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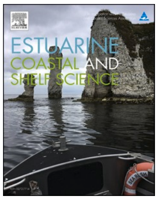

Spatiotemporal patterns and environmental drivers of *Physalia physalis* strandings along mainland Portugal (northeastern Atlantic)

Patrícia Carvalho [a,b], Clara Cordeiro [c,d,e], Soraia Pereira [e,f], Antonina dos Santos [a,g,*]

[a] IPMA - Portuguese Institute for Sea and Atmosphere, Av. Doutor Alfredo Magalhães Ramalho, 6, 1495-165, Algés, Portugal
[b] Universidade Católica Portuguesa, Portugal
[c] Departamento de Matemática, Faculdade de Ciências e Tecnologia, Universidade do Algarve, Portugal
[d] Center for Research and Development in Mathematics and Applications (CIDMA), Department of Mathematics, University of Aveiro, 3810-193, Aveiro, Portugal
[e] CEAUL - Centre of Statistics and its Applications, University of Lisbon, Portugal
[f] CMAT - Centre of Mathematics, University of Minho, Portugal
[g] CIIMAR - Interdisciplinary Centre of Marine and Environmental Research, Terminal de Cruzeiros do Porto de Leixões, Av. General Norton de Matos S/N, 4450-208, Matosinhos, Portugal

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ABSTRACT

Physalia physalis is a cosmopolitan colonial organism frequently observed in Portuguese waters. The species has long tentacles, provided with cnidocytes, which release a strong poison when in contact with other organisms, and cause skin reactions and severe pain in humans. Events of rapid reproduction, common in these species, may have important economic and social consequences. This study explores for the first time, the relationships between long-term assessment of *P. physalis* strandings, using data from the GelAvista citizen science project, and environmental variables - Sea Surface Temperature (SST), wind direction and intensity, the North Atlantic Oscillation (NAO), and upwelling indices - along the Portuguese coast, using a Generalized Linear Mixed-Effects Model.

Strandings of *P. physalis* were concentrated along the western coast and were rare in the south. More than 54 % of the records corresponded to a single individual. Sightings peaked from November through May (winter and spring), mirroring the negative correlation with SST. Wind patterns strongly influenced stranding events: winds likely pushed colonies toward the shore, while calm conditions facilitated their arrival on beaches. In March 2018, an upwelling event in the south coast combined with a series of storms likely underlay the high stranding numbers observed in the southern area, with more than 50 individuals of *P. physalis* per record.

A positive trend in sightings over the study period suggests that *P. physalis* occurrences may be rising, even after accounting for wind and SST, which might be linked to climate change. Our findings underscore the value of ongoing jellyfish monitoring via citizen science platforms like GelAvista and highlight the need for expanded high-resolution environmental datasets. Moreover, this work establishes a foundation for experimental studies to elucidate the mechanisms behind *P. physalis* strandings. For future research, time series techniques for imputing missing values may be utilized to enhance the completeness of environmental datasets and strengthen analytical robustness in subsequent studies focused on time series analysis.

1. Introduction

Physalia physalis Linnaeus, 1758, or the Portuguese man o'war, is a colonial organism that floats at the ocean's surface (e.g. (Licandro et al., 2017)). It inhabits tropical to temperate waters from 51°N to 38°S (Mapstone, 2014) and is often found along the Portuguese coast, including in the Azores and Madeira (GelAvista, 2025). The colony comprises multiple polypoid zooids: the pneumatophore, a gas-filled float, ensures buoyancy, gastrozooids manage feeding and digestion processes, gonozooids handle reproduction, and dactylozooids manipulate via tentacles (e.g. (Munro et al., 2019)). Those tentacles contain cnidocytes with stinging toxins for prey capture and defence (Labadie

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* Corresponding author. IPMA - Portuguese Institute for Sea and Atmosphere, Av. Doutor Alfredo Magalhães Ramalho, 6, 1495-165, Algés, Portugal.

E-mail addresses: patcarvalho@ucp.pt (P. Carvalho), ccordei@ualg.pt (C. Cordeiro), soraia.pereira@math.uminho.pt (S. Pereira), antonina@ipma.pt (A. dos Santos).

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et al., 2012). Accidental human contact with tentacles can cause painful stings, leading to symptoms like skin necrosis, neurological issues, and rarely fatal complications (Ward et al., 2012).

The Portuguese man o'war is a carnivorous predator that preys on multiple species, including fish and their larvae (e.g. Pagès and Madin, 2010), using cnidocytes, which release a toxin that paralyses prey (Munro et al., 2019). It can be preyed on by turtles, fishes, nudibranchs, and crabs (e.g. (Tiralongo et al., 2022)). It reproduces sexually with external fertilization (Prieto, 2018). Both juvenile and adult stages float on the ocean surface, supported by their pneumatophore, while all the other zooids remain submerged (Munro et al., 2019).

The dispersion and distribution of this siphonophore are primarily influenced by the wind and surface oceanic currents, as the pneumatophore functions like a sail. Its pleustonic nature suggests that its spatial distribution could also be affected by upwelling events, the dynamics of the North Atlantic Oscillation (NAO) and of the Arctic Oscillation Index (AOI), and fluctuations in sea surface temperatures (e.g. (Pires et al., 2018); (Torres-Conde, 2022)). Prieto et al. (2015) investigated a significant arrival of this species along the Mediterranean coast in 2010, attributing the event to various meteorological and oceanographic factors, including wind patterns. Ferrer & Pastor (Ferrer and Pastor, 2017) researched the stranding of these organisms on the Basque coast (North of Spain), concluding that *P. physalis* originates in the northern part of the North Atlantic Subtropical Gyre, with wind being the primary cause of its occurrence. Multiple studies confirm the wind's influence on *P. physalis* spatial distribution (e.g. (Iosilevskii and Weihs, 2009); (Headlam et al., 2020)).

The Atlantic Ocean plays a critical role in thermohaline circulation, facilitating the transfer of heat from tropical regions toward the poles and contributing to the regulation of global temperatures. However, global warming with rising sea levels have been causing concern with some significant alterations at the major ocean water masses transport (e.g. (Santana-Toscano et al., 2025)). Several significant changes have been documented in the Atlantic Ocean, including variations in seawater temperature, increased acidification, rising sea levels, alterations to water mass circulation patterns, and a higher occurrence of extreme weather events such as hurricanes and tropical storms (e.g. (England et al., 2025)). This climate change has been associated with an increase of gelatinous species outbursts all over the world, including the Atlantic Ocean (e.g. (Magalhães et al., 2020)). *Physalia physalis* strandings occur frequently in coastal areas (e.g. (Bachouche et al., 2022)). Mass stranding events, however, are considered uncommon, and typically result from unusual environmental conditions often linked to climate change (e.g. (Torres-Conde and Rodríguez-Martínez, 2024)). For example, these events can lead to increased predation by *P. physalis*, impacting marine ecosystems stability ((Torres-Conde and Rodríguez-Martínez, 2024)). Additionally, there are socio-economic effects, notably reducing the attractiveness of coastal tourism (e.g. (Prieto et al., 2013); (Gómez and Gutiérrez-Hernández, 2020); (Ruiz-Frau, 2022)), affecting fisheries and aquaculture (e.g. (Bosch-Belmar et al., 2020)), and presenting public health risks due to the envenomation threat posed by the toxin in the Portuguese man o'war tentacles (e.g. (Labadie et al., 2012)). Given the potential human health risk and the possibility of an increase in mass stranding events, likely due to climate change, monitoring this species distribution and abundance is crucial.

Recent research on *P. physalis* has spanned various scientific fields. Numerous studies have concentrated on its abundance and distribution (e.g. (Iosilevskii and Weihs, 2009); (Prieto et al., 2015); (Bourg et al., 2022)), while other investigations have targeted its physiology (e.g. (Munro et al., 2019)). Additionally, there is extensive research on its toxins and human envenomation (e.g. (Bañón-Boulet and Gonzalez-Arnay, 2025); (Maharani and Widiastuti, 2021)). Despite these efforts, substantial gaps remain in our understanding of the species' distribution, ecology and biology, partly due to its irregular occurrence ((Munro et al., 2019); (Chebaane et al., 2024)). A recent comparative study analysing *P. physalis* occurrences in both the Azores and the Australian East coasts found, through machine learning models, that regional wind patterns and increased primary productivity may be key factors behind these events (Colaço Martins et al., 2024).

Citizen science projects are essential in addressing these knowledge gaps. They offer long-term data on biodiversity, occurrence, abundance and population dynamics while covering extensive areas that are challenging for researchers to monitor independently (e.g. (Dickinson et al., 2010); (Magalhães et al., 2020)). GelAvista (2025), a Portuguese citizen science project focusing on the monitoring of gelatinous organisms in Portugal. Has been actively collecting scientific data on the distribution and abundance of these organisms since 2016 (GelAvista, 2025).

This study aims to analyse the distribution and frequency of *Physalia physalis* strandings along mainland Portuguese coast, with a focus on monthly and yearly trends. It considers environmental factors such as Sea Surface Temperature (SST), wind direction and intensity, the NAO and Upwelling indexes to better understand the causes behind these strandings. As *P. physalis* is mainly influenced by surface ocean currents and winds, it is expected that wind direction and intensity significantly affect shore occurrences. Strandings are expected to be more frequent outside the main upwelling season when surface waters move offshore. Considering the climate change and reports of increased jellyfish population (e.g. (Attrill et al., 2007); (Condon et al., 2013)), a rise in both sighting frequency and individuals per sighting is anticipated over time. This analysis uses data from the GelAvista citizen science project (2016–2022).

2. Materials and methods

2.1. Study area

Portugal, situated in the southwestern Europe, lies along the eastern boundary of the North Atlantic (Fig. 1). The coastline of mainland Portugal is divided into three distinct regions based on its oceanographic and biological characteristics ((Santos et al., 2007); (Baptista et al., 2018)). The northern and southwestern coasts mark the transition between the temperate and subtropical regions of the northeast Atlantic ((Santos et al., 2001); (Baptista et al., 2018)). In contrast, the southern coast of mainland Portugal exhibits influences from both the subtropical Atlantic Ocean and the Mediterranean Sea ((Baptista et al., 2018); (Cardoso et al., 2019)).

During spring and summer, coastal upwelling on the western coast generates northward jet stream winds that create an Equator-bound current, bringing cold, nutrient-rich water ((Peliz et al., 2002); (Relvas et al., 2007); (Biguino et al., 2023)). In winter, downwelling occurs due to southerly winds (Alvarez et al., 2008). Upwelling areas boost primary production, supporting zooplankton growth and strong food webs (Pires and Dos Santos, 2020). Studies have found Copepoda as the most abundant zooplankton along the Portuguese coast, with notable gelatinous species like siphonophores also present (e.g. (D'Ambrosio et al., 2016); (Domínguez et al., 2017); (Pires et al., 2018); (Dos Santos et al., 2023)). The Portuguese coastline, features a combination of sandy beaches, rocky cliffs, bays, estuaries and lagoons (Rocha et al., 2020), is highly influenced by the North Atlantic Oscillation which can induce alterations on the sea surface temperatures and upwelling patterns ((Santos et al., 2007); (Ferreira et al., 2019)) and consequently on the distribution and abundance of zooplankton communities.

To capture the diverse coastal environments across the country and the patterns of sightings, the Portuguese coast was divided into five areas: North, Center, Lisbon & Setúbal, Southwest and South (Fig. 1). This division considers geographical features (e.g. capes and rivers) and demographics along the coast. The North area extends from the Minho River to the Douro River. The Center spans from the Douro River to cape Carvoeiro. Lisbon & Setúbal includes the Tagus and Sado estuaries. Southwest stretches from south of Sado river mouth to cape S. Vicente. The South covers cape S. Vicente to the Guadiana River (Fig. 1).

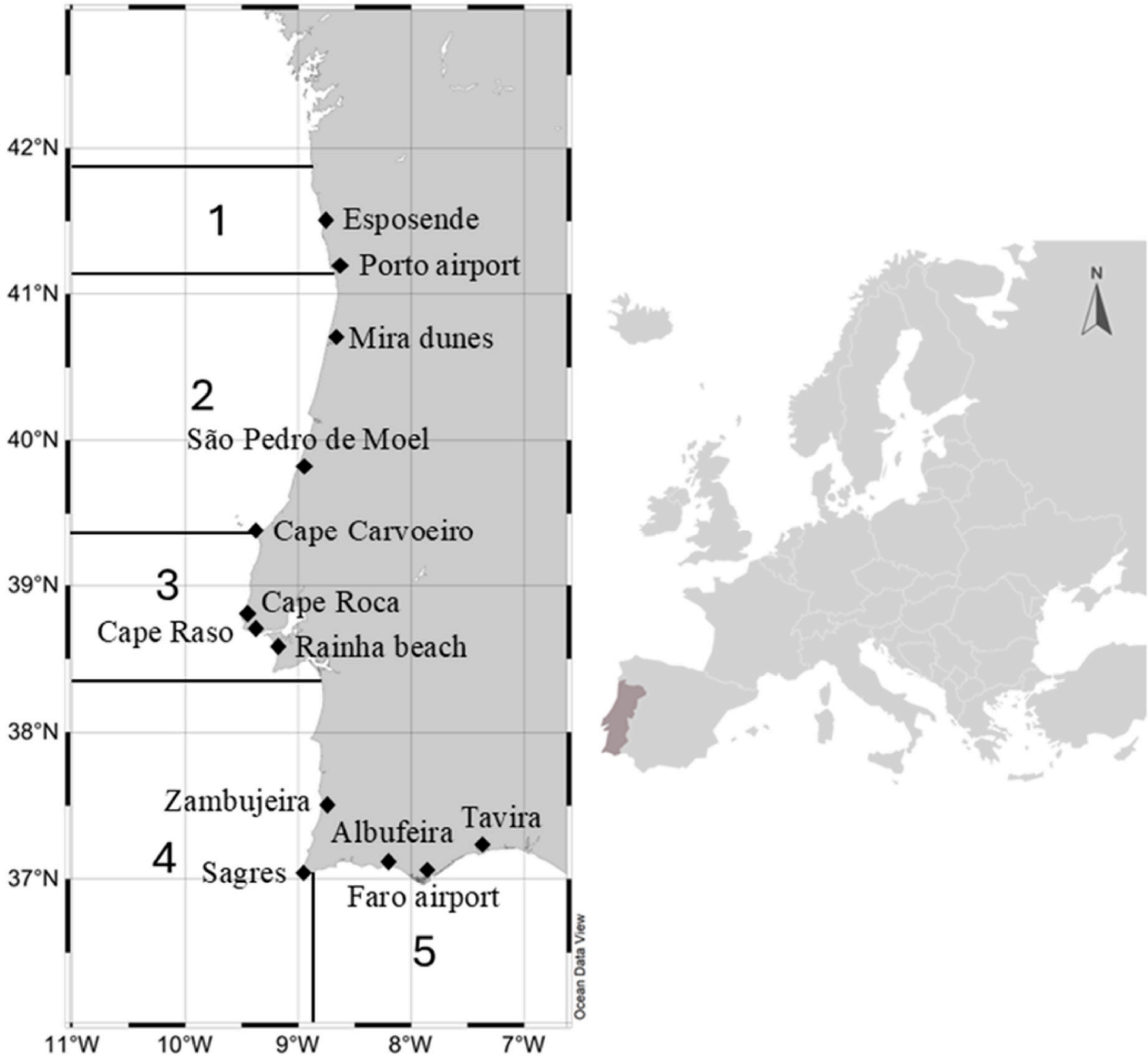

Fig. 1. The Portuguese coast divided into five areas: 1- North; 2- Center; 3- Lisbon & Setúbal; 4- Southwest; 5- South. Black diamonds indicate the meteorological stations used for wind data extraction.

2.2. Citizen science data

Citizen sighting data are submitted via the GelAvista app, email, and social media. Each submission requires location, date, time, and an estimated count of specimens sighted, which are grouped by rank: 1, 2–5, 6–10, 11–50, >50, >100, >1000. Photographs or videos are also requested to confirm the species identification.

For each record, a confidence level is set, based on the positive identification by GelAvista experts and on complete information provided. The confidence level has three grades. Level 3 (low) lacks photographic evidence or key details, level 2 (intermediate) is assigned to uncertain photos (e.g. significant deterioration of the organism) and level 1 (high) is attributed to records with complete information and confirmed identification.

Records with a confidence level of 1 (high) were selected for analysis, while those with a confidence level 3 (low) were excluded. Records classified with a confidence level of 2 (intermediate) underwent individual evaluation to determine their suitability for the study. For simplification of subsequent data analysis, the number of organisms sighted was converted from ranks to numerical values to avoid amplification of abundance sighted they were converted into the lowest value of the rank: rank 2–5 was transformed into 2, rank 6–10 in 6, and >100 in 101, >1000 in 1001, etc. The bias, if any, will be against high occurrences of the species at the shores. To allow a comparison between regions with varying population densities and beach usage throughout the year, the number of *P. physalis* sightings was weighted by the total number of reports received relative to the number of citizens contributing information. This approach enabled the calculation of an abundance index.

Over seven years, GelAvista received 2600 sightings of *P. physalis* (Fig. S1). After excluding those from the Azores and Madeira, the dataset had 1036 sightings. For statistical analysis, 681 sightings were used due to limited environmental data.

2.3. Environmental variables

The environmental variables were: sea surface temperature (°C), average wind intensity (m/s), wind direction (0- calm; 1-NE; 2-E; 3-SE; 4- S; 5- SW; 6-W; 7-NW; 8- N), North Atlantic Oscillation index, and Upwelling index.

The wind data was obtained from the Instituto Português do Mar e da Atmosfera (IPMA) website (www.celsius.ipma.pt) and selected meteorological stations were: Albufeira (n° 0874); Almada - Rainha beach (n° 0773); Cape Carvoeiro (n° 0531); Cape Roca (n° 0750); Cape Raso (n° 0765); Mira dunes (n° 0704); Esposende (n° 2126); Faro aerodrome (n°0554); Porto aerodrome (n° 0545); Sagres (n° 0533); São Pedro de

Moel (n° 0721); Tavira (n° 0833) and Zambujeira (n° 0788) (Fig. 1). Daily average values were considered from the selected stations.

Sea surface temperature data was sourced from Copernicus Marine Service (www.data.marine.copernicus.eu), using daily temporal resolution and a spatial resolution of 0.05° × 0.05°. The NAO index came from NOAA (https://www.ncei.noaa.gov/access/monitoring/nao/), in monthly values. The Upwelling index was obtained from the Spanish Oceanographic Institute (http://www.indicedeafloramiento.ieo.es/index_UI_es.html), using monthly values.

2.4. Statistical analysis

To quantify relative abundance while accounting for variable sampling effort, we computed an abundance index by dividing the number of observed specimens by the number of observers per sampling occasion. This approach enables comparison across areas, months, and years while accounting for sampling effort. Regions like Lisbon and Setúbal, being densely populated, tend to yield more sightings. Areas with rocky, non-bathing shores are likely to have fewer visitors, and more sightings are expected during weekends and warmer seasons. All subsequent analyses were conducted using both the abundance index and the raw counts of sightings; both approaches yielded consistent results with respect to the effects of covariates.

We investigated the relationships between sighting counts (or index values) and explanatory factors using Generalized Linear Model (GLMs). Unlike ordinary linear regression, GLMs allow the response variable to follow non-Gaussian distributions, such as Poisson or negative binomial, while linking its expected value to a linear predictor via a suitable link function (e.g. (Arnold et al., 2020)). In general, a GLM takes the form:

$$g(E[Y_i]) = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \ldots + \beta_k X_{ik},$$

where Y_i is the response for the i-th observation, $X_{i1}, \ldots, X_{ik}$ are the corresponding covariated, β_0 is the intercept, and $\beta_1, \ldots, \beta_k$ are the regression coefficients. The function g() is the canonical link that transforms the mean of Y_i into the linear predictor. For example, when modelling count data with a Poisson distribution, one typically uses the log link:

$$\log(E[Y_i]) = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \ldots + \beta_k X_{ik}.$$

In our analysis, we first compared Poisson and negative binomial families to model the discrete count of *Physalia physalis* sightings, incorporating the total number of sightings as an offset term. The offset ensures that model estimates are adjusted for differing total sample sizes or survey effort across observations.

Because observations were collected across multiple areas and months, we subsequently extended the model to a Generalized Linear Mixed-Effects Model (GLMM). We fitted GLMMs with a log link to count responses, comparing Poisson and Negative Binomial (NB) families. Fixed effects were: wind direction, SST, NAO, upwelling, and year. We included i.i.d. (unstructured) random intercepts for month and area to capture latent temporal and spatial heterogeneity not explained by the covariates. We investigated overdispersion via exploratory analysis of the mean–variance relationship and residual diagnostics. This framework allows us to include random intercepts for area and for month, thereby accounting for unobserved heterogeneity. Formally, the GLMM can be written as:

$$g(E[Y_{ijm}]) = \beta_0 + \beta_1 X_{ijm1} + \beta_2 X_{ijm2} + \ldots + \beta_p X_{ijmp} + u_j + v_m$$

Where:

*Y_{ijm} is the count of sightings in area j, month m, and sampling unit i.
*$X_{ijm1}, \ldots, X_{ijmp}$ are the fixed-effect covariates.
*β_0 is the global intercept.
*$\beta_1, \ldots, \beta_p$ are the fixed-effect coefficients.
*$u_{j} \sim N(0, \sigma_u^2)$ is the random intercept for area j.
*$v_{m} \sim N(0, \sigma_v^2)$ is the random intercept for month m.

Under this specification, u_j and v_m capture between-area and between-month variability in abundance, respectively, beyond what is explained by the fixed covariates.

Model selection and assessment were guided by the Akaike Information Criterion (AIC), which balances goodness-of-fit against model complexity (Davis et al., 2011). For a candidate model with likelihood L and k estimated parameters, the AIC is defined as:

$$AIC = -2 \ln L + 2k$$

Lower AIC values indicate a more parsimonious model that is expected to generalize better to new data. This approach favours simple models, as the criterion rewards models with fewer parameters while still achieving good fit. Consequently, the model with lowest AIC is considered the most parsimonious fit of the data (Davis et al., 2011).

For a GLMM with a log link function, the estimated coefficients (β) are expressed on the log scale. To make them more interpretable, the Incidence Rate Ratio (IRR), calculated as IRR = exp(β), along with the 95 % Confidence Intervals (CIs) for IRR, were obtained. Note that if the 95 % CI for the IRR does not include 1, the effect is considered significant.

All statistical analyses were conducted in R 4.5.2 (R Core Team, 2025) using several contributed packages. Data manipulation relied on functions from the dplyr package (version 1.1.4 (Wickham et al., 2023);). For fitting linear mixed-effects models, glmer() and glmer.ng() from lme4 (version 1.1–37 (Bates et al., 2015);) were used. Model diagnostics were carried out using the DHARMa package (version 0.4.7 (Hartig, 2024);), with simulateResiduals() to generate residual-based QQ plots and testDispersion() to evaluate potential overdispersion. Data visualisation was performed with ggplot2 (version 4.0.1 (Wickham, 2016);), ggeffects (version 2.3.1 (Lüdecke, 2018);), and spatial data were visualised with the sf package (version 1.0–22 (Pebesma, 2018);) and the rnaturalearth package (version 1.1.0 (Massicotte and South, 2025);).

Throughout the analysis, statistically significant effects were only considered whenever p-value ≤0,05.

3. Results

3.1. Physalia physalis distribution

Most observations during the study period reported one *P. physalis* per record, accounting for 54,5 % of records. Sightings were more frequent on the West coast than the South. The first two years showed a low number of specimens per record (Fig. 2). In March 2018, a peak was noted in the South with over 50 individuals per record, the highest for this area. In 2019, the number increased, especially in April in Lisbon & Setúbal, July–August in the Southwest, and December across all areas except the South.

In 2020, the Center area had 50 to 100 individuals per record during February, March, May, June and December. January 2021 saw the highest average of nearly 600 organisms per observation (Fig. 2). Numbers dropped in February but remained higher than usual, especially in the North area. The rest of 2021 and all of 2022 had low numbers per record.

Sightings of *P. physalis* were typically less than 3 per month, except in 2018 with 5, in 2019 with around 10, and January 2021 with about 15 in the Lisbon & Setúbal area (Fig. 3). This period had the highest numbers per sighting. *Physalia physalis* was most frequently observed between November and May, especially in the winter months.

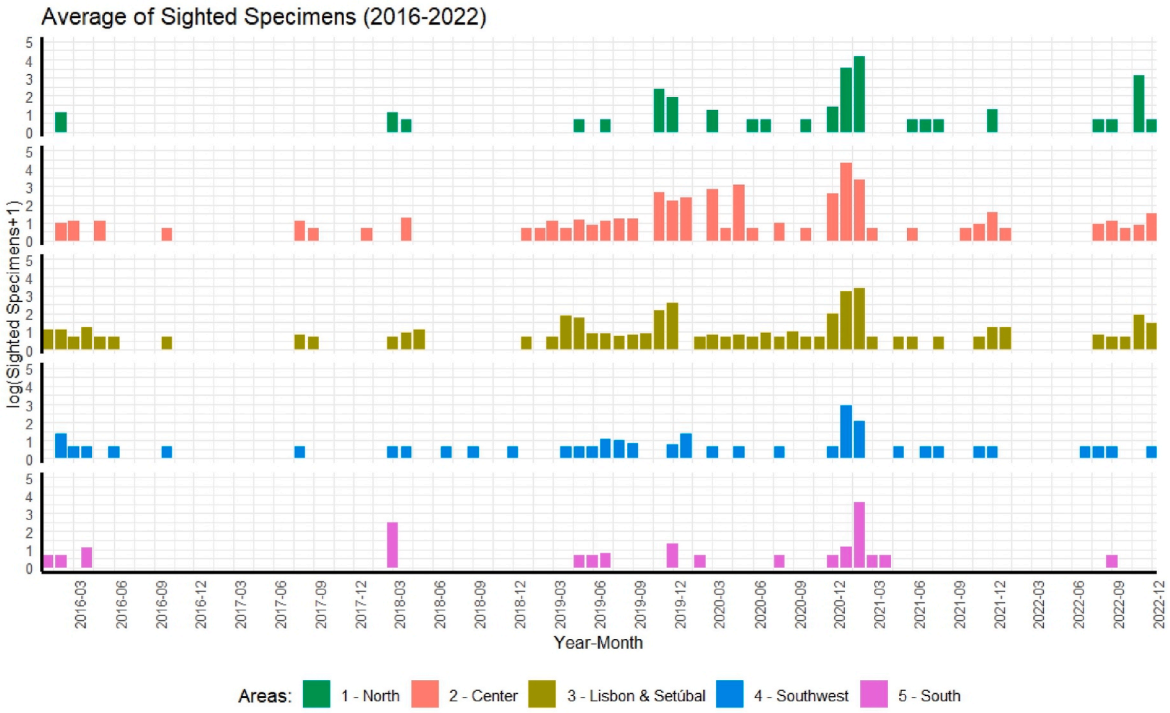

Fig. 2. Average monthly sighted specimens per area (2016–2022).

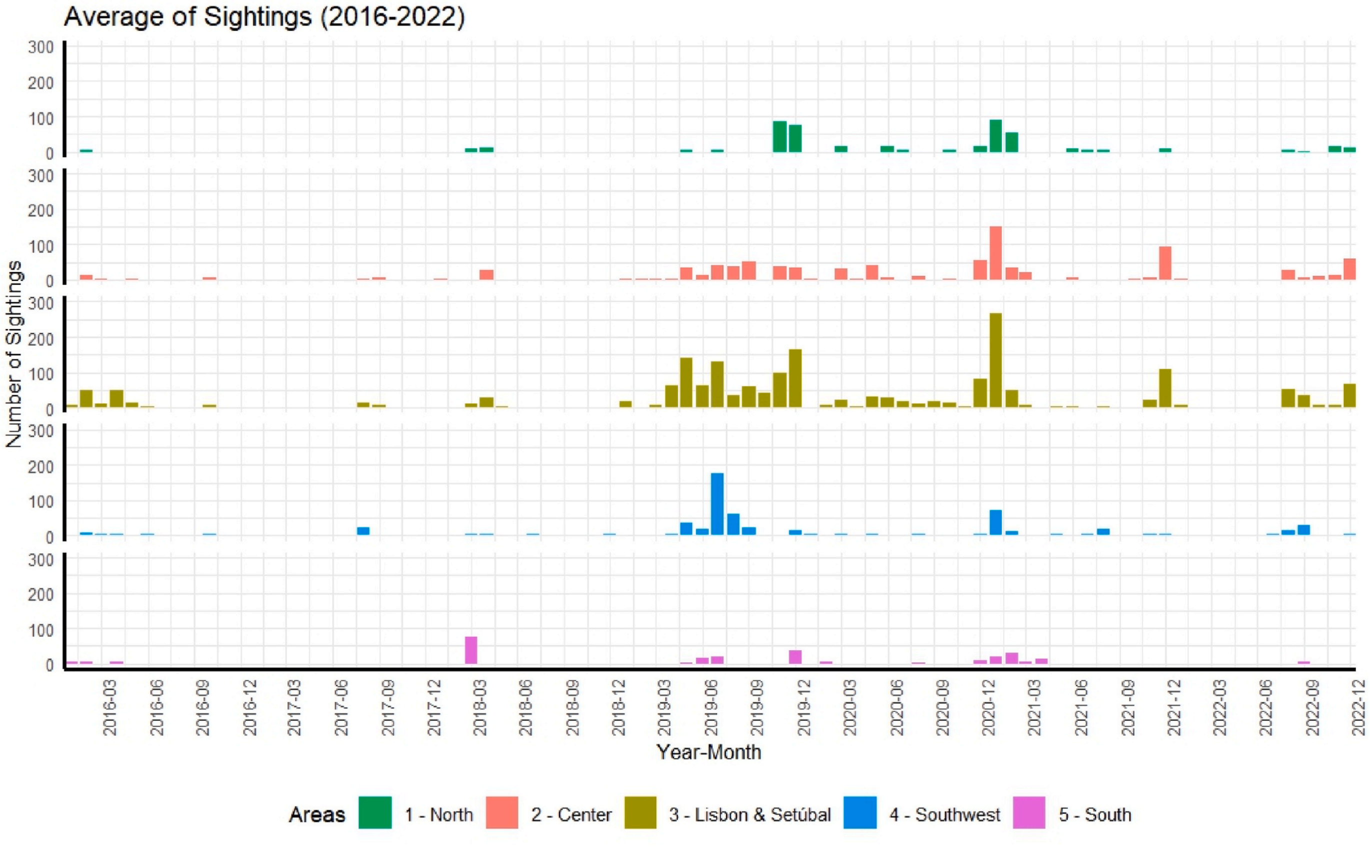

Fig. 3. Average monthly sightings by area, 2016–2022.

3.2. Environmental variables

3.2.1. Sea surface temperature

During the study period, SST along the mainland Portugal coast showed consistent seasonal patterns. Winter temperatures (December–March) were lower (Fig. 4), while summer temperatures (June–September) were higher (Fig. 4), ranging from about 15 °C in winter to 21–22 °C in summer, with the south generally warmer than the north. Upwelling during summer showed coastal SSTs between 14 °C and 18 °C. Spring and summer months exhibited more variation, with some years showing higher SST than others. The summer of 2021 had notably lower SSTs along the west coast compared to the other years, whereas 2022 recorded the highest SST values of the study period.

From a monthly perspective, January 2020 exhibited the lowest sea surface temperatures (SST) along the coast, particularly in the northern region (Fig. 4). In contrast, January 2016 presented relatively high SSTs compared to the other years studied. February 2018 recorded the lowest SST values along almost the entire coastline of mainland Portugal coast (Fig. 4). March displayed notably low SSTs along the coastline in both 2016 and 2018, whereas in 2017, these variable values ranged between 14° and 16 °C (Fig. 4).

In April 2021, SSTs in the South reached 18 °C, higher than in the other years. In contrast, SSTs were lower in 2016, 2018, 2019, and 2022 (Fig. 4). More specifically, SSTs were low along most of the coast in 2016 and 2018, while in 2019 and 2022, the lowest SSTs were in the North, Center and Lisbon & Setúbal areas.

In May 2020, sea surface temperatures along the mainland Portugal coastline were higher (Fig. 4). Conversely, this month had the lowest SST values in 2018 (below 15 °C). In June 2018, 2019, and 2020, coastal SSTs showed the lowest observed values, being at or below 16 °C (Fig. 4). In contrast, 2016 and 2017 exhibited higher SSTs, particularly in the South in 2017 where the values exceeded 20 °C.

July 2021 had the lowest SSTs (Fig. 4). In 2020 Lisbon & Setúbal and the South regions recorded sea surface temperatures above 22 °C. Similarly in August 2016, the South, especially near the Guadiana estuary, registered high SSTs, while lower values were observed in 2021 (Fig. 4).

September 2017 showed lower SSTs in the northern area (Fig. 4), while 2021 had the highest. In October, SSTs peaked at 22 °C in the South in 2018, but October 2016 recorded higher values overall, with 2020 showing the lowest (Fig. 4). November 2019 had low coastal SSTs, but these were unusually high in November 2022 (Fig. 4). December SSTs mirrored November's (Fig. 4). In 2022, SSTs were notably high, contrasting with the lowest records in 2019.

3.2.2. North Atlantic Oscillation (NAO)

During the study period most of the winter months exhibited positive NAO index values, whereas the summer months presented negative NAO values (not shown). The NAO index was not statistically significant with *P. physalis* data for the period studied.

3.2.3. Wind direction and intensity

The wind direction prevailed throughout the years suggesting a general trend of winds blowing from the North/North-Northwest (Fig. 5). For years 2016–2020, the North direction was dominant, with statistical significance for all years, except 2020. In 2021 and 2022 the Northwest direction was the prevailing one.

Regarding wind intensity, the ranges of 2–4 m/s and 4–6 m/s were dominant, indicating a common frequency of low to moderate wind speed, which was a clear trend in 2021. Although the wind reached higher intensities (14–16 m/s) along the study period, it was more noticeable in 2022.

Monthly wind data from 2016 to 2022 shows a seasonal trend in direction and intensity (Fig. 6). In winter, winds were mainly Northeast and East; in summer, they ranged between North and Northwest. Wind intensity was higher in summer months than in winter. These patterns

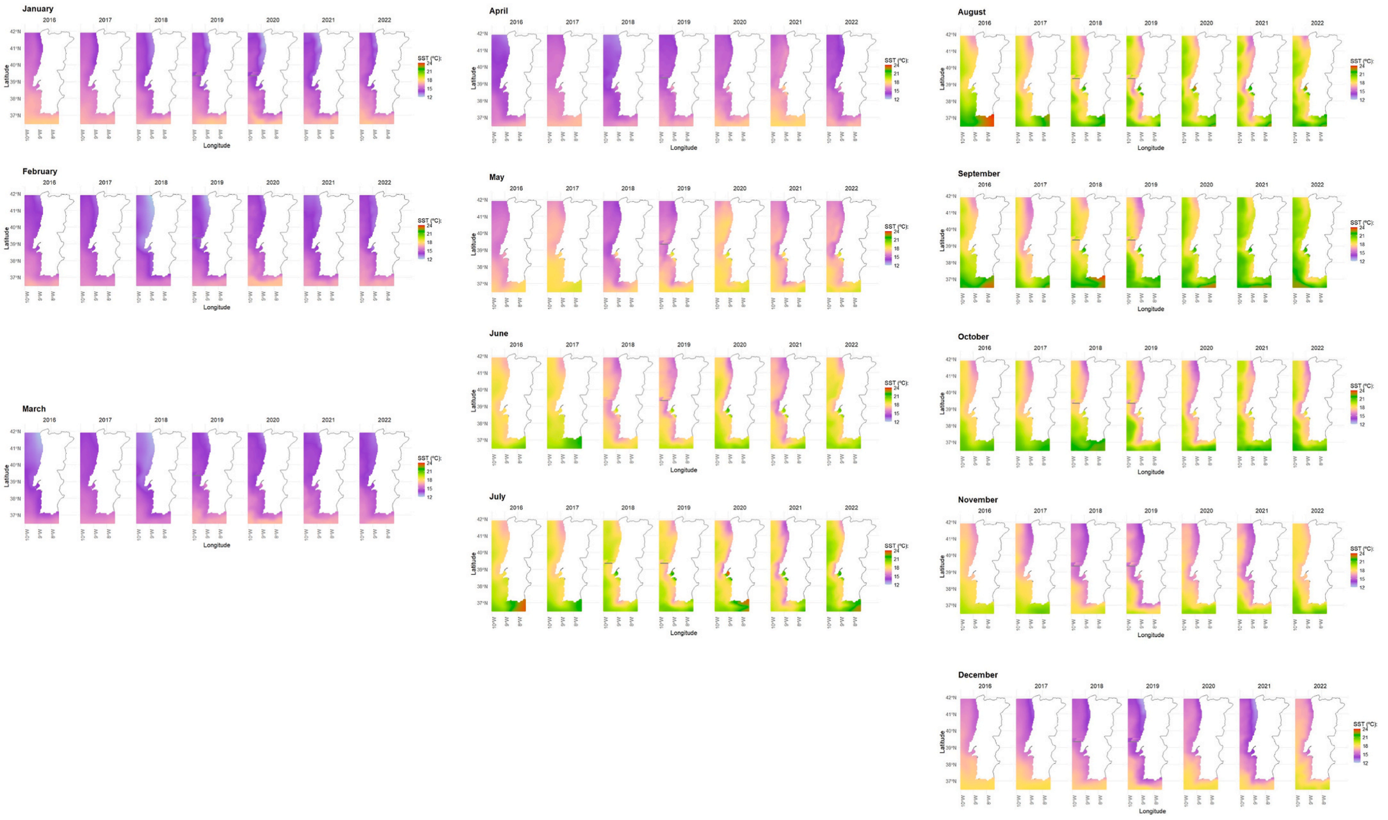

Fig. 4. Sea surface temperature (°C) in mainland Portugal from 2016 to 2022; grey areas indicate missing data.

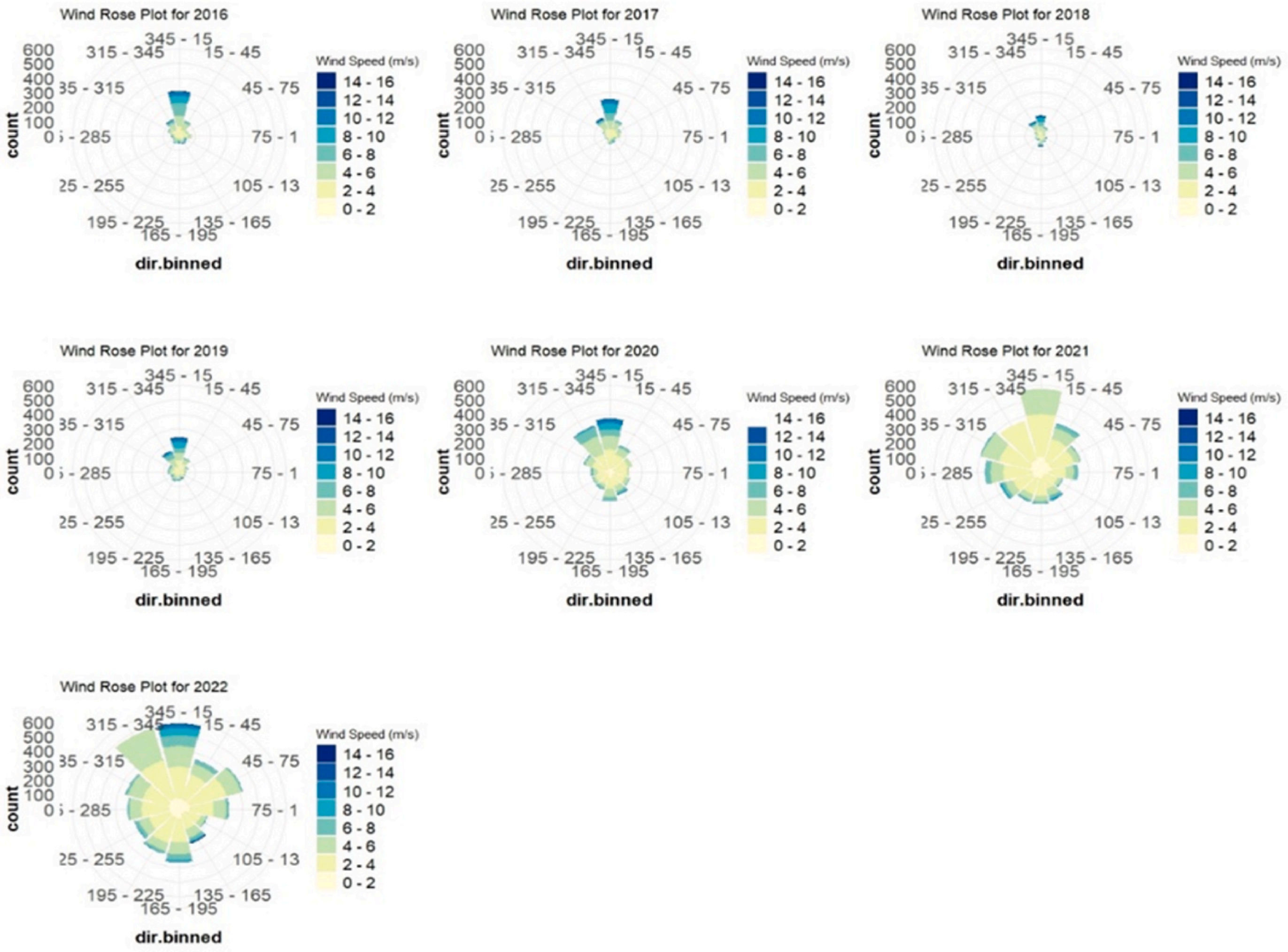

Fig. 5. Annual wind rose plots display wind speed (m/s) and direction (°) for mainland Portugal from 2016 to 2022. Plot segment sizes reflect data availability. For example, 2022 shows larger segments due to more data available for that year.

are related to upwelling and downwelling on the Portuguese coast.

3.2.4. *Upwelling*

The Upwelling index per area (Fig. 7) revealed that events were more intense in the North.

In January of 2016, downwelling was recorded in the North and Center regions. During the same year, upwelling was observed from June to October across all regions except the South. This phenomenon was particularly intense in July within the North, Center, and Lisbon & Setúbal areas. Similarly, in 2017, upwelling events were noted in all regions, excluding the South, from June to October, albeit with lower intensity.

In March 2018, the South area experienced its highest upwelling values of the year. Conversely, during the same month, downwelling events took place in the North and Center areas. The upwelling period occurred from June to October in all areas, except in the South. Throughout 2019, downwelling events were infrequent. Upwelling events were also less intense and occurred in May and July in all regions, except the South, and in September in the North and Center areas. In 2020, upwelling was more pronounced than in other years of study, with the peak observed in July in the North, Center, Lisbon & Setúbal, and Southwest areas. The North area registered the highest index values. No downwelling events were documented this year. In the following year, upwelling was noted between May and August. In December, downwelling phenomena were recorded in all the studied areas, except for the South, with the North areas showing the highest index values.

In 2022, the upwelling was weak, beginning in April in the Southwest region. It occurred again in July and August in the North, Center, Lisbon & Setúbal, and Southwest regions, with the North having the highest values. In October, downwelling events occurred in North and Center regions. It was observed later in December in all regions, except in the South and, reaching the highest values for that year.

Upwelling was predominantly associated with summer months (June to September), while downwelling was linked to winter months (December to March) (Fig. 7).

3.3. *Data modelling*

3.3.1. *Species distribution in relation to environmental variables*

As an initial data-processing step, all variables were aggregated by Area and Year-Month, and any rows containing missing values were removed to ensure a complete dataset for inclusion in the statistical model. Prior to the analysis, categorical variables were converted to factors, and continuous variables were standardized (z-scores) to facilitate model convergence and comparability effect sizes. Initially, a Generalized Linear Model (GLM) was fitted and the outcomes were satisfactory, however an even more adequate model could be assessed. After analysing the results, the Poisson Generalized Linear Mixed-Effects

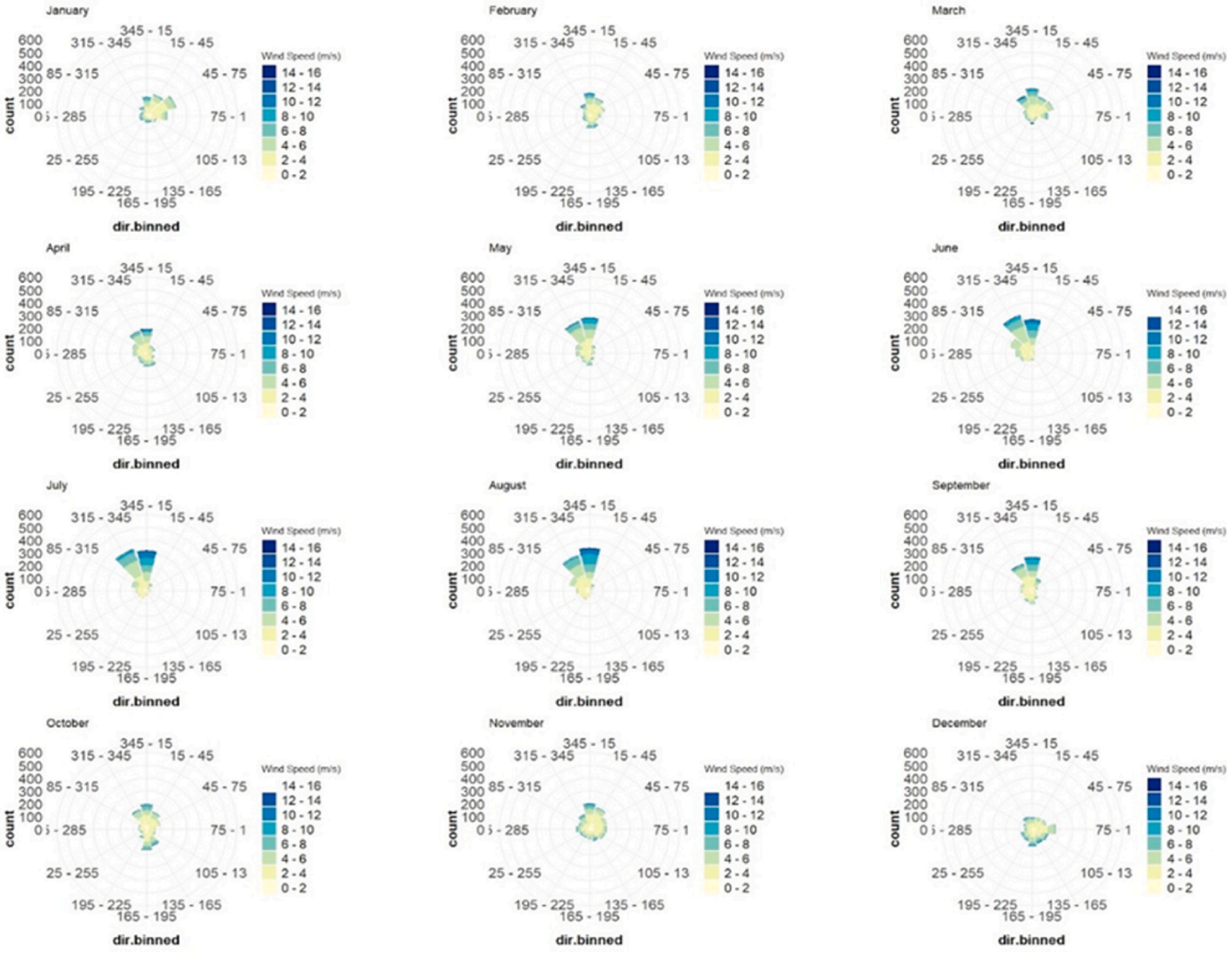

Fig. 6. Monthly wind rose charts showing wind speed (m/s) and wind direction (°) for mainland Portugal from 2016 to 2022.

Model (GLMM) was fitted to the count data. However, ecological and observational count data very often exhibit overdispersion. The diagnostic of overdispersion was performed and so, the negative binomial GLMM was estimated with dispersion parameter 2586. A comparison between the models (Table S1) showed that the negative binomial distribution presented a lower AIC when compared to the Poisson distribution. This indicates that the negative binomial is more suitable for this study, as the optimal fitted model is determined by the minimum AIC value (Cavanaugh and Neath, 2019). The residuals diagnostic (Fig. S2) shows that they do not exhibit a noticeable pattern, which is an ideal outcome. Nevertheless, there appears to be a slight structure when it comes to their independence, making it impossible to affirm that the residuals are totally independent. Despite the presence of some outliers, the QQplot (Fig. S2) confirms that there is no evidence the chosen distribution is not appropriate for the data under study. This model indicated that wind intensity, the NAO and upwelling did not have statistically significant effects (Table S2). Also, the variance in the monthly random intercepts (Table S3) is greater than that of the area random intercepts. This suggests that monthly variation has a stronger influence on *P. physalis* occurrences than spatial (area-based) variation.

The GLMM was refitted without the random effect area and without the fixed effects NAO, WindInt and Upwelling, removed one at a time, and the results are presented in Table 1. In addition, to interpret the strength and the direction of the effects, the coefficients were converted to IRR, where IRR<1 indicates fewer sightings, IRR = 1 no effect, and IRR>1 indicates more sightings. The GLMM, fitted by maximum likelihood using Laplace Approximation, indicated statistically significant effects for SST (Estimate = −0,41) and the variable year (Estimate = 0,24) (see Table 1). The negative value obtained for SST estimate suggests that as these variable decreases, the number of individuals sighted (n° ind/record) increases. In fact, SST exhibited a significant negative effect (IRR = 0,66; 95 % CI: 0,54-0,82), indicating a 34 % decline in sightings for every 1 Standard Deviation (SD) increase in temperature. Conversely, the positive correlation between year and the numbers of *P. physalis* per sighting implies an increasing trend over time. The year had a significant positive effect on organism sightings (IRR = 1,27; 95 % CI: 1,05-1,52), suggesting a 27 % long-term increase in the expected number of sightings along the time. Wind directions, except South (WindDir4) and West (WindDir6), also had statistically significant effects, with calm wind (WindDir0) linked to a high number of individuals sighted per record. Relative to the reference wind direction (calm), several directions reduced sightings by 28 %–86 %, with IRR values between 0,14 and 0,72. Overall, most wind directions were associated with substantially lower counts compared to the reference direction, highlighting that wind direction strongly influences sightings. To visualise the fixed effects of the negative binomial GLMM, model-based predictions were generated using the function ggpredict() from ggeffects (Lüdecke, 2018) and plotted with ggplot2 in Fig. 8. These plots

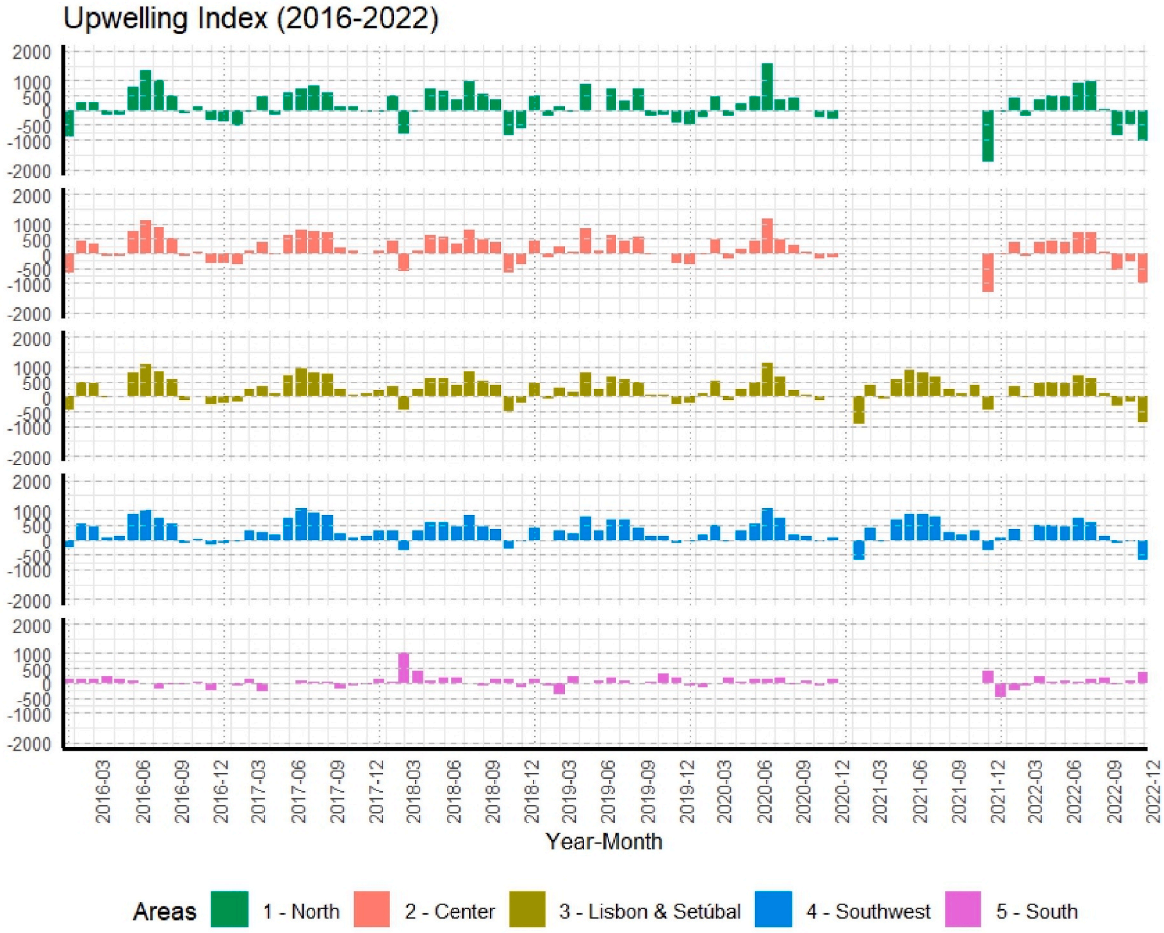

Fig. 7. Monthly Upwelling index data covers 2016–2022, except January 2021. From February to November 2021, only Lisbon & Setúbal and Southwest regions have data.

provide an intuitive and interpretable visualisation of the fixed effects of the final model by converting the log-scale coefficients into meaningful predictions on the natural count scale, highlighting the negative influence of SST and the positive trend over the time.

4. Discussion

This study used GelAvista data to analyse the spatial and temporal patterns of *Physalia physalis* along Portugal's coast. The extensive area made comprehensive scientific field research impractical, but citizen science provided a larger dataset on species occurrence. Therefore, engaging the public in observation through citizen science projects is a promising method for studying jellyfish communities (e.g. (Pires et al., 2018); (Gueroun et al., 2022)). The GelAvista project was initiated following the observation of a *P. physalis* specimen near Lisbon in early January 2016. At that time, this species was regarded as rare on mainland Portugal, being more commonly found in the Madeira and Azores archipelagos during the summer months. It is now considered one of the most abundant gelatinous species on the Portuguese mainland (https://gelavista.ipma.pt/wp-content/uploads/2024/01/Ponto-Situacao-GelAvista_compressed.pdf). Given its status as the most dangerous species of its kind along our coasts, there has been an increased willingness among the public to report sightings of *P. physalis*. Observer effort was influenced by (1) public awareness of the GelAvista project, especially in its first three years, (2) low population density in some coastal areas, and (3) fewer beach visitors during winter. To address this, *P. physalis* sightings were weighted to correct for sample imbalance due to uneven coastal populations and seasonal beach use. Although this proceeding could potentially cause overrepresentation, we believe this was not the case, as GelAvista received far more reports during summer months (https://gelavista.ipma.pt/wp-content/uploads/2023/11/Numero-avistamentos-recebidos-GelAvista-PT-1.pdf).

The Lisbon & Setúbal area had the most records and the highest numbers of *P. physalis* per record. This region has the highest population density among the areas studied (PORDATA, 2025). As a result, more people use the coastal areas and are willing to report data to GelAvista. This area also includes a coastline with several sandy beaches, which consist of 13 km of the Almada coast and 45 km of Grândola, contributing to the population at the shore available to report jellyfish sightings. The Southwest area has one of the lowest population densities (PORDATA, 2025), a coastal landscape featuring cliffs and coves with small beaches, which may contribute to the lower frequency of sightings reported to GelAvista. The lower number of jellyfish observed in the Southwest area may be due to its narrower continental shelf compared to northern areas (e.g. (Dos Santos and Peliz, 2005); (Pochelon et al., 2017)). Dos Santos & Peliz (Dos Santos and Peliz, 2005) also linked the absence of the Norway lobster larvae (*Nephrops norvegicus)* in this area to both the narrow shelf and local oceanographic conditions. The authors note that frequent mesoscale eddy activity linked to the Slope current and Mediterranean undercurrent disrupts plankton retention on the continental shelf, which may also affect jellyfish retention.

Results showed a positive correlation between the variable year and *P. physalis* numbers per record, indicating an increased tendency of this species sightings over the years. Climate change is often pointed as a

Table 1
Fixed effects of the Generalized Linear Mixed-Effects Model displaying raw coefficients (Estimate, β); Standard Errors (SE); z-value, which indicates the observed value of the statistic test; p-values (Pr(>|z|), Incidence Rate Ratio (IRR) and its 95 % Confidence Interval (CI). The wind directions from 1 to 8 correspond to WindDir0-calm; WindDir1-Northeast (NE); WindDir2-East (E); WindDir3-Southeast (SE); WindDir4- South (S); WindDir5- Southwest (SW); WindDir6-West (W); WindDir7-Northwest (NW); WindDir 8- North (N) were obtained considering a reference Wind Direction (WindDir0). Statistically significant results (*p-value* < 0.05) are highlighted in boldface.

Variable	β (Estimate)	SE	z-value	p-value	IRR	95 % CI IRR
(Intercept)	1,69	0,21	8,23	<0,01	5,42	3,62-8,11
WindDir1 (NE)	−1,77	0,49	−3,6	0,000322	0,17	0,07-0,45
WindDir2 (E)	−1.94	0,86	−2,26	0,02	0,14	0,03-0,77
WindDir3 (SE)	−1,33	0,4	−3,3	0,000976	0,26	0,12-0,58
WindDir4 (S)	−0,43	0,29	−1,45	0,15	0,65	0,37-1,16
WindDir5 (SW)	−0,84	0,37	−2,28	0,02	0,43	0,21-0,89
WindDir6 (W)	−0,32	0,3	−1,07	0,29	0,72	0,40-1,31
WindDir7 (NW)	−1,05	0,25	−4,12	0,0000379	0,35	0,20-0,54
WindDir8 (N)	−1,19	0,25	−4,77	0,00000152	0,33	0,21-0,52
SST	−0,41	0,11	−3.83	0,000126	0,66	0,54-0,82
Year	0,24	0,09	2,52	0,01	1.27	1,05-1,52

potential factor influencing marine species distribution and abundance, including *P. physalis* (e.g. (Canepa et al., 2020); (Torres-Conde and Rodríguez-Martínez, 2024)). The increased number of sightings could be related to GelAvista reaching a larger audience. Therefore, the present results must be interpreted with caution and emphasizes the importance of continuing monitoring jellyfish species through GelAvista to verify whether these trends are accurate. Although we observed a positive temporal trend in sightings over the study period, we cannot directly attribute this trend to climate change. SST and wind direction were associated with the observed pattern, but other factors, such as changes in observer effort or unmeasured ecological drivers, may also play a role. Therefore, these results indicate correlations rather than direct causation, and further research is needed to identify the underlying drivers of the observed trends.

Simultaneously, lower sea surface temperature was associated with a higher number of occurrences of *P. physalis*. Throughout the year, *P. physalis* was observed in higher numbers during winter months, which can be attributed to colder sea surface temperatures and downwelling conditions, while its summer strandings are likely linked to lower SST values associated with upwelling events. These findings contrast with previous works that reported a positive correlation between SST and the occurrence of the Portuguese man o'war. In particular, two studies conducted along the Chilean coast, revealed that SST had a positive correlation with stranding colonies ((Canepa et al., 2020); (Fierro et al., 2021)). Therefore, further research, such as laboratory studies, are necessary to better understand the correlation between sea temperature and the strandings of this species.

As a result of climate change, upwelling events are expected to intensify due to changes in pressure gradients between continental and oceanic areas (e.g. (Rykaczewski and Dunne, 2010); (Pires and Dos Santos, 2020)). Thus, an increase in sightings is expected during winter and spring, during periods of downwelling. During the summer, strandings of *P. physalis* are expected to be minor. As a pleustonic organism, this species could experience alterations in its distribution patterns due to faster offshore transport ((Rykaczewski and Dunne, 2010); (Sydeman et al., 2014); (Pires and Dos Santos, 2020)). Additionally, circulation shifts driven by climate change might affect its population dynamics by altering behaviour, reproduction and growth (Pires and Dos Santos, 2020). While previous studies have shown that jellyfish are resilient to environmental changes, with some upwelling

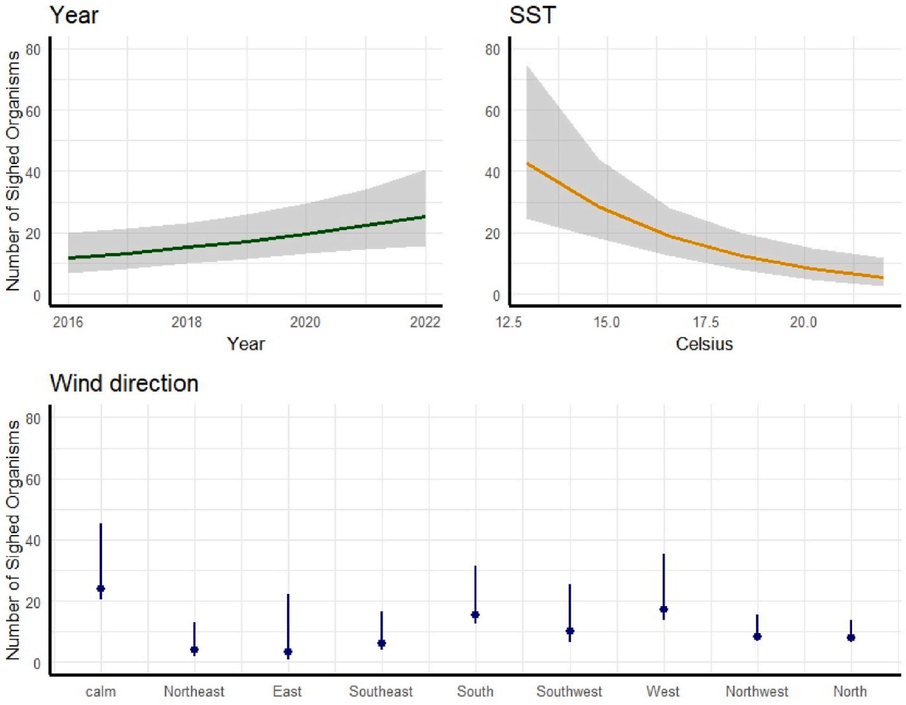

Fig. 8. Predicted number of sightings from a negative binomial GLMM. Top left: Predicted counts over time (Year). Top right: Predicted counts as a function of sea surface temperature (SST, °C). Bottom: Predicted counts for different wind directions (WindDir; 0 = reference direction). Shaded areas and vertical error bars indicate 95 % confidence intervals around the predictions. All continuous predictors were standardized.

regions reporting an increase in its populations (e.g. (Condon et al., 2013)), insufficient evidence to confirm these trends remains.

P. physalis distribution is significantly controlled by the wind ((Ferrer and Pastor, 2017); (Headlam et al., 2020)) and sea surface currents. The statistical analysis showed a significant correlation between wind direction and the numbers of *P. physalis* per record. Although periods of calm winds (Wind Direction 0) were found to be particularly influential on the number of individuals observed per record, South and West winds directions, also played a role, with statistical significance. These winds may facilitate the transport of the specimens closer to the shore. When weakened, the consequent calm wind will eventually promote *P. physalis* stranding on the beach. Conversely, the influence of northerly winds on the mainland Portugal coast has been highlighted in numerous studies, notably due to their association with the upwelling patterns (e.g. (Leitão et al., 2019)). Ferrer & Pastor (Ferrer and Pastor, 2017) identified a combination of west-southwesterly and northwesterly winds as the main cause of an unusual mass stranding of this species along the Basque coast in 2010. Moreover, Torres-Conde & Rodríguez-Martínez (Torres-Conde and Rodríguez-Martínez, 2024) suggested that northeasterly winds were the possible cause for a mass stranding in Cuba in 2022. Although these studies provide useful findings, it should be noted that wind conditions along the Basque coast and in Cuba differ considerably from those in the Portuguese coast. These highlight the diverse effects that local environmental factors, such as wind patterns, can have on species distribution. Accordingly, Colaço-Martins et al. (Colaço Martins et al., 2024) in their comparative work of one region in the North Atlantic and one in the Southeast Pacific concluded that *Physalia* blooms are driven by region-specific wind patterns. Regarding wind intensity, the analysis did not reveal any statistical significance. This unexpected outcome may be due to the incomplete wind data set for various periods and areas. Further research in the possible influence of previous wind conditions, days or weeks, could provide valuable insights on how past patterns could affect *P. physalis* strandings.

During the study period, two uncommon events were observed, characterized by an increased number of records and specimens per record of *Physalia physalis*. The first event occurred in the southern region between 4th and March 14, 2018 showed no statistical correlation with any tested environmental variables. This can be partially explained by the absence of the wind data for the area and the low resolution for the upwelling data (monthly versus weakly sightings data) in the period considered. However, during this period, daily air temperatures consistently remained below the average (IPMA, 2018). Additionally, it recorded unusually high upwelling values for the area, which were also the highest observed nationwide for the year. Moreover, between February 28th and March 28th, 2018, three different depressions -Emma, Giselle and Félix-impacted the area under study (IPMA, 2018), notably affecting the southern region (Ploamaritis et al., 2019). The unusual high upwelling values and storms on the South coast may explain the *P. physalis* occurrence in this region, although upwelling was not statistically significant, probably due to absence of upwelling data. Several authors have documented occurrences of *P. physalis* in the western Mediterranean Sea during the same period, attributing these events to a combination of meteorological and oceanographic factors. Macías et al. (2021), reported occurrences of the Portuguese man o'war in the Cadiz region from March 2nd to April 16th, with initial sightings noted in February in the Alboran Sea (western Mediterranean Sea). Previously, Mghili et al. (2020), reported this species' first observations on March 26th at Fnideq beach (southwestern Mediterranean Sea). In the following months, it extended to other Moroccan beaches influenced by the easterly winds (Mghili et al., 2020) and to the northwestern coast of Algeria (Boughamou and Ladoul, 2022).

The second event that occurred in January 2021, across all areas of the western coast, with particular significance in the Center region could not be linked to any specific environmental variable tested. Previous research has linked the NAO negative phase to higher abundance of *P. physalis* (e.g. (Prieto et al., 2015); (Torres-Conde and Rodríguez-Martínez, 2024)) but this inference cannot be made in our case because the NAO index in this period was positive. Therefore, the need for further research between NAO index and this species strandings should be reinforced, as has been emphasized (e.g. (Prieto et al., 2015)). However, we can infer that during this period there would have been a large population of *Physalia* off the Portuguese coast, as they washed up in large numbers.

5. Conclusion

This study has provided valuable insights into spatial and temporal distribution patterns of *Physalia physalis* along the Portuguese coast. The species was common all over the western coast and was scarce in the South. The stranding pattern is characterized by one individual per record, although with several exceptions. The species exhibited a pattern of higher frequency between November and May, with an increased number of individuals per record during the winter months. Accordingly, results revealed *P. physalis* sightings associated with low sea surface temperatures.

The influence of wind direction proved to be significant in the sighting patterns of *P. physalis*, with calm and possibly south and west winds conducting the stranding events. Winds drive *P. physalis* closer to the coast, while the calm wind might facilitate their stranding on the shore.

There is a positive temporal trend, indicating that occurrence of sightings has increased over the study period, even after accounting for wind and SST, which might be linked to climate change.

This study underscores the importance of ongoing jellyfish monitoring conducted by GelAvista, as well as the necessity for a comprehensive database encompassing all relevant environmental variables. In addition, synthesizing insights from prior research with experimental approaches can yield a more consistent understanding of the mechanisms underlying Portuguese man o'war strandings. Furthermore, the application of statistical methodologies that incorporate structured random effects will improve the modelling of temporal and spatial dependencies across various months and geographic regions. For future research, time series techniques for imputing missing values may be utilized to enhance the completeness of environmental datasets and strengthen analytical robustness in subsequent studies focused on time series analysis.

CRediT authorship contribution statement

Patrícia Carvalho: Writing – review & editing, Writing – original draft, Validation, Investigation, Formal analysis, Data curation. **Clara Cordeiro:** Writing – review & editing, Validation, Formal analysis. **Soraia Pereira:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis. **Antonina dos Santos:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Data availability statement

The data, models and code used to support the findings of this study are available from the corresponding author upon request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109674.

Data availability

Data will be made available on request.

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