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Analysis of the temporal and spatial variability of whale shark (*Rhincodon typus*) aggregation in the South Ari Marine Protected Area, Maldives, Indian Ocean

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Abstract
Whale sharks are known to aggregate in coastal areas. In the South Ari Marine Protected Area (Maldives) a aggregation, mostly represented by young males with a high level of residency, has been described in the literature. Despite the worldwide interest in the natural resources of the Maldives, this population is increasingly subjected to anthropogenic pressure and major concern regards the flourishing tourist industry. In this study, data collected by the Maldives Whale Shark Research Programme between 2014 and 2017 have been used to detect both temporal and spatial patterns of occurrence. Favourable environmental conditions to visually detect whale sharks have been defined for the studied area. Accordingly, a total of 1077 shark encounters have been analysed in this study. Environmental conditions (i.e. sea surface temperature, monsoon occurrence) have been used to detect possible factors affecting the spatial and temporal variability of *Rhincodon typus* aggregations. A two-way ANOVA has been performed to detect temporal trends in animal occurrence, sea surface temperature pattern and to investigate the sea bottom depth variability during encounters. Significant differences in the monthly occurrence of whale sharks within the same year and among different years have been detected. Similar patterns have been observed for environmental parameters such as sea surface temperature and depth. A different spatial distribution has also been detected as a function of the Indian Monsoon reversal (north-eastern and south-western) affecting the area. During the northeast monsoon period, whale sharks appeared to concentrate in a smaller longitudinal range closer to the western-central part of the MPA, where deeper water conditions occur due to the proximity of a deep depression (submarine canyon). Results from this study provide new pieces of information for the implementation of dedicated management actions to protect the whale sharks population inhabiting the South Ari Marine Protected Area.

Keywords: *Whale shark,* Rhincodon typus*, Maldives, South Ari Atoll, Indian Ocean*

1. Introduction

The whale shark (*Rhincodon typus*, Smith 1828) is the largest shark on earth (Pierce & Norman, 2016) and one of three known planktivorous shark living species (Colman 1997; Compagno 2001; Rowat & Brooks 2012). The species occurs seasonally in coastal and oceanic-pelagic environments of the circumtropical, tropical, and warm temperate waters between 30°N to 35°S, both in the Atlantic and Indo-Pacific Oceans (Colman 1997; Compagno 2001; Rowat & Brooks 2012; Sequeira et al. 2014a).

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Most of the knowledge about the species ecology is limited to coastal areas, where whale sharks seasonally aggregate for foraging on a variety of prey, including spawning fish, zooplankton blooms, baitfish, and crab larvae (Graham et al. 2005; Meekan et al. 2009; Rowat & Brooks 2012; Robinson et al. 2013; Pierce & Norman 2016; Copping et al. 2018; Boldrocchi & Bettinetti 2019). In these feeding areas, individuals of different sizes and genders have been observed (Aca & Schmidt 2011; Ketchum et al. 2013; Cochran et al. 2019; Whitehead et al. 2020; Allen et al. 2021). Due to their feeding and thermoregulatory behaviours (Thums et al. 2013), whale sharks spend a large amount of time in proximity to the surface, making them easier to spot but also leaving them exposed to various dangers (Boldrocchi et al. 2020; Allen et al. 2021). Currently, whale sharks are listed as "Endangered" by the International Union for Conservation of Nature (IUCN) Red List of Threatened species and in Appendix II of the Convention on International Trade in Endangered Species (CITES), as a result of a severe decline of its population (>50%) over the last 75 years due to the past overfishing (Schmidt et al. 2009; Pierce & Norman 2016).

Owing to their life history (i.e., long lifespan, late maturity, and slow growth) and habitat use, sharks are exposed to pressure coming from different anthropogenic activities and therefore are subject to a higher risk of extinction if compared to other vertebrates (Lieber et al. 2020). The main threats are represented by targeted harvesting (Li et al. 2012; Cochran et al. 2016; Perry et al. 2018), bycatch, illegal fishing, habitat modification, vessel strikes (Speed et al. 2008), and contaminant exposure (Boldrocchi et al. 2020).

Globally, whale sharks are also an important socioeconomic source. Shark watching or "swimming with whale sharks" are profitable activities in many countries (Gallagher & Hammerschlag 2011; Araujo et al. 2017). However, unregulated ecotourism can be a source of disturbance thus threatening the well-being of whale sharks (Quiros 2007; Trujillo-Córdova et al. 2016; Araujo et al. 2017; Allen et al. 2021; Harvey-Carroll et al. 2021). The establishment of Marine Protected Areas (MPAs) and the regulation of activities within their borders are known to bring both mid- and long- term benefits to marine biodiversity (FAO 2007; West et al. 2009; Ibarra-García et al. 2017). MPAs are also widely considered a critical conservation tool for the protection of many elasmobranch species (Davidson & Dulvy 2017; Rigby et al. 2019; Birkmanis et al. 2020).

In the coastal waters of the Republic of Maldives, whale sharks are seasonally present and show a semi-annual residency pattern. They move along the western atolls during the northeast monsoon (from December to April), and along the eastern atolls during the southwest monsoon (from May to November) (Anderson & Ahmed 1993; Riley et al. 2010; Anderson et al. 2011; Cagua et al. 2014; Donati et al. 2016). Movements of whale sharks along the double chains of atolls of the Maldives, appear to be affected principally by the seasonal variability in productivity (Anderson et al. 2011) and by ocean currents (Anderson & Ahmed 1993; Wilson et al. 2001). The south region of Ari Atoll (Alif Dhaalu Atoll) represents an exception compared to the other atolls in the Maldives. Indeed, although the driver of aggregation has not to be defined yet, this area hosts year-long aggregations, mainly composed of juvenile males (Riley et al. 2010; Donati et al. 2016; Perry et al. 2018; Allen et al. 2021; Harvey-Carroll et al. 2021). The high re-sighting rate of some individuals suggests a high site fidelity over the years, and the absence of adult, neonates, and female indicates that this area might be a "secondary nursery area" and a developmental habitat for juvenile males (Perry et al. 2018; Allen et al. 2021; Harvey-Carroll et al. 2021). To protect this species, the Government of Maldives banned hunting of the whale sharks in 1995 (Cagua et al. 2014) and the fishing industry has been replaced with ecotourism (Zimmerhackel et al. 2019; Harvey-Carroll et al. 2021). In 2009, the South Ari Marine Protected Area (SAMPA, Ari Atoll, Maldives) was established as the largest Maldivian area to specifically protect the whale shark aggregation present in the Ari Atoll (Environmental Protection Agency, Cagua et al. 2014; Stevens et al. 2015; EPA 2019), and to promote long-term human well-being by protecting the marine ecosystem (Rasheed & Abdulla 2020). In the SAMPA, as in the entire Maldives, the regular presence of whale sharks represents a profitable attraction, as this involves thousands of people every year engage in "whale sharks' excursions" (Cagua et al. 2014) and therefore, ecotourism has become an integral part of conservation strategies (Sanzogni et al. 2015). Despite the agreements between stakeholders, the management planning in the SAMPA is yet to be implemented (Cagua et al. 2014; Rasheed et al. 2016; EPA 2019; Rasheed & Abdulla 2020) therefore whale sharks are still considered at risk as showered by the high number of injured individuals (i.e., presenting collision marks) reported in the SAMPA area (Allen et al. 2021; Harvey-Carroll et al. 2021).

More extensive knowledge about whale shark's populations is necessary to develop effective management and conservation actions that account for the protection of the different life stages of animals (West et al. 2009; Grüss et al. 2011; Breen et al. 2015; Haupt et al. 2017) and their habitats (Haupt et al. 2017; Copping et al. 2018). Understanding whale shark presence and use of the habitat is a key issue to inform decision-making processes that aim to implement the dedicated management actions and to support any future conservation plans at the MPA level (Heupel et al. 2014). Therefore, this study aims to provide additional pieces of information on the whale shark occurrence in the SAMPA by investigating the temporal and spatial variability of this species within and between different seasons.

2. Materials and methods

2.1. *Study area*

The study area is located within the waters of the SAMPA (Latitude range: 3°38′10 N – 3°32′15 N; Longitude range: 72°42′18E – 72°55′58E) (Rasheed et al. 2016) in the southern part of the Ari Atoll (Figure 1), the largest atoll of the Maldives (Gischler 2006). The SAMPA boundaries extend along the seaward fringe of South Ari atoll and comprise the adjacent 1 km buffer zone, moving from Dhigurah Island to Rangali Island, from east to north-west, for a total area of 42 km^2. The MPA includes four islands (Dhigurah, Maamigili, Dhiddhoo, and Fenfushi), resort islands reefs (Rasheed & Abdulla 2020) and a pass area where the lagoon communicates with the channel Ariadhoo kandu between Ari Atoll and North Nilandhe Atoll.

Bathymetry is relatively shallow within the atolls and lagoons if compared to the open ocean. Lagoons can reach 50–60 m of depth, oceanward margins up to 2000 m, while the inner seaside reaches a few hundred meters (Fürstenau et al. 2010; Betzler et al. 2016). The depth of the channel Ariadhoo kandu ranges from about 400 m to 1000 m from east to west.

The forereef shows the same geomorphological characteristics typical of the atolls of the Maldives (Fürstenau et al. 2010; Betzler et al. 2016). The northeast-southwest sector (from Dhigurah to Dhiddhoo) is characterized by a narrow and steep forereef, whereas the east-west sector (from Maamigili to Rangali) displays a larger and gentler slope. The slope, here, is interrupted between Maamigili and Fenfushi islands, close to the edge of the buffer zone, by an abrupt reef slope that leads to deep waters (Figure 1).

Climate and hydrography are strongly influenced by the Indian Monsoon reversal (Gischler et al. 2014; Betzler et al. 2016). Notably, the area experiences two monsoons annually. The southwest monsoon blows from May to November; it brings increased average rainfall, wind speeds, and cloud

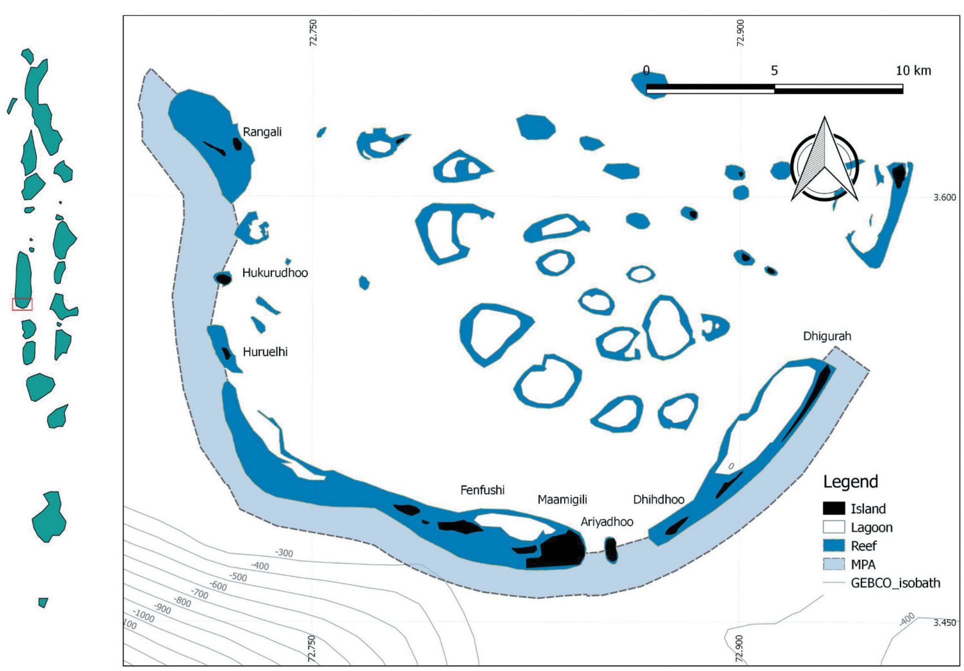

Figure 1. Map of South Ari Marine Protected Area (SAMPA) – The map shows the 1 km buffer zone defined by the MPA and isobaths; it is possible to note the differences of depths between Dhigurah and Fenfushi Islands.

cover, which causes rougher seas, and a dominant current that flows from west to east. The northeast monsoon, on the contrary, blows from December to April, it brings blue skies, calm and clear waters for most of the time, with the dominant current flowing from east to west (Anderson & Ahmed 1993; Wilson et al. 2001; Rowat 2007; Stevens et al. 2015; Betzler et al. 2016).

2.2. Research effort

The Maldives Whale Shark Research Programme (MWSRP) is the only long-term research-based conservation charity dedicated to the study of whale sharks in the Maldives, and it has conducted annual research and surveys in the area since 2012.

Surveys were undertaken along the outer reef within the MPA, on board a 15 meters wooden hull motorized local boat, called *dhoni*, following protocols described by Riley et al. (2010). Transect routes were designed parallel to the upper margin of the forereef drop off and they followed two directions: from northeast to southwest and from southwest to northeast, starting from and returning to Dhigurah Island (see Figure 1). The extension, number, and time (start and ending time) of the surveyed transects varied, depending on the daily weather conditions, mainly due to any possible rough navigational conditions during both monsoon seasons. Visual effort was conducted, during daylight hours, by three trained team members that looked, from the upper deck, for a dark silhouette underwater or the dorsal fin tips of a whale shark at the surface.

2.2.1. Environmental data. During each encounter, the following data were collected: i) general data (i.e., date, time, position) and ii) environmental data such as cloud coverage (classified as clear, partially covered, totally covered), wind speed (using Beaufort scale) and direction.

In-situ Sea Surface Temperature (SST, °C) was collected from the lower deck of the boat, using a digital thermometer.

Derived Sea Surface Temperature (hereafter called SST_SAMPA) from remote sensing (MODIS, monthly average at 4 km resolution), and monthly rate precipitations (Tropical Rainfall Measuring Mission 2011 and TMPA/3B43 Rainfall Estimate, 0.25 degree x 0.25 degree spatial grid) were also extracted from the NASA Ocean Biology Processing Group (OBPG) through the Giovanni system

(©Giovanni.gsfc.nasa.gov - https://giovanni.gsfc.nasa.gov/giovanni/-).

Depth data were obtained from the General Bathymetric Chart of the Oceans (GEBCO, 2014, 30 arcsec spatial grid resolution) (Table I).

Table I. Summary of environmental data used for analysis.

Summary of the environmental data		
In situ		
Value	*Units*	
SST	°C	
Cloud coverage	clear	
	partially covered	
	totally covered	
Wind speed	Beaufort scale	
From remote sensing		
Value	*Units*	*Resolution*
SST_SAMPA	°C	4 km
Depth	m	30 arcsec
Rain Precipitation	mm/month	0.25°

2.3. Data preparation for the analysis

This study analysed data collected between 4 years, 2014 and 2017, and only during months presenting more than 6 research days were considered. It is well known that weather conditions could affect the detectability of marine vertebrates (e.g., cetaceans - Reid et al. 2003; Evans & Hammond 2004; Dunshea et al. 2020; seabirds - Webb & Durinck 1992; turtles - Eguchi et al. 2007; and sharks - Sims et al. 2005). Therefore, to reduce the bias induced by the heterogeneity in sampling conditions, only data collected in standardized Favourable Environmental Conditions (hereafter called FEC) were considered in this study.

FEC are defined as i) wind speed not exceeding 3 in the Beaufort scale, and ii) clear or partial cloud coverage of the sky. These criteria, from Sims et al. (2005), allowed to characterize the most favourable condition to detect whale sharks during boat surveys in the SAMPA.

In this study, Sightings Per Unit Effort (SPUE) was calculated, for each month and year, as the number of whale shark encounters collected in FEC per day of research effort.

Sightings collected between May and November were classified as collected under the influence of the southwest Monsoon, whereas those collected from December to April under the influence of the northeast Monsoon based on Anderson and Ahmed (1993).

2.3.1. Data analysis. The temporal variability in the SPUE among the years and months, as well as the SST variability, were investigated by using a two-way ANOVA that allowed estimating the effect of two factors on a continuous dependent variable. The relationship between environmental variables and their association has been investigated using Pearson's Correlation coefficient.

Differences in the position (descriptive statistics of latitude and longitude and depth) of the whale sharks as a function of the Indian Monsoon reversal (north-eastern and south-western) were investigated using a Kruskall Wallis test.

Maps were generated using the software QGIS (Version 2.18.16) and all statistical analyses were undertaken using SPSS Statistics (version 25, IBM, New York, USA, https://www.ibm.com/it-it/products/spss-statistics).

3. Results

Between 2014 and 2017, a total of 451 research days were conducted by MWSRP reporting 1244 whale shark sightings (Figure 2). Research days varied among the years, with a minimum of 93 days recorded in 2014 and a maximum of 124 days in 2017, with a monthly average of 12.5 days (Table II). FEC conditions were respected 84% of the days (n = 378).

Out of the total number of sightings, 1077 (86%) were collected in FEC, with a yearly average of 269 encounters, a minimum of 247 in 2015, and a maximum of 283 encounters in 2014 (Table II - Figure 3). Only 167 sightings were reported with unfavourable environmental conditions throughout the entire research period. These sightings were excluded from the analysis.

3.1. *Temporal variability of SPUE*

The two-way ANOVA did not show any significant difference (P-level > 0.05) in the SPUE amongst different years (see Table III and Figure 4). Conversely, differences in the monthly occurrence of the species were identified (Table III). Specifically, the occurrence of whale sharks was significantly different among months of the same year (P-level < 0.01) and between the same months of different years (P-level < 0.01) (Figure 5).

In the attempt to explain these results, the variability of the in situ SST (°C) (averaged values across the time period: mean = 29.5 ± 0.04; median = 29.5; min = 27; max = 33; SD = 0.78) was tested againts time (months, years). As for the SPUE, the analysis showed significant differences in the average values of in situ SST between years (P-level < 0.01), months of the same year (P-level < 0.01) and months of different years (P-level < 0.01) (Table IV; Figure 6).

The variability of average sea bottom depth in the areas, where encounters occurred, was also tested on a yearly and monthly basis (averaged values across the time period: mean = 115 ± 2.6; median = 92; min = 3; max = 342; SD = 86). The analysis showed significant differences in the average values of depth between years (P-level < 0.01), months of the same year (P-level < 0.01), and months of different years (P-level < 0.01) (Table V, Figure 7).

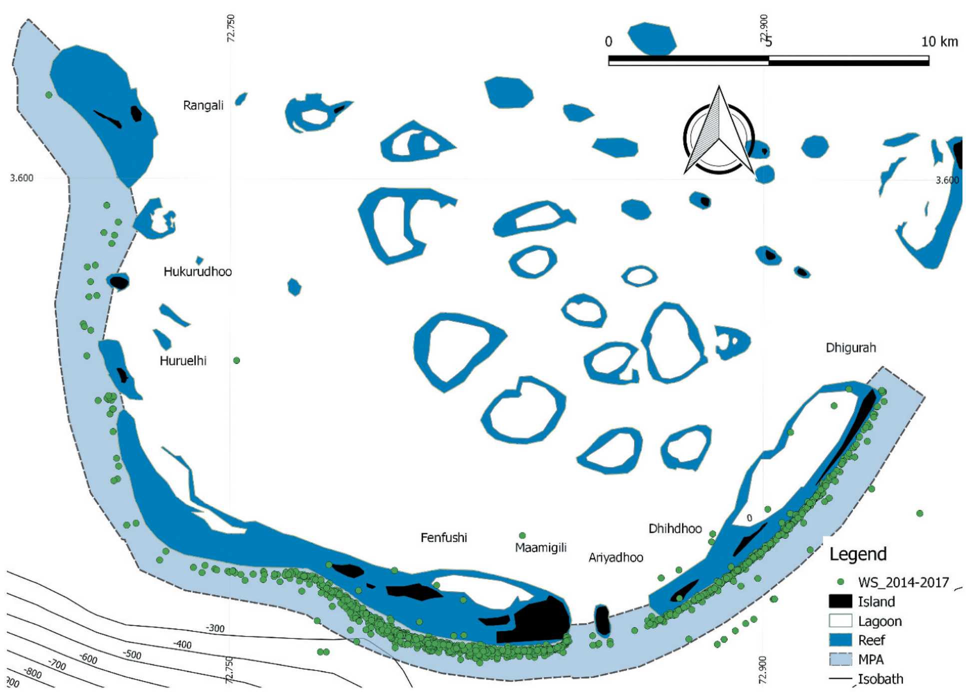

Figure 2. Total number of encounters during the whole study period.

Table II. Total numbers of days at sea, days under favourable environmental conditions and encounters during the whole study period.

Year	Days at sea	Days under FEC	Sharks encounters under FEC
2014	93	83	283
2015	120	100	247
2016	114	96	276
2017	124	99	271
Total	451	378	1077

3.2. *Correlations between SPUE and environmental variables*

No significant correlation between in-situ SST and SPUE was observed (P-level > 0.05), however, a significant correlation between monthly average of in-situ SST and derived SST_SAMPA was detected (Pearson correlation N = 36; r = 0.5; P-level < 0.05). Therefore, the relation of SPUE with SST_SAMPA, collected by remote sensing was tested. An inverse correlation close to the significant level was found between average monthly values of SST_SAMPA and SPUE (Pearson correlation N = 36; r = −0.31; P-level = 0.06). This could be due to the temporal resolution of the remote sensing data. However, no significant linear relationship was found between sea surface temperature and the occurrence of whale sharks. Finally, the analysis showed a significant inverse correlation between the SPUE and the monthly average values of precipitation (mm/month) derived from remote sensing (Pearson correlation N = 36; r = −0.6; P-level < 0.05).

Table III. Two-way ANOVA – SPUE variability between years, months of the same year, and months of different years. Significant results are highlighted in bold.

Source	Type III sum of squares	df	Mean square	F	P level
Corrected Model	1,626[a]	35	0.046	2.389	0.000
Intercept	0.047	1	0.047	2.393	0.123
year	0.119	3	0.04	2.044	0.107
month	**0.68**	**10**	**0.068**	**3.495**	**0.000**
year * month	**0.892**	**22**	**0.041**	**2.087**	**0.003**
Error	9.604	494	0.019		
Total	11.23	530			
Corrected Total	11.23	529			

3.3. *Spatial variability of the encounters during Indian Monsoons*

A significant inverse correlation between the SPUE and the monthly average values of precipitation (mm/month) derived from remote sensing (Pearson correlation N = 36; r = −0.6; P-level < 0.05) was observed. To further investigate this result, the position (latitude and longitude) of the encounters were compared during the two Indian monsoons seasons (north-eastern, N = 499; SD = 84 and south-western, N = 569; SD = 81). During the northeast monsoon season, encounters occurred in areas with average depth of about 140 m while during the southwestern monsoon they occured in areas with shallower depths, at average depth of 93 m. The difference in latitudinal variability in whale shark's encounters was statistically significant (H = 136.8; df = 1; P-level < 0.001) (Figure 8).

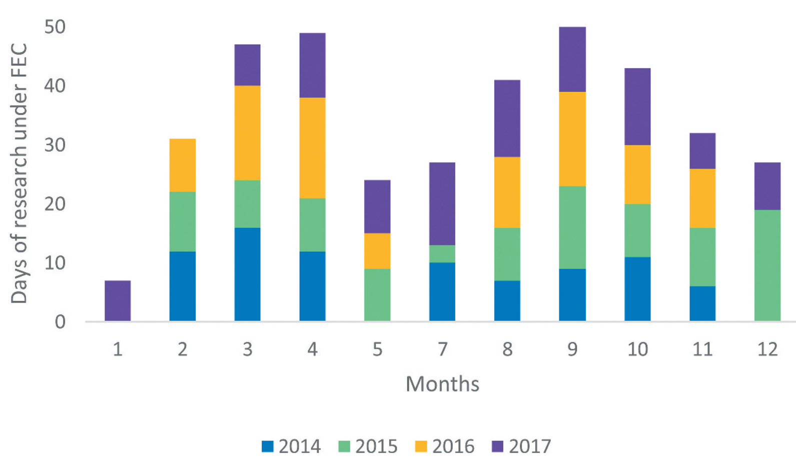

Figure 3. Number of research days under Favourable Environmental Conditions (FEC) per month and per year.

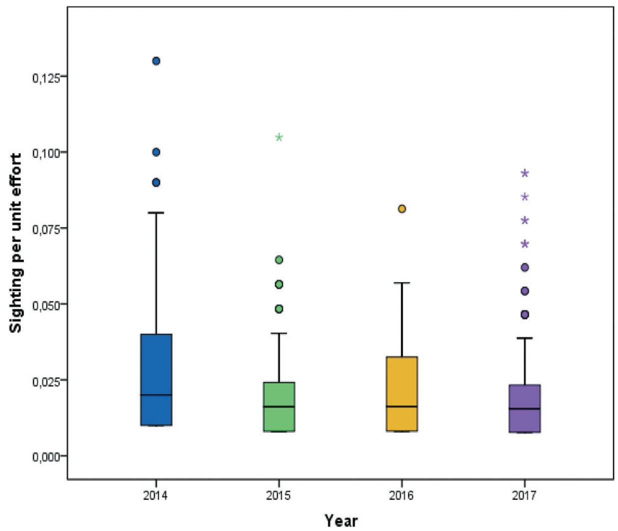

Figure 4. Box plot showing whale sharks sighting per unit effort (SPUE) during the study period (2014–2017).

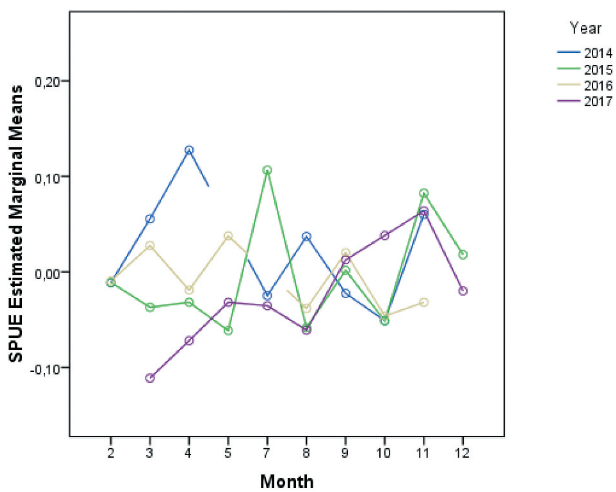

Figure 5. Whale sharks sighting per unit effort (SPUE) monthly variability across the years (2014–2017).

4. Discussion

This study provided new information on the temporal and spatial variation of whale sharks aggregation within the South Ari Marine Protected Area (SAMPA, Maldives). Different studies on whale sharks were focused on understanding animal occurrence and distribution throughout ocean-basins scale (Sequeira et al. 2012, 2013, 2014a, 2014b). Several species of sharks are pelagic and they travel great distances in high seas areas where their conservation is extremely difficult or almost impossible. By protecting critical habitats for reproduction and feeding, MPAs can play an important role in their conservation (Norse 2010; Escalle et al. 2015). However, substantial uncertainty remains regarding the effectiveness of MPAs and their specific benefits to sharks' populations (MacKeracher et al. 2019). In this framework, there is a growing demand from MPA managers to supply more accurate results on the occurrence and distribution of target species in order to develop appropriate conservation actions, especially for small scale MPAs (<100 km^2) (Rigby et al. 2019). Results presented in this study allow to better understand the monthly variability of species occurrence at SAMPA site, and to further investigate potential drivers of occurrence of whale sharks in the area.

4.1. *The importance of environmental conditions*

The present study is the first to include environmental conditions to assess whale sharks relative abundance (expressed as SPUE) in the area, through the application of criteria previously used to study basking sharks (Sims et al. 2005). Results show that most of the encounters (86% of the dataset) occurred in favourable environmental conditions for visual detection from the surface (wind speed < than 3 Beaufort; clear or partial cloud coverage of the sky). The exclusion of data for which FEC requirements were not met, allowed to minimize biases induced by the research effort (i.e., reducing false negative encounters), as weather conditions could affect the detectability of many marine species (e.g., cetaceans (Reid et al. 2003; Evans & Hammond 2004; Dunshea et al. 2020), seabirds (Webb & Durinck 1992; Arroyo et al. 2020), turtles (Eguchi et al. 2007)).

4.2. *Monthly variability in sharks presence*

Results from this study confirmed the year-round presence of whale sharks in the South Ari Atoll previously described as one of a few coastal areas where whale sharks can be frequently encountered yearlong, showing high site fidelity and residency behaviour (Riley et al. 2010; Donati et al. 2016; Perry et al. 2018; Allen et al. 2021; Harvey-Carroll et al. 2021). In particular, this study highlighted significant oscillations in the number of encounters among months, both in the same year and between months of different years, indicating that sharks' relative abundance changes within and between years. Despite the presence of a monthly variability, the absence of seasonal peaks confirms that whale sharks are regularly present in the area during the entire year. In the time interval investigated in this study (four years period), the yearly

Table IV. Two-way ANOVA – SST variability between years, months of the same year, and months of different years. Significant results are highlighted in bold.

Source	Type III sum of squares	df	Mean square	F	P level
Corrected Model	159,313[a]	35	4.552	16.263	0.000
Intercept	179,920.78	1	179,920.775	642,828.73	0.000
year	**4.699**	**3**	**1.566**	**5.596**	**0.001**
month	**77.203**	**10**	**7.72**	**27.584**	**0.000**
year * month	**67.807**	**22**	**3.082**	**11.012**	**0.000**
Error	115.874	414	0.28		
Total	392,311.62	450			
Corrected Total	275.187	449			

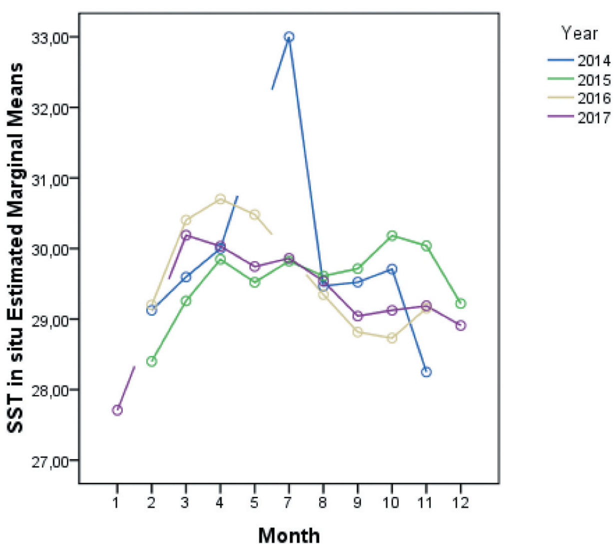

Figure 6. Sea Surface Temperature (SST; °C) monthly variability across the years (2014–2017).

relative abundance appeared to be homogeneous, and no trends were detected; however, a recent study by Harvey-Carroll et al. (2021), where a longer time period was considered (six years), detected a decreasing trend in whale shark presence in the SAMPA. This result highlighted the importance to consider an adequate time interval when assessing the existence of a temporal trend for the species in the SAMPA area.

4.3. Drivers of occurrence in SAMPA

Despite, no linear relationship was found between sea surface temperature and the temporal occurrence of whale sharks in SAMPA area, the inverse

Table V. Two-way ANOVA - Depth variability between years, months of the same year, and months of different years. Significant results are highlighted in bold.

Source	Type III sum of squares	df	Mean square	F	Sig.
Corrected Model	1,964,964.405[a]	42	46,785	8.1	0.0000
Intercept	3,975,360.7	1	3,975,361	686.8	0.0000
Year	**55,179.356**	**3**	**18,393**	**3.2**	**0.0234**
Month	**735,307.57**	**11**	**66,846**	**11.5**	**0.0000**
Year * Month	**526,628.65**	**28**	**18,808**	**3.2**	**0.0000**
Error	5,932,976.5	1025	5788		
Total	22,060,677	1068			
Corrected Total	7,897,940.9	1067			

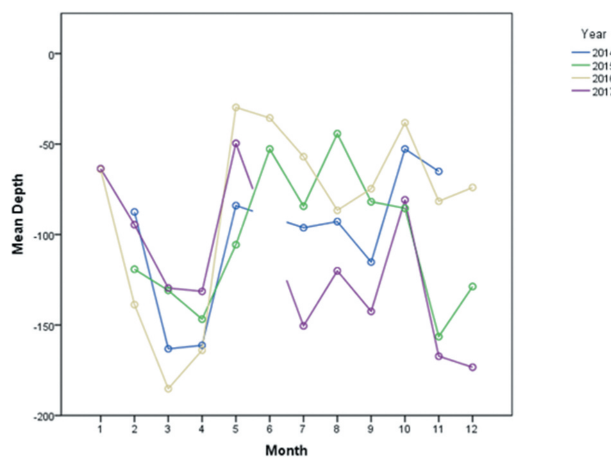

Figure 7. Depth (m) monthly variability across the years (2014–2017).

correlation, almost close to the significant level, with monthly valued of derived SST suggests that temperature likely plays a role in sharks' habitat selection at this scale. Sequeira et al. (2012) classify the SST as the main variable affecting the relative occurrence of whale sharks at Indian Ocean-scale suggesting that whale sharks used only a small band of averaged temperatures for their large-scale movements and they might move outside this range for other activities (e.g. foraging). The limited area considered in this study might constitute a limitation to capture an adequate temperature variability to describe variation in sharks' relative abundance across the year and among years. As reported in many studies, one of the most influential factors for filter feeders aggregations is food abundance (e.g., fish and coral spawning, high-density patch of zooplankton) (Anderson et al. 2011; Sequeira

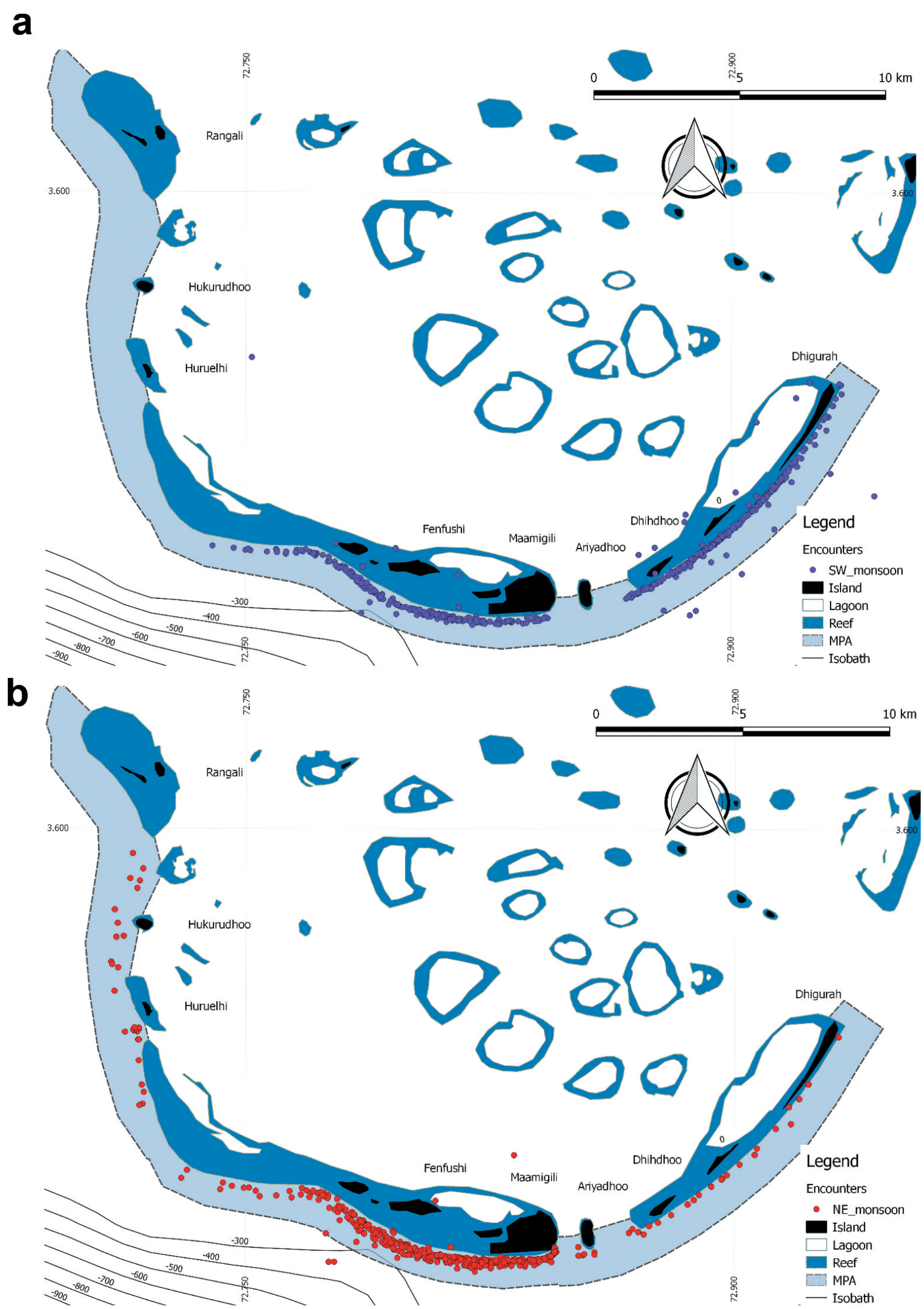

Figure 8. Position of whale sharks encounters during the southwest (a) and the northeast (b) monsoon.

et al. 2012; Robinson et al. 2013; Cárdenas-Palomo et al. 2015; Cárdenas-Palomo et al. 2018; Harris et al. 2020). Although the feeding activity is not confirmed in the SAMPA area, if available, zooplankton biomass data, rather than SST, can represent a suitable variable to understand the occurrence of whale sharks in SAMPA and the rest of Maldives.

The present study found an inverse correlation between SPUE and average values of rainfalls.

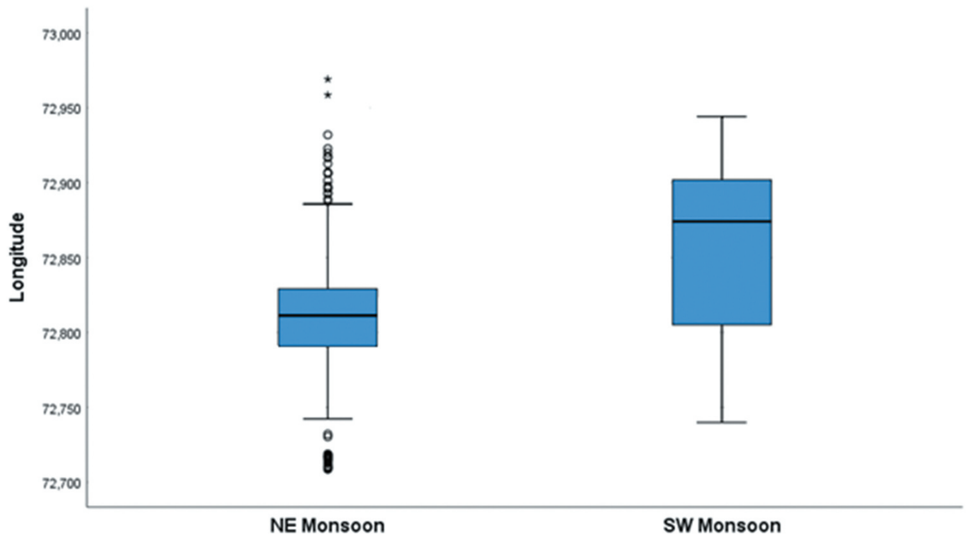

Figure 9. Differences in longitudinal position of whale sharks encounters during the northeast and the southwest monsoons.

Maldives climate is tropical equatorial and characterized by two main seasons influenced by the Indian Monsoon. The northeast monsoon, from December to April, brings the "dry season" with limited rainfalls, whilst the southwest monsoon "wet season" occurs from May to November bringing increased rainfalls (Anderson & Ahmed 1993; Wilson et al. 2001; Rowat 2007; Stevens et al. 2015). The findings from the present study highlighted the presence of whale shark especially during the dry season (northeast monsoon) but data did not show a seasonal peak in the first half of the year. Along the entire Maldives archipelago, whale sharks show a pattern of distribution strongly related to the monsoon seasons (Anderson & Ahmed 1993; Anderson et al. 2011), this spatial pattern is confirmed by the results of our study at a much smaller spatial scale (MPA scale; 42 km^2). In the SAMPA during the northeast monsoon period, whale sharks appeared to be more concentrated in a smaller longitudinal range (Figure 8(b)) closer to the western-central part of the MPA. In this area, deeper waters conditions occur due to the proximity to a deep depression (Figures 1–9) close to the forereef, which could be considered an "accumulation" zone for nutrients and preys.

The direct correlation between latitudinal position of whale sharks and sea bottom depth recorded during the encounters (Pearson correlation $N = 1068$; $r = 0.56$; P-level < 0.001) indicated that bathymetrical features could play a role in the shark distribution at SAMPA especially during monsoon seasons. During the northeast monsoon season, encounters occurred in areas with average depth of about 140 m while during the southwestern monsoon they occur in areas with shallower depths. (Figure 10). This result suggested a potential influence of deep canyon systems, and related oceanographic factors, with the habitat selection, during the dry season.

This key role played by oceanographic geomorphological features is supported by other studies. Copping et al. (2018) showed that coastal whale sharks aggregations occur typically in the shallow forereef and lagoon areas which have steep slopes and deep water in their proximity. Canyons are well known to induce upwelling events and to be characterized by high productivity (Copping et al. 2018). The influence of currents on sharks aggregation was also reported in southern Mozambique (e.g., whales sharks aggregation in Praia de Tofo) where the presence of eddies was indicated as important factors affecting shark aggregation along the coast (Sleeman et al. 2010; Rohner et al. 2013; Donati et al. 2016).

Additionally, studies indicated that whale sharks feeding activity could occur in deep water and then, successively the animals surfaced in shallower and warmer waters, to thermoregulate and recover (Motta et al. 2010; Copping et al. 2018; Allen et al. 2021). In SAMPA canyon areas could be used by shark for feeding purposes especially during dry season. However, results presented in this study

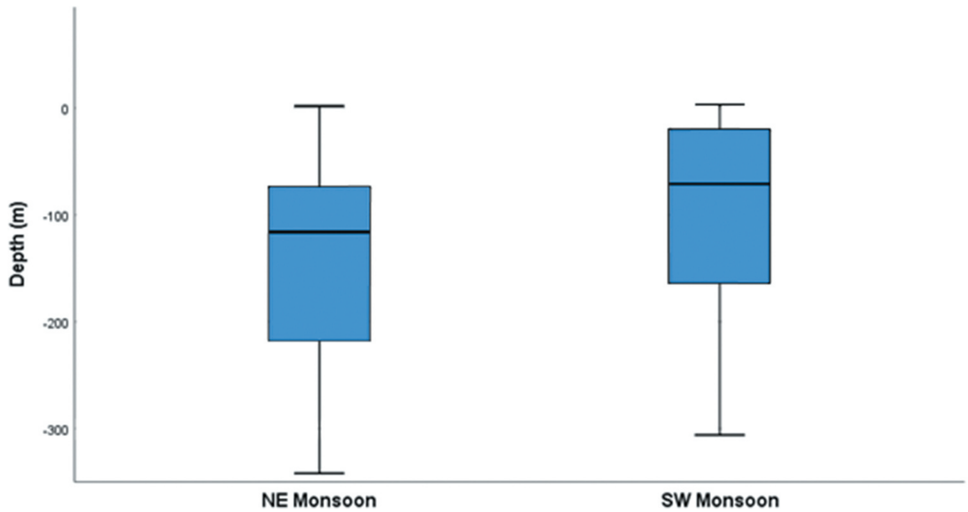

Figure 10. Differences in sea bottom depth recorded during whale sharks encounters during the northeast and the southwest monsoons.

focused only on data collected in shallow waters, and further data (e.g., tagging data, zooplankton samples or foraging evidence, oceanographic data collected as a function of depth) from the canyon area, are needed to support this hypothesis.

Here, at the scale of MPA, the strongest drivers of whale sharks temporal occurrence and distribution appear to be related to seasonal rainfalls events (monsoon influence) or bathymetric features (canyon presence), rather than productivity or sea surface temperature, widely used in literature (Sequeira et al. 2014a, 2014b) to explain sharks movements and habitat selection at a larger scale. To fully assess the population status of whale sharks it is necessary to understand the key elements affecting their occurrence and the influence that climate change-related events may have on their distribution at the local scale.

Despite the worldwide interest in the natural resources of the Maldives, the whale shark population from this area is increasingly subjected to anthropogenic pressure mainly coming from tourism-related activities. The results presented in this work provided additional elements to increase the knowledge about whale shark aggregations in South Ari Atoll and to inform decision-making processes that aim to implement dedicated management actions and to protect this fragile population inhabiting SAMPA.

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Disclosure statement

No potential conflict of interest was reported by the author (s).

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