Whale shark-tuna associations, insights from a small pole-and-line fishery from the mid-north Atlantic

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1. Introduction

Tunas represent about 10% of the global seafood trade, with about 6 million tons landed annually (FAO, 2019). The growing global demand for tuna and the increasing efficiency of the fishing fleets have resulted in the exploitation of most stocks up to its full capacity, and even to its overexploitation in some cases (Coulter et al., 2020; Cullis-Suzuki and Pauly, 2010). Despite such large pressure on tuna stocks, our knowledge of the complex ecology of tunas is still quite incomplete, mostly due to the practical challenges of investigating these highly migratory oceanic species. This limitation often leads to inefficient or complex management schemes for transnational tuna stocks, usually shared among multiple national exclusive economic zones and high seas (Allen et al., 2010).

A particularly striking knowledge gap is the behavioural ecology of tuna and their interactions with other oceanic species, such as whale shark Rhincodon typus Smith 1828, the largest fish on earth and other sensitive megafauna (Escalle et al., 2019). Fisherman have known and explored the association between tuna and whale sharks for centuries. Just as in the past, present day industrial fishers search for the presence of whale shark as cue to locate tuna schools. These whale shark-tuna associations have been usually assumed to result from the same ecological drivers that govern the attraction of tunas and other fishes towards floating objects or Fish Aggregation Devices (FAD). Yet, this assumption has never been explicitly investigated. As a result, the ecological (evolutionary) significance of the whale shark-tuna associations and the potential impacts of fishing these associations remain unclear. Here, we set out to test a set of predictions expected under the framework of the ‘indicator-log’ and the ‘meeting-point’ hypotheses, originally proposed in the context of the tuna-FAD associative behaviour, by contrasting inter-annual fishing patterns, over 16-years, across highly variable whale shark abundance periods and comparing whale shark associated tuna schools and free swimming schools in the Azores. In addition we also analysed the tuna fishing fleet behaviour over periods of high and low whale shark abundance across the archipelago.

We found an overall south and eastward migration of fishing effort towards lower latitudes, where most whale sharks were reported, compared to the low whale shark occurrence period. Overall we found that the whale shark associated school differed from free swimming schools and fishing yields were also influenced by the presence of the whale shark. Specifically, we found that skipjack, bigeye, albacore and yellowfin tuna are caught in higher quantities when associated with whale sharks. Whale shark associated schools were more diverse and yielded smaller fish on average than free-swimming schools, as predicted under the theoretical framework of tuna-FAD associations. Our results highlight the possibility that whale shark behaviour may play an active role in the association dynamics, and that these associations may be mutually beneficial. We argue that whale sharks may represent a “meeting point” for the aggregation of small tunas and that this behaviour is more likely to be size dependent than species oriented. Finally, we discuss the potential implications of our findings for the management and conservation of both tunas and whale sharks.

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and be more diverse (Andrzejaczek et al., 2019; Escalle et al., 2016) megafauna, such as whale sharks. In light of these arguments, it is tuna with drifting objects, anchored FADs and slowly moving marine (2000) extend the meeting point hypothesis to explain associations of (Escalle et al., 2018) to 1% in the Indian ocean (Capietto et al., 2014), J. Fontes, et al.

motivated by the same forces driving tunas and other Ocean Tuna Commission (IOTC), Western and Central Pacific Fisheries Commission (WCPFC), and Inter-American Tropical Tuna Commission (IATTC), imposed a moratoria on the intentional net setting on whale sharks (Escalle et al., 2018).

Despite the growing interest in assessing the impact of fishing practices on these vulnerable and emblematic megafauna, quantitative studies on the catch composition in whale shark associated fishing events are extremely scarce, in contrast with the volume of information available for free school and FAD associated fishing (Andrzejaczek et al., 2019). The few studies that have addressed whale shark-tuna associations have predominately focussed on the bycatch and survival of the whale sharks (e.g. Andrzejaczek et al., 2019; Capietto et al., 2014; Román et al., 2018; Romanov, 2002).

Whale shark-tuna associations have been usually assumed to be motivated by the same forces driving tunas and other fishes to associate with floating objects or Fish Aggregation Devices (FAD) (Freon and Dagorn, 2000), an assumption that has supported its classification under the same category as vessel and log associations in the purse-seine tropical fisheries (Pallarés and Petit, 1998; Pianet et al., 2000). The theory and empirical evidence to explain the associative behaviour of tuna with floating objects was comprehensively reviewed, and essentially consider the combined advantages of the ‘indicator-log’ and the ‘meeting-point’ hypotheses as the most credible drivers of this behaviour (Castro et al., 2002; Freon and Dagorn, 2000). The indicator-log hypothesis postulates that tunas may use natural floating objects as indicators of productive areas, either because most natural floating objects originate in rich areas (i.e., river mouth, mangrove swamps) and remain within these rich bodies of water, or because they aggregate in rich frontal zones. The meeting point hypothesis assumes that individual tuna will increase their encounter rate with other isolated or schooling individuals by associating with floating objects, thus potentially benefitting from the evolutionary advantages of schooling: reduced risk of predation (via a dilution effect), faster location of food, increased time for feeding, increased effective sampling and (social) information transfer, and opportunity for learning by social facilitation (Fréon and Misund, 1999; Pitcher and Parrish, 1993). Freon and Dagorn (2000) extend the meeting point hypothesis to explain associations of tuna with drifting objects, anchored FADs and slowly moving marine megafauna, such as whale sharks. In light of these arguments, it is reasonable to expect that, as in FADs, whale shark associated tuna schools will be composed of smaller fish (Hallier and Gaertner, 2008) and be more diverse (Andrzejaczek et al., 2019; Escalle et al., 2016) than free-swimming schools. However, there are no specific empirical or experimental studies to date designed to evaluate the dynamics of the whale shark-tuna interaction per se.

In the Azores archipelago, mid-north Atlantic, tunas represent more than half of the total seafood landed (350,000 tons from 1950 to 2010 - Pham et al., 2013). Tuna fishing in this oceanic region has remained artisanal, relying exclusively on pole-and-line and hand-line fishing with live bait carried out by the local small to medium sized (up to 30 m long) boats (Morato et al., 2008b). Skipjack (Katsuwonus pelamis) and bigeye (Thunnus obesus) tunas are the most important species, with albacore (T. alalunga), yellowfin (T. albacares) and bluefin tunas (T. thynnus) caught in much smaller quantities. The wider Azores region represents the fringing (northern limit) habitat for the three tropical tuna, skipjack, bigeye and yellowfin, and the northern distribution and thermal limit of whale sharks in the Atlantic. Whale sharks have been known to occur in the region for some time but the first official records date from the mid-nineties (Santos et al., 1995, 1997). Historically, whale shark sightings in the Azores have been typically low or null, until the dramatic increase observed in 2008, attributed to a concomitant rise in average water temperature (Afonso et al., 2014). As in other tuna fisheries, the local fleet has also learned to opportunistically use whale shark-tuna associations to locate and fish tunas. Data from the Azorean Fisheries Observer program (POPA) shows that, when whale sharks are present in the region, nearly 100% of the whale shark sightings (over 2000 from 1998 to 2013) were associated with tuna schools and resulted in the catch of tunas (Afonso et al., 2014). There are no records of bycatch or incidental hooking of whale sharks in this highly selective fishery (Afonso et al., 2014; Silva et al., 2002). However, as for industrial tuna fisheries, there is no information regarding the potential impact of artisanal pole-and-line fishing on the vulnerability of both tunas and whale sharks.

In summary, our current knowledge about the nature of whale shark-tuna associations, their ecological (evolutionary) significance and drivers, as well as the potential impacts from fisheries, remains poor. In order to address this gap, we first need to understand the basic dynamics of whale shark-tuna associations and the fine-scale interactions with fisheries. Here we set out to analyse the extensive POPA observer database (from 1998 to 2013) for the pole-and-line tuna fishery in the Azores to investigate how the presence of whale sharks may impact fisheries yields and the vulnerability of associated tunas. Specifically, we sought to test the following hypothesis: i) is the spatial distribution of fishing events related to the presence of whale sharks? ii) does whale shark-associated fishing events equate to higher fishing yields? iii) are whale shark-associated tunas smaller than free-swimming tuna? iv) are whale shark-associated tuna schools more diverse than free-swimming schools?

2. Materials and methods

2.1. Study site

The Azores archipelago is located along the northern mid-Atlantic ridge and is composed of nine islands broadly grouped into a western, a central and an eastern island groups (Fig. 1). The region is characterized by its isolation form other land masses, by the presence of a high number seamounts of varying heights and summit depths (Morato et al., 2008a), and by an oceanographic regime that broadly sets the region’s ecoregion position between warm temperate and subtropical characters (Caldeira and Reis, 2017).

2.2. Fisheries related data

Whale shark sightings, which resulted in whale shark associated fishing events in almost 100% of cases, were extracted from the database of the Azorean pole-and-line tuna fisheries observer programme (POPA). The program deploys trained observers since 1998 in about 50% of the fleet during the entire tuna (warm) season, which typically extends from May to November. Boats actively search for tuna at the surface to fish during the day, and will come into port every 2–8 days, depending on the amount of fish caught. Observers record georeferenced data of all fishing events, including duration of fishing events and catch (number of individuals, species and estimated size/weight), as well as other scientifically relevant information such as the sighting of associated or non-associated species including turtles, seabirds, marine mammals and whale sharks. An observer will consider a whale shark associated fishing event if a whale shark is spotted within 15 m of the boat during a fishing event (Afonso et al., 2014). The average speed of the tuna vessels when searching is approximately eight knots (~15 km h⁻¹), and the vessel will typically cover an average of 1300 linear km over a week. Whale sharks are known to spend the majority (80%) of their daytime very close to the surface (e.g. Berumen et al., 2014; Brunnschweiler and Sims, 2011; Eckert and Stewart, 2001). Therefore, we can reasonably assume that the probability of daytime whale shark detections by observers should be high (Afonso et al., 2014). Yet, it is possible that the observers may underestimate the abundance of whale sharks and tuna, simply because they are not within detectable range and depth 100% of the time. Nevertheless, this bias should not affect our results as they do not depend on the absolute
density and this bias should be similar across the study period. Whale sharks were frequently observed by dive operators from Sta. Maria island between 2008 and 2013. Yet, no systematic records were made thus precluding the use of this additional information source. For this study, we considered data from all the tuna species fished in the Azores except Atlantic bluefin tuna as it was only caught in 59 fishing events. Although captured in much lower numbers, the albacore and yellowfin were captured during enough whale shark associated fishing events to be modelled. Tuna catches were derived from direct observer counts of the number of individuals per species fished during a given event, while fish size and weight were derived from the captain’s estimations of average fish size and weight per species for each fishing event. As a result, the catch per unit effort was calculated dividing the number of individuals collected over the duration of each fishing event (CPUE; number of individuals min\(^{-1}\)). We calculated the CPUE for each species at each event.

### 2.3. Statistical analyses

In the Azores, the whale shark occurrence patterns were quite unpredictable since 1998. Whale shark associated fishing events were very few until 2007, peaked in 2008, and remained relatively high compared to the previous period (up to 9% vs. ~0.1 % of all events) (Table 1, Sup 1). Thus, we investigated the effect of whale shark presence on the location of fishing events (hypothesis i. is the spatial distribution of fishing events related to the presence of whale sharks?) by comparing the average annual location of fishing events and average whale shark sighting locations. We computed the annual 75% Kernel Utilisation Distribution (75% KUD) for each tuna species. We also computed the center of gravity for all tuna species fishing events on free swimming schools and whale shark associated to illustrate any spatial changes in

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<tr>
<td>All events</td>
<td>20,078</td>
<td>5777</td>
<td>729</td>
</tr>
<tr>
<td><em>K. pelamis</em></td>
<td>13,274</td>
<td>3160</td>
<td>689</td>
</tr>
<tr>
<td><em>T. obesus</em></td>
<td>7781</td>
<td>3160</td>
<td>317</td>
</tr>
<tr>
<td><em>T. alalunga</em></td>
<td>1027</td>
<td>532</td>
<td>11</td>
</tr>
<tr>
<td><em>T. albacares</em></td>
<td>319</td>
<td>152</td>
<td>18</td>
</tr>
<tr>
<td>Whale shark</td>
<td>743</td>
<td></td>
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</table>

To test hypotheses ii. (does whale shark-associated fishing events equate to higher CPUE?), hypothesis iii. (are whale shark-associated tuna schools more diverse than free-swimming tuna?) and hypothesis iv. (are whale shark-associated tuna schools more diverse than free-swimming schools?) we focused our analysis on the 2007–2013 period, from June through September, when whale sharks were most abundant and each fishing event was classified as a free swimming (FSS) or whale shark-associated tuna school. An exploratory analysis revealed that the relationships between the response variables and several predictor variables were non-linear, so we chose a binomial generalised additive model (GAM) for these analyses. In order to analyse the effect of whale shark presence on tuna CPUE and average size, we set the statistical model response variable as the binomial classifier (FSS or whale shark-associated). We also included distance of each fishing event to the nearest seamount and the sea surface temperature (SST) in these models as those environmental factors seem important for the distribution of whale sharks in the Azores region (Afonso et al., 2014). GAMs allow for more complex relationships to be modelled and use smoothing splines in place of linear coefficients as covariates. To reduce potential over-fitting, we limited the smoothing splines to a maximum of 4 estimated degrees of freedom. Variable selection followed the procedure outlined by (Marra and Radice, 2013) where a double penalty approach is used in combination with a maximum likelihood estimator of the regression splines. The extra penalty approach provides a robust way of removing any variables that do not contribute significantly to the model and removes any bias through stepwise selection measurements (Whittingham et al., 2006).

Hypothesis iv. (are whale shark-associated tuna schools more diverse than free-swimming schools?) was tested by means of comparing the tuna diversity fished at FSS and whale shark-associated. We used an ANOVA to model the differences in tuna species diversity of FSS vs. whale shark-associated schools. We used the number of tuna species captured at each fishing event as measure of diversity, ranging from 1 (monospecific catch) to 4 (all species present in the catch). All statistical analysis was done using the R programming environment (R-Core-Team, 2013).
3. Results

We analysed 20,079 fishing events recorded by observers between 1998 and 2013, 753 of these events were associated with whale sharks. Most fishing events were recorded around the islands and large seamounts south of the central group. Annual tuna landing in the Azores have been highly variable, for all three species, across the entire period of this study. We also found no correlation between annual tuna landings for any of the species, and whale shark sightings from 1998 to 2013 (Sup 1). Between 1998 and 2007, most fishing events were recorded around the central islands. However, after 2007, both the COG and 75 % KUD for both skip jack and bigeye tuna shifted south-eastward, closer to Santa Maria island, where most whale shark associated sets were concentrated. The exception was the year 2012 (Fig. 2a and b respectively) when most skipjack and bigeye were fished south of the central group. This spatial shift in fishing events and whale shark associated fishing events was coincident with the westward displacement of the 22 °C isotherm. Albacore and yellowfin tuna, although caught in substantially lower numbers, show an identical trend although less robust (Sup 2).

A more detailed analysis showed that the distance between annual COG for skipjack (ANOVA, F1,13 = 8.23, p = 0.013) and bigeye (ANOVA, F1,13 = 17.51, p = 0.001) tuna and the locations of whale shark became significantly smaller on the period following 2007 (except 2012) (Fig. 3). The annual distances changed from 350–400 km to ~120 km on the post 2007 period. We also found a small (< 50 km) distance between the COG averaged across all years of both tuna species. Changes in the COG for albacore and yellowfin between the two periods were not significant.

Whale shark presence was positively correlated with CPUE for all four tuna species, suggesting that larger yields are expected for whale shark-associated fishing events. The strongest relationships were found for the two most abundant tuna species (skipjack and bigeye), for which positive residuals were found when CPUEs were above 40–50 individuals min⁻¹ (Fig. 4a-b). For albacore and yellowfin tuna, positive residuals were only found for CPUEs higher than 150 individuals min⁻¹ (Fig. 4c-d).

We also found the mean individual size of whale shark-associated tuna to be significantly smaller than free swimming tunas, for skipjack (4 cm smaller), bigeye (17 cm) and albacore tuna (20 cm) (Fig. 5a–c).

There was no significant difference in the mean size of free-swimming and whale shark-associated yellowfin tuna. The deviance explained by the CPUE and average size models was 35.3 % and 32.5 % respectively (Table 2). Distance to seamount and SST both came out as significant variables in both models (hypothesis ii and iii), showing that whale sharks were found at intermediate distances (~20–60 km) from the summit of larger seamounts and at temperatures warmer than 22 °C (Fig. 6).

Species diversity was significantly greater in whale shark-associated events compared with FSS events (mean richness 1.36 vs 1.15, F1,6469 = 64.6, p < 0.001) (Fig. 7).

4. Discussion

We analysed sixteen years of fisheries observer data to investigate the fishing patterns, catch composition and CPUE of four important tunas in the Azorean pole-and-lime tuna fishery. Our goal was to investigate how the presence of whale sharks may influence the spatial patterns of tuna fishing in the archipelago, CPUE and catch composition. Two contrasting periods of whale shark abundance emerge from this dataset: a period of sporadic whale shark associated fishing events, from 1998 to 2007 (0–2 events per year), followed by a dramatic increase in annual whale shark-associated fishing events (2008–2013) (Afonso et al., 2014).
The tuna fishing boats in the Azores typically search for tuna across the entire region’s EEZ and even beyond, but will often converge to locations where successful fishing events have recently been reported, including those associated with whale sharks (Afonso et al., 2014). Given that nearly all whale sharks sighted were reported to be associated with tuna and that most whale sharks were found southeast of the central group, it’s not surprising that both the 75% KUD and COG for tuna fishing events during the high whale shark abundance period (2008−2013) shifted south relative to the 1998−2007 period. Even in 2012, when whale shark−associated fishing events decreased, there was a notable westward shift in the tuna fleet consistent with the shift in whale shark COG towards the Princess Alice seamount region. The information about the presence of whale sharks in a given area is commonly spread across the fleet, thus potentially favouring an overlap between whale shark rich areas and the fishing fleet. Reports of whale sharks presence at a given area are likely to influence captains’ decisions and fishing patterns, which likely resulted in the observed overlap between fisheries and whale sharks.

Given that this is a fringing seasonal habitat for both the tropical tunas and whale sharks, it’s thus worth posing the question ‘who follows who’, or ‘are tunas following whale sharks or are the whale sharks following the tuna?’ It may be the case that tuna and whale shark converge to this high latitude in favourable (including high temperature) years, possibly responding to the same environmental cues (e.g. water temperature, food availability, etc.). The correlation between whale shark abundance in the Azores and water temperature reported by Afonso et al. (2014) suggests this is the case for the whale sharks. Although the distribution of tuna and whale sharks within the Azores is complex and difficult to predict, some marine predators like skipjack and bigeye tuna, the common dolphin (Delphinus delphis) and Cory’s shearwater (Calonectris diomedea borealis) are more likely to occur in the proximity of seamounts’ summits shallower than 400 m (Morato et al., 2008b). Afonso et al. (2014) also reported that whale shark occurrence within this region were more likely closer to the seamounts, coinciding with higher chlorophyll-a biomass, probably associated to increased feeding opportunities. In fact, 63% of all large seamounts are located south of the central group (Morato et al. 2008a), where most whale sharks were reported and where the COG of the two most abundant tuna lay following 2007. It is thus reasonable to assume that, the distribution patterns of tunas in the Azores is likely influenced by a combination of seamount landscape, environmental cues and whale shark habitat use patterns, as shown by the clear southward shift of tuna 75% KUD and COG (skipjack and bigeye) after 2007. Major shifts in tuna distribution and fishing patterns have been previously documented in the tropics where most industrial fisheries operate. In some cases, these shifts have been attributed to the massive deployment of FADs that displaced the tunas away from traditional areas of log (natural FADs) fishing (Freon and Dagorn, 2000).

Although the motivation and advantages of whale shark-tuna associations remain elusive, a few hypotheses have been put forward (Reviewed in Freon and Dagorn, 2000). Among these propositions, the “meeting point” and “indicator-FAD” hypotheses seem more credible (Hallier and Gaertner, 2008). Under this theoretical framework, tunas are attracted to FADs and marine megafauna in order to facilitate the formation of large schools, towards the same evolutionary advantages of schooling (Castro et al., 2002) and food finding (Freon and Dagorn, 2000). The distribution patterns of tunas in the Azores during the high whale shark abundance period seem to support the view that FADs and whale sharks may have a similar ecological effect on tunas, as suggested by Pianet et al. (2000). Our finding that whale shark-associated schools were typically composed of smaller individuals (except yellowfin) and typically harboured more diverse tuna schools relative to free-swimming schools is also in line with this hypothesis. Moreover, a recent study by Escalle et al. (2019) also found that purse seine sets around
FADs and whale sharks, in the Atlantic, tend to be more diverse and produce average smaller size catch of the three major tuna species (skipjack, bigeye and yellowfin tuna), compared to free-swimming school sets, especially due to the capture of large yellowfin tuna.

It is not surprising that smaller tunas, which are typically more vulnerable to predators, seem to be more likely to associate with FADs or whale sharks as this behaviour is expected to reduce predation risk through the dilution effect (Castro et al., 2002; Hoare et al., 2000; Pitcher and Parrish, 1993). On the other hand, the higher tuna diversity typically associated with whale sharks suggests that whale sharks may act as a "meeting point" for the aggregation of small tunas and this behaviour is more likely to be size dependent than species oriented. It is expected that different species may gather in a single school to benefit from the advantages of larger schools (Fréon and Misund, 1999; Pitcher and Parrish, 1993).

While small and immature fishes associated to FAD and whale sharks may benefit from reduced predation risk, i.e. decreased natural mortality, our results suggest they may be more vulnerable to fishing compared to free-swimming schools. Similar patterns have been reported for example, in the eastern Atlantic Ocean, where FAD associated sets typically generate more than twice the catch than free swimming schools, even though the average fish size of FAD associated fish is smaller (Fonteneau et al., 2000). Escalle et al. (2019) also reported that free school sets had the lowest set success rate (more than one ton of catch) compared to whale shark sets and FAD sets. Ultimately, it can be argued that fishing whale shark-associated schools is less sustainable than fishing free swimming schools given the higher proportion of immature fish captured with apparently higher captureability.

**Table 2**

GAM results exploring the effect of whale sharks on the CPUE and average size of individuals for each of the four tuna species. In addition to the the four tuna species, each model included two environmental variables, the distance to seamounts and SST. For each term the estimated degrees of freedom (Est. df.) and Chi squared statistic (Chi sq.) is shown. Significance is denoted as: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant.

**Response: WSp/a ∼ CPUE**

<table>
<thead>
<tr>
<th>s(term, k = 4)</th>
<th>Est df</th>
<th>Chi sq.</th>
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<tbody>
<tr>
<td>Log$_{10}$(Skipjack CPUE)</td>
<td>4.0</td>
<td>111.1***</td>
</tr>
<tr>
<td>Log$_{10}$(Bigeye CPUE)</td>
<td>1.9</td>
<td>98.4***</td>
</tr>
<tr>
<td>Log$_{10}$(Albacore CPUE)</td>
<td>2.2</td>
<td>18.2***</td>
</tr>
<tr>
<td>Log$_{10}$(Yellowfin CPUE)</td>
<td>2.4</td>
<td>17.9***</td>
</tr>
<tr>
<td>Distance to Seamount</td>
<td>1.9</td>
<td>64.25***</td>
</tr>
<tr>
<td>SST</td>
<td>2.3</td>
<td>222.1***</td>
</tr>
<tr>
<td>Dev. Explained = 35.3 %</td>
<td>n = 6471</td>
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**Response: WSp/a ∼ mean size cm.**

<table>
<thead>
<tr>
<th>s(term, k = 4)</th>
<th>Est df</th>
<th>Chi sq.</th>
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<tbody>
<tr>
<td>Skipjack cm.</td>
<td>1.8</td>
<td>13.73**</td>
</tr>
<tr>
<td>Bigeye cm.</td>
<td>2.5</td>
<td>44.0***</td>
</tr>
<tr>
<td>Albacore cm.</td>
<td>1.8</td>
<td>20.5***</td>
</tr>
<tr>
<td>Yellowfin cm.</td>
<td>0.1</td>
<td>0.0ns</td>
</tr>
<tr>
<td>Distance to Seamount</td>
<td>1.3</td>
<td>75.6***</td>
</tr>
<tr>
<td>SST</td>
<td>1.9</td>
<td>229.8***</td>
</tr>
<tr>
<td>Dev. Explained = 32.5 %</td>
<td>n = 6471</td>
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Even if some parallel can be found between FAD and whale shark-associated schools, one fundamental difference remains, whale sharks are not objects passively drifting on the surface of the ocean. In fact, whale shark are exactly the opposite: they are complex organisms with acute sensory capabilities and complex behaviour, performing transoceanic migrations, dynamic diel vertical behaviour, capable of extreme dives with complex feeding ecology (Borrell et al., 2011; Brunnschweiler et al., 2009; Cárdenas-Palomo et al., 2018; Rohner et al., 2018; Sampaio et al., 2018).

The whale shark is generally known as a filter-feeder mainly targeting zooplankton and micronekton, including fish spawn (de la Parra Venegas et al., 2011; Meekan et al., 2009; Rowat and Brooks, 2012; Sampaio et al., 2018). Yet, there are increasingly more evidence to suggest that whale sharks consume more fish than previously anticipated (Boldrocchi and Bettinetti, 2019; Borrell et al., 2011; Cárdenas-Palomo et al., 2018; Sampaio et al., 2018). Nevertheless, it is still unclear how they are able to prey large quantities of small highly mobile fish. We speculate that the association with tunas may facilitate access to this abundant resource as tunas force the formation of compact baitballs, making it accessible to slow moving whale sharks (e.g. https://www.youtube.com/watch?v=BBqiQeDri0). This feeding interaction may represent an important benefit for whale sharks, particularly when and where baitfish is the only staple available. This is arguable the case in the Azores, during the summer months, when whale shark aggregate, primary production is lowest (Woods and Barkmann, 1995) and zooplankton concentrations decrease to its minimum (Carmo et al., 2013). While it could also be argued that whale sharks and tunas are competing for the same prey, it is also safe to say that this interaction enables whale sharks to explore a resource that otherwise would not be accessible.

Recognising that whale sharks are vulnerable, ecologically important and emblematic, the Western and Central Pacific Fisheries Commission and the Indian Ocean Tuna Commission banned the setting of nets around whale sharks as a precautionary measure to mitigate both lethal and sub-lethal impacts of bycatch (Capietto et al., 2014). In contrast, similar measures are still lacking for the Atlantic, even if whale shark is considered endangered (IUCN red-list). There are no restrictions to pole-and-line fishing on whale shark-associated schools, possibly because the current perception is that this artisanal fishery does not represent a direct threat to the whale sharks since bycatch is impossible and sub-lethal effects are not considered. However, if these associations are indeed ecologically meaningful, i.e., advantageous for tunas and whale sharks, then targeting these associations may result in unknown detrimental effects on whale sharks over the long term.

This 16 year data set was uniquely placed at a time when whale sharks went from a rare visitor to a regular annual visitor to this region. It presented a valuable opportunity to investigate, for the first time, the influence of the endangered whale shark on pole and line tuna fishery dynamics and the vulnerability of the associated tuna species. We found evidence that suggest a link between the spatial dynamics of whale sharks and fishing fleet behaviour in the region, either directly through interspecific interactions and/or indirectly by responding to the same environmental cues (e.g. water temperature). On the other hand, the presence of whale shark is associated with a significant change the catch composition and yields compared to free swimming school fishing events. This suggests that fishing whale shark-associated schools is potentially less sustainable than free swimming schools since whale shark-associations typically harbour higher proportion of immature fishes and are more vulnerable to fishing mortality. We argue that future investigations should clarify the relevance of whale shark-tuna associations and the implications of targeting whale shark-tuna associations.

**Ethical approval**

This article does not contain any studies with animals performed by any of the authors.
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CRediT authorship contribution statement

Jorge Fontes: Conceptualization, Investigation, Methodology, Writing - review & editing, Data curation, Formal analysis, Funding acquisition, Writing - original draft. Niall McGinty: Conceptualization, Investigation, Methodology, Writing - review & editing, Data curation, Formal analysis, Writing - original draft. Miguel Machete: Conceptualization, Investigation, Methodology, Writing - review & editing, Data curation, Project administration. Pedro Afonso: Conceptualization, Investigation, Methodology, Writing - review & editing, Funding acquisition, Writing - original draft.

Declaration of Competing Interest

Authors declare that there are no conflicts of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found in the online version, at doi:https://doi.org/10.1016/j.fishres.2020.105598.

References


