



Monsoon variability and sea surface temperature influence the presence of tiger sharks around Fuvahmulah, Maldives

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Abstract

Environmental variability plays a crucial role in shaping the site use of apex predators, yet its influence under human-modified conditions remains unclear. From August 2021 to March 2024, we conducted 911 visual surveys of tiger sharks (*Galeocerdo cuvier*) at Fuvahmulah, Maldives. We used photo-ID to identify individual tiger sharks, and agglomerative hierarchical clustering to classify sharks into residency clusters. We fitted generalized additive models to residency clusters and life-stage groups to test whether sea surface temperature, monsoon phase, lunar–tide interactions, and wind and wave metrics influenced shark abundance at the Tiger Harbour dive site. Models explained 24–38% of deviance and revealed that resident, relatively larger females preferred warm temperatures and monsoonal cycles, whereas transient, relatively smaller sharks responded more to weather patterns, wind direction, and lunar–tidal effects. Our results underscore that natural environmental rhythms continue to influence tiger shark sightings even under regular provisioning, informing ecological insights consistent with findings from other provisioned shark aggregations.

Keywords GAMs · Photo-ID · Apex predator · Environmental influence · Tiger shark · Maldives

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Introduction

Predatory sharks are declining worldwide largely due to overfishing (Dulvy et al. 2021). The lack of such predators can alter food web-structure and ecosystem functioning (Baum and Worm 2009). Yet, the presence of sharks is driven by a complex combination of anthropogenic, ecological and environmental factors (Heupel and Simpfendorfer 2014; Schlaff et al. 2014; Hammerschlag et al. 2022). Temperature, depth, tidal regimes, lunar phases, and seasonal variability have been identified as key drivers of shark and ray movements (Schlaff et al. 2014). Temperature has a strong influence on shark metabolism and drives diel, seasonal, and long-term distribution shifts (Bernal et al. 2012; Sims et al. 2006; Ketchum et al. 2014; Osgood et al. 2021). Moreover, evidence of behavioural thermoregulation is linked to reproduction and foraging, whereby sharks seek thermal optima to maximize the efficiency of metabolic processes (Sims et al. 2006; Speed et al. 2012; Watanabe et al. 2021). Tidal cycles influence habitat use in species such as bull sharks *Carcharhinus leucas*, blacktip reef *C. melanopterus*, and lemon sharks *Negaprion brevirostris* (Heupel et al. 2010; Lea et al. 2020), and in combination

with lunar phase, correlate with occurrence in at least nine elasmobranch species (Andrzejczek et al. 2024).

Tiger sharks *Galeocerdo cuvier* are apex predators that play a central ecological role across a wide range of marine habitats. As keystone species, they shape prey populations and promote connectivity between coastal and pelagic ecosystems (Papastamatiou et al. 2015; Vaudo et al. 2014). Tiger sharks have been associated with ecological effects across multiple marine habitats, including potential influences on herbivore dynamics and habitat structure, although these effects are context-dependent (Dedman et al. 2024). These sharks exhibit highly variable movement patterns that span multiple spatial and temporal scales, with behaviour influenced by environmental gradients, physiological demands, and prey availability, supporting a context-dependent ecological framework (Lubitz et al. 2022).

In the western Indian Ocean (WIO), tiger sharks show both site fidelity and long-distance migrations (Ebert et al. 2021; Heithaus et al. 2007). Across regions such as La Réunion, South Africa, and Madagascar, tiger sharks display sex-specific and seasonal shifts in spatial behavior and parturition timing (Jaquemet et al. 2013; Blaison et al. 2015; Dicken et al. 2016). In Western Australia, seasonal variation is also observed, with higher occurrences reported between September and May, likely linked to prey abundance in foraging habitats like Shark Bay (Heithaus 2001; Simpfendorfer et al. 2001; Wirsing et al. 2006). These patterns highlight how tiger shark movements respond to environmental cues and resource availability across the Indian Ocean (Ferreira et al. 2015); however, such data are lacking for the Maldives, a central yet understudied region, despite its designation as a Shark Sanctuary (Vossgaetter et al. 2024).

Provisioning sharks has become a common and lucrative activity in recent years for tourism purposes, generating substantial revenues for local economies (Gallagher and Hammerschlag 2011; Cisneros-Montemayor et al. 2013). However, it also presents potential challenges for both humans and sharks (Brena et al. 2015; Gallagher et al. 2015). Provisioning sharks refers to the use of food-based attractants to increase the probability of shark encounters, although encounters remain variable and not guaranteed (Meyer et al. 2009). Provisioning sites offer a controlled framework for conducting scientific research and for monitoring external factors that might impact the likelihood of encounters with marine fauna at a small spatial scale. Human-altered ecosystems where food is predictably available year-round, such as in Fuvahmulah, Maldives, could potentially alter the strength of natural environmental drivers on shark occurrence (e.g. whale sharks *Rhincodon typus*, Legaspi et al. 2020). Fuvahmulah hosts reproductive adult females year-round, along with juveniles and occasional adult males (Sulikowski et al. 2024; Vossgaetter et al. 2024).

Assessing the influence of environmental variables on year-round-provisioned tiger sharks in Fuvahmulah is crucial for understanding how these variables affect their spatial ecology despite continuous provisioning. As shark provisioning continues to expand globally, studies that provide time-space, fishery-independent data on the parameters affecting shark movement, distribution, and behaviour are vital for managing the target species. Tiger sharks are currently provisioned worldwide at several locations (Séguigne et al. 2023), although the environmental conditions that may influence encounters at these sites are often overlooked.

At provisioned sites, individual sharks often exhibit heterogeneous site use, with some individuals returning frequently over long periods while others appear only sporadically. This variability in site fidelity may reflect differences in foraging strategy, reproductive state, or tolerance of local conditions, and it may influence how strongly environmental drivers shape encounter rates. Therefore, separating individuals by residency patterns can help identify whether environmental responses differ among sharks with contrasting site-use strategies.

Here, we aim to (a) investigate the influence, if any, of environmental variables on tiger shark abundance at Fuvahmulah in the Maldives; (b) and test whether environmental predictors of tiger shark sightings differ between groups of individuals with contrasting site fidelity as defined from photo-ID encounter histories and between life stages (adults vs. juveniles).

Methods

Study Site

Fuvahmulah is a single-island-atoll located in the southern part of the Maldivian Archipelago, nearly 30 km south of the equator, surrounded by the Indian Ocean (lat, -0.30° , lon 73.43°). The island is made of an oceanic platform reef surrounded by a fringing reef and lacks a lagoon, unlike any other atolls in the Maldives. A 2-km spur reef (Farikede in the local language) is present in the south-eastern edge of the island, made by a moderate sloping coral reef (depth 0–20 m) and a drop-off over the site. Near-atoll bathymetry typically ranges from 30 to 80 m depth, even though the abyssal plain reaches depths $>2,000$ m. Meteorological data displays the presence of two predominant monsoonal phases, the Northeast monsoon (Dec–Apr) and the Southwest monsoon (Jun–Oct), which alternate with inter-seasonal monsoons in May and November (Schott et al. 2009; Su et al. 2021), and a mixed semidiurnal tidal regime (1.1 m maximum range) (UHSLC, Caldwell et al. 2015). Our study site encompasses the area outside the harbour, at a dive site

named ‘Tiger Harbor’. The dive site (previously described by Vossгаetter et al. 2024 and Reinero et al. 2025) is shallow (<11 m), where tiger sharks are provisioned with tuna heads or fish discards hidden under rocks daily, year-round, for an average time of 30–40 min per dive. All surveys were conducted at this same provisioning location, and divers remained within a consistent shallow depth range (<11 m) during each observation period, ensuring standardized survey depth across sampling days (Fig. 1).

Data collection

Surveys were conducted between August 2021 and March 2024 and comprised a total of 877 dives. Sampling occurred year-round across all months, with monthly effort ranging from 29 dives (June) to 114 dives (November), spanning four calendar years (2021–2024). Tiger shark sightings were recorded systematically by resident marine biologists, following the methodology adopted by Vossгаetter et al. (2024). Unique individuals were identified based on distinctive physical characteristics that were reliable over time and reduced double counts (Vossгаetter et al. 2024).

The response variable was the number of unique photo-identified tiger sharks observed per calendar day during

standardized provisioning dives. Dives were conducted daily at the same site and followed a consistent protocol, including standardized duration (55–60 min) and uniform baiting using tuna heads. Shark counts were recorded from the onset of the food drop until the conclusion of the dive. Because dive location, duration, and baiting protocol were consistent across sampling days, daily shark counts were considered directly comparable without additional effort correction.

Life stage (juvenile vs. adult) was assigned according to the size categories used by Vossгаetter et al. (2024) in their characterization of tiger sharks at the same Fuvahmulah aggregation, based on total length estimates from photo-ID and photogrammetry. Environmental conditions were monitored using a combination of in situ and remotely sensed environmental datasets (see Table 1).

Sea Surface Temperature (SST, °C) was collected using calibrated dive computers, whereas wind speed and direction, as well as wave height and direction, were acquired from *Wisuki.com*, following the same approach as Ionuzzi et al. (2023). Weather was collected in-situ using a categorical weather-state variable classification with four levels: (a) ‘Sunny’, ‘Rainy’, ‘Cloudy’, ‘Partly Cloudy’.

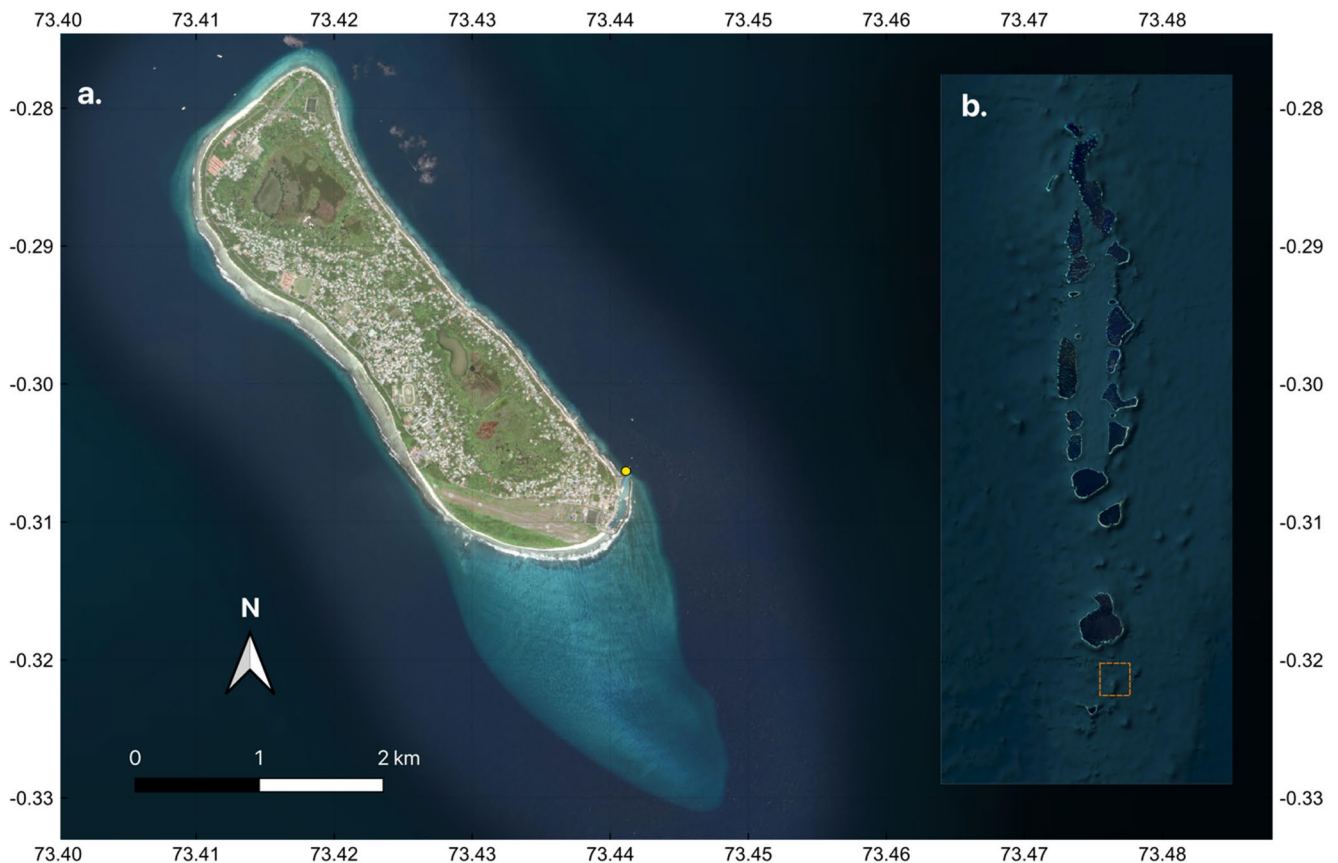


Fig. 1 (a) Map of Fuvahmulah Island, Maldives, showing the location of Tiger Harbour (0.30°N, 73.43°E, yellow dot) on the southern coastline. (b) Regional map of the Maldives archipelago with a dashed, orange rectangle indicating the position of Fuvahmulah within the country

Table 1 Environmental variables chosen for the models in this study and their corresponding dataset and source

Variable	Type	Data Source	Collection Methods
SST (°C)	Continuous	Dive Computer	In-Situ
Weather	Categorical	Satellite-derived	Wisuki.com
Wind Speed	Continuous	Satellite-derived	Wisuki.com
Wind Direction	Categorical	Satellite-derived	Wisuki.com
Wave Height	Continuous	Satellite-derived	Wisuki.com
Wave Direction	Continuous	Satellite-derived	Wisuki.com
Lunar Phases	Categorical	Data-driven	'lunar' package (RStudio)
Tides	Categorical	Satellite-derived	tidecharts.com
Monsoon	Categorical	Date	Derived from the calendar month
Dive Time	Continuous	Dive Computer	In-Situ
Observation Depth	Continuous	Observer	In-Situ
Visibility	Continuous	Observer	In-Situ

Lunar phases were obtained using the 'lunar' package in R (Version 2024.12.1+563) and matched with the appropriate date, facilitating the alignment of environmental data with the lunar cycle, a potential influencer of shark behavior (RStudio, 2024).

Site fidelity clusters

To assess the effect of environmental variables on groups of sharks, we clustered individuals with differing degrees of site fidelity to isolate potential individual-level patterns. The analysis was conducted based on the global site fidelity index (SFI) used by Séguine et al. (2023). SFI was computed as the proportion of dives within the sampling period during which a shark was observed, calculated by dividing the number of dives with sightings by the total number of dives conducted. Values range from 0 to 1, where lower SFI indicates weaker site fidelity to the study area and higher SFI indicates stronger site fidelity.

Based on individual SFI values, an agglomerative hierarchical cluster (AHC) analysis was performed to separate sharks exhibiting similar degrees of residency. Dissimilarity among individuals was calculated using Euclidean distance, and Ward's method was used as the clustering algorithm. Clustering was conducted using the `hclust` function in the R package `stats` with `method = "ward.D2"` (Murtagh and Legendre 2014), following Kaufman and Rousseeuw (1990) and Legendre and Legendre (2012). The optimal number of clusters was determined using the average silhouette method implemented in the R package `cluster` (Maechler et al. 2021).

Generalized Additive Models (GAMs)

To investigate how environmental and temporal variables influenced daily tiger shark occurrence, we modeled the number of uniquely identified tiger sharks observed per calendar day as a function of environmental predictors. Each observation represented a single standardized provisioning dive conducted at a consistent site, depth, and duration, resulting in comparable sampling effort across dives; therefore, no offset term was included in the models. Given the count-based nature of the response variable (number of individual tiger sharks per calendar day) and environmental predictors, generalized additive models (GAMs) were fitted to the data using the `mgcv` package (Wood 2017) in RStudio, with a Poisson distribution and log link to understand the influence, if any, of environmental and temporal variables on shark numbers. All predictors were included as parametric terms (i.e., no spline smoothers were specified); therefore, basis dimensions (knots) were not applicable. Accordingly, diagnostics specific to smooth terms (e.g., basis-dimension checks and concurvity) were not applicable; model fit was assessed using residual diagnostics and overdispersion checks, and predictor collinearity was assessed using variance inflation factors. Environmental and temporal factors were included as exploratory variables (i.e. wave height in meters, wind direction in cardinal directions, water temperature in Celsius, eight unique lunar phases, tide category, monsoon season, and weather; see Table 1). Model selection began with a full model including all candidate predictors. Predictors were sequentially removed in a backward stepwise manner, with models compared at each step using Akaike's Information Criterion (AIC) (Papastamatiou et al. 2015). The final model retained the combination of predictors that minimized AIC. After selecting the best-fit model, we fitted a separate GAM including a tide \times lunar-phase interaction term to test whether the effect of tide on tiger shark counts varied across lunar stages. Collinearity among predictors was assessed using variance inflation factors, and model fit was assessed through residual diagnostics (i.e. residuals vs. fitted values, overdispersion ratios) to ensure that the assumptions were met (Ackerman et al. 2000). Separate models were fitted for (i) residency clusters identified through hierarchical clustering and (ii) life-stage categories (adults and juveniles) to evaluate whether environmental drivers differed among site-fidelity groups and ontogenetic classes.

Results

Two distinct clusters were identified in the agglomerative hierarchical clustering (AHC) analysis, comprising 30 individuals in Cluster 1 and 190 individuals in Cluster 2. The AHC cut-off value was set at a height of 1.05, and the cophenetic correlation coefficient was 0.845, indicating good representation of the underlying dissimilarities.

Clustering was based on the Site Fidelity Index (SFI) values, a unitless index ranging from 0 to 1, with higher values indicating stronger site fidelity. Cluster 1 exhibited significantly higher SSFI values (mean \pm SD = 0.1698 ± 0.0428) and was composed entirely of females (100% female; 73.3% classified as adults). Many individuals in this group were observed pregnant (Sulikowski et al. 2024). This cluster is hereafter referred to as ‘highly resident’ (HR).

Cluster 2 exhibited substantially lower SFI values (mean \pm SD = 0.0269 ± 0.0307), including individuals sighted only once during the study period. This cluster comprised both juveniles and adults and was predominantly female (82.1% female; 51.6% adults). This group is hereafter referred to as ‘less resident’ (LR).

The Generalized Additive Models (GAMs) explained between 24.3% and 38.2% of the deviance in tiger shark sightings, with adjusted r^2 values ranging from 0.188 to 0.232 (Table 2). Significant predictors varied across residency clusters and life stages.

For HR tiger sharks (Cluster 1, Table 2), the model explained 29.6% of the deviance ($r^2 = 0.208$). Sightings increased with SST ($p = 0.019$). Wind from the east-northeast (ENE), north (N), and southeast (SE) also significantly influenced sightings ($p = 0.014$, $p = 0.016$, $p = 0.008$). Lunar and tide effects were observed, with increased sightings during the full moon and rising tide ($p = 0.04$).

For LR tiger sharks (Cluster 2 - Table 2), the model explained 38.2% of the deviance ($r^2 = 0.232$). Sightings were positively associated with the northeast monsoon ($p = 2.9 \times 10^{-7}$), rainy ($p = 0.018$) and sunny weather ($p = 0.04$), and surface winds from the south (S) ($p = 0.008$), southwest (SW) ($p = 0.017$), west (W) ($p = 0.006$), and west-southwest (WSW) ($p = 0.0019$). Significant lunar and tidal interactions were detected during high tide and the waning gibbous moon ($p = 0.0118$, $p = 0.023$).

For Juvenile sharks (Table 2), the model explained 24.3% of the deviance ($r^2 = 0.188$). Sightings were positively linked to the full moon ($p = 0.03$), monsoon phase ($p = 9.2 \times 10^{-6}$), and SST ($p = 0.009$). Increased sightings were also observed during partly cloudy ($p = 0.017$) and rainy weather ($p = 0.047$) and with winds from the west-southwest (WSW) ($p = 0.031$). Lunar and tide interactions were significant during the rising tide ($p = 0.02$) and the first quarter moon.

For Adult sharks (Table 2), the model explained 25% of the deviance ($r^2 = 0.197$). Sightings were influenced by surface SST ($p = 1.2 \times 10^{-5}$) and the full moon ($p = 0.008$). Monsoon season ($p = 0.001$) and wind direction from the east-southeast (ESE) ($p = 0.02$), northeast (NE) ($p = 0.03$), and south-southeast (SSE) ($p = 0.04$) were also significant predictors. Lunar and tide interactions were detected during high tide and the waning gibbous moon ($p = 0.043$).

Influence of seasonal and thermal conditions on tiger shark sightings

Sea surface temperature (SST) emerged as a consistent positive predictor of tiger shark sightings across all four groups (Fig. 2; Table 2). SST was significantly and positively associated with shark sightings for highly resident individuals (Estimate = 0.0739, SE = 0.0316, $z = 2.3350$, $p = 0.0195$), less resident individuals (Estimate = 0.0507, SE = 0.0208, $z = 2.4347$, $p = 0.0149$), juveniles (Estimate = 0.0799, SE = 0.0308, $z = 2.5952$, $p = 0.0095$), and adults (Estimate = 0.0917, SE = 0.0210, $z = 4.3763$, $p < 0.001$). Collectively, these patterns indicate increased sightings under warmer surface temperatures across residency groups and life stages.

Similarly, monsoonal phases also emerged as impact factors on tiger shark sightings, with consistently higher sightings during the NE monsoon across all groups (Fig. 3). The effect was strongest among adult sharks (Estimate = -0.55, SE = 0.12, z -score = -4.60, $p < 0.001$) and highly resident individuals (Estimate = -0.47, SE = 0.13, z -score = -3.56, $p < 0.001$), indicating significantly reduced sightings during the SW monsoon relative to the NE. Less resident sharks exhibited a significant seasonal response (Estimate = -0.42, SE = 0.14, $z = -2.97$, $p = 0.003$), while juveniles showed a weaker, non-significant trend (Estimate = -0.26, SE = 0.17, $z = -1.53$, $p = 0.126$) (Table 2). Ultimately, these results highlight a seasonal distribution of tiger sharks at the study location, with a sharp presence during the NE monsoonal phase among highly resident and adults.

Discussion

General trends

This study reveals clear temporal patterns in tiger shark sightings in Fuvahmulah; our results show that a combination of seasonal and short-term environmental variables explains a substantial portion of the variance in sighting frequency. Shark sightings at Tiger Harbour are not random but linked to environmental cues, even at this provisioning site. Monsoonal phases and sea surface temperature emerged

Table 2 Generalized Additive Models (GAM) results assessing the influence of environmental predictors on tiger shark (*Galeocerdo cuvier*) sightings at Fuvahmulah, Maldives. GAM models were run across Highly Resident (HR, Cluster 1), Less Resident (LR, Cluster 2), Adult, and Juvenile groups. The significance of the single variables is reported with estimate, SE, z-score, and *p*-value (*p* < 0.05) highlighted in bold

Model	Variable	Estimate	SE	z-score	<i>p</i> -value
Cluster 1	Lunar Full	-0.5543	0.2570	-2.1573	0.0310
Cluster 1	Monsoon (NE)	0.1664	0.0790	2.1059	0.0352
Cluster 1	Monsoon (SW)	-0.4143	0.0726	-5.7091	0.0000
Cluster 1	SST(°C)	0.0739	0.0316	2.3350	0.0195
Cluster 1	Wind Direction (ENE)	-0.4460	0.1828	-2.4403	0.0147
Cluster 1	Wind Direction (N)	-0.3879	0.1614	-2.4031	0.0163
Cluster 1	Wind Direction (SE)	-0.4292	0.1641	-2.6146	0.0089
Cluster 1	Tide Rising x Lunar Last quarter	-0.4803	0.2352	-2.0416	0.0412
Cluster 2	Lunar Full	-0.3286	0.1287	-2.5542	0.0106
Cluster 2	Monsoon (NE)	0.2393	0.0467	5.1260	0.0000
Cluster 2	Monsoon (SW)	-0.4404	0.0498	-8.8379	0.0000
Cluster 2	Weather Rainy	-0.1838	0.0780	-2.3573	0.0184
Cluster 2	Weather Sunny	0.0829	0.0416	1.9908	0.0465
Cluster 2	SST(°C)	0.0507	0.0208	2.4347	0.0149
Cluster 2	Wind Direction (S)	0.4854	0.1837	2.6423	0.0082
Cluster 2	Wind Direction (SW)	0.4287	0.1797	2.3860	0.0170
Cluster 2	Wind Direction (W)	0.4825	0.1784	2.7055	0.0068
Cluster 2	Wind Direction (WNW)	0.3822	0.1853	2.0629	0.0391
Cluster 2	Wind Direction (WSW)	0.5857	0.1889	3.1000	0.0019
Cluster 2	Tide High x Lunar Full	0.4765	0.1892	2.5178	0.0118
Cluster 2	Tide High x Lunar Waning gibbous	0.6631	0.2919	2.2713	0.0231
Cluster 2	Tide High x Lunar Waning crescent	0.4850	0.1677	2.8924	0.0038
Juvenile	Lunar Full	-0.4507	0.2121	-2.1248	0.0336
Juvenile	Monsoon (NE)	0.3128	0.0705	4.4350	0.0000
Juvenile	Monsoon (SW)	-0.7344	0.0775	-9.4698	0.0000
Juvenile	Weather Partly Cloudy	-0.2436	0.1026	-2.3749	0.0176
Juvenile	Weather Rainy	-0.2343	0.1182	-1.9817	0.0475
Juvenile	SST(°C)	0.0799	0.0308	2.5952	0.0095
Juvenile	Wind Direction (WSW)	0.4793	0.2228	2.1511	0.0315
Juvenile	Tide Rising x Lunar First quarter	0.5020	0.2173	2.3098	0.0209
Juvenile	Tide Rising x Lunar Full	0.5804	0.2422	2.3967	0.0165
Juvenile	Tide High x Lunar Waning crescent	0.6214	0.2671	2.3261	0.0200
Adult	Lunar Full	-0.3641	0.1376	-2.6463	0.0081
Adult	Monsoon (NE)	0.1848	0.0484	3.8174	0.0001
Adult	Monsoon (SW)	-0.3613	0.0490	-7.3726	0.0000
Adult	Weather Rainy	-0.2017	0.0813	-2.4790	0.0132
Adult	SST(°C)	0.0917	0.0210	4.3763	0.0000
Adult	Wind Direction (ESE)	-0.3573	0.1545	-2.3130	0.0207
Adult	Wind Direction (NE)	-0.3004	0.1414	-2.1238	0.0337
Adult	Wind Direction (SSE)	-0.3530	0.1729	-2.0412	0.0412
Adult	Tide High x Lunar Waning gibbous	0.7473	0.3696	2.0221	0.0432
Adult	Tide Rising x Lunar Last quarter	-0.3417	0.1459	-2.3420	0.0192

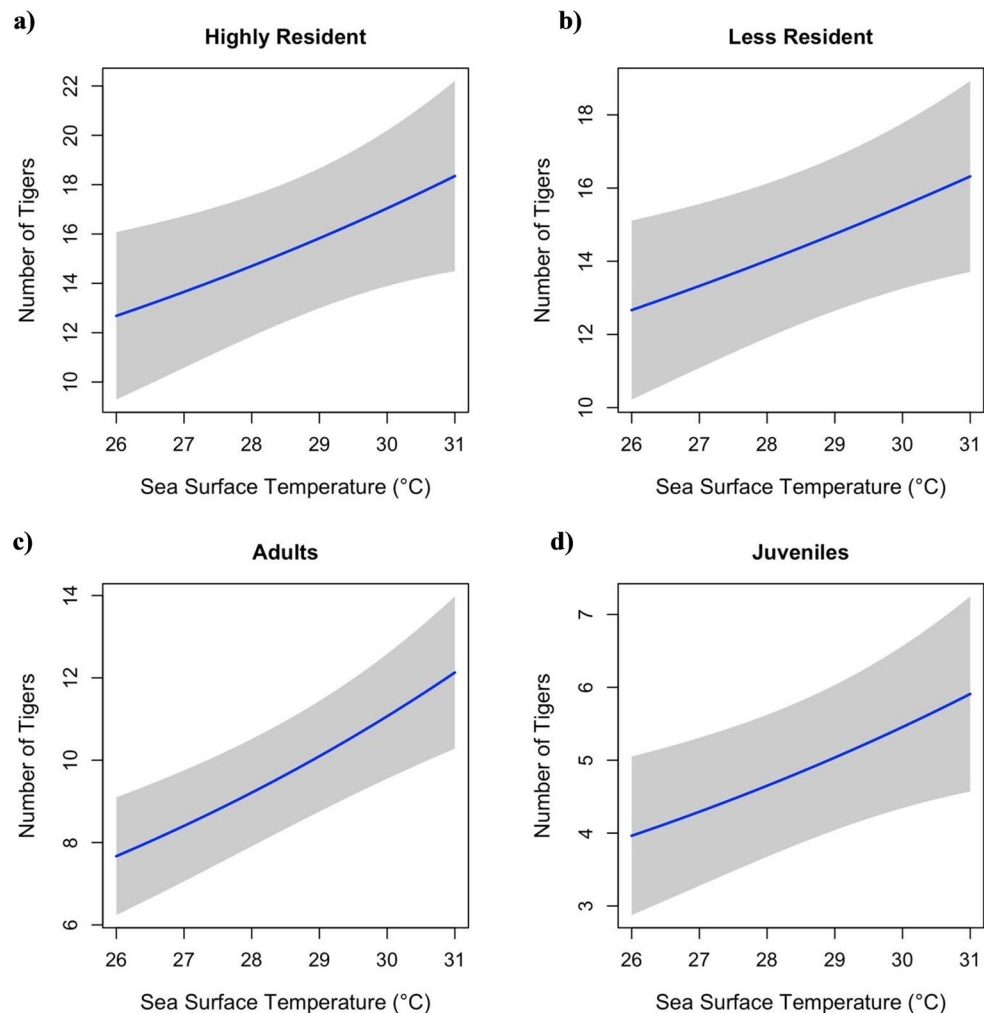
as key predictors across life stages and residency groups. GAM trends suggest that tiger sharks adjust their visitation in response to broad seasonal shifts and finer-scale cycles, likely as part of their behavioural strategy to optimise feeding and balance it with physiological conditions, rather than being an artefact of provisioning alone. As documented in other species, shark populations can respond dynamically to their surrounding environment in a context-dependent site use (Papastamatiou et al. 2015; Lubitz et al. 2022). Our results suggest a stronger seasonal occurrence influenced by monsoonal phases, SST, and lunar-tidal cycles, significantly

shaping patterns, with noticeable differences between life stages and residency groups. The differences between groups may also reflect life-stage-specific movement strategies: more transient juveniles respond to broader-scale environmental conditions, while resident adults respond more strongly to local environmental variation.

Seasonality and monsoon

A pronounced seasonal signal was evident in tiger shark sightings closely aligned with the regional monsoon cycle.

Fig. 2 Effect of sea surface temperature (SST) on tiger shark (*Galeocerdo cuvier*) sightings predicted from generalized additive models (GAMs) across four groups: (a) Highly Resident, (b) Less Resident, (c) Adults, and (d) Juveniles. Lines represent the modelled smooth functions for SST, with shaded bands indicating 95% confidence intervals. Models were fitted with a Poisson error structure, and predictions were generated while holding all other covariates constant at their median (continuous) or reference (categorical) values. All groups exhibited a positive relationship between SST and shark sightings

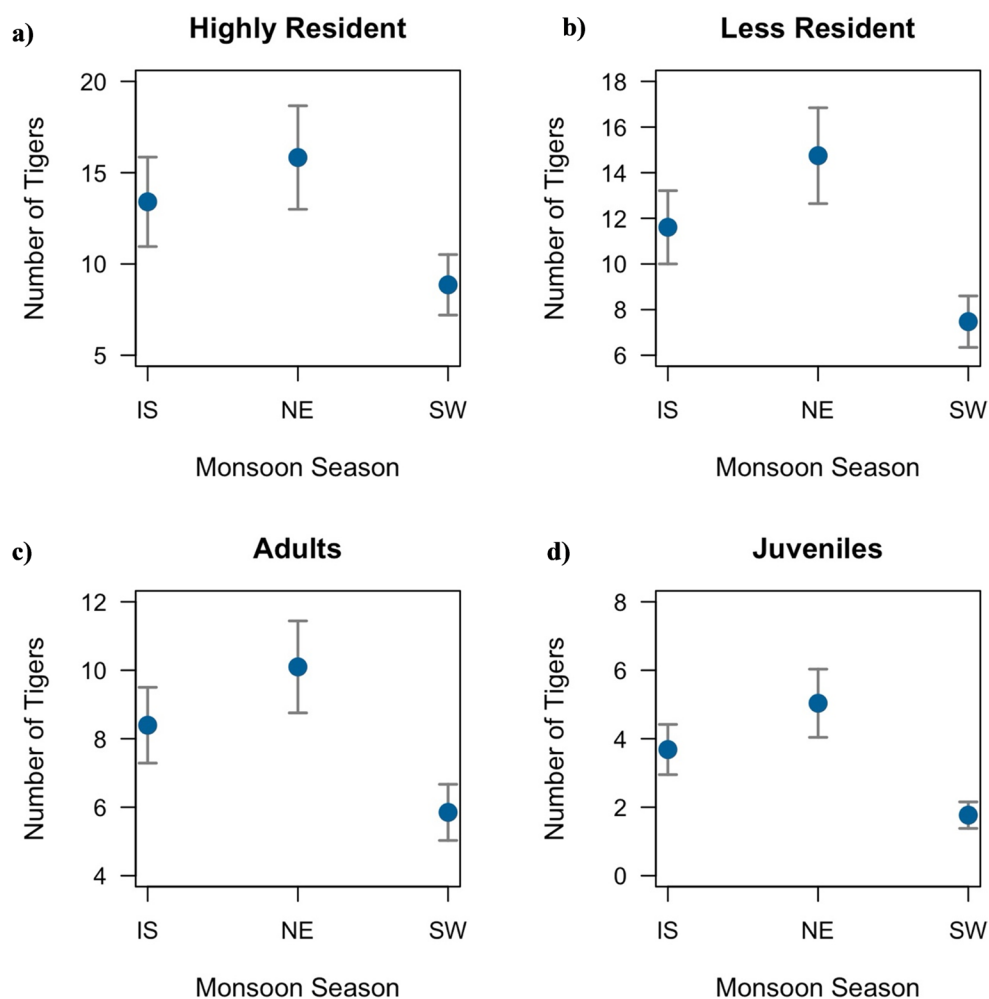


This pattern was corroborated by long-term photographic identification data from the same site where males were almost entirely absent from July to September and female sightings peaked from November to April (Vossgaetter et al. 2024). The seasonal decline in sightings during the Southwest monsoon suggests that a portion of the population, especially males and possibly near-term pregnant females, disperses or reduces the usage of the site. According to Betzler et al. (2018), the Northeast monsoon brings in the Maldives calmer seas and often clearer waters with different current patterns. These conditions could maximise foraging opportunities and encourage sharks to aggregate locally in greater numbers. Takemoto et al. (2014) found that the monsoons influence reef and pelagic food webs, such that prey fishes or scavenging opportunities could be more abundant or accessible during certain months. Tiger sharks are opportunistic feeders (Lowe et al. 1996), and they may time their residency at Fuvahmulah to coincide with periods of higher foraging payoff, in addition to an energetically efficient patrolling of the area and interactions with divers promoted by calmer conditions of the ocean.

Conversely, the Southwest monsoon is characterized by stronger winds, higher rainfall, and overall rougher sea conditions, along with decreased food availability due to the low tourist season; these conditions might lead sharks to seek alternative areas or more sheltered habitats, resulting in fewer sightings at the provisioning site. In the Bahamas, it is hypothesized that tiger sharks could use provisioning grounds in such a way that provisioning activities alone would not be the sole plausible driver for restricting their habitat utilisation and movement patterns to shark feeding sites. Other drivers could explain residency patterns and space use at high-use areas exposed to shark tourism, such as prey preferences and availability, and reproduction (i.e., gestation or parturition) (Hammerschlag et al. 2012, 2017). Similar patterns have also been reported at shark provisioning sites in Fiji (Brunnschweiler and Barnett 2013) and French Polynesia (Séguigne et al. 2023), where environmental variability continues to influence shark presence despite consistent provisioning.

The observed monsoonal pattern in tiger shark sightings is consistent with seasonal habitat shifts documented

Fig. 3 Predicted effect of monsoon season on tiger shark (*Galeocerdo cuvier*) sightings across four groups: (a) Highly Resident, (b) Less Resident, (c) Adults, and (d) Juveniles. Estimates were derived from generalized additive models (GAMs) with monsoon phase included as a categorical predictor. Points represent fitted values and vertical bars denote 95% confidence intervals, with all other covariates held at their median or reference values. Monsoon phases are abbreviated as IS=Inter-Seasonal, NE=Northeast, and SW=Southwest. All groups exhibited a peak in predicted sightings during the Northeast monsoon



in other large elasmobranchs of the region. For example, whale sharks in the Maldives exhibit a monsoon-linked distribution, shifting between opposite sides of atolls as monsoon currents reverse; congregating where plankton blooms develop in each season (Anderson and Ahmed 1993). In South Ari Atoll, whale sharks and manta rays move between eastern and western reef zones depending on monsoonal plankton dynamics, effectively tracking productivity pulses driven by the monsoon cycle (Anderson et al. 2011; Valsecchi et al. 2021).

Seasonal site fidelity of large sharks tied to reproductive cycles is another consideration (Hammerschlag et al. 2011). Many shark species undertake seasonal migrations, or habitat shifts to coincide with mating or pupping seasons (Heupel et al. 2015). In the Western Atlantic, for instance, adult female tiger sharks migrate seasonally, presumably to give birth or mate in specific areas at specific times (Hammerschlag et al. 2012; Sulikowski and Hammerschlag 2023). In our study, the timing of reduced sightings (mid-year) corresponds to late spring and summer. This period may represent when pregnant females might leave the aggregation to

give birth, if a synchronous pupping season exists (Castro 2009). Thus, the monsoonal decline could be explained by an exodus of near-term gravid females to distant pupping grounds, after which some return by the late-year Northeast monsoon. This inference is corroborated by a recent study in Fuvahmulah (Sulikowski et al. 2024) where a multitude of pregnant females were found pregnant at different stages in May, a few months before the start of the Southwest monsoon. While direct tracking data would be needed to confirm such movements, the strong seasonality we observed aligns well with the idea that tiger sharks use this site cyclically in tune with monsoon-driven environmental changes and their life-history schedule.

Temperature

Among the environmental variables tested, sea surface temperature stood out as a dominant predictor of tiger shark sightings, especially for the highly resident sharks. Sightings increased markedly with warmer water temperatures, suggesting that these ectothermic sharks are

selective for thermal conditions that favour their life-history requirements.

Temperature is known to be a key driver of shark movement and habitat selection, as it directly affects metabolic rates and energy balance (Bernal et al. 2012; Schlaff et al. 2014). Numerous studies have highlighted that sharks often exhibit behavioural thermoregulation, moving toward preferred temperature zones to optimize biological functions and maximise fitness-related processes (Sims et al. 2006; Araujo et al. 2020; Pillans et al. 2021). In our study, the positive relationship between temperature and shark sightings likely occurs as a concentration of individuals around the coastal waters of the island during warmer periods, in line with the possibility of capitalizing on the metabolic benefits of elevated water temperatures. Furthermore, warmer waters can accelerate processes like digestion and, crucially, gestation for pregnant sharks by increasing metabolic and embryonic growth rates (Speed et al. 2012; Watanabe et al. 2021). We indeed observed that the cluster of sharks with the strongest site fidelity was dominated by mature female adults, many of which were confirmed pregnant by Sulikowski et al. (2024). Recent non-invasive ultrasound surveys at this location found embryos in 93% of all mature females scanned, providing direct evidence that this site serves as a gestation ground for tiger sharks (Sulikowski et al. 2024). Given that viviparous tiger sharks have lengthy gestation periods (~12–16 months) and relatively low reproductive output, the ability to thermoregulate by selecting warm-water refuges could serve an adaptive strategy to enhance reproductive success, as detected for other shark species (Hight and Lowe 2007; Matich et al. 2015), or reheat after diving in cooler waters at depth.

Interestingly, the effect of temperature was most pronounced for adult sharks and less so for juveniles, hinting at significant differences in space use connected to thermal preferences. Larger females may have a greater incentive to select warmer habitats due to the demands of gestation, whereas juveniles might be more tolerant of a range of temperatures or might roam more widely in search of food (Sulikowski et al. 2016). In Fuvahmulah, adult females could be using the site as a quasi-nursery for developing young, staying within a comfortable thermal window. The presence of two distinct embryonic cohorts observed via ultrasound (Sulikowski et al. 2024) suggests that different females may be at different stages of pregnancy, possibly indicating an asynchronous or staggered reproductive cycle among the population. Some females might be in mid-gestation while others are near parturition, which could explain why not all adult females leave the site simultaneously. This flexibility would align with emerging evidence that tiger shark reproductive cycles can vary by region and individual (Whitney et al. 2007; Manuzzi et al. 2022), rather than all

sharks following a strictly synchronized biennial schedule. It is plausible that Fuvahmulah provides a year-round safe haven with optimal temperatures, allowing pregnant females on varying schedules to remain until they need to depart to give birth. After pupping, females may return to the site, either to recuperate in warm, food-rich waters or to mate and gestate again if on a shorter reproductive cycle.

Several limitations temper our interpretation of the temperature–sightings relationship. First, our temperature data reflect surface conditions during dives; we lacked continuous in situ temperature logging and information on temperature at depth. It is possible that microhabitat selection could modulate their experienced temperatures in ways we could not resolve. However, given that most shark–diver interactions occurred in relatively shallow water, the measured temperature likely captures the conditions influencing their behaviour at the site. Second, while it is tempting to conclude that warmer water causes higher shark presence, it could also be that some other factor correlated with seasonal temperature, such as monsoon-related changes in currents or prey, is partly responsible. We attempted to control for monsoon season in the models, and temperature still emerged as a strong independent predictor, lending credence to a true thermal preference. Additionally, social cues and individual-level hierarchies could be responsible for the lesser presence of juveniles at the site year-round (Voss-gaetter et al. 2024). Larger female tiger sharks show higher testosterone levels and dominate provisioning sites in the Bahamas (Rangel et al. 2022). Similarly, in Fuvahmulah, larger, adult females exert an influence on smaller conspecifics and prevail in provisioning contexts (Reinero et al. 2025), which leads to reduced sightings of juveniles in the presence of adults and explains less pronounced effects of environmental variables on juveniles.

Nonetheless, experimental or tracking studies would be valuable to confirm active thermoregulatory behaviour. Finally, we acknowledge that provisioning could confound natural patterns – if sharks are fed, they might tolerate suboptimal temperatures. The fact that they still preferred warmer conditions indicates that even with provisioning, their innate thermal ecology is a driving force. This finding highlights the importance of considering physiological drivers like temperature when managing shark aggregation sites, especially those serving as critical habitats for reproduction.

Tidal effects

Our analysis detected a weak but statistically significant influence of tidal phase on shark sightings. In general, tiger shark sightings were slightly higher during certain tide conditions, notably around rising or high tide, as evidenced by a few significant tide–moon interactions (e.g. increased

sightings during rising tide on quarter moon nights, and at high tide during waning gibbous moon). The modest impact of tides is not unexpected given the characteristics of our study site. Tiger Harbour is a shallow reef slope environment near the equator, where tidal ranges are small (on the order of 1 m or less) and the geomorphology does not create extreme tidal currents, unlike estuarine or lagoonal habitats, where tides can dramatically alter depth and force sharks to relocate, as evidenced by Ackerman et al. (2000). Altogether, these conditions might allow the sharks to remain in the area through all tidal states, and any preferences are subtle, possibly related to ease of swimming or the movement of prey with slight currents.

Previous studies have shown that tidal cycles can shape the behaviour and habitat use of coastal sharks (Andrzejczek et al. 2024), especially juveniles in shallow nurseries. For example, juvenile bull sharks in a river mouth nursery move with the tide to exploit inundated habitats, and reef-associated sharks like blacktip reef and lemon sharks often show increased activity or abundance during incoming tides that bring prey (Wetherbee et al. 2007; Heupel et al. 2010; Lea et al. 2020). One notable consideration, despite the negligible contribution of tidal cycles alone, is the interaction between tide and lunar phase. The combination of a particular moon phase and tide (e.g., rising tide during the first-quarter moon) yielded a slight uptick in sightings for juveniles, suggesting that the timing of tides relative to nocturnal light levels might influence shark activity. Many reef organisms synchronize activity with lunar illumination and tides, potentially creating windows of increased foraging success for sharks, as evidenced by Hammerschlag et al. (2017). However, given the complexity of isolating such effects and the multiple comparisons involved, we urge caution in over-interpreting these interactions.

We also acknowledge some limitations in our tidal analysis, due to the regional scale of the forecasts, which may overlook fine-scale variation or timing offsets at the exact site. Additionally, dives were typically conducted during daylight hours for safety; thus, any shark responses to tides at night, when observers were absent, would not have been detected in our dataset. If, for example, sharks patrol closer to shore on high tides at night to scavenge, we would miss that pattern. Despite these caveats, the inclusion of tidal terms in the best-fit models indicates that even in a low-amplitude system, tiger sharks exhibit slight behavioural adjustments with the tide. Therefore, management or tourism operations need not heavily revolve around tide tables, although avoiding extreme currents is sensible for diver safety.

Hydrodynamic conditions

Several wind-driven and wave-driven variables were significant predictors of tiger shark sightings, particularly for less resident sharks (Cluster 2). Sharks were more abundant when winds blew from the south, southwest, west, and west-southwest directions that predominate during the Southwest monsoon and generate on-reef currents (Lea et al. 2020). These winds may enhance olfactory plumes of bait or natural prey carrion, drawing sharks into the harbour. Conversely, highly resident sharks (Cluster 1) showed reduced sightings during easterly winds (ENE, NE, SE), perhaps because offshore currents might distribute scent plumes along the reef edge, making them more detectable to patrolling sharks and increase site visitation, as proposed by Papastamatiou et al. (2015).

Similarly, wave height and direction were weak but significant in certain models, suggesting that surface agitation modulates visibility and prey transport. Given the low-energy fringing reef at Tiger Harbour, wave effects were modest, but they nonetheless contribute to fine-scale variation in shark presence.

Conclusion

The present study provides novel insights into the environmental drivers of tiger shark encounters in Fuvahmulah, Maldives. Despite the anthropogenic influence from the provisioning activities at the site, tiger shark sightings was evidently influenced by natural environmental rhythms. Our results suggest a stronger seasonal occurrence influenced by monsoonal phases, SST, and lunar-tidal cycles, significantly shaping patterns, with noticeable ontogenetic differences across residency groups and life stages. Adult females with high site fidelity were strongly influenced by water temperature, consistent with thermoregulatory behaviour during gestation. On the contrary, less resident individuals, including juveniles and occasional adults, responded more to the alternation of monsoon phases, wind direction, and broader weather patterns, suggesting seasonal site use tied to foraging or dispersal. These distinct responses indicate that Fuvahmulah offers ideal conditions for long-term residency of reproductive females and transient visitors of other demographic groups, fulfilling multiple life-history requirements within a single reef system.

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Data availability All data is available upon reasonable request to the authors.

Declarations

Conflict of interest The authors disclosed no conflict of interest to this work.

Ethical approval No ethical approval was required since this is an observational study. The study was conducted following the guidelines and under the research permits issued by the Environmental Protection Agency (annually renewable permit: EPA/2021/PA-F01) and the Ministry of Fisheries, Marine Resources and Agriculture, Maldives (annually renewable permit: 30-D/PRIV/2021/190). The methods employed were non-invasive in nature with no harm caused to the animals involved.

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