result in shark trajectories following these currents. Conversely, a weak correlation between shark trajectories and currents would suggest a low association rate with FADs. As such, a methodology was developed here to estimate this association rate, using tracks of silky sharks obtained with pop-up archival tags compared with outputs of a Lagrangian passive drift model from the western Indian Ocean.

2 | MATERIALS AND METHODS

2.1 | Electronic tagging

Twenty-six silky sharks were caught at FADs in central western Indian Ocean in water surrounding the Seychelles and in the Mozambique Channel. Sharks were tagged with Pop-up Satellite Archival Tags (miniPAT; Wildlife Computers, Redmond, WA, USA) between 2010 and 2012 (see Table S1 for additional information). All sharks were caught and released in association with drifting FADs. Sharks were either captured during purse-seine operations or during dedicated tagging cruises when baited hand lines were used. The majority of the silky sharks were juveniles, with total length ranging from 87 to 235 cm (median: 111.5 cm). Tags were either attached using a tethered anchor inserted into the dorsal musculature near the base of the dorsal fin, or directly to the dorsal fin using a threaded nylon rod to which the tag was tethered. Tags were programmed to automatically release from the animal after either 100 or 150 days. Following release, the tags floated to the surface (popped up) and transmitted archived data, including light levels recorded during the deployment, via the ARGOS satellite system. The deployment period of the 26 tagged sharks ranged from 27 to 141 days with a mean of 55.2 days (SD 33.9 days).

2.2 | Geolocation estimates

Geographical positions were reconstructed from light intensity data, with some positions determined accurately through acoustic tagging. This information, along with sea surface temperature and depth data, was processed using the GPE3 model available on the Wildlife Computers Data Portal (http://my.wildlifecomputers.com/data/) to provide the most likely positions on a daily basis. In a few cases, double tagging with acoustic tags allowed the position of the shark to be determine accurately due to their time-stamped detection by acoustic receivers on FADs and its associated GPS data. Apart from the accurate locations obtained through acoustic tagging, the light-based geolocation estimates are subject to considerable errors (Teo et al. 2004). To account for this error, the overall uncertainty of the geolocation (herein referred to as the *radius of uncertainty*) was estimated as the average distance to the 99% likelihood contour estimated over all the trajectories (Figure 1).

2.3 | Relationship between shark trajectories and ocean surface currents

2.3.1 | Brief overview of the method

Shark trajectories were compared with trajectories of simulated drifting particles released in the proximity of the shark geolocation estimate, within the *radius of uncertainty*. Divergence of shark subtrajectories from surface currents was assessed through an evaluation of the distance between a shark's position and simulated particles. To assess the validity of the method, the same approach was applied to trajectories of oceanographic drifters that are known to follow ocean currents. Geographical areas where the method was invalidated were
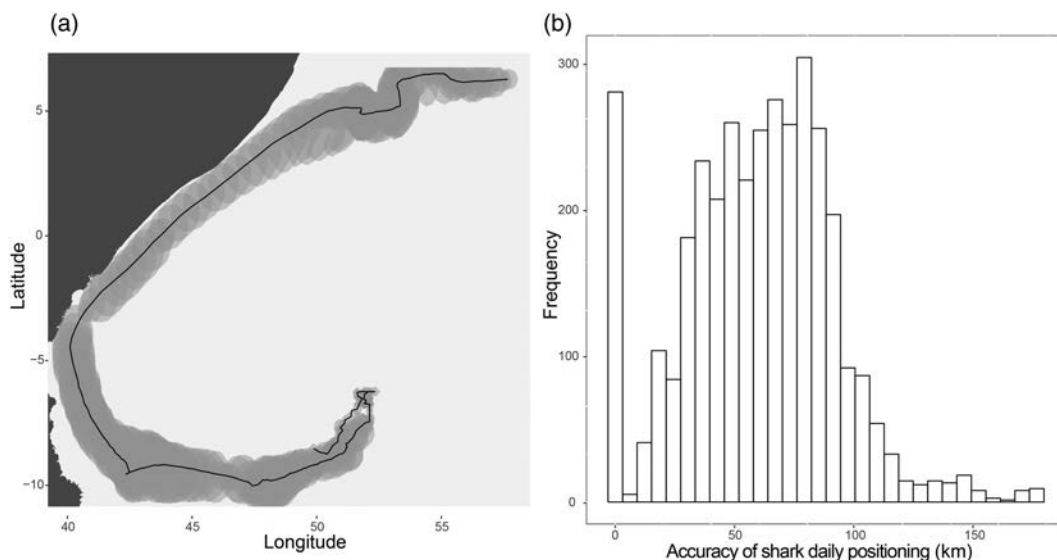

FIGURE 1 Accuracy of shark positioning. (a) The black line corresponds to the most likely daily positions of an individual shark, shaded grey presents the daily 99% likelihood contours of the individual's daily positions. (b) Average distance from most likely positions to the 99% likelihood contour was calculated for each daily shark position, the distribution of these daily average distances is plotted here

thereby removed from the analyses. For retained areas, the increasing tendency of shark trajectories to separate from simulated particles compared to drifter trajectories was used to draw conclusions about sharks' divergence from surface currents.

2.3.2 | Details of the method

From each shark trajectory, sliding window portions of x days were sampled. The final part of the trajectory corresponding to $x-1$ days was excluded from the analysis (for example a 20 days long trajectory with a 6-day sliding window resulted in 15 portions each six days long and each one day later than the preceding portion). For each x days long track portion, the hypothesis H_0: the animal follows sea surface circulation; was tested. For this purpose, a cloud of 1,000 virtual particles was released within the *radius of uncertainty R* of 100 km around the initial position of the track portion. The choice of R was based on a rounded value of the estimated average 99% likelihood contour (Figure 1). The trajectories of the virtual particles were simulated as passively drifting for x days with the Ichthyop software (Lett et al., 2008), forced with modelled ocean near-surface current data from the OSCAR product ($1/3°$ spatial resolution, five days temporal resolution) (ESR, 2009). To assess if the final position of the shark track portion was consistent with passive drift, the distance to the closest simulated particles was measured (CD_{animal}: for 'Closest Distance' = average distance to the N_{CD} = 10 closest simulated particles), and compared with distances obtained from strictly drifting objects ($CD_{strict\ drift}$), i.e. measured from simulated trajectories. The latter was obtained by randomly sampling a number N_{sample} of simulated particles. If CD_{animal} was observed to be greater than 95% of $CD_{strict\ drift}$, i.e. the animal position separated significantly from the cloud of simulated particles, H_0 was rejected and the animal track portion was considered as incompatible with passive drift.

The analysis was conducted considering track portions of x = 6 days. This duration of six days was selected according to the average ocean surface current speed (v = 0.2 m/s = 17 km/d) and the subsequent required time for a virtual particle strictly moving straight

forward to leave the initial 100-km release radius. Accordingly, for durations less than six days, H_0 would not even be rejected for a stationary animal as its position would remain within the cloud of simulated drifting particles. In summary, both the spatial scale of 100 km and the temporal scale of six days are larger than the OSCAR resolution, which limits the bias induced by mesoscale features not represented by the OSCAR product. Figure 2 illustrates the classification approach, H_0-accepted or -rejected, for two animal tracks.

To assess the accuracy of our classification method and to identify potential biases, the same method was applied to trajectories from a set of oceanographic drifters from the Global Drifter Program (GDP) (Centurioni, Horányi, Cardinali, Charpentier, & Lumpkin, 2016) as these were known to follow the movements of water masses. The GDP dataset was subsampled for trajectories within the study period (2010–2012) and the geographical extent of shark trajectories (central western Indian Ocean), resulting in a dataset of 190 trajectories, encompassing a total of 14,030 daily positions. This comparison allowed for the identification of regions where our method systematically misclassified track portions as having not followed surface currents. To facilitate the comparison and identify areas of systematic error, a 2° resolution grid was applied to the central western Indian Ocean. Grid cells for which more than a given percentage threshold (named below T%) of drifter track portions were classified as H_0-rejected were removed from the shark trajectory analysis. The baseline analysis was conducted considering a percent threshold T = 50% and sensitivity analysis was conducted for the following values of T%: 20, 30, 40, 60, 70 and 80%.

Even within the selected cells, drifter track portions were not always classified as H_0-accepted for all of the GDP samples. The proportion P' of misclassified GDP track portions was used to establish a lower bound for the proportion of time that a shark actively diverged from the ocean surface currents. As such, if every animal track portion was actually following surface currents as drifters do, there would be a proportion P' of them that would still be classified as H_0-rejected due to the inherent uncertainty within the method. If P is defined as the fraction of animal track portions classified as H_0-rejected, then a
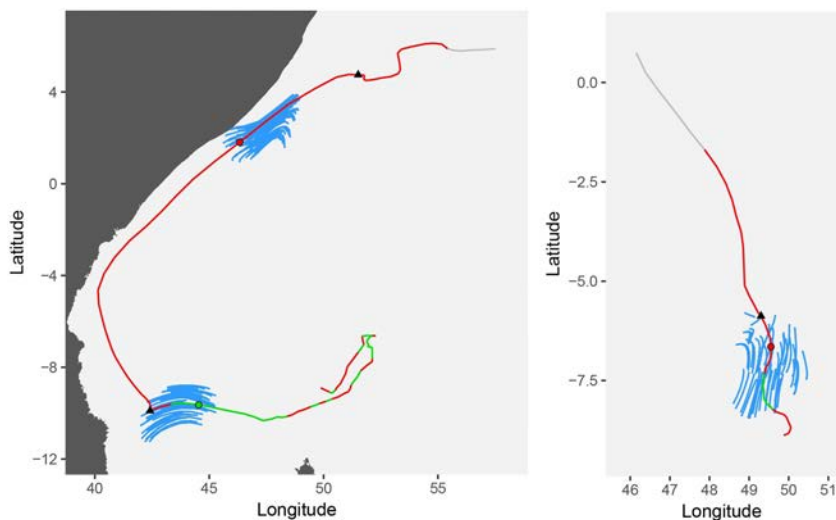

FIGURE 2 Example of classification for compliance with the passive drift hypothesis for two individual shark tracks. Track portions are considered over six days and their starting point are coloured in green if compatible with passive drift hypothesis (H_0-accepted) and in red if not (H_0-rejected). Blue tracks represent Ichthyop virtual particles released around specific examples of track positions (circled black dots) and tracked for passive drift for six days. The respective animal positions after six days are represented by black triangles. The animal trajectory portion in grey corresponds to the last five days of the track and was therefore not considered in the analysis

minimum proportion $\Pi = (P - P')$ of animal track portion would be classified as H_0-rejected due to actual divergence from the sea surface currents and not because of the method error. The remaining proportion P' that is H_0-rejected could either follow the current but be misclassified (like the drifters), or truly diverge from circulation. As such, the value of Π provided a lower bound for the proportion of time that a shark actively diverged from the sea surface currents.

Standard deviations of P, P' and Π were calculated through a bootstrap procedure over the selected grid cells (100 random samples with replacement of threshold-selected grid cells). All analyses were conducted using R 3.3.2 (R Core Team, 2018).

3 | RESULTS

The comparison between the Lagrangian model and the oceanic drifter data outlined a spatially-heterogeneous performance of the model (Figure 3a). Regions where the Lagrangian model was not in agreement with the drifter track portions were mainly located in the Mozambique Channel, the equatorial ocean, and the coastal regions close to eastern Africa. Namely, in these regions, the hypothesis H_0 that the drifter followed the simulated surface currents was mainly rejected (see red drifter track portions in Figure 3a). Using a threshold $T = 50\%$ over the 234 grid cells considered in the analysis, 104 grid cells where the percentage of incorrectly classified drifter track portions was less than $T\%$ were found (Figure 3a). These cells contained 3,646 six-day long track portions, corresponding to 29% of the overall drifter track portions.

The overall shark trajectory dataset encompassed 1,434 daily positions and the average distance to the 99% likelihood contour estimated over all the trajectories corresponded to 79.3 km (Figure 1). Within the above-identified 104 cells, 842 shark track portions were selected, corresponding to 66% of the overall shark track portions. Within the selected cells, proportions $P = 52\%$ (SD 5%) of shark track portions and $P' = 20\%$ (SD 1.5%) of drifter track portions were found

to be incompatible with H_0, i.e. did not follow the simulated surface currents tracks (Figure 3). As such, the lower bound for the proportion of shark track portions that diverged from the sea surface currents was estimated as $\Pi = 32\%$ (SD 5%; see also Figure S2).

Interestingly, the sensitivity analysis demonstrated that these estimated values of Π mean ($\sim$30%) and SD ($\sim$5%) remained stable for a large range of the $T\%$ threshold values (30–80%, Figure 4a) in the baseline case (i.e. using a track portion duration of $x = 6$ days and $R = 100$ km). By contrast, Π showed a higher sensitivity relative to the track portion length x and the *radius of uncertainty R* and increased with x (Figure 4b). When $R = 50$ km was compared with $R = 100$ km in the baseline case ($T = 50\%$), Π increased faster with x for R = 50 km, before levelling off at an approximately equivalent level. However, as explained in the methods section, with $R = 50$ km, the baseline value of x would be three days. This duration of three days can be obtained considering the average ocean surface current speed ($v = 0.2$ m/s = 17 km/d) and the subsequent required time for a virtual particle strictly moving straight forward to leave the initial 50-km release radius. For these values of $R = 50$ km and $x = 3$ days, values of $\Pi \sim 30\%$ and SD $\sim$5% were again found (Figure 4b). Finally, the sensitivity of Π relative to x was tested for different thresholds $T\%$ and was higher for lower values of the threshold $T\%$ (Figure S3). The other parameters that were tested (N_{CD}: the number of particles across which CD was calculated, and N_{sample}: the number of $CD_{strict\ drift}$ calculated to assess the control distribution and its 95% threshold) had little effect on Π (Figures S4 and S5).

4 | DISCUSSION

This study provides the first quantitative estimate of the amount of time that silky sharks spend between associations with floating objects. Furthermore, the comparison of *in situ* animal trajectories derived from pop-up archival tags with outputs of a Lagrangian passive drift model provides a novel approach for estimating the
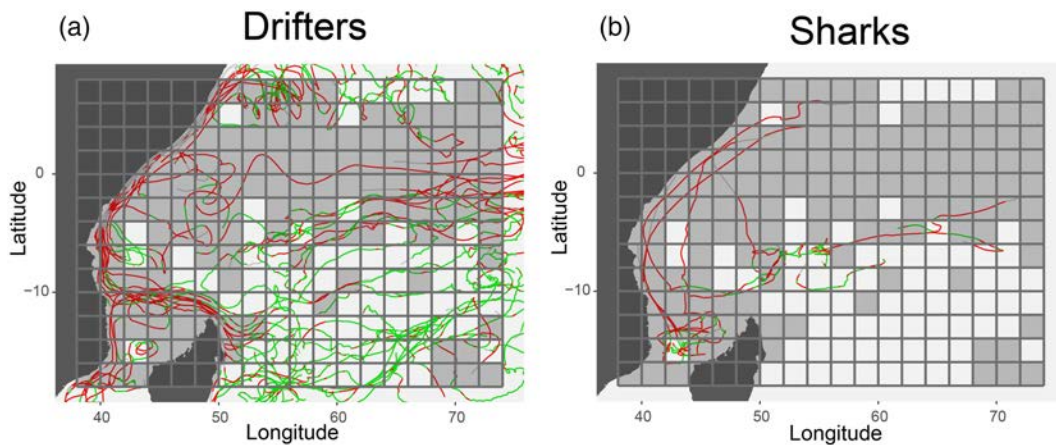

FIGURE 3 Classification for compliance with the passive drift hypothesis of oceanographic drifter (a) and shark (b) track datasets. Track portions are coloured as detailed in Figure 1. A 2° resolution grid applied to the region (central western Indian Ocean) indicates the cells for which >50% of drifter track portions were incorrectly classified as H_0-rejected and were removed from the analysis (in grey)
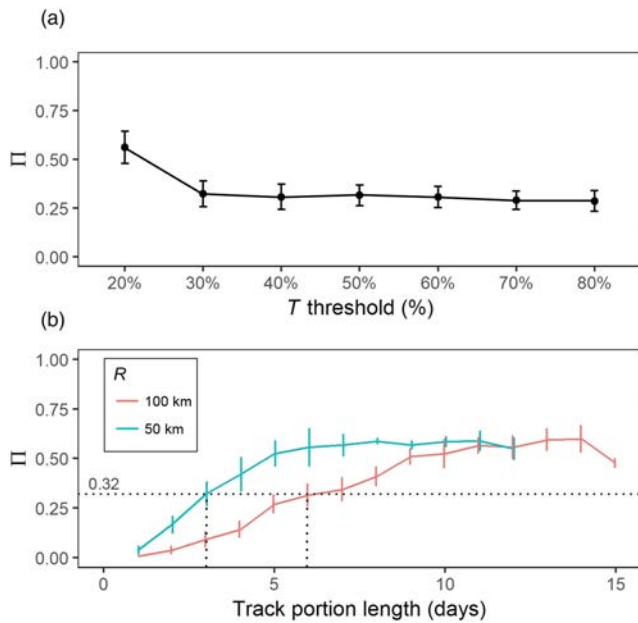
FIGURE 4 Effect of *T* threshold and *R* radius on the lower bound Π of the proportion of shark track portions that diverged from the sea surface currents. (a) The threshold value (*T%*) controls the removal of 2° grid cells, according to the maximum tolerated proportion of incorrectly predicted drifter track portions inside the cell. Error bars represent standard deviation values obtained through bootstrapping of subsequently sampled 2° grid cells. (b) The value of *R* controls the radius in which virtual particles were released to estimate track correlation with sea surface circulation. The resulting lower bound of the proportion of shark track portions that diverged from the sea surface circulation is displayed according to track portion length (in days)

prevalence of this behaviour. While recent acoustic tagging experiments conducted around drifting FADs successfully estimated the average time that silky sharks spend associated with the same FAD (Filmalter et al., 2015), nothing was known about the amount of time that sharks spent in an unassociated state. This information is key for assessing the impacts of FADs on silky shark populations, since the time that they spend between associations can both affect the rate of entanglement (if FADs in the region are built with nets, not following non-entangling FAD design criteria, Murua et al., 2016), bycatch (direct impacts), and their vulnerability related to the potential influence of artificial floating objects on their movements and ecology (indirect impacts).

Given the large uncertainty related to the position estimates derived from light–based geolocation applied to pop-up satellite tag data (average radius of 99% likelihood contours of nearly 80 km) and the fact that the position of surrounding FADs were unknown, this study required the development of a novel methodological framework that could overcome the low accuracy and uncertainties in the available data. Our method relies on passive drift simulations of virtual particles released around the estimated position of the sharks, using a Lagrangian model. A direct comparison of shark trajectories with those of near-by drifters or FADs would have been a

valid approach; however, the number of tracked drifting objects within a meaningful radius of the shark was too small to allow such an approach. Furthermore, even if this were the case, if shark and drifter diverged, it would remain impossible to exclude the possibility that they were following divergent currents. As such, the method developed in this study is able to account for such possible divergences in a statistical manner through the consideration of a large set of particles rather than on comparing two trajectories. In regions where divergence is prominent, all particles will spread over a large distance. In this case, should the shark be located within the cloud of particles but does not follow any of them, the rejection of H_0 remains impossible. A similar approach was used by Briscoe et al. (2016), who interpreted the discrepancies between observed and simulated paths of young sea turtles as an indication of active swimming. However, Putman, Lumpkin, Sacco, and Mansfield (2016) showed that these differences could also partly be explained by uncertainties in the model predictions. To account for such uncertainties, the approach was first applied to oceanographic drifters, and only the areas where the model predictions were satisfactory were selected. Also, the model predictions obtained for the drifter datasets were used to derive a robust lower bound for the time that sharks spent between associations. Another way of understanding the construction of this lower bound (Π) is to deconstruct the model's error into type I and type II errors (Table S6). Let P_{real} be the actual proportion of times the animals separated from the sea surface currents, and the proportion P be an estimate of P_{real}. The type I error can be approximated by P', the proportion of portion tracks that do follow surface currents but are H_0-rejected. Nonetheless, the input of the type II error is of unknown magnitude so the only certainty concerns the lower bound of the P_{real} value ($\Pi << P - P' < P_{real}$).

It is also possible that the direct effect of wind (i.e. windage; Johns et al., 2020; Trinanes et al., 2016) and waves (i.e. Stokes drift; Dobler et al., 2019; Fraser et al., 2018) influence the drift of FADs, and as such the separation of sharks from surface current correctly indicating non-associative behaviour may require further validation.

Finally, an oceanographic ocean near-surface current product (OSCAR) was used, which relies on remote-sensing data, to force a Lagrangian model. Despite their coarse spatial resolution, such products were shown to successfully simulate surface drifter trajectories with equal (or even higher) accuracies than higher-resolution oceanographic model outputs (Amemou, Koné, & Verley, 2018; Scott et al., 2012).

Nonetheless, a limitation of our model in evaluating oceanographic drifter trajectories comes from the tendency for OSCAR to underestimate current speed (Imzilen et al., 2019). This limitation could be of particular importance for areas of high surface current velocity, such as coastal waters off the Somalia horn and off Cape Amber (Northern Madagascar), as illustrated by Peng et al. (2015), where our model resulted in high levels of rejection in the drifter control tests. As a result, it was not possible to draw any conclusions about the relationship between shark movements and surface currents for several shark tracks located in these areas. Another potential

source of rejection of the drifter control test could be the low resolution of ocean current data (1/3°, ~37 km). In certain areas such as the east coast of Africa and the Mozambique Channel, such resolution may not be sufficient to account for mesoscale features and coastal currents, resulting in rejections in our approach. Furthermore, the method could be improved by conducting the drifter control tests on a local spatial and temporal scale around each individual animal track portion, rather than globally. However, the limited number of drifter tracks available in our study was insufficient to facilitate such an approach.

The sensitivity analysis allowed us to assess the robustness of our approach. The 30% lower bound that was found for shark association with FADs was insensitive to our model parameters except to track portion duration. For longer durations, higher proportions of track portions were uncorrelated with surface currents, indicating that for an animal initially located in a given water mass, the longer it is subsequently monitored, the higher the likelihood of observing it actively swimming out of that water mass.

When focusing on long track portion duration (>6 days), increasing the level of demand regarding control by the oceanographic drifters track portions (= decreasing the threshold $T\%$) provided better predictions in subsequently selected areas, but naturally reduced the size of the analysed animal track dataset (smaller selected area). This trade-off could be resolved by favouring the use of a threshold of 30%, given the drop of in the dataset size from 30 to 20% (579 for $T = 30\%$ to 137 for $T = 20\%$ selected shark track portions, Table S7).

Our results can also provide insights on residence times, i.e. the time spent at the same FAD. As the mean duration of our shark complete tracks was 55 days, the lower bound of 30% amounts to an average of 16.5 days spent between two consecutive associations during the monitoring period. Considering that multiple departure events could occur, this result indicates that association to the same FAD for a time period longer than 40 days is very unlikely. This is consistent with the maximum residence time of 30.6 days at the same floating object observed by Filmalter et al. (2015). Additionally, in light of the average FAD-association duration of 15 days estimated in Filmalter et al. (2015), the 30%-lower bound for the total time spent unassociated provides a lower bound for the mean absence time (i.e. a mean time between two FAD associations) of approximately six days. Indeed, given the average residence time (CRT_{mean}) and the average absence time (CAT_{mean}) and the fact that the number of association events equals the number of unassociation events, the proportion of time spent unassociated can also be expressed as the ratio $CAT_{mean}/(CRT_{mean} + CAT_{mean})$. From this equality and the measured value $CRT_{mean} = 15$ days, it is straightforward to obtain $CAT_{mean} > 6$ days.

For the first time, it was possible to demonstrate that juvenile silky sharks can move independently of surface currents, and thus FADs, for at least 30% of their time. As this value is a lower bound threshold, it is difficult to compare with estimates of association rates of yellowfin and bigeye tuna (Capello et al., 2016; Phillips et al., 2017; Schaefer & Fuller, 2010). Nonetheless, a lower value was expected, considering their relative long residence times at FADs (average of 2 weeks) and their high rate of occurrence as a

bycatch species within the FAD fisheries which contrasts with the declining population trends of silky sharks (IUCN, 2017). This striking result provides some optimistic vision, as their vulnerability to purse seiners is strongly correlated to the time they spend associated with FADs. Long residence times at FADs, such as those observed by Filmalter et al. (2015), reveal that floating objects play an important role in the ecology of juveniles of the species. Consequently, one could assume that when an individual leaves a floating object, the motivation to associate with another floating object is strong. In areas with high densities of FADs, this should lead to individuals rapidly re-associating with a new floating object, resulting in short inter-association periods. Such behaviour should also lead to some individuals re-associating with the same FAD after a long excursion (>24 hours). This has never been observed (Filmalter et al., 2015), except for sharks returning after recovering from the stress of capture and tagging, which tends to validate that silky sharks are able to home back to an FAD. Given the potential impacts of FADs on shark populations, the precautionary approach implies reducing the numbers of FADs. Indeed, increasing FAD densities would be likely to decrease the total time they spend in a free-swimming state, increasing their vulnerability to FAD-based purse-seine fisheries, and the potential risk of ecological trap.

Using these results to evaluate the impacts of increasing numbers of FADs on silky sharks is not straightforward. Extrapolating these results obtained from a geographical subset of the Indian Ocean to the entire silky shark population can be deceptive. Typically, the areas retained in these analyses are heterogeneous in terms of FAD densities, with high values of FADs densities in the north of Madagascar but lower values to the east (Imzilen et al., 2019; Maufroy et al., 2017). One could expect for sharks located in areas with lower floating object densities to be less prone to associative behaviour and thus for their movements to be less correlated with surface currents. However, due to the reduced sample size of our study, a comparative analysis that accounted for the role of the density of FADs could not be conducted.

As such, future work in this area should aim to quantify the time that silky sharks spend moving independently of surface currents in different time area windows, with contrasting environmental data (e.g. density of floating objects), in order to investigate their effects. Besides a need to get spatially consistent model outputs, this would clearly require that more silky sharks be tagged with pop-up archival tags in more areas during different periods, as well as the collection of data on the density of natural and artificial floating objects released by all fishing fleets. In parallel, further studies investigating changes in the vertical behaviour of silky sharks associated with FADs could directly facilitate the assessment of association rates, as has been achieved for bigeye tuna (Phillips et al., 2017; Schaefer & Fuller, 2010). Finally, instrumenting an array of drifting floating objects with acoustic receivers and tagging silky sharks with acoustic tags within this array would allow the duration of inter-association periods as a function of inter-FAD distance to be accurately measured, thus providing a complete picture of the association dynamics of this species.

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