

Article

Environmental Variability and Chlorophyll-a Are Associated with Immature Whale Shark Surface Sightings in Nosy Be, Madagascar

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Abstract

Whale shark aggregations in tropical coastal systems are linked to environmental variability and prey dynamics, yet the drivers of surface sightings remain poorly understood. In Nosy Be, Madagascar, a seasonal aggregation of immature whale sharks occurs within a productive coastal ecosystem. This study investigated the relationship between daily environmental conditions and whale shark surface sighting probability while accounting for heterogeneous sampling effort. Boat-based survey data collected from 2019 to 2025 were aggregated by sampling day, and daily whale shark surface sighting probability was analysed using a bias-reduced grouped binomial Generalized Linear Model. Environmental covariates included sea surface temperature, sea surface chlorophyll-a concentration, cloud cover, wind speed, and precipitation, while El Niño–Southern Oscillation variability was assessed as an interannual climatic descriptor. Using data from 103 recorded whale shark surface sightings, chlorophyll-a emerged as the strongest predictor, showing a positive association with daily sighting probability, whereas other environmental variables exhibited weaker and inconsistent effects. These findings suggest that whale shark surface sightings in Nosy Be are primarily associated with prey aggregation processes driven by local productivity rather than with direct responses to local physical environmental conditions. By integrating environmental variability and sampling effort into ecological models, this study provides insights into whale shark habitat use and supports ecosystem-based management of sustainable whale shark tourism in tropical coastal ecosystems.

Keywords: *Rhincodon typus*; Indian Ocean; environmental drivers; sampling effort; sustainable marine tourism

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1. Introduction

In Nosy Be, Madagascar (western Indian Ocean), the occurrence of whale sharks (*Rhincodon typus*, Smith, 1828) is closely associated with the regional high biological productivity [1]. The continental shelf off north-western Madagascar promotes the rapid development of zooplankton and micronekton communities, generating abundant prey resources for planktivorous megafauna, including whale sharks [1]. Productivity peaks occur during the austral summer, when north-easterly monsoon winds drive seasonal coastal upwelling, resulting in relatively cooler, chlorophyll-a-rich waters than the surrounding offshore waters. The interaction between coastal upwelling and regional eddy circulation enhances biological productivity along the northwestern coast of Madagascar, including the waters surrounding Nosy Be [2,3]. Therefore, Nosy Be hosts one of the largest known seasonal feeding aggregations of whale sharks in the western Indian Ocean, occurring primarily between September and December, when whale sharks are frequently observed feeding at the surface [1,4,5]. The area appears to function primarily as a juvenile foraging ground, and the seasonal aggregation is predominantly composed of immature males [1,4–6].

Whale sharks primarily feed on zooplankton, although fish spawn and small pelagic fishes may also represent important dietary components [1,4,5,7–17]. In Nosy Be, surface zooplankton communities are mainly dominated by copepods, followed by appendicularians, molluscs, and chaetognaths [17,18]. However, prey availability in this system is highly heterogeneous and often concentrated within localized surface feeding events known as *chasse*, where schools of tuna and small pelagic fishes aggregate prey near the surface, generating dense and short-lived trophic hotspots that also attract seabirds and other predators [1,4,5]. These events represent ephemeral, multi-trophic hotspots where plankton, micronekton, and fish larvae become simultaneously available, and where whale sharks are commonly observed feeding at the surface. Recent observations suggest that environmental variability may be associated with the occurrence and intensity of these feeding events, thereby affecting immature whale shark surface feeding behaviour [5]. Therefore, whale shark surface sightings in this system appear to be associated not only with background productivity but also with environmentally driven trophic processes operating at relatively fine temporal scales.

Despite the ecological importance of whale shark aggregations, estimating absolute abundance for highly mobile marine megafauna remains challenging. Consequently, relative indices derived from surface sightings are commonly used to investigate temporal occurrence patterns and habitat use, although these observations inherently reflect both ecological and observation processes, including variation in sampling effort and detection probability [19–31]. Surface sightings should therefore be interpreted as outcomes of a coupled ecological–observation system, in which environmental conditions may be associated with both the probability of whale sharks occurring near the surface and the probability of detecting them during surveys.

Environmental variability may influence whale shark occurrence through both direct and indirect pathways. Direct effects can involve physiological constraints and behavioural responses to environmental conditions, whereas indirect effects are typically mediated through prey availability and trophic aggregation processes [5,31–35]. As a result, temporal variability in whale shark surface sightings is often interpreted in relation to environmental proxies such as sea surface temperature, sea surface chlorophyll-a concentration, and other oceanographic variables [35]. Previous studies have reported both positive and negative associations between these environmental variables and whale shark occurrence depending on the spatial and temporal scale considered [13,31,36–44].

In Nosy Be, previous research has primarily focused on whale shark population structure, occurrence, residency, movement patterns, and surface feeding behaviour

[1,4,5,45]. However, the environmental drivers underlying fine-scale temporal variability in whale shark surface sightings remain poorly understood. To date, studies integrating heterogeneous sampling effort with both local environmental drivers and large-scale climatic forcing are still largely lacking in the whale shark literature.

Beyond their ecological relevance, whale shark aggregations also have increasing socio-economic importance, particularly in regions such as Nosy Be where marine wildlife tourism is rapidly expanding [6]. Understanding the environmental drivers associated with whale shark surface sightings is therefore essential not only for ecological interpretation but also for the development of sustainable management strategies capable of balancing conservation objectives with human activities in dynamic coastal ecosystems.

To address these knowledge gaps, the present study adopted an effort-standardized day-level analytical framework to investigate immature whale shark surface sightings in Nosy Be. This approach allows local environmental variability to be distinguished from broader interannual climatic variability while explicitly accounting for heterogeneous sampling effort. Within this framework, we tested the hypothesis that whale shark surface sightings in Nosy Be are primarily associated with productivity-related environmental conditions reflecting environmentally mediated trophic dynamics. Although localized feeding events such as *chasse* were not explicitly quantified, they provide important ecological context for interpreting the observed relationships.

The aims of this study were therefore to: (i) evaluate how daily environmental conditions are associated with the probability of whale shark surface sightings in Nosy Be; (ii) identify the environmental covariates most consistently associated with surface sighting dynamics after accounting for variation in sampling effort; and (iii) assess the robustness of these relationships across alternative model formulations.

2. Materials and Methods

2.1. Sampling Area

Nosy Be (13°39' S, 48°20' E), located in the Antsiranana Province of northwestern Madagascar, is a volcanic island situated within the Mozambique Channel approximately 8 km offshore from mainland Madagascar. The island is part of an archipelago including Nosy Sakatia, Nosy Tanikely and Nosy Komba, and is characterised by a relatively shallow continental shelf. The study area exhibited a relatively homogeneous bathymetry, with water depths of approximately 40 m throughout the surveyed area. The region is recognised as a biodiversity hotspot [46] and supports important aggregations of marine megafauna, including whale sharks [45]. Whale sharks in this area are frequently associated with feeding aggregations of schools of tuna targeting small pelagic fishes [1], and the aggregation is predominantly composed of immature individuals, as commonly observed in tropical coastal feeding aggregations [14].

Sampling activities were conducted in the coastal waters between Nosy Sakatia and Nosy Tanikely (Figure 1), within approximately 5 km of the coastline. Survey routes were not spatially fixed and varied among sampling days according to field conditions, sea state, and the occurrence of surface feeding activity.

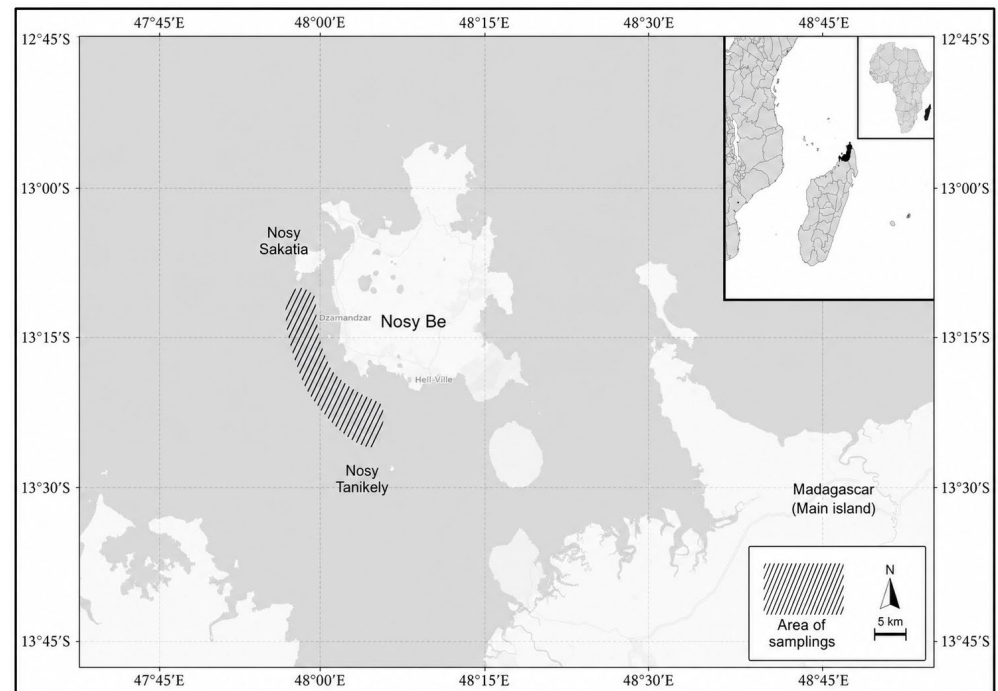


Figure 1. Nosy Be (Madagascar) and the sampling area between Nosy Sakatia and Nosy Tanikely.

2.2. Sampling Effort and Survey Design

Boat-based whale shark surveys were conducted along the southwestern coast of Nosy Be with logistical support from the partner operator Manta Diving. Surveys were performed during morning hours (approximately 09:00–13:00), when sea conditions were generally most favourable for visual detection. Surveys were conducted from a 10-m vessel, with observers positioned approximately 0.5 m above the water surface. Visual searches were performed using polarized sunglasses to reduce surface glare and facilitate the detection of feeding-associated bird aggregations (*chasses*). When a *chasse* was detected, the vessel approached the area to verify the presence or absence of whale sharks before in-water observations were initiated.

Five scientific expeditions were conducted in 2019, 2022, 2023, 2024, and 2025, excluding the SARS-CoV-2 pandemic years (2020–2021). Sampling took place during November and December, corresponding to the peak seasonal period of whale shark occurrence in the region [4]. Overall, approximately 256 h of monitoring effort were conducted across the study period: one month in 2019 (14 November–6 December; 60 h over 15 survey days), one week in 2022 (30 November–4 December; 20 h over 5 survey days), one week in 2023 (3–8 December; 20 h over 5 survey days), one month in 2024 (21 November–13 December; 72 h over 18 survey days), and one and a half months in 2025 (5 November–14 December; 84 h over 21 survey days).

These figures describe the overall field-monitoring effort. For the statistical analyses, field records were screened for analytical consistency, matched with the available environmental covariates, and aggregated by sampling date. Consequently, the number of analytical sampled days used in the models is slightly lower than the total number of field survey days reported above.

Sampling effort varied substantially among years in terms of both survey duration and daily spatial coverage. To account for this heterogeneity, effort was explicitly quantified as the number of observational units recorded per sampling day. An observational unit was defined as a discrete field record corresponding to a search or encounter entry during a sampling day. This effort metric was subsequently incorporated into the

statistical framework to standardise daily sighting probability and sighting rate across sampling days.

2.3. Whale Shark Sightings and Field Observations

Following whale sharks' detection, standardised field observations were collected by trained volunteers and research staff from the Sharks Studies Centre–Scientific Institute of Massa Marittima, Italy. All whale shark interactions complied with Madagascar Government regulations and established whale shark tourism guidelines [47]. To minimise disturbance, no more than four people entered the water simultaneously and a minimum distance of 3 m from the animals was maintained. Whale sharks were frequently observed feeding at the surface in association with zooplankton patches and bait balls generated by schools of tuna preying on juvenile fishes, often accompanied by aggregations of seabirds. These feeding events, locally referred to as *chasse*, represent transient multi-trophic feeding hotspots and are strongly associated with survey trajectories [4]. Although *chasse* events were frequently observed, they were not systematically measured and thus were excluded from the statistical analyses.

All sightings, including repeated observations of the same individuals, were retained within the analytical dataset. The response variable therefore reflects sighting frequency relative to sampling effort rather than the abundance of unique individuals.

2.4. Photo-Identification and Biological Data

Upon each whale shark sighting, individuals were photographed underwater by snorkelers swimming at the surface (approximately 0–1 m depth) to allow individual photo-identification based on their unique spot patterns following Arzoumanian et al. [48], supported by the documentation of scars and wounds [49]. All re-sightings were preserved in the sighting dataset.

Sex was determined from the presence or absence of claspers [5], and total length (TL), when available, was estimated using laser photogrammetry following Matsumoto et al. [50]. Laser photogrammetry was only employed between 2022 and 2025.

These biological data were used solely to describe the aggregation and confirm that it was composed primarily of immature male individuals; they were not included as explanatory variables in the environmental models.

2.5. Environmental Data Collection

Environmental variables were collected for all study years (2019, 2022–2025) using a combination of in situ measurements and external environmental databases. All environmental covariates were matched to the corresponding sampling dates and subsequently aggregated at the day level to ensure consistency with the analytical framework adopted for the statistical analyses. Given the heterogeneous spatial and temporal resolutions of the different data sources, environmental covariates should be interpreted as proxies of local and regional environmental conditions potentially associated with whale shark surface sightings.

Sea surface temperature (SST, °C) was recorded in situ during field surveys using underwater dive computers operated by the research team. Measurements were taken at the location and time of each whale shark sighting, immediately after entering the water. When multiple SST measurements were available from different dive computers during the same sampling day, daily mean values were calculated to represent the average thermal conditions for that day.

Wind speed (Wind, knots) and precipitation (Precipitation, mm/h) were obtained from the Windguru database for the Nosy Be Ambondrona region (<https://www.windguru.cz/121089>; accessed 15 January 2026). Hourly Wind and Precipitation values

corresponding to the time of each whale shark sighting were retrieved and associated with the corresponding sampling day. These variables were selected because local atmospheric conditions may influence both prey aggregation dynamics and observational conditions during field surveys.

Sea surface chlorophyll-a concentration (Chl-a, mg/m³), used as a proxy for marine primary productivity, was extracted from the Copernicus Marine Service database (<https://data.marine.copernicus.eu/>; accessed 15 January 2026) using the GLOBAL_ANALYSISFORECAST_BCG_001_028 product. This product provides daily mean fields at a spatial resolution of 0.25° × 0.25° (approximately 25 km²). Daily Chl-a values corresponding to the Copernicus grid cell encompassing the survey area were matched to each sampling day and used as a proxy for local marine productivity. Chl-a was included because productivity-related processes are known to be linked to zooplankton biomass and trophic aggregation dynamics within tropical coastal systems [16,41,51].

Cloud cover (Cloud) was visually estimated in situ at the location and time of each whale shark sighting following the oktas system described by Rees [52], ranging from 0 (completely clear sky) to 8 (fully overcast sky). Cloud cover was included because it may be associated with both visual detectability during surface surveys and local prey aggregation dynamics through changes in light penetration and atmospheric conditions.

Large-scale climatic variability was represented by El Niño–Southern Oscillation (ENSO) using the Multivariate ENSO Index (MEI), obtained from the NOAA Climate Prediction Center (https://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensو_advisory/ensodisc.shtml; accessed 15 January 2026). As the MEI is provided at monthly temporal resolution, the corresponding monthly ENSO value was assigned to all sampling days within the same month. However, ENSO was interpreted as a low-frequency climatic descriptor reflecting broad interannual variability rather than a local day-level environmental condition, consistent with the established use of MEI as an index of large-scale ENSO variability [53].

Consequently, ENSO was treated separately from the local environmental covariates during the inferential analyses.

2.6. Statistical Analysis

2.6.1. Descriptive Overview

Prior to inferential modelling, the final analytical dataset was summarised descriptively to (i) characterise the observation process, (ii) quantify sampling effort across years, and (iii) evaluate the frequency of positive sightings and non-detections. These descriptive metrics were used to guide the subsequent modelling strategy and to assess the suitability of the dataset for effort-standardised analyses.

Annual sampling effort was defined as the total number of observational units, as defined in Section 2.2, recorded within each campaign year, whereas sampled days represented the number of distinct survey dates. Mean daily effort was calculated as the ratio between total effort and sampled days (*mean daily effort* = *effort units/sampled days*), and the annual positive rate was defined as the proportion of observational units with at least one whale shark surface sighting (*positive rate* = *positive sightings/total observational units*). At the day level, sampling dates were classified as “*positive days*” when at least one whale shark surface sighting occurred and “*zero-days*” otherwise.

Because ENSO represents a lower-frequency climatic index rather than a fine-scale environmental variable, annual ENSO variability was summarised descriptively at the campaign-year level rather than incorporated directly into the day-level environmental framework. In contrast, fine-scale environmental variables (SST, Chl-a, Cloud, Wind, and Precipitation) were summarised using descriptive statistics calculated from the day-level analytical dataset.

2.6.2. Multicollinearity Assessment

Potential overlap among environmental covariates was assessed prior to model fitting in order to evaluate whether any predictors carried redundant information capable of affecting model stability or coefficient interpretation. Pairwise Pearson correlation coefficients were calculated among the day-level local environmental covariates, namely SST, Chl-a, Cloud, Wind, and Precipitation, using the *cor()* function from the stats package in RStudio v2026.05.0-218 [54].

Correlation analyses were performed on the day-level aggregated dataset to avoid artificial inflation of dependence arising from repeated observations collected within the same sampling day. Variance Inflation Factors (VIFs) were subsequently calculated using the *vif()* function from the *car* package in R [55] to assess whether any predictor could be approximated as a linear combination of the remaining covariates.

These diagnostics indicated limited collinearity among the local day-level predictors. Pairwise Pearson correlation coefficients were below $|0.5|$ for all predictor pairs except Chl-a and Wind, which showed a moderate negative association ($r = -0.519$). VIF values were low for all predictors, ranging from 1.076 to 1.591, indicating no evidence of problematic multicollinearity. Because the correlation between Chl-a and Wind slightly exceeded the predefined $|0.5|$ threshold, these two predictors were not allowed to enter the same candidate model during the Akaike Information Criterion (AIC)-based model-selection procedure. The complete Pearson correlation matrix and VIF tables are provided in the Supplementary Materials (Tables S1 and S2).

ENSO was not included in either the day-level correlation matrix or the VIF diagnostics because it was treated as a lower-frequency climatic descriptor rather than as a fine-scale local environmental covariate. Instead, ENSO was evaluated separately through temporal-scale diagnostics (Table S2) examining: (i) the proportion of ENSO variability explained by year; (ii) the relative magnitude of within-year and between-year variability; and (iii) the auxiliary association between ENSO and SST. This approach allowed ENSO to be evaluated at an appropriate temporal scale without artificially inflating the dependence structure among the day-level environmental predictors.

Following these preliminary diagnostics, two complementary modelling frameworks were then used to describe the same day-level sighting process from different but related perspectives: (i) a grouped binomial model for effort-standardised sighting probability and (ii) a count-based model for effort-standardised sighting rate.

2.6.3. Grouped Binomial Sighting-Probability Model

The primary inferential analysis was conducted on the day-level aggregated dataset using a grouped binomial formulation, reflecting the binary nature of the response at the observational-unit level. Aggregation by sampling date was adopted to avoid pseudo-replication arising from multiple observations collected within the same day and to ensure that each analytical unit represented a distinct daily sampling event. For sampling day d , n_d denoted the total number of observational units and y_d denoted the number of observational units containing at least one whale shark surface sighting; consequently, $n_d - y_d$ represented the corresponding number of non-detections. The model therefore retained the complete number of positive observations and non-detections recorded under the daily sampling effort, rather than reducing each day to a single presence/absence outcome.

A bias-reduced grouped binomial Generalized Linear Model (GLM) was fitted using the *brglm2* package [56], as follows:

$$y_d \sim \text{Binomial}(n_d, p_d)$$

$$\text{logit}(p_d) = \beta_0 + \beta_1 \text{SST}_d + \beta_2 \text{Chl} - a_d + \beta_3 \text{Cloud}_d + \beta_4 \text{Wind}_d + \beta_5 \text{Precipitation}_d + \text{year effects}$$

where p_d is the probability that an observational unit recorded on sampling day d contained at least one whale shark surface sighting; β_0 is the model intercept; and β_1 – β_5 are the regression coefficients associated with the day-level environmental covariates. SST_d , $\text{Chl} - a_d$, Cloud_d , Wind_d , and Precipitation_d denote the day-level environmental conditions described in Section 2.5. Year was included as a categorical fixed effect to account for interannual differences among sampling campaigns.

Environmental predictors were retained as continuous variables without discretisation or threshold-based categorisation. For reporting purposes, environmental covariates were standardised using z-score transformation to facilitate comparison of effect sizes across predictors measured on different scales.

A bias-reduced grouped binomial GLM was adopted to improve estimation stability given the relatively limited sample size and the presence of sparse outcomes in some campaign years. The model was estimated using bias-reduced maximum likelihood for binomial-response GLMs, following a Firth-type/mean bias-reduction approach implemented in the *brglm2* package [56]. This approach reduces small-sample estimation bias and mitigates instability associated with quasi-complete or near-complete separation, which may arise when some campaign years contain very high proportions of positive observations. Year was included as a nuisance adjustment accounting for campaign-level heterogeneity rather than as a biological predictor of interest.

ENSO was excluded from the primary day-level specification because its variability was predominantly organised at the interannual scale. Its association with whale shark surface sightings was therefore evaluated separately using the annual exploratory model described in Section 2.6.5.

Given the relatively limited number of sampling days, model complexity was intentionally kept low by restricting the analysis to biologically interpretable covariates. An automated AIC-based model-selection procedure was then used to identify the most parsimonious day-level grouped binomial model. All possible combinations of the local day-level environmental predictors were compared using the *dredge()* function from the *MuMIn* package in R [57], while retaining year as a fixed nuisance effect in all candidate models to account for campaign-level heterogeneity. Because Chl-a and Wind showed a pairwise correlation slightly above the predefined $|0.5|$ threshold, these two predictors were not allowed to enter the same candidate model. Candidate models were ranked according to AIC, and the model with the lowest AIC was retained as the selected model. Model calibration was additionally inspected by comparing observed daily sighting proportions with fitted probabilities from the selected grouped binomial model.

2.6.4. Count-Based Sighting-Rate Model

As a secondary sensitivity analysis, the same ecological relationship was also evaluated using a count-based Poisson model. This alternative formulation modelled the daily number of positive observational units while including the logarithm of daily sampling effort as an offset. The Poisson model was not intended to replace the grouped binomial analysis, because the observed counts originated from a bounded number of binary observational units. Instead, it was used to assess whether the main Chl-a association remained consistent under an alternative rate-based parameterisation. The count-based model was specified as:

$$\text{sightings}_{\text{day}} \sim \text{Poisson}(\mu_{\text{day}})$$

$$\log(\mu_{\text{day}}) = \alpha_0 + \alpha_1 \text{SST} + \alpha_2 \text{Chl-a} + \alpha_3 \text{Cloud} + \alpha_4 \text{Wind} + \alpha_5 \text{Precipitation} + \text{year controls} + \log(\text{effort}_{\text{day}})$$

where μ_{day} is the expected number of whale shark surface sightings on a given sampling day; α_0 is the model intercept; α_1 – α_5 are the regression coefficients associated with the day-level environmental covariates; $\log(effort_{day})$ is the offset term used to standardise expected sighting counts according to differences in daily sampling effort; and *year controls* were included as a categorical fixed effect to account for interannual differences among sampling campaigns.

Model dispersion was evaluated using the Pearson residual dispersion ratio together with simulation-based residual diagnostics implemented in the *DHARMa* package [58] to assess whether overdispersion was present and whether a Negative Binomial specification was required. The Poisson distribution was retained because diagnostic analyses did not indicate overdispersion requiring a Negative Binomial specification.

Simulation-based residual diagnostics did not indicate significant deviations from residual uniformity for either the grouped binomial sighting-probability model or the count-based sighting-rate model. The uniformity test was non-significant for both models (grouped binomial: $p = 0.961$; count-based Poisson: $p = 0.128$), and no outliers were detected (outlier test: $p = 1.000$ for both models). Dispersion tests indicated deviations from the expected dispersion structure (grouped binomial: $p = 0.002$; count-based Poisson: $p < 0.001$), with the count-based model showing underdispersion rather than overdispersion. This finding was consistent with the Pearson residual dispersion ratio being below 1 and therefore did not support switching to a Negative Binomial specification.

To facilitate biological interpretation of the selected grouped binomial model, the marginal effect of Chl-a concentration on predicted whale shark surface sighting probability was visualised using the *visreg* package [59].

2.6.5. Annual ENSO Exploratory Model

The association between ENSO and whale shark surface sightings was evaluated separately using an exploratory bias-reduced annual grouped binomial GLM with a logit link. For each campaign year t , N_t denoted the total number of observational units and Y_t denoted the number of observational units containing at least one whale shark surface sighting; consequently, $N_t - Y_t$ represented the corresponding number of non-detections. The model was specified as:

$$Y_t \sim \text{Binomial}(N_t, q_t)$$

$$\text{logit}(q_t) = \gamma_0 + \gamma_1 \text{ENSO}_t^*$$

where q_t denotes the annual probability that an observational unit contained at least one whale shark surface sighting, γ_0 is the model intercept, γ_1 is the ENSO coefficient, and ENSO_t^* is the standardised annual mean MEI for campaign year. The model was fitted using the mean bias-reduction approach implemented in the *brglm2* package [56]. Given the limited temporal replication across five campaign years and the uneven distribution of annual sampling effort, the ENSO model was intended to characterise the direction and magnitude of the broad interannual association rather than to support definitive inference on large-scale climatic effects.

All statistical analyses were conducted in R [54] using RStudio v2026.05.0-218. Data import, processing, date handling, string manipulation, tabular outputs, and graphical summaries were performed using functions from the *tidyverse* [60], including *lubridate* [61] for date handling and *ggplot2* [62] for graphical outputs. Count-based robustness models were fitted using base R GLM functions and the *MASS* package [63] when required.

3. Results

3.1. Population Overview

A total of 103 raw whale shark sightings, corresponding to 62 photo-identified individuals, were recorded during the study period. When sex could be determined, the aggregation was predominantly male-biased, comprising 21 males and 6 females.

Total length (TL) estimates ($n = 11$) ranged from 2.30 to 7.40 m (mean $\pm$ SD: 4.53 ± 1.67 m), indicating that the aggregation was composed primarily of immature individuals [64].

All sightings, including repeated encounters of the same individuals, were retained in the analytical dataset, as the response variable was defined as sighting frequency relative to sampling effort rather than the abundance of unique individuals.

3.2. Descriptive Overview

The final analytical dataset consisted of 111 observational units distributed across 63 sampling days and five campaign years (2019, 2022–2025). Sampling effort was heterogeneous among years, with 2019 accounting for the largest number of observational units and the most recent campaigns (2023–2025) characterised by lower mean daily effort (Table 1).

Table 1. Annual sampling effort, whale shark surface sightings, and ENSO conditions by campaign year. Mean effort per day was calculated as the number of effort units divided by the number of sampled days. Positive rate represents the percentage of observational units containing at least one whale shark surface sighting. Annual ENSO values represent mean MEI values for each campaign year.

Year	Effort Units	Sampled Days	Mean Effort Per Day	Positive Sightings	Non-Detections	Positive Rate (%)	Annual ENSO
2019	43	15	2.87	41	2	95.3	0.400
2022	18	5	3.60	18	0	100.0	−1.300
2023	6	5	1.20	6	0	100.0	1.100
2024	19	16	1.19	6	13	31.6	−0.458
2025	25	22	1.14	10	15	40.0	−0.236
Total	111	63	/	81	30	/	/

Of the 111 observational units, 81 (72.97%) included at least one whale shark surface sighting, whereas 30 (27.03%) were classified as non-detections. After aggregation by sampling date, 34 of the 63 sampling days (53.97%) included at least one whale shark surface sighting, whereas 29 days (46.03%) were classified as zero-sighting days. This distribution ensured that both positive and zero-sighting days were represented in the subsequent modelling analyses. Annual mean ENSO values varied substantially among campaign years, ranging from strongly negative conditions in 2022 (−1.300) to positive conditions in 2023 (1.100). However, because only five campaign years were available and annual sampling effort was highly heterogeneous, ENSO was interpreted descriptively at the annual scale rather than incorporated into the primary day-level inferential framework.

The fine-scale environmental conditions recorded during the study period are summarised in Table 2. SST ranged from 23.00 to 30.03 °C (mean $\pm$ SD: 28.81 ± 1.06 °C), whereas Chl-a concentrations ranged from 0.084 to 0.361 mg/m³ (mean $\pm$ SD: 0.131 ± 0.060 mg/m³). Wind varied between 0 and 7 knots (mean $\pm$ SD: 3.47 ± 1.72 knots), Cloud ranged from 0 to 7 oktas (mean $\pm$ SD: 3.38 ± 2.04), and Precipitation ranged from 0 to 16.60 mm/h (mean $\pm$ SD: 2.22 ± 3.78 mm/h). These descriptive statistics provide ecological context for the analytical dataset and facilitate comparison with environmental conditions reported from other whale shark aggregation studies.

Table 2. Descriptive statistics for the fine-scale environmental variables included in the day-level analyses. Values were calculated from the analytical dataset ($n = 63$ sampling days) and are reported as mean $\pm$ standard deviation (SD), median, minimum, and maximum.

Variable	Mean $\pm$ SD	Median	Minimum	Maximum
SST ($^{\circ}$ C)	28.81 $\pm$ 1.06	28.98	23.00	30.03
Chl-a (mg/m^3)	0.131 $\pm$ 0.060	0.119	0.084	0.361
Cloud (oktas)	3.38 $\pm$ 2.04	3	0	7
Wind (knots)	3.47 $\pm$ 1.72	3.56	0.00	7.00
Precipitation (mm/h)	2.22 $\pm$ 3.78	0.42	0.00	16.60

Pairwise correlations among the local environmental variables were generally low, and VIFs indicated no evidence of problematic multicollinearity (Tables S1 and S2).

3.3. Grouped Binomial Sighting-Probability Model

The grouped binomial GLM was fitted on the day-level aggregated dataset, comprising 63 sampling days, 111 observational units, 81 positive observational units and 30 non-detections. The final bias-reduced grouped binomial model achieved a deviance-based pseudo- R^2 of 0.680 and an AIC of 61.41.

Including year as a categorical fixed effect substantially improved model performance compared with the corresponding model without year effects, resulting in a lower AIC (61.41 vs. 88.08) and higher explanatory power (pseudo- $R^2 = 0.680$ vs. 0.413). These results indicate that accounting for interannual sampling heterogeneity improved the overall fit of the environmental model.

Among the environmental covariates, Chl-a showed the clearest and most consistent positive association with daily whale shark surface sighting probability and represented the only environmental predictor with evidence of a non-zero effect at the 5% significance level (Table 3). By contrast, SST, Cloud, Wind, and Precipitation exhibited 95% confidence intervals (CI) overlapping zero, providing weaker evidence of an association with whale shark surface sighting probability.

Table 3. Standardized environmental effects from the main binomial model. Standardized environmental coefficients estimated from the reporting version of the bias-reduced grouped binomial GLM. All environmental predictors were standardised using z-scores prior to coefficient estimation, so that coefficients represent the expected change in log-odds associated with a one-standard-deviation increase in the corresponding predictor. Odds ratios are reported for interpretative purposes.

Variable	Estimate	95% CI	Odds Ratio	p -Value
SST	−0.065	[−0.695, 0.565]	0.937	0.840
Chl-a	3.993	[0.625, 7.362]	54.237	0.020
Cloud	0.311	[−0.740, 1.362]	1.364	0.562
Wind	0.637	[−0.550, 1.825]	1.892	0.293
Precipitation	−0.494	[−1.773, 0.785]	0.610	0.449

The standardized reporting model indicated that a one-standard-deviation increase in Chl-a was associated with a 54.24-fold increase in the odds of daily whale shark surface sightings (OR = 54.237; 95% CI for the OR: 1.868–1574.983; $p = 0.020$). Although this estimate provides evidence of a positive association, the wide CI indicates considerable uncertainty regarding the precise magnitude of the effect. SST and Precipitation showed negative but non-significant effects, whereas Wind and Cloud exhibited positive but statistically uncertain associations.

The automated AIC-based model-selection procedure identified the model retaining Chl-a and year effects as the top-ranked specification (Table 4). This selected model had the lowest AIC among the candidate models (AIC = 54.0, Δ AIC = 0.0, AIC weight = 0.421), representing a substantial improvement over the full standardized model including all local environmental predictors (AIC = 61.4). Despite its simpler structure, the selected model retained virtually the same explanatory performance as the full model (deviance-based pseudo- R^2 = 0.676 versus 0.680). Chl-a remained positively associated with whale shark surface sighting probability and statistically significant (estimate = 3.391, p = 0.016; OR = 29.7), supporting its interpretation as the most robust environmental correlate of whale shark surface sighting probability.

Table 4. AIC-based model-selection results for the grouped binomial sighting-probability model. Candidate models were compared using the *dredge()* function from the *MuMIn* package. Year effects were retained in all candidate models as nuisance controls. Only the top-ranked candidate models are shown.

Rank	Environmental Predictors	AIC	Δ AIC	AIC Weight
1	Chl-a	54.0	0.0	0.421
2	Chl-a + SST	55.8	1.8	0.169
3	Chl-a + Cloud	56.3	2.3	0.132
4	Chl-a + Precipitation	56.4	2.5	0.122
5	Chl-a + Cloud + SST	58.1	4.2	0.052
6	Chl-a + Precipitation + SST	58.4	4.4	0.046
7	Chl-a + Cloud + Precipitation	58.6	4.6	0.042
8	Chl-a + Cloud + Precipitation + SST	60.6	6.7	0.015
9	Wind	84.7	30.8	0.000
10	Intercept-only environmental model	85.5	31.5	0.000

The marginal-effect plot showed that the predicted probability of whale shark surface sighting increased from approximately 0.08 at the lowest observed Chl-a concentration (0.084 mg/m³) to approximately 0.98 at 0.20 mg/m³. The predicted probability approached 1.00 at approximately 0.25 mg/m³ and then plateaued at higher Chl-a concentrations (Figure 2).

3.4. Count-Based Robustness Model

The count-based Poisson model was fitted as a sensitivity analysis and produced the same principal ecological conclusion as the primary grouped binomial model. Chl-a remained positively and statistically significantly associated with whale shark surface sightings (rate ratio = 2.06; 95% CI for the OR: 1.28–3.31; p = 0.003). However, the Poisson model showed underdispersion rather than overdispersion (Pearson dispersion ratio = 0.391), consistent with the bounded structure of the daily counts. The agreement in the direction and statistical significance of the Chl-a association therefore supports the robustness of the primary grouped binomial results. Full results of the count-based sensitivity analysis and the comparison between modelling frameworks are reported in Table S3.

3.5. Exploratory Annual ENSO Analysis

The exploratory bias-reduced annual grouped binomial GLM with a logit link did not provide clear evidence of a statistically significant association between annual mean ENSO conditions and whale shark surface sighting probability. The standardised ENSO coefficient was positive but not statistically significant (estimate = 0.449; 95% CI: −0.125–1.023; OR = 1.567; p = 0.125). The model explained only a small proportion of annual variation (deviance-based pseudo- R^2 = 0.044). Given the limited temporal replication across

five campaign years and the uneven distribution of annual sampling effort, the ENSO analysis was used to characterise the direction and magnitude of the broad interannual association rather than to support definitive inference on large-scale climatic effects.

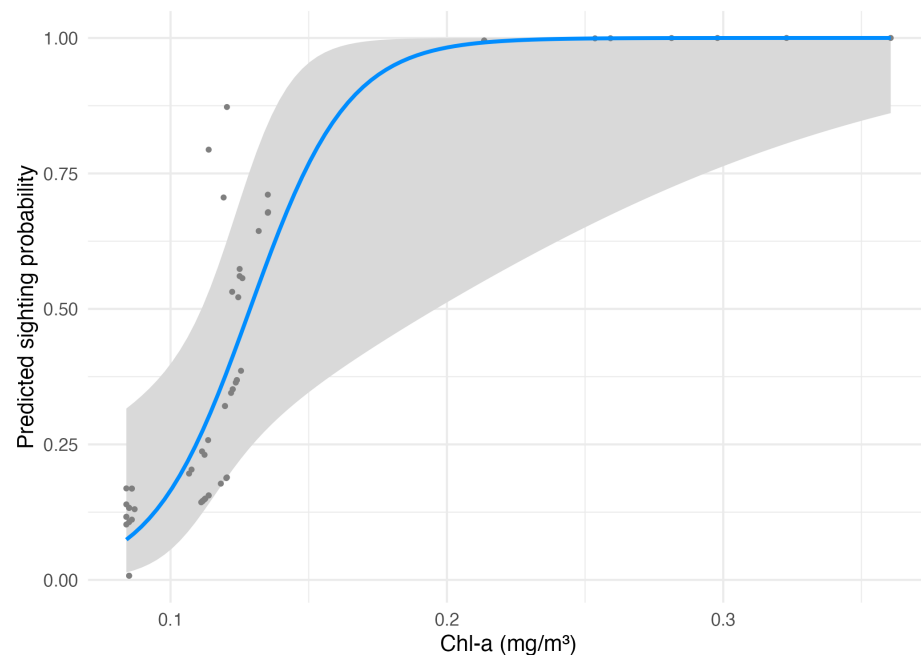


Figure 2. Predicted effect of Chl-a on daily whale shark surface sighting probability. The curve shows the predicted probability of whale shark surface sighting across the observed range of Chl-a values, estimated from the AIC-selected grouped binomial model with year effects retained as nuisance controls. The shaded band represents the 95% confidence interval (CI). Points represent model partial residuals for individual sampling days and illustrate the day-level variation around the fitted Chl-a relationship.

4. Discussion

The study shows that fine-scale environmental variability is associated with immature whale shark surface sightings in Nosy Be, with Chl-a being the most consistent environmental correlate after accounting for uneven sampling effort and campaign-level variability. By adopting an effort-standardized day-level analytical framework, the analyses provide a more robust interpretation of immature whale shark surface sighting patterns by accounting for heterogeneous sampling effort and reducing observation-related bias.

The population structure observed during this study further confirms that the whale shark aggregation in Nosy Be is primarily composed of immature individuals and is strongly male-biased, consistent with demographic patterns commonly reported for tropical coastal whale shark feeding aggregations worldwide [1,5,7,16,31,35,65,66]. Although information on sex and body size was collected primarily to characterize the aggregation rather than to explain sighting patterns, such description provides important ecological context for interpreting the environmental models. These variables were therefore not incorporated into the statistical analyses, which focused specifically on the environmental correlates of daily whale shark surface sightings rather than on demographic drivers. The predominance of immature individuals is consistent with the role of productive tropical coastal habitats as important juvenile foraging grounds for the species [67]. Within this context, the environmental relationships identified in the present study are likely to reflect feeding-related habitat use by immature whale sharks, driven primarily by prey availability, rather than broader demographic or reproductive processes. Consequently, caution

should be exercised when extrapolating these findings to populations with different demographic structures or to regions where adult individuals or females are more prevalent.

The positive and significant association between Chl-a and daily sighting probability is most consistent with productivity-mediated trophic processes influencing immature whale shark surface sightings in Nosy Be. Chl-a is widely used as a proxy for primary productivity and is commonly associated with enhanced zooplankton biomass and trophic transfer [16,41,51]. Similar relationships between whale shark occurrence and elevated Chl-a have been reported across several aggregation sites worldwide, where increased productivity promotes prey availability and creates favourable feeding habitats [16,19,31,37,68]. Although Chl-a does not directly measure prey abundance, it provides a robust ecological indicator of bottom-up processes linking phytoplankton production to zooplankton biomass and, ultimately, to whale shark feeding opportunities [16]. In Nosy Be, this relationship is most plausibly interpreted within the ecological context of localized feeding events known as *chasse*, during which predatory fishes such as schools of tuna aggregate prey near the surface, generating transient but highly concentrated feeding opportunities for whale sharks [1,4,5]. The consistency of the Chl-a effect across both grouped binomial sighting-probability model and the count-based Poisson sighting rate model supports the interpretation that productivity-related processes represent a robust ecological signal associated with immature whale shark surface sightings during the seasonal aggregation period. More broadly, these trophic dynamics occur within a productive oceanographic system influenced by seasonal upwelling and mesoscale circulation processes in the Mozambique Channel [2,3]. Previous studies have shown that predator distributions in this region are associated with productivity hotspots and dynamic oceanographic features [17,69]. Within this framework, Chl-a likely acts as an indirect proxy for environmental conditions favouring prey aggregation processes rather than as a direct driver of whale shark surface sightings.

In contrast, SST, Wind, Cloud, and Precipitation showed weaker and less consistent relationships with immature whale shark surface sightings than Chl-a, suggesting that productivity-related processes were more strongly associated with day-to-day sighting probability than the remaining environmental variables at the temporal scale considered here.

Previous studies conducted over broader spatial and temporal scales have identified SST as an important predictor of whale shark occurrence because it integrates large-scale oceanographic conditions influencing seasonal movements, habitat selection, and the formation or persistence of aggregations [38,39,41,43,51,68]. More recently, Ornelas et al. [44] also demonstrated that the relative importance of oceanographic and atmospheric drivers varies across seasons and years, highlighting that environmental controls on whale shark abundance are inherently scale dependent. By contrast, the present study was intentionally restricted to the seasonal aggregation period within the established aggregation area of Nosy Be. Consequently, the objective was not to explain why whale sharks occur in Nosy Be, but rather to identify which local environmental conditions best explain day-to-day variation in surface sightings within an established seasonal aggregation. These findings do not suggest that SST is ecologically unimportant; rather they indicate that once a seasonal aggregation has formed, short-term variation in whale shark surface sightings is more closely associated with local productivity than with relatively stable thermal conditions. Similarly, the weaker effects of Wind, Cloud, and Precipitation suggest that these variables may influence surface sightings only indirectly, through their effects on prey aggregation or visual detectability during surveys [35]. Consequently, productivity-related variables such as Chl-a, acting as proxies for local prey availability, are expected to exert a stronger influence than broad-scale environmental drivers. Importantly, the absence of strong multicollinearity among predictors indicates that the dominance of Chl-a

is not an artefact of correlated covariates but instead reflects a stronger and more direct ecological signal linked to prey availability and aggregation processes [5,35]. Future studies integrating standardized surveys across the entire annual cycle and a broader geographic range will be essential to determine how the relative importance of SST and productivity-related variables changes across spatial and temporal scales.

A major strength of the present analytical framework is the explicit temporal-scale separation between local environmental variability and broader climatic forcing represented by ENSO. Temporal diagnostics showed that ENSO variability was overwhelmingly structured among campaign years rather than within the daily sampling framework, indicating that ENSO functions primarily as a low-frequency climatic descriptor rather than a fine-scale environmental covariate. Consequently, ENSO was excluded from the main day-level model and evaluated separately through annual exploratory analyses. Although no significant ENSO effect was detected, this should not be interpreted as evidence that ENSO lacks ecological relevance within the regional system. Instead, ENSO likely acts as a distal climatic driver associated with whale shark surface sightings indirectly by modifying regional oceanographic conditions, including SST, primary productivity, and prey dynamics over broader spatial and temporal scales [36,38,70], consistent with recent findings [44]. In contrast, Chl-a represents a more proximal ecological indicator of local trophic conditions and therefore provides a stronger predictor of fine-scale variation in immature whale shark surface sightings within the temporal window analysed here.

Another important contribution of this study is the explicit incorporation of heterogeneous sampling efforts into the modelling framework. Whale shark sightings are inherently influenced by both ecological and observation processes, including variability in search intensity, detectability, and environmental conditions [19,29]. By modelling surface sightings relative to effort through grouped binomial and offset-based count formulations, the analyses help reduce biases associated with uneven sampling intensity and improve comparability among campaigns. The comparison between models with and without year controls further highlights the importance of accounting for campaign-level heterogeneity. Including year effects substantially improved model fit, indicating that inter-annual variability contributed significantly to observed surface sighting dynamics. Treating year as a nuisance adjustment rather than a biological predictor allowed local environmental effects to be interpreted separately from broader campaign differences.

Overall, the results support a conceptual view of Nosy Be as a dynamic, prey-driven foraging system structured around transient aggregation processes. Immature whale shark surface sightings appear to reflect episodic responses to short-lived feeding opportunities rather than continuous habitat use. This interpretation is consistent with growing evidence that whale sharks exhibit considerable behavioural flexibility in their foraging strategies, adjusting their feeding behaviour according to local prey distribution and environmental conditions [5,71]. Within this framework, Chl-a acts as a proxy for environmental conditions that facilitate trophic interactions, while other variables operate indirectly or upstream. This interpretation accords with previous studies indicating that immature whale sharks target spatially and temporally patchy concentrations of high-density prey [14,33] and is consistent with recent evidence from Nosy Be linking surface feeding behaviour to transient and heterogeneous prey distributions [5].

Despite these strengths, several limitations should be acknowledged. First, the environmental variables analysed here represent indirect proxies rather than direct measurements of prey abundance or trophic aggregation dynamics. Moreover, potentially relevant local-scale variables, including wind direction, the occurrence of feeding-associated bird aggregations (*chasses*), and the presence of associated fauna, were not systematically recorded during field surveys and therefore could not be included into the statistical analyses. In addition, surveys were intentionally conducted only under favourable sea

conditions, resulting in limited variation in sea state among sampling days. Future studies should explicitly quantify these variables to further refine models of whale shark surface sightings. Second, although sampling effort was explicitly incorporated into the analyses, detectability may still vary due to unmeasured observational factors, including variation in whale shark vertical position within the water column, water visibility, and other behavioural or environmental conditions that were not systematically quantified during field surveys. Third, the relatively limited number of sampling days and the uneven distribution of annual effort may reduce statistical power for weaker environmental effects. Finally, the present findings should be interpreted within the temporal scope of the study. Field surveys were intentionally conducted during the known seasonal whale shark aggregation period (September–December) and during daytime hours, when surface sightings are most frequent. Consequently, the environmental relationships identified here describe the factors associated with whale shark surface sightings within the aggregation season rather than year-round occurrence or habitat use. Future studies extending standardized environmental monitoring across the entire annual cycle will be necessary to determine whether these relationships remain consistent beyond the seasonal aggregation period.

Importantly, the present study does not explicitly quantify the occurrence or intensity of *chasse* events, which likely represent a key intermediate mechanism linking environmental variability to whale shark surface behaviour [5]. Future studies should therefore aim to incorporate direct or proxy measures of these events, as they potentially play a major role in determining fine-scale whale shark surface sighting patterns. This would also facilitate a more comprehensive characterization of whale shark feeding behaviour under different ecological conditions, complementing recent efforts to develop standardized behavioural ethograms for whale sharks and providing a broader behavioural framework for interpreting feeding-related observations [71]. In addition, several environmental and ecological variables not included in the current model may be critical for a more comprehensive understanding of whale shark aggregation dynamics in Nosy Be. These include direct measurements of prey availability, such as zooplankton biomass and community composition [17], together with estimates of micronekton and small pelagic fish density, particularly in relation to tuna-driven aggregations, and assessments of tuna abundance and behaviour as primary drivers of *chasse* formation. Future studies should also incorporate fine-scale oceanographic variables, including fronts, eddies, and vertical stratification [3,68], as well as current velocity and direction, which may influence prey concentration and retention. Lunar phase and diel cycles should also be considered because they have been linked to plankton dynamics and predator behaviour in other systems [13,72]. Finally, the integration of high-resolution satellite data would improve the characterization of fine-scale variability in productivity and thermal structure, providing a more comprehensive understanding of the environmental processes influencing whale shark surface sightings. The integration of these variables within hierarchical or spatially explicit modelling approaches may provide a stronger basis for examining the links between environmental forcing, trophic dynamics, and whale shark behavioural patterns.

From a conservation and management perspective, the present findings may contribute to the development of evidence-based whale shark tourism practices in Nosy Be. Because whale shark surface sightings were frequently associated with transient feeding events (*chasses*), these periods likely represent ecologically sensitive situations in which minimizing human disturbance should be a management priority. Rather than prescribing universal operational thresholds, future site-specific management plans should consider regulating the number of vessels and swimmers allowed to approach feeding aggregations, establishing appropriate approach distances, and implementing behavioural monitoring to evaluate the effectiveness of these measures. Similar adaptive management

frameworks have been successfully developed at other whale shark tourism destinations, where long-term ecological, behavioural, and tourism-monitoring studies have informed visitor guidelines and codes of conduct designed to reduce disturbance while maintaining sustainable ecotourism activities, including Ningaloo Reef (Australia) [47,73] and Donsol (Philippines) [74]. These examples demonstrate how integrating scientific evidence into management decisions can support both effective conservation and sustainable wildlife tourism. Integrating long-term ecological monitoring with adaptive management strategies may therefore provide an effective framework for balancing whale shark conservation with the continued development of sustainable marine ecotourism in Madagascar.

5. Conclusions

This study provides the first effort-standardized quantitative assessment of the environmental drivers of immature whale shark surface sightings in Nosy Be, Madagascar. By explicitly incorporating both presence and non-detection data while accounting for heterogeneous sampling effort, the proposed analytical framework offers a robust approach for investigating fine-scale ecological drivers of whale shark surface sightings. The results identify chlorophyll-a concentration as the principal environmental correlate of whale shark surface sightings during the seasonal aggregation period, emphasizing the importance of productivity-mediated trophic processes in shaping the habitat use of immature whale sharks. Beyond these findings, the present study identifies several priorities for future research. Direct measurements of prey availability, zooplankton biomass, and trophic aggregation dynamics are now required to move beyond environmental proxies and better understand the mechanisms underlying whale shark surface sightings. Future studies should also systematically quantify feeding-associated bird aggregations (*chasses*), tuna abundance and behaviour, associated fauna, and additional oceanographic variables to improve the ecological interpretation of whale shark aggregations. Integrating behavioural observations with environmental monitoring will further clarify how whale sharks respond to both natural prey dynamics and increasing tourism pressure. Emerging technologies, including Unmanned Aerial Vehicles (UAVs), high-resolution satellite imagery, and biologging approaches, offer considerable potential to expand survey coverage, improve the detection and characterization of feeding events, quantify predator–prey interactions, and reduce observational bias. Extending standardized monitoring across the entire annual cycle and over longer temporal scales will also be essential to evaluate inter-annual variability, assess the influence of large-scale climatic processes under future climate scenarios, and develop predictive habitat models capable of identifying periods and areas of increased whale shark occurrence. Finally, the integration of long-term ecological research with adaptive management strategies will provide the scientific foundation for evidence-based conservation and sustainable whale shark tourism in Madagascar.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/oceans7040069/s1>, Table S1: Pairwise correlation matrix of the local day-level environmental covariates included in the inferential analyses; Table S2: Variance Inflation Factors (VIFs) and ENSO temporal-scale diagnostics. Panel A reports VIFs computed for the local day-level environmental covariates retained in the inferential models. Panel B summarises the temporal-scale diagnostics used to evaluate ENSO behaviour; Table S3: Count-based Poisson sensitivity analysis and comparison with the primary grouped binomial model. Panel A reports goodness-of-fit statistics for the Poisson model fitted to the daily number of positive observational units, with the logarithm of daily sampling effort included as an offset. Panel B compares the estimated Chl-a effect between the primary grouped binomial model and the count-based Poisson sensitivity model. Estimates, 95% confidence intervals (CI), effect measures, *p-values*, and the

percentage of deviance explained by Chl-a are reported to assess consistency across the two modelling frameworks.

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Abbreviations

The following abbreviations are used in this manuscript:

TL	Total length
SST	Sea surface temperature
ENSO	El Niño–Southern Oscillation
MEI	Multivariate ENSO Index
VIFs	Variance Inflation Factors
GLM	Generalized Linear Model
Chl-a	Sea surface Chlorophyll-a
Cloud	Cloud cover
Wind	Wind speed
AIC	Akaike Information Criterion
UAVs	Unmanned Aerial Vehicles
SD	Standard Deviation
CI	Confidence Intervals

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