Ocean and Coastal Management 266 (2025) 107694

Contents lists available at ScienceDirect

Ocean and Coastal Management

journal homepage: www.elsevier.com/locate/ocecoaman

# Distribution modelling of jellyfish in Spanish coastal areas: An approach based on the maximum entropy principle

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ARTICLE INFO

*Keywords:*
*Pelagia noctiluca*
Maximum entropy model
Beach management
Citizen science
West editerranean coast

ABSTRACT

Jellyfish blooms are natural events with significant ecological and socio-economic impacts, particularly in regions like the Andalusian Mediterranean coast, where tourism is an important industry. This study employs Maximum Entropy (MaxEnt) species distribution model to predict jellyfish presence using citizen science data from the Infomedusa app and environmental variables derived from the Copernicus platform. In particular, while users reports do not enforce species-level identification, *Pelagia noctiluca* likely dominated the sightings in our study region. Presence-only data from summer 2019 were analyzed alongside key environmental factors from March to September. The models consistently identified the mixed layer depth in April as the most influential variable, contributing between 72.7 % and 93.9 % to the probability distribution, highlighting the role of early spring conditions in shaping summer jellyfish dynamics. The results revealed spatial and temporal patterns in jellyfish presence, providing valuable insights for coastal management and early-warning systems. To validate the MaxEnt predictions, observed absence data were used to compare areas of low predicted probability of jellyfish presence with high densities of observed absences, revealing a moderate level of agreement, with 22.58 %–37.13 % coincidence between low-probability MaxEnt predictions and areas of high absence density. While the study is limited to a single summer season due to data availability, it highlights the potential of integrating advanced modeling techniques with crowd-sourced data, this study underscores the value of citizen science for marine ecology and highlights the importance of proactive strategies to mitigate the socio-economic impacts of jellyfish blooms on local communities and ecosystems. These findings can inform regional planning and contribute to global efforts to address gelatinous zooplankton proliferation.

## 1. Introduction

Jellyfish blooms are natural events that have occurred recurrently in marine ecosystems throughout history (Condon et al., 2012; Marambio et al., 2021). In particular, the Mediterranean Sea has been consistently affected by dense blooms of various jellyfish species over time (Canepa et al., 2014). The increase in frequency and intensity of jellyfish blooms has been the subject of intense debate and scientific study in recent decades (Sanz-Martín et al., 2016; Pitt et al., 2018). Despite the ambiguity in long-term trends, it is evident that jellyfish blooms are a natural part of marine ecosystems, with a notable presence in the Mediterranean Sea and various effects on both human and ecosystem services (Bergamasco et al., 2022). Jellyfish blooms are not only ecological events but also socio-economic phenomena with the potential to impact various sectors. While jellyfish play essential roles in regulation, support, provisioning, and cultural services (Doyle et al., 2014; Graham et al., 2014), their negative effects on human activities have increased over time (Purcell et al., 2007). As human interactions with coastal ecosystems increase, so too will encounters with jellyfish blooms.

The Andalusian region (southern Spain) is highly dependent on

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https://doi.org/10.1016/j.ocecoaman.2025.107694
Received 17 December 2024; Received in revised form 2 April 2025; Accepted 9 April 2025
Available online 15 April 2025

tourism, with the sector directly linked to the region's economic growth (Tugcu, 2014; Bernier et al., 2014). Jellyfish blooms have had a significant economic impact on this coastal region, notably reducing tourism and causing financial losses in the recreational sector (Ghermandi et al., 2015; Cantarero-Prados et al., 2023). Despite efforts to mitigate the problem, blooms of *Pelagia noctiluca* (Forsskäl, 1775), the most conspicuous Mediterranean jellyfish (Brotz and Pauly, 2012), can result in beach closures along the coast to protect public health, severely affecting the summer tourist season (Ghermandi et al., 2015). The presence of jellyfish not only poses public health risks due to stings but also negatively affects the region's tourist image, leading to significant economic losses. Given this situation, it is crucial to understand the ecological dynamics that drive these blooms and develop effective strategies for their management and mitigation.

Several studies have employed various environment-resource modelling techniques to understand the distribution and proliferation of jellyfish. For instance, Canepa et al. (2014) and Gutiérrez-Estrada et al. (2021) used Generalised Additive Models (GAM) to explore environmental factors, such as wind direction and wind speed, influencing the stranding of jellyfish on western Mediterranean beaches. The same modelling technique was used by Siapatis et al. (2008) to predict the potential habitat of the invasive ctenophore *Mnemiopsis leidyi* in the Aegean Sea. Benedetti-Cecchi et al. (2015) utilized a hierarchical Bayesian analysis to model *Pelagia noctiluca* blooms along the Catalan coast. This model incorporated environmental variables such as sea surface temperature (SST), primary production, chlorophyll concentration, and geostrophic currents to predict jellyfish proliferations. Edelist et al. (2022) employed a Lagrangian particle tracking model combined with jellyfish data provided by citizen science and genetic analysis to study the dispersal patterns of *Rhopilema nomadica* in the Eastern Mediterranean Sea. Castro-Gutiérrez et al. (2022) applied an explainable artificial intelligence model based on fuzzy logic to predict jellyfish outbreaks in southern Spain, identifying wind direction and speed as key factors in the occurrence of jellyfish swarms in the studied area.

Most of these traditional approaches rely on the availability of both presence and absence data, and while these models are useful, they require high-quality and extensive coverage data, which is not always feasible in jellyfish studies. According to Brotz et al. (2012), jellyfish were often underrepresented in historical marine research due to methodological limitations and the general lack of attention in scientific surveys. Currently, despite growing interest, their targeted research is costly and requires innovative technologies (Hamel et al., 2021).

Given the scarcity of data in traditional marine studies, citizen science has emerged as a key tool for monitoring jellyfish populations, leveraging the collective efforts of the public to gather valuable data across vast marine areas (for example, Garcia-Soto et al., 2021). This collaborative approach not only democratises scientific research but also significantly extends the scope and scale of observations, capturing jellyfish population fluctuations and distribution patterns in real time. In this context, the Diputación of Málaga, in collaboration with Aula del Mar of Málaga, developed the Infomedusa app in 2013 (https://auladelmarmed.org/infomedusa/). This mobile app allows citizens to monitor the presence of jellyfish along the Andalusian coast and also functions as a forum where users can discuss other topics related to their beach experiences. Although this initiative provides valuable data, the information generated is not controlled by a structured scientific programme, which introduces bias, as users tend to report jellyfish presence more frequently than absence in an attempt to inform others of beach conditions. Nevertheless, previous studies have successfully used Infomedusa data to analyze jellyfish distribution patterns and develop predictive models (e.g. de la Fuente Roselló et al., 2024; Cantarero-Prados et al., 2024; Castro-Gutiérrez et al., 2024), demonstrating the potential of this tool for ecological research despite its inherent biases.

In this study, Maximum Entropy (MaxEnt) models were used, which are statistical models widely employed to predict the potential distribution of species based on presence data. Its name derives from "maximum entropy", a principle that suggests that, in the absence of additional information, the best prediction for a species distribution is the most uniform or the one that maximises entropy (Phillips et al., 2006).

MaxEnt has proven to be an effective tool for modeling jellyfish distribution in various marine ecology studies. For example, Bentlage et al. (2009) applied this model to infer the distribution of cubozoan jellyfish of the genus *Chirodropus* revealing habitat patterns based on specific environmental variables. Guo et al. (2023) used MaxEnt to evaluate the environmental factors determining the distribution of large jellyfish along the northern coast of China, identifying temperature and chlorophyll concentration as key variables for their proliferation. Another study, conducted by Pantiukhin et al. (2024), employed an adapted three-dimensional version of MaxEnt to model the climate-driven shift of gelatinous zooplankton species toward the Arctic, highlighting MaxEnt utility in predicting species distribution changes under future environmental scenarios. Moreover, citizen science data have also been utilized in MaxEnt models. Record et al. (2018) developed a jellyfish sighting forecasting system based on MaxEnt, integrating data collected through social networks to generate real-time maps of areas with a high probability of jellyfish encounters.

Building upon this framework, the present study aims to model the distribution of jellyfish sightings during the summer of 2019 along the Andalusian coast using the MaxEnt modelling technique and utilizing data from the Infomedusa APP. By integrating environmental variables from the Copernicus platform, we hypothesize that specific oceanographic conditions, including those occurring in the months preceding jellyfish sightings, play a crucial role in determining their spatial distribution. Thus, the main objective of this study is to identify the key factors driving jellyfish distribution and predict the areas of highest and lowest occurrence. The present study aims to provide robust, spatially explicit predictions that can inform future management strategies, enhance beach safety measures, and mitigate the socio-economic impacts of jellyfish blooms in the region.

## 2. Material and methods

### 2.1. Study area

This study was conducted along the Mediterranean coast of Andalusia, located in the south of Spain (Fig. 1). This region includes the provinces of Málaga, Granada, and Almería, stretching from the Strait of Gibraltar in the west to Pulpí, the easternmost municipality of Almería bordering the Region of Murcia. The Andalusian coast, approximately

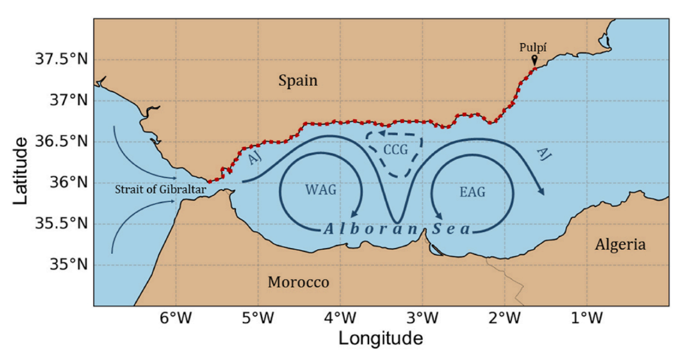


**Fig. 1.** Map of the Andalusian Mediterranean coast, highlighting the study area with a red dotted line, extending from the Strait of Gibraltar in the west to the east, with Pulpí bordering the Region of Murcia. The map shows the upper 200 m general circulation patterns of the Alboran Sea, dominated by the Atlantic Jet (AJ), which forms two major anticyclonic gyres: the Western Alboran Gyre (WAG) and the Eastern Alboran Gyre (EAG). A smaller cyclonic gyre (CCG) lies between these two systems. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

500 km long, borders the Alboran Sea, where the surface circulation is highly dynamic and characterized by strong currents, frontal zones, and mesoscale structures (Vargas-Yáñez et al., 2021). The circulation in these layers is dominated by the frontal jet of Atlantic water (Atlantic Jet), which enters the Alboran Sea in a northeasterly direction and, around 3–4°W, turns south, encircling two large anticyclonic gyres: the Western Alboran Gyre (WAG) and the Eastern Alboran Gyre (EAG). Between these two anticyclonic gyres lies a smaller cyclonic gyre. The physicochemical characteristics of these structures have been described in detail by Sánchez-Garrido and Nadal (2022). In addition to the inflow of Atlantic waters, different Mediterranean water masses, mainly Levantine Intermediate Water (characterised by its high salinity) and Western Mediterranean Deep Water (denser and colder), as well as the Tyrrhenian Dense Water, also flow from 200 m depth to the sea bottom through the Strait of Gibraltar towards the Atlantic (García-Lafuente et al., 2017; Vargas-Yáñez et al., 2021). These dynamics contribute to the sea's unique features, including its circulation patterns, marine biodiversity, and ecosystems (García-Lafuente et al., 2021).

### 2.2. Jellyfish sighting data

The data on jellyfish presence and absence were obtained through the mobile application Infomedusa, developed by the Aula del Mar in Málaga in collaboration with the Diputación Provincial de Málaga. Infomedusa is a non-driven citizen science tool that allows users to report in real-time the conditions of Andalusian beaches, including observations on the presence or absence of jellyfish. A total of 9433 comments were collected in 2019 from the southern coast of Spain, corresponding to the entire Andalusian region, spanning from 5 January to 8 December.

Each comment was analyzed to assess its relevance to jellyfish information. A value of 1 (presence) or 0 (absence) was assigned to each observation, depending on whether the user explicitly mentioned the presence or absence of jellyfish. Comments that did not provide specific information on jellyfish were classified as NA (Not Available) and excluded from further analysis. This methodology is detailed in previous studies on the processing of data from the Infomedusa app (Castro-Gutiérrez et al., 2024). The Infomedusa application allows users to report jellyfish presence without specifying the species observed. Therefore, all jellyfish sightings were considered collectively, regardless of taxonomic classification.

The temporal distribution of comments showed a higher concentration during the summer months. Due to the scarcity of jellyfish data in other months, the analysis of sightings focused on the summer period from June to September 2019. Additionally, as this study focuses on the Alboran Sea region, only observations from municipalities within this area were considered. Records from municipalities along the Atlantic-facing Andalusian coast were excluded due to the lower availability of jellyfish sightings and limitations in obtaining a spatial-temporal regular grid of environmental data from Copernicus for those areas.

The presence and absence data were organised into two separate databases. Presence observations were grouped by month and exported as individual ".csv" files, meeting the requirements of the MaxEnt software for species distribution modelling. Absence observations, although not directly used in the MaxEnt model, were retained for subsequent validation analysis.

### 2.3. Environmental data

To understand the environmental factors influencing jellyfish distribution, oceanographic and biogeochemical variables were obtained from two products of the Copernicus Marine Environment Monitoring Service (CMEMS): the Mediterranean Sea Physical Reanalysis Product (Escudier et al., 2020, 2021; Nigam et al., 2021) and the Mediterranean Sea Biogeochemistry Reanalysis (Teruzzi et al., 2021a, 2021b).

From the physical reanalysis product, variables such as sea surface temperature (°C) and sea floor potential temperature (°C) were selected. Potential temperature represents the temperature a parcel of seawater would have if brought adiabatically to sea surface pressure, accounting for the effects of pressure on temperature. Additionally, sea surface height above the geoid (m) was included, where the geoid is a surface of constant geopotential representing the mean ocean surface if the ocean were at rest. The sea surface height above geoid measures the difference between the actual sea surface height at any given time and place and that of the geoid. The ocean mixed layer thickness defined by sigma theta (m) was also considered (hereinafter 'Mixed layer depth'). This variable represents the depth where the potential density increases by 0.01 kg $m^{-3}$ compared to the density at 10 m depth, indicating subtle stratification in the upper ocean. Sea surface salinity (Practical Salinity Units, PSU) and eastward and northward seawater velocities ($m \cdot s^{-1}$) were included as well. The eastward and northward components were used to calculate the direction of marine currents in degrees, combining both to represent the general water flow.

From the biogeochemistry reanalysis product, the mass concentration of chlorophyll-a in seawater ($mg \cdot m^{-3}$) and the net primary production of biomass (mg $C \cdot m^{-3} \cdot day^{-1}$) were incorporated.

Environmental data were obtained as NetCDF files with a horizontal grid resolution of 1/24° (approximately 4–5 km) in both products. The selection of variables was based on previous studies that identified their relevance in jellyfish dynamics (e.g. Richardson et al., 2009; Canepa et al., 2014). All variables were averaged monthly. The environmental data covered the period from March to September 2019, starting before the peak of jellyfish observations to enable analysis of potential temporal lags between environmental conditions and jellyfish appearances. Each environmental variable was converted and separated into monthly ASCII files, adhering to the requirements of MaxEnt.

### 2.4. Preprocessing and exploratory analysis

To assign a precise geographical location to each comment, an external database was used to geolocate the observations according to the corresponding coastal municipality. Although a municipality may include several beaches, the comments were grouped at the municipal level to homogenize the information and facilitate spatial analysis. Geolocation was carried out by assigning the coordinates of the urban center of the municipality to each observation. Subsequently, the municipality locations were adjusted to the nearest point with available environmental data on the grids obtained from Copernicus, which allowed for effectively linking the jellyfish presence and absence data with the corresponding environmental conditions.

#### 2.4.1. Exploratory analysis of environmental data

To address possible multicollinearity among the environmental variables and reduce the dimensionality of the dataset, a Principal Component Analysis (PCA) was performed (Abdi and Williams, 2010; Forkman et al., 2019). The PCA was used to identify the optimal number of principal components necessary to adequately represent the variability of the data without losing essential information (Jolliffe, 2002).

After identifying the relevant principal components, the environmental variables with a significant contribution to these components were selected. This selection was based on the values of the loadings associated with each variable, considering significant those with absolute values greater than 0.2 in at least one of the selected principal components. This variables were identified as the most influential in the data structure and were retained for subsequent analyses.

To visualize the relationships among the selected variables and better understand their influence on the principal components, a three-dimensional plot was generated representing the loadings of the variables in the space defined by the selected principal components. This graphical representation facilitated the identification of possible groupings among the environmental variables. In order to statistically group the highly correlated variables and address multicollinearity, the k-means clustering algorithm was applied to the set of selected variables to classify them into groups based on their proximity in the principal component space, identifying clusters of variables with similar behaviors. Within each group, multicollinearity was evaluated by calculating the Variance Inflation Factor (VIF) for each variable.

The VIF quantifies how much the variance of the estimated coefficient of an explanatory variable increases due to its collinearity with the other variables in the model. It is calculated for each variable as shown in Eq. (1).

$$VIF_i = \frac{1}{1 - R_i^2} \quad \text{(Eq. 1)}$$

where $R_i^2$ is the coefficient of determination obtained by regressing the variable $X_i$ against all other explanatory variables. VIF values above 10 indicate high collinearity and suggest that the variable may be redundant (O'Brien, 2007). Among the variables of each identified cluster, the following procedure was carried out: (1) VIFs were calculated for the variables within each cluster, (2) Variables with VIFs exceeding the threshold of 10 were eliminated to reduce multicollinearity, (3) This procedure was repeated until all variables had VIFs below the threshold. In situations where, after all possible iterations of VIF calculation, two variables with mutual explained variance greater than 10 persisted but corresponded to different months, both variables were retained in the analysis due to their temporal relevance. This approach aligns with O'Brien (2007) recommendation to consider contextual relevance alongside multicollinearity reduction, allowing for the selection of a final set of representative and non-collinear environmental variables for the MaxEnt model.

The processing and analysis of the jellyfish information data and environmental data were carried out in Python (version 3.9.18). A flowchart summarizing the data preprocessing and steps is shown in Fig. 2.

### 2.5. MaxEnt modelling

The potential distribution of jellyfish was modeled using MaxEnt software (versión 3.4.4) (Phillips et al., 2006). An independent model was generated for each month with jellyfish observations, adjusting the environmental variables according to the specific month. For example, for June, only variables up to that month were included, without considering subsequent environmental data.

In the model configuration, the 'autofeature' option was selected, allowing MaxEnt to automatically determine the most appropriate feature functions to describe the model's response to environmental conditions (Phillips et al., 2017). The maximum number of iterations was set to 500 with a convergence threshold of 0.00001. A regularization multiplier of 1 was applied to prevent overfitting (Phillips et al., 2006). The number of background points was set to 10,000, randomly selected from the study area to represent the environmental conditions available to the species. Duplicate presence records within the same grid cell were removed to avoid spatial sampling bias.

The selected output format was 'cloglog' (complementary log-log), which offers a direct interpretation of probability of presence on a continuous scale between 0 and 1. This format is based on the Inhomogeneous Poisson Point Process (IPP) model, where presence records are modeled as points in space with an intensity $\lambda$ that varies according to environmental conditions (Phillips et al., 2017).

Under this model, the number of individuals in a cell follows a Poisson distribution with mean $\lambda$. Therefore, the probability that at least one individual is present in a cell is calculated using the formula (Eq. (2)):

$$\text{Probability of presence} = 1 - e^{-\lambda} \quad \text{(Eq. 2)}$$

where $e^{-\lambda}$ is the probability of observing zero individuals in a cell. By applying the 'cloglog' transformation, MaxEnt outputs the estimated probability of presence for each cell, which is appropriate for presence-only data. This output provides an intuitive measure of how likely it is to find jellyfish in different areas based on the modeled environmental variables.

The performance of each MaxEnt model was evaluated using the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve calculated on the training data. The ROC curve was plotted by graphing the true positive rate (sensitivity) against the false positive rate (1 - specificity) for different threshold values. An AUC of 1 indicates a perfect model, while a value of 0.5 suggests performance equivalent to random chance (Bradley, 1997). However, in MaxEnt, specificity is defined using the predicted area instead of true commission, implying that the maximum achievable AUC is less than 1 (Phillips et al., 2006).

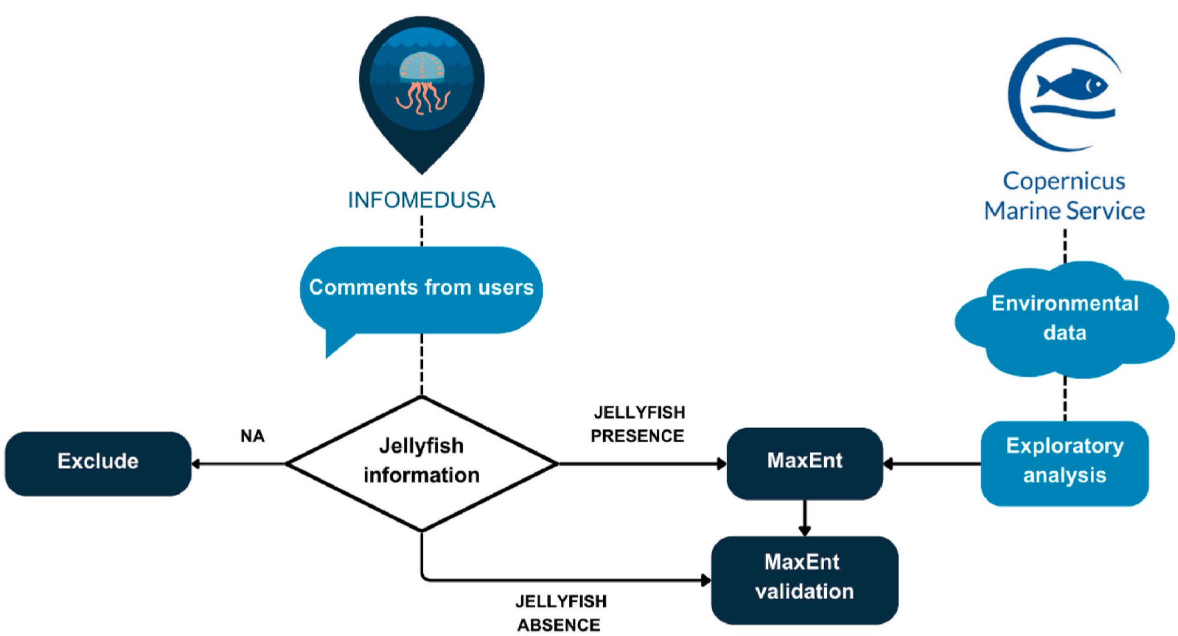


**Fig. 2.** Flow chart illustrating the process of obtaining, processing and preparing both jellyfish occurrence and environmental data for integration into the MaxEnt model.

Variable contribution analysis and permutation importance were used to estimate the influence of each variable on the model's performance. The variable contribution estimates the proportion in which each variable explains the variation in the presence data, based on the increase in regularized gain during the training process. The permutation importance evaluates the decrease in model performance when the values of a variable are randomly permuted, providing a measure of the model dependence on that variable (Phillips et al., 2006). The jackknife analysis was also activated to evaluate the relative importance of each variable in the model. Additionally, the generation of response curves was enabled to visualize the relationship between each environmental variable and the probability of jellyfish presence.

### 2.5.1. MaxEnt validation approach through absence data

To validate the predictions of the MaxEnt model and evaluate its ability to identify areas of low probability of jellyfish presence, a comparative analysis was performed using observed absence data.

A heat map representing the spatial distribution of jellyfish absences was generated using the absence observations from each corresponding month. A regular grid with the same resolution of the MaxEnt output was created for the study area. The number of absence records within each cell was counted to obtain the absence density. To smooth local variations and reduce noise, a Gaussian filter with a sigma value of 1 was applied to the absence density map, helping to generalize absence patterns and highlight areas of consistently high absence density.

To coherently compare the MaxEnt model predictions with the observed absence densities, both datasets were aligned by ensuring they shared the same spatial dimensions and valid data points. This alignment was achieved by applying masks that excluded any cells containing missing values (NaNs) in either dataset. By directly matching the grids of the MaxEnt probability maps and the absence density map, we ensured a consistent basis for comparison without the need for resampling or interpolation. Spatial masks were applied to limit the analysis to coastal zones, excluding offshore areas where jellyfish absence data were unavailable.

Thresholds were established to identify areas of low probability from the MaxEnt predictions and areas of high absence density from the observed data. For the MaxEnt predictions, cells with predicted probabilities below 0.50 were classified as low-probability areas. For the observed absences, cells with absence densities above 0.1 were considered high absence density areas. Binary masks were generated for both datasets based on these thresholds, assigning a value of 1 to cells meeting the criteria and 0 to others.

The binary masks of low-probability areas and high absence density areas were overlaid to identify cells where the predictions and observations coincided. The degree of overlap was quantified by calculating the total number of coinciding cells and the percentage of coincidence relative to the total number of cells classified as high absence density.

## 3. Results

The 9433 comments collected through the Infomedusa application in 2019 were distributed unevenly throughout the year, with a strong concentration during the summer months, coinciding with the peak of beach tourism (Table 1). The number of comments mentioning jellyfish presence or absence information was significantly higher between June and September, which aligns with the period when citizen engagement in the application is at its highest.

The dataset was filtered to include only records from municipalities within the Alboran Sea region. After this selection, the final dataset for the summer period (June–September) consisted of 1166 comments (12,4 % of the 9433 total comments) after filtering for the Alboran Sea region and the summer period (Table 1), of which 117 corresponded to jellyfish presence and 1049 to jellyfish absence. In June, 76 observations were recorded (18 presences and 58 absences), in July 508 observations (40 presences and 468 absences), in August 479 observations (47 presences and 432 absences), and in September 103 observations (12 presences and 91 absences).

**Table 1**
Monthly summary of comments submitted via the Infomedusa app throughout 2019, reporting jellyfish presence or absence along the Andalusian coast, including specific records from the Andalusian Alboran Sea coast during the summer months (June–September). Values are broken down by month, including the total number of published comments, those reporting jellyfish presence, and those reporting their absence.

| Month | Total of comments | Presence (All Andalusia) | Absence (All Andalusia) | Presence (Alboran, summer only) | Absence (Alboran, summer only) |
|---|---|---|---|---|---|
| January | 6 | 0 | 0 | – | – |
| February | 0 | 0 | 0 | – | – |
| March | 12 | 1 | 0 | – | – |
| April | 39 | 0 | 9 | – | – |
| May | 181 | 3 | 14 | – | – |
| June | 779 | 19 | 58 | 18 | 58 |
| July | 3675 | 53 | 471 | 40 | 468 |
| August | 3765 | 60 | 442 | 47 | 432 |
| September | 879 | 12 | 92 | 12 | 91 |
| October | 93 | 0 | 0 | – | – |
| November | 0 | 0 | 0 | – | – |
| December | 4 | 0 | 0 | – | – |
| **Total** | **9433** | **148** | **1086** | **117** | **1049** |

### 3.1. Environmental variables exploratory analysis

The initial Principal Component Analysis (PCA) included 56 environmental variables, considering monthly measurements of each variable from March to September. The first three principal components (PCs) were identified as the most representative, jointly explaining 66 % of the total variance in the data. The loadings of the principal components were analyzed after applying a threshold filter of 0.2. Table 2 shows the environmental variables that contributed significantly (absolute loading >0.2) to at least one of the first three principal components, along with their loading values. These variables were selected for subsequent analyses due to their relevance in explaining the observed variability.

The three-dimensional plot of the PCA loadings (Supplementary Material 1) revealed groupings of environmental variables based on their contributions to the first three principal components. To identify clusters of highly correlated variables, we applied the k-means clustering algorithm, resulting in the identification of four clusters. The first cluster grouped variables related to sea floor potential temperature from March to September, together with mass concentration of chlorophyll-a in March and April and net primary productivity in the same months. The second cluster included marine currents direction in April, mass concentration of chlorophyll-a in July and sea surface temperature in March and April. The third cluster comprised sea surface salinity in March, April and June, as well as sea surface temperature from May to September. The fourth cluster grouped the mixed layer depth in April and the sea surface height above geoid from June to September.

After calculating the Variance Inflation Factor (VIF) for the variables within each cluster, multicollinearity was identified and reduced through an iterative procedure. The results obtained after these iterations indicated that some variables had VIF values exceeding the threshold of 10.

In the first cluster, the variables sea floor potential temperature in September and surface primary productivity in April showed VIF values of 23.65. Despite exceeding the threshold, both variables were retained as they correspond to different months and could provide important temporal information from an ecological point of view. In the second cluster, the variables surface water direction in April and surface phytoplankton concentration in July had low VIF values, approximately

**Table 2**
Environmental variables that contributed significantly (absolute loading >0.2) to at least one of the first three principal components (PC). Absolute load values greater than 0.2 are marked in bold.

| Variable | Month | Loading | | |
|---|---|---|---|---|
| | | PC1 | PC2 | PC3 |
| Sea floor potential temperature | March | 0.007 | **0.240** | 0.085 |
| | April | 0.008 | **0.238** | 0.089 |
| | May | 0.008 | **0.234** | 0.095 |
| | June | 0.012 | **0.226** | 0.095 |
| | July | 0.017 | **0.213** | 0.086 |
| | August | 0.016 | **0.208** | 0.091 |
| | September | 0.020 | **0.211** | 0.091 |
| Water direction | April | 0.040 | 0.043 | **−0.250** |
| Mixed layer depth | April | −0.010 | **−0.215** | 0.078 |
| Mass concentration of chlorophyll-a | March | −0.144 | 0.089 | **0.200** |
| | April | −0.066 | 0.159 | **0.231** |
| | July | **−0.210** | 0.065 | −0.087 |
| Net primary productivity | March | −0.052 | 0.126 | **0.251** |
| | April | 0.007 | 0.174 | **0.226** |
| Salinity | March | **0.204** | −0.006 | 0.088 |
| | April | **0.207** | 0.089 | 0.063 |
| | June | **0.202** | 0.040 | −0.060 |
| Sea surface height | June | −0.083 | −0.121 | **0.211** |
| | July | −0.030 | −0.198 | **0.230** |
| | August | 0.002 | −0.137 | **0.281** |
| | September | 0.008 | −0.119 | **0.214** |
| Sea surface temperature | March | −0.136 | −0.110 | **−0.237** |
| | April | −0.064 | **−0.212** | −0.110 |
| | May | **0.209** | −0.008 | 0.057 |
| | June | **0.208** | −0.059 | 0.096 |
| | July | **0.218** | −0.019 | 0.072 |
| | August | **0.204** | −0.035 | 0.095 |
| | September | **0.210** | −0.043 | 0.104 |

1.01, indicating non collinearity. Therefore, both variables were retained. The third cluster included the variables sea surface salinity in June and sea surface temperature in July, both of which showed high VIF values of 391.28. Although these values indicate high collinearity, the variables correspond to consecutive months and may capture relevant environmental dynamics in the summer period. Consequently, it was decided to keep both variables. In the last cluster, the variables mixed layer depth in April and sea surface height above geoid in August obtained VIF values of 9.74, which is below the critical threshold.

### 3.2. MaxEnt results

To better understand the spatial distribution of jellyfish observations before modeling their potential habitat, we analyzed the density of presence records obtained through the Infomedusa application along the Andalusian Mediterranean coast. Fig. 3 presents the spatial distribution of jellyfish presence density for each month from June to September 2019. The density values represent the number of presence reports per grid cell, illustrating areas with higher and lower jellyfish sightings.

These maps reveal spatial heterogeneity in jellyfish occurrences, with some coastal areas exhibiting a higher concentration of presence records. The highest densities were observed in localized hotspots, particularly in Malaga city capital, coinciding with the peak tourist season when citizen science contributions were more frequent.

The performance of the MaxEnt models generated for each month are shown in Fig. 4. The ROC curves indicated a high ability of the models to discriminate between areas of presence and absence of jellyfish. The June model performed best, while the August model showed a slight decrease in accuracy.

#### 3.2.1. Environmental variables importance analysis

The variable contribution and permutation importance analyses in the MaxEnt models from June to September revealed that the mixed layer depth in April was consistently the most influential variable in predicting the potential presence of jellyfish in all the months studied (Table 3). This variable showed the highest percentage contributions and permutation importance values in each model.

The other environmental variables had lesser contributions and varied in their influence depending on the month. For example, net primary production in April and sea surface salinity in June had more notable contributions in the MaxEnt models for July and August. Marine current direction in April also showed some relevance, especially in August, although its contribution was lower than that of the mixed layer depth in April.

The jackknife test corroborated the importance of the mixed layer depth in April, as its use alone produced the highest training gain, and its omission resulted in the greatest decrease in gain in all models. This indicates that the mixed layer depth in April contains essential information not present in the other variables and is crucial for the predictive performance of the model.

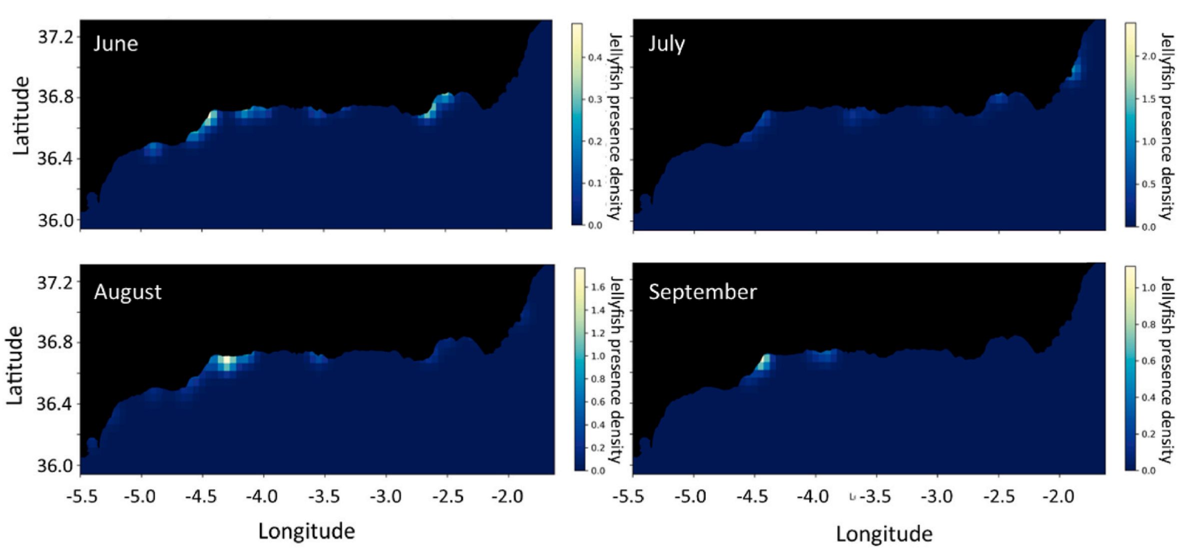


**Fig. 3.** Spatial distribution of jellyfish presence density along the Andalusian Mediterranean coast from June to September 2019, based on Infomedusa user reports. The density values represent the number of presence reports per grid cell, highlighting areas with higher or lower jellyfish sightings.

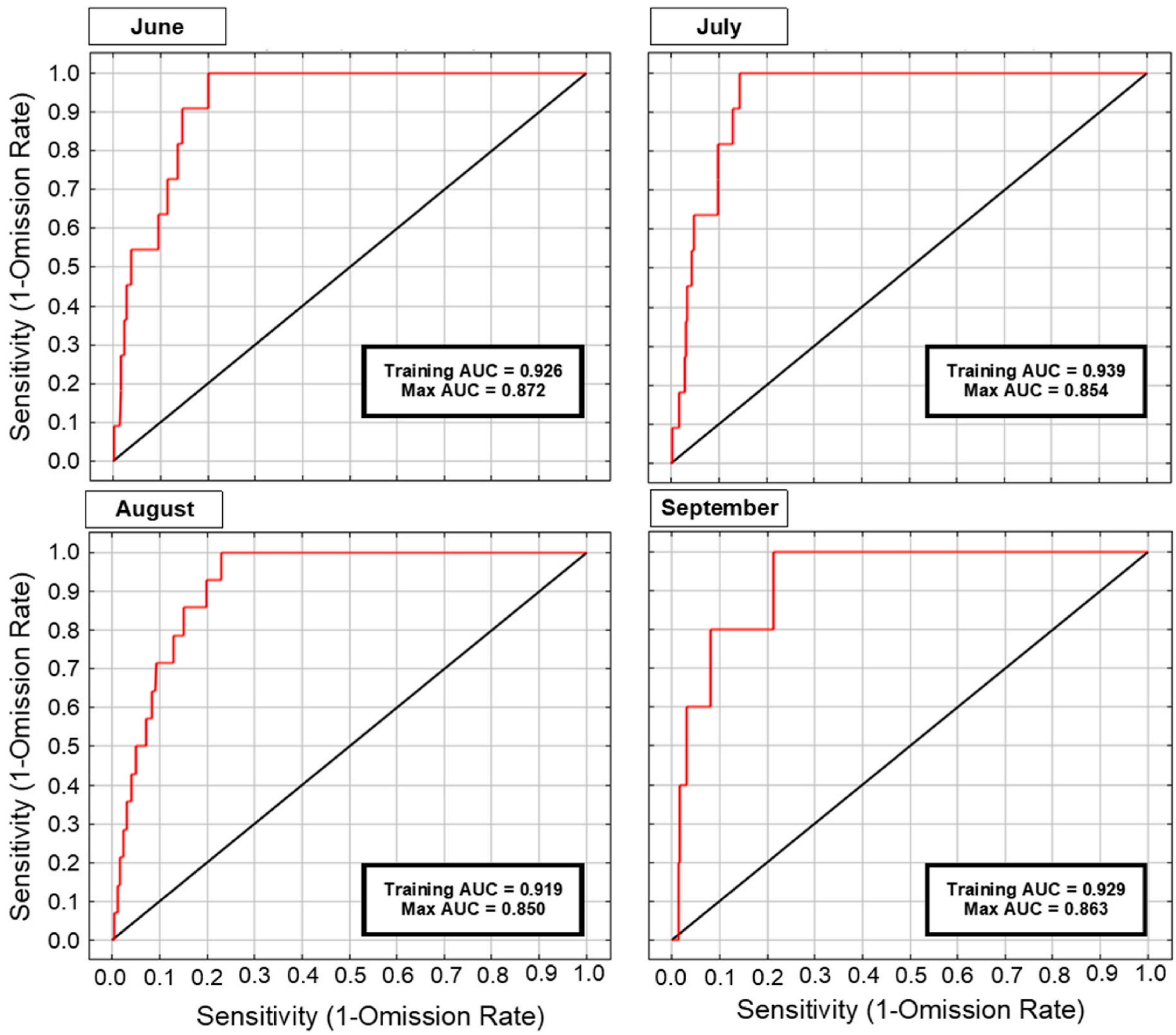


**Fig. 4.** ROC curves for MaxEnt models from June to September 2019.

**Table 3**
Percentage contribution (%C) and importance per permutation (%P) of the environmental variables in the MaxEnt models for each month studied.

| Environmental variable | MaxEnt Model | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | June | | July | | August | | September | |
| | %C | %P | %C | %P | %C | %P | %C | %P |
| Mixed layer depth (April) | 90 | 90.4 | 77.1 | 62.7 | 72.7 | 65.5 | 93.9 | 98.3 |
| Net primary productivity (April) | 7.3 | 4.6 | 0.1 | 8.8 | 12.9 | 6.4 | 6.1 | 1.7 |
| Sea surface salinity (June) | 1.5 | 3.2 | 12 | 11.1 | 2.8 | 4.9 | 0 | 0 |
| Marine currents direction (April) | 1.3 | 1.8 | 9.9 | 14.2 | 7.7 | 20.2 | 0 | 0 |
| Sea surface temperature (July) | – | – | 1 | 3.2 | 0 | 0 | 0 | 0 |
| Mass concentration of chlorophyll-a (July) | – | – | 0 | 0 | 1.7 | 3 | 0 | 0 |
| Sea surface height aborve geoid (August) | – | – | – | – | 2.1 | 0 | 0 | 0 |
| Sea floor potential temperature (September) | – | – | – | – | – | – | 0 | 0 |

The response curves of the most influential environmental variables are presented in Fig. 5. Each panel illustrates how the predicted probability of jellyfish presence changes with variations in the environmental variable across different months. In Fig. 5A, the mixed layer depth in April consistently shows a significant influence on jellyfish presence. Across all months, the probability of presence decreases with increasing mixed layer depth. This suggests that shallower mixed layers in April are associated with higher jellyfish presence later in the summer. Fig. 5B depicts the response to net primary production in April. The probability of presence increases with higher net primary production levels. This suggests that higher productivity in early spring may enhance jellyfish presence during the summer months. In Fig. 5C, the relationship with sea surface salinity in June varies between months. The strongest relationship is found in July, while in other months the effect is less pronounced. This variable did not have any effect in the MaxEnt model for September. Fig. 5D displays the response curves for marine current direction in April across the months studied. The influence of this variable is consistent across months, with higher predicted probabilities of jellyfish presence associated with water directions near 0°, corresponding to northward-moving currents.

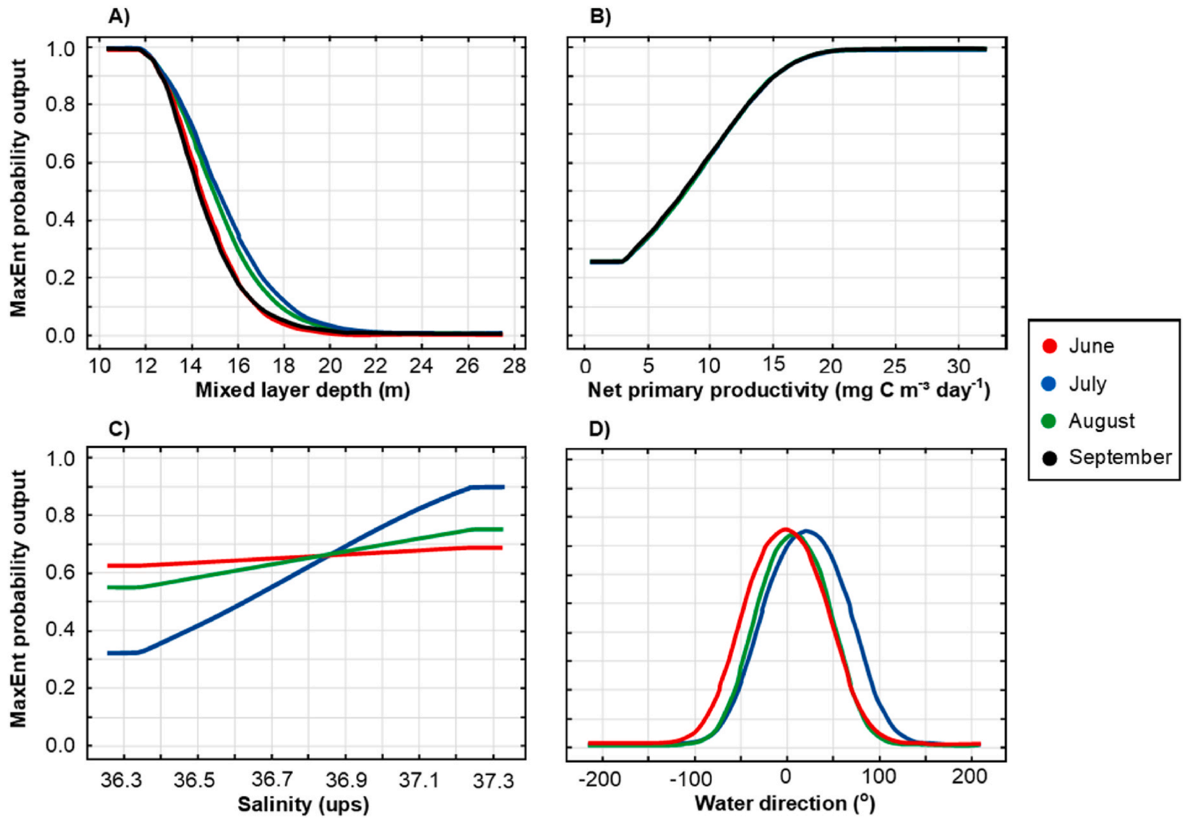


**Fig. 5.** Response curves of key environmental variables influencing the predicted probability of medusa presence from June to September 2019. Each panel displays the response of a specific variable across the four months studied. Red lines represent June, blue lines represent July, green lines represent August, and black lines represent September. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

### 3.2.2. Jellyfish probability distribution maps

The maps generated by MaxEnt (Fig. 6) showed spatial and temporal variations in the probability of jellyfish presence along the coast. The maps show a coastal gradient, in which the areas with the highest probability of jellyfish presence (red and yellow colours) are predominantly concentrated near the coastline. The blue areas represent areas with a relatively low probability, indicating a lower predisposition to jellyfish presence in these locations.

### 3.2.3. Model validation with absence data

The dataset of jellyfish absence observations collected between June and September 2019 was used to generate absence density maps. A regular grid with cells of 0.05° resolution was created over the study area, and the absence observations were counted in each grid cell. To smooth local variations and highlight spatial trends, a Gaussian filter with a sigma of 1 was applied to the density matrix, resulting in smoothed heat maps for each month.

To evaluate the agreement between the MaxEnt model predictions and the absence observations, the jellyfish presence probability maps were overlaid with the absence density maps. Thresholds were established to identify areas of low probability of presence in the MaxEnt predictions (values less than 0.50 of jellyfish presence probability) and areas of high absence density in the heat maps (values greater than 0.1 of the normalized absence density). The results of the areas identified using thresholds, along with the overlapping regions for the four months studied, are shown in Fig. 7.

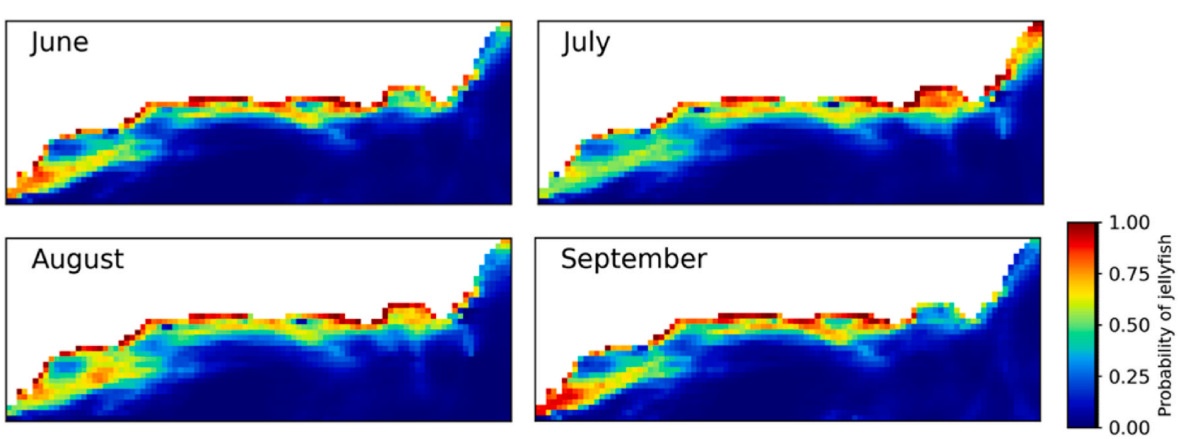


**Fig. 6.** Jellyfish occurrence probability maps predicted by MaxEnt from June to September 2019 for the mediterranean Andalusian coast.

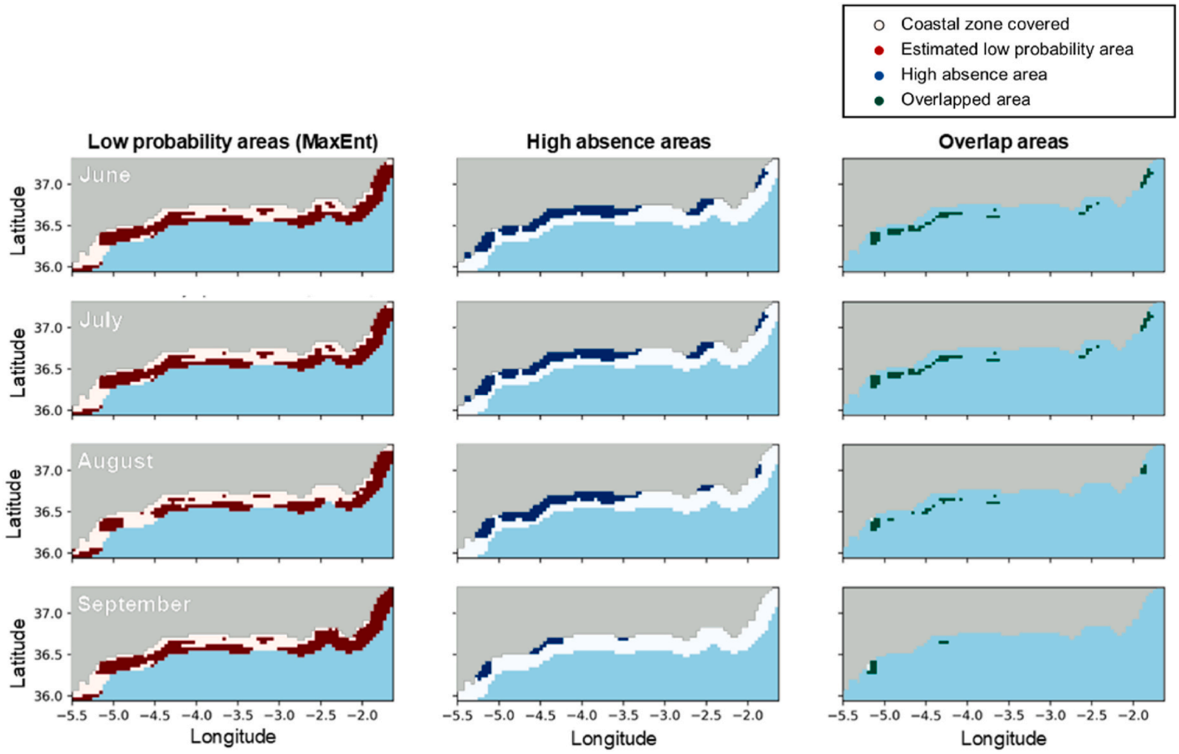


**Fig. 7.** Overlay of low probability areas predicted by MaxEnt and areas of high absence density observed for each month. The left column represents areas where the MaxEnt model predicted a low probability of jellyfish presence (red). The middle column displays areas with high observed absence density based on Infomedusa user reports (blue). The right column highlights the spatial overlap between both datasets, where MaxEnt low-probability predictions coincide with high observed absence densities (green). The study area's coastal zone is shown in white, while offshore waters are depicted in light blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The extent of coincidence between MaxEnt predictions and absence observations for each month was quantified. The total number of cells where the areas of low probability and high absence density coincided was calculated, as well as the percentage of coincidence with respect to the total areas of high absence density. The results are shown in Table 4.

The results indicate that the MaxEnt model was able to identify a moderate proportion of the areas of high jellyfish absence in the months of June, July and September, with coincidence percentages ranging from 30.77 % to 37.13 %. In August, the coincidence percentage was lower (22.58 %), suggesting a decrease in the model's ability to correctly predict jellyfish-free areas during this month.

## 4. Discussion

This study utilized MaxEnt to model the distribution of jellyfish along the Andalusian coast during the summer of 2019, using presence data collected from the Infomedusa app user reports and environmental variables obtained from the Copernicus platform. The models consistently identified the mixed layer depth in April as the most influential predictor of jellyfish presence across all months studied. Other environmental variables, such as net primary production and marine current direction in April, and sea surface salinity in June, also contributed to the models but to a lesser extent.

**Table 4**
Results of the coincidence between MaxEnt predictions and absence observations per month.

| Month | Total low probability areas | Total high absence areas | Coincidences (n) | Coincidence (%) |
|---|---|---|---|---|
| June | 301 | 96 | 33 | 34.38 |
| July | 301 | 167 | 62 | 37.13 |
| August | 249 | 155 | 35 | 22.58 |
| September | 329 | 39 | 12 | 30.77 |

The interpretation of our results is supported by the fact that *Pelagia noctiluca* is the most abundant and conspicuous jellyfish species in the Mediterranean Sea (Brotz and Pauly, 2012) and the most commonly reported species in our study area, the Andalusian Mediterranean coast (Gutiérrez-Hernández and Rubio-Gómez, 2023). Although Scyphozoa are the predominant group in the region, it is possible that some reports included other gelatinous zooplankton, such as *Cotylorhiza turbelata* and *Rhizostoma pulmo* (Rubio-Gómez and Gutiérrez-Hernández, 2020; Mghili et al., 2024). However, because the Infomedusa app does not require mandatory species identification or photo verification, it was not possible to verify the taxonomic accuracy of all observations. Previous studies and communications with the Infomedusa team indicate that the vast majority of user reports correspond to *P. noctiluca*, which is the most commonly photographed species by the Infomedusa users. Its prevalence in the dataset suggests that the environmental variables influencing jellyfish distribution primarily affect this species. Given that *P. noctiluca* is a holoplanktonic jellyfish (Lucas et al., 2012), its occurrence is strongly dependent on surface water conditions, which likely explains the strong correlation between its presence and key oceanographic variables identified in our models.

The consistent importance of the mixed layer depth in April suggests that early spring oceanographic conditions play a key role in determining jellyfish distributions in the summer months. In this study, the variable mixed layer thickness defined by sigma theta was used as a proxy measure of mixing layer depth (MLD). A shallower MLD in spring can lead to early stratification, increasing surface temperatures and favouring phytoplankton blooms (Wihsgott et al., 2019). This increase in primary productivity provides a greater food supply for the early stages of *P. noctiluca* (Ottmann et al., 2021), as well as more water column stability that could favor survival and reproduction (Molinero et al., 2005). Notably, *P. noctiluca* has been shown to reproduce throughout the year, with peak reproductive activity occurring in spring (Mghili et al., 2020), further highlighting the ecological significance of this season in shaping population dynamics. Furthermore, a shallower mixed layer can influence the distribution of small pelagic fish, such as anchovies and sardines, by concentrating them near the surface. This increased aggregation can enhance their catchability and potentially lead to higher fishing pressure (Báez et al., 2022). Since small pelagic fish prey on the early life stages of *P. noctiluca* (Ottmann et al., 2021), intensified fishing activity may reduce their populations, thereby decreasing predation on ephyrae and other juvenile stages. This reduction in predatory pressure could, in turn, promote the survival and proliferation of *P. noctiluca* medusae, highlighting a potential link between early spring oceanographic conditions, fisheries, and jellyfish bloom dynamics. This is in line with the results found for net primary productivity during the same month, which indicates higher phytoplankton biomass. An increase in phytoplankton abundance supports greater populations of zooplankton, the primary food source for the early life stages of *P. noctiluca* (Ottmann et al., 2021). As stated by Boero et al. (2008) jellyfish abundance peaks are energetically supported by both phytoplankton and herbivorous zooplankton. Thus, early spring conditions with high primary productivity can, therefore, enhance the growth and survival rates of juvenile medusae by providing food resources.

Sea surface salinity (SSS) in June was also identified as an influential variable, although its impact was less pronounced compared to MLD and primary productivity. The positive correlation observed between sea surface salinity in June and the probability of jellyfish presence in our models is consistent with previous studies (Tegaccia, 1983; Aouititen et al., 2021). Canepa et al. (2014) showed that salinity has a positive relationship with the presence of *Pelagia noctiluca*. Salinities between 35 and 38 are a consequent of low rainfall, which in turn translates as a lower influence of freshwater inputs and a higher stability of the water column. Since Ottmann et al. (2021) showed that salinity had no significant effect on the earliest stages of *P. noctiluca*, it is plausible that the effect of this variable is explained by the stability of the water column.

Marine current direction in April was another variable that contributed to the models, suggesting that ocean circulation patterns during early spring have a role in determining jellyfish distributions in the summer. Northerly currents could facilitate the transport of *P. noctiluca* individuals from spawning areas to the Andalusian coast (Gutiérrez-Estrada et al., 2021; Castro-Gutiérrez et al., 2022; 2024). In the Alboran Sea, the inflow of Atlantic water through the Strait of Gibraltar (known as the Atlantic Jet) interacts with the Western Alboran Gyre (WAG) to shape ocean circulation and, consequently, the distribution of gelatinous plankton (Bellido et al., 2020). The WAG often serves as a retention zone that gathers large numbers of jellyfish, mainly along its periphery, where food resources tend to be concentrated (Bellido et al., 2020). However, disruptions in this gyre, often caused by incoming Atlantic fronts or shifts in the strength and trajectory of the Atlantic Jet, can spawn cyclonic eddies that may carry substantial jellyfish aggregations toward the continental shelf (Sánchez-Garrido et al., 2013). Once closer to shore, local factors such as wind forcing or coastal topography can steer these aggregations into areas like the Bay of Málaga or the Gulf of Almería. Meanwhile, the Almería-Oran Front functions as an ecological boundary that generally keeps blooms contained within the Alboran Sea, preventing further dispersion into the Western Mediterranean (Pérez-Portela et al., 2019). In years with a robust and stable WAG, jellyfish may remain offshore, resulting in fewer swarms reaching the coast. Conversely, when the WAG weakens or disorganizes, the likelihood of coastal strandings and high-density blooms increases, highlighting the pivotal role of mesoscale oceanographic processes in driving distribution patterns of gelatinous species (Bellido et al., 2020). Even though the marine current variable from this study represents conditions in April, its effect can manifest later as the transported individuals grow and develop, leading to higher jellyfish abundances in the summer months. The MaxEnt model identifies correlations between environmental variables and species presence without accounting for temporal delays, so it can detect relationships where earlier oceanographic conditions influence later biological patterns (Wang et al., 2018). Therefore, marine currents in April may set the initial distribution of jellyfish populations that persist into the summer, highlighting the importance of considering temporal dynamics in ecological jellyfish models.

Although sea surface temperature (SST) was not retained as a key predictor in our MaxEnt models due to collinearity issues, its role in jellyfish population dynamics is widely supported in the literature (Aouititen et al., 2024). SST often correlates with other key environmental parameters, such as chlorophyll-a concentration and primary productivity, which influence jellyfish population dynamics by affecting food availability for early life stages (Canepa et al., 2014; Zavodnik, 1987). Several studies have demonstrated that SST can significantly influence jellyfish occurrences, with warmer conditions often promoting higher densities of medusae (Purcell, 2005; Canepa et al., 2014; Brotz and Pauly, 2012). This effect may be linked to an increase in reproductive success, as higher temperatures have been shown to accelerate egg and ephyrae development (Avian et al., 1991), leading to increased bloom potential. Furthermore, the literature indicates that the peak spawning of *P. noctiluca* occurs in spring, peaking when the temperature is around 17 °C (Augustine et al., 2014), suggesting seasonal variation in jellyfish populations. This underscores the importance of considering specific jellyfish species and their reproductive cycles when examining the effect of SST on their presence. Additionally, variations in SST can influence jellyfish transport and aggregation patterns by modifying water column stability and stratification (Graham et al., 2001; Messié and Chavez, 2017). Areas with higher SST may facilitate the retention of jellyfish near coastal zones due to reduced vertical mixing and increased prey availability. It should be clarified that, due to the availability of data mainly in the summer months, these findings may not fully reflect patterns of jellyfish occurrence in other seasons, nor may they apply to jellyfish species other than *P. noctiluca*.

Wind forcing, while not included in our models, is also an environmental factor widely recognized as a key driver in jellyfish transport and coastal strandings (Long et al., 2024), specially in the Costa del Sol study area (Castro-Gutiérrez et al., 2022). Onshore winds tend to promote jellyfish beaching events in the eastern Costa del Sol, while parallel winds to the coast promote this events in the western Costa del Sol. Several studies have demonstrated that wind patterns play a crucial role in jellyfish beaching events not only along the Andalusian Mediterranean coast but also on the southern shores of the Alboran Sea (Mghili et al., 2020a, 2020b, Mghili et al., 2020a, 2020b).

Additionally, wind-driven mixing is a key process controlling vertical stratification, nutrient availability, and primary production (Bindoff et al., 2019). While this study focused on large-scale environmental drivers rather than short-term transport mechanisms, incorporating wind-related variables in future analyses could improve the predictive accuracy of jellyfish occurrence models, particularly for short-term forecasting of beaching events.

According to Olivero et al. (2016), Maxent models tend to overfit and require higher spatial resolution. However, in our study case the spatial resolution was limited, and the use of MaxEnt modeling allowed for the effective utilization of presence-only data from the Infomedusa app. This approach eludes the limitations associated with the lack of absence data in jellyfish studies. MaxEnt ability to handle complex relationships between environmental variables and species occurrences makes it well-suited for modeling jellyfish distributions (Bentlage et al., 2009; Record et al., 2018; Guo et al., 2023; Pantiukhin et al., 2024).

### *4.1. Implications for management and mitigation*

Evidence suggests that certain blooms of jellyfish species, notably *Pelagia noctiluca*, are increasing in the Mediterranean Sea (Brotz and

Pauly, 2012). This underscores the need for proactive management strategies that address jellyfish blooms through a comprehensive understanding of their causes (Boero, 2013). Immediate local measures, such as removing jellyfish from recreational waters and installing anti-jellyfish nets, help reduce risks to public health and minimize economic impacts on tourism (Piraino et al., 2016; Macías et al., 2021). According to Ruiz-Frau (2023), such initiatives in the western Mediterranean can reduce by up to 83 % the percentage of tourists deterred by jellyfish presence, mitigating economic impacts on coastal communities. Cantarero-Prados et al. (2023) highlight that the beaches of Málaga, Marbella, and Torrox are among the most impacted by jellyfish blooms, resulting in decreased tourist activity and significant economic losses. Similar events have occurred in other regions, such as the Mar Menor, where massive outbreaks of *Cotylorhiza tuberculata* required the removal of thousands of tons of jellyfish to protect tourism. The Costa del Sol has experienced severe jellyfish events, with *Pelagia noctiluca* outbreaks in 2012 leading to beach closures and affecting the summer season (Ghermandi et al., 2015). On the Moroccan coasts, numerous cases of *P. noctiluca* stings affecting tourists and residents have been documented, with a considerable percentage of those affected requiring medical assistance (Mghili et al., 2020c). Furthermore, jellyfish blooms have caused considerable economic losses to local fisheries, not only through reduced catches due to interaction with nets, but also through the additional time and costs involved in repairing damaged fishing gear (Mghili et al., 2022). These effects reinforce the urgency of implementing monitoring and mitigation strategies that integrate collaboration between the tourism, fisheries and public administration sectors to minimize the impacts of these events in the Alboran sea. Public awareness initiatives, including warning flags indicating jellyfish presence (Bordehore et al., 2016), and citizen science programs that facilitate real-time reporting (Marambio et al., 2021), have also proven effective.

However, these interventions do not tackle the underlying factors driving jellyfish proliferations. Long-term management requires an ecosystem-based approach that integrates continuous monitoring and research to understand ecological dynamics (Richardson et al., 2009). Collaborative efforts among stakeholders (government agencies, the tourism sector, fisheries, and the public) are essential for implementing effective measures tailored to regional conditions (Macías et al., 2021). Adopting a combination of immediate and long-term strategies is crucial. Preventive measures focusing on early detection, coordinated responses, and sustained monitoring can help mitigate the impacts of jellyfish blooms and contribute to better marine resource management (Richardson et al., 2009).

Citizen science data significantly expanded the spatial and temporal coverage of jellyfish observations (Aouititen et al., 2024). The Infomedusa app engaged the public in data collection, resulting in a rich dataset that might not have been feasible through traditional scientific surveys. This collaborative approach not only provided valuable data but also increased public awareness of jellyfish issues. By incorporating environmental variables from the Copernicus platform, the study benefited from high-resolution data. This integration enhanced the accuracy of the models and allowed for a more detailed understanding of the environmental factors influencing jellyfish distribution.

### *4.2. Limitations of the study*

While citizen science data offer many advantages, they also introduce potential biases. Users may preferentially report jellyfish sightings over absences, leading to an overrepresentation of presence data. Additionally, reports may be concentrated in easily accessible or popular beaches, resulting in spatial bias.

While the use of citizen science data from the Infomedusa app provided valuable insights into jellyfish distribution along the Andalusian coast, there are inherent limitations associated with this data source. In the version of Infomedusa utilized during our study, users interacted with the app in a manner similar to a forum. Although the app was intended to record jellyfish observations, users were not required to input specific information about jellyfish presence or absence. Instead, they could post comments freely, resulting in unstructured data that varied in content and detail. This format needed the manual processing of each comment to extract relevant information about jellyfish sightings. The unstructured nature of the data introduced due to uneven reporting efforts. Moreover, because Infomedusa does not record personal user identifiers, we were unable to filter or exclude multiple, potentially duplicate comments from a single user, adding uncertainty to the dataset.

Another important limitation of this study is the temporal availability of data. Although long-term time series can improve the robustness of jellyfish species distribution models by capturing interannual variability (Rosa et al., 2013; Condon et al., 2012; Sanz-Martín et al., 2016; Fernández-Alías et al., 2024), the Infomedusa application is predominantly used during the summer months. As a result, we lack sufficient data outside this period to perform a robust multi-annual analysis. The current dataset only allows for a seasonal assessment (June–September 2019), limiting our ability to analyze potential year-to-year changes in jellyfish presence. Nevertheless, other studies have shown that the monthly scale is widely accepted for modelling jellyfish distribution using MaxEnt models (e.g. Record et al., 2018; Guo et al., 2023).

Since our study, the Aula del Mar de Málaga (now refunded as Fundación Aula del Mar Mediterráneo) has released an updated version of the app, Infomedusa 2.0 (https://auladelmarmed.org/infomedusa/), which addresses these limitations. A key enhancement in the new version is the implementation of a structured data entry system. When users report on beach conditions, they are now prompted to provide information about jellyfish presence or absence. This standardization facilitates more consistent and accurate data collection, reducing the need for manual data processing and minimizing potential biases associated with unstructured input. Additionally, the structured data entry system opens new opportunities for broader participation from key stakeholders, including fishers, tourism operators, and local authorities, who can contribute valuable information on jellyfish occurrences.

Efforts are underway to encourage year-round use of the Infomedusa app, which could provide a more continuous dataset in the future. Expanding the temporal coverage of citizen science data will enable future studies to assess interannual trends and validate the reliability of MaxEnt models over longer timeframes. Future studies leveraging data from Infomedusa 2.0 are likely to benefit from more comprehensive and precise datasets, enhancing model accuracy and providing deeper insights into the factors influencing jellyfish distributions.

## 5. Conclusions

This study demonstrates that early spring environmental conditions, particularly the mixed layer depth in April, are key predictors of jellyfish presence along the Andalusian coast during the summer months, suggesting that early stratification processes play a fundamental role driving jellyfish presence during the summer. Other relevant variables included net primary productivity in April, which likely reflects food availability for early life stages, and marine current direction in April, which may influence the transport of jellyfish populations to the study area. Additionally, sea surface salinity in June showed a positive relationship with jellyfish presence, potentially linked to water column stability. Sea surface temperature and sea surface height above the geoid were also considered in the models but showed lower contributions, likely due to collinearity with other variables. The use of MaxEnt models with citizen science data proved effective in predicting jellyfish distributions without the need for absence data. These findings contribute to a better understanding of the factors driving jellyfish blooms and have practical implications for managing their socio-economic impacts.

The identification of early spring environmental conditions as predictors of summer jellyfish presence offers new insights into the temporal dynamics of *P. noctiluca* populations. By identifying critical environmental predictors and leveraging innovative data sources, this research offers valuable insights for coastal management and highlights the potential of combining advanced modeling techniques with citizen science in marine ecology. Continued efforts in data collection, model development, and collaborative approaches will enhance our ability to predict and mitigate the effects of jellyfish blooms in the future. Establishing long-term monitoring programs would allow for the assessment of interannual variability and trends in jellyfish populations. Expanding the geographic scope to include other regions of the Mediterranean could facilitate comparative studies and enhance regional management strategies.

## CRediT authorship contribution statement

**Jairo Castro-Gutiérrez:** Writing – original draft, Visualization, Validation, Software, Investigation, Formal analysis, Data curation. **Juan Carlos Gutiérrez-Estrada:** Writing – review & editing, Validation, Supervision, Resources, Investigation, Conceptualization. **Juan Jesús Bellido:** Writing – review & editing, Investigation. **José Carlos Báez:** Writing – review & editing, Supervision, Resources, Conceptualization.

## Data availability statement

The data supporting the findings of this study are openly available in Zenodo (Souviron-Priego et al., 2024).

## 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.

## Acknowledgements

The authors would like to express their sincere gratitude to the team at the Fundación Aula del Mar Mediterráneo for their continuous support throughout this research. We also extend our thanks to the technical team behind the Infomedusa app for their dedication to improving data collection tools. We would like to acknowledge all Infomedusa users who contributed their feedback and observations, enriching the dataset and making this study possible. Finally, we sincerely thank the anonymous reviewers for their valuable comments and constructive suggestions, which have significantly contributed to improving the clarity and robustness of this manuscript. Funding for open access charge: Universidad de Huelva / CBUA.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2025.107694.

## References

Abdi, H., Williams, L.J., 2010. Principal component analysis. Wiley interdisciplinary reviews: Comput. Stat. 2 (4), 433–459.

Aouititen, M., Mrhraoui, A.R.M., Luan, X., 2021. Causes of outbreak in M'diq beach, *Pelagia noctiluca* northwest Moroccan mediterranean coastline. Indian J. Ecol. 48 (2), 519–523.

Aouititen, M., Ravibhanu, A., Ang, S.C., et al., 2024. New records of two jellyfish species Rhizostoma luteum (Quoy and Gaimard 1827) and Cotylorhiza tuberculata (Macri 1778) in the Moroccan northwest Mediterranean coast. Discov Life 54, 5.

Augustine, S., Rosa, S., Kooijman, S.A., Carlotti, F., Poggiale, J.C., 2014. Modeling the eco-physiology of the purple mauve stinger, *Pelagia noctiluca* using Dynamic Energy Budget theory. J. Sea Res. 94, 52–64.

Avian, M., Rottini Sandrini, L., Stravisi, F., 1991. The effect of seawater temperature on the swimming activity of *Pelagia noctiluca* (Forsskål). Ital. J. Zool. 58 (2), 135–143.

Báez, J.C., Pennino, M.G., Albo-Puigserver, M., Coll, M., Giraldez, A., Bellido, J.M., 2022. Effects of environmental conditions and jellyfish blooms on small pelagic fish and fisheries from the Western Mediterranean Sea. Estuar. Coast Shelf Sci. 264, 107699.

Bellido, J.J., Baez, J.C., Souviron-Priego, L., Ferri-Yanez, F., Salas, C., López, J.A., Real, R., 2020. Atmospheric indices allow anticipating the incidence of jellyfish coastal swarms. Mediterr. Mar. Sci. 21 (2), 289–297.

Bentlage, B., Peterson, A.T., Cartwright, P., 2009. Inferring distributions of chirodropid box-jellyfishes (Cnidaria: cubozoa) in geographic and ecological space using ecological niche modeling. Mar. Ecol. Prog. Ser. 384, 121–133.

Bergamasco, A., Cucco, A., Guglielmo, L., Minutoli, R., Quattrocchi, G., Guglielmo, R., Palumbo, F., Pansera, M., Zagami, G., Vodopivec, M., Malej, A., Granata, A., 2022. Observing and modeling long-term persistence of *P. noctiluca* in coupled complementary marine systems (Southern Tyrrhenian Sea and Messina Strait). Sci. Rep. 12 (1), 14905. https://doi.org/10.1038/s41598-022-18832-2.

Bernier, E.T., Sánchez, R.R., Díaz, B.R., 2014. La crisis económica en el sector turístico. Un análisis de sus efectos en la Costa del Sol. Revista de análisis turístico (18), 11–18.

Bindoff, N.L., Cheung, W.W.L., Kairo, J.G., Arístegui, J., Guinder, V.A., Hallberg, R., et al., 2019. Changing Ocean, marine ecosystems, and dependent communities. In: Pörtner, H.-O., Roberts, D.C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegría, A., Nicolai, M., Okem, A., Petzold, J., Rama, B., Weyer, N.M. (Eds.), IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Boero, F., 2013. Review of jellyfish blooms in the mediterranean and black sea. General Fisheries Commission for the Mediterranean. Studies and Reviews 92, I.

Boero, F., Bouillon, J., Gravili, C., Miglietta, M.P., Parsons, T., Piraino, S., 2008. Gelatinous plankton: irregularities rule the world (sometimes). Mar. Ecol. Prog. Ser. 356, 299–310.

Bordehore, C., Alonso, C., Sánchez-Fernández, L., Canepa, A., Acevedo, M., Nogué, S., Fuentes, V.L., 2016. Lifeguard assistance at Spanish Mediterranean beaches: jellyfish prevail and proposals for improving risk management. Ocean Coast Manag. 131, 45–52.

Bradley, A.P., 1997. The use of the area under the ROC curve in the evaluation of machine learning algorithms. Pattern Recogn. 30 (7), 1145–1159.

Brotz, L., Pauly, D., 2012. Jellyfish populations in the Mediterranean Sea. Acta Adriat. 53 (2), 213–232.

Canepa, A., Fuentes, V., Sabates, A., Piraino, S., Boero, F., Gili, J.M., 2014. *Pelagia noctiluca* in the Mediterranean Sea. In: Pitt, K.A., Lucas, C.H. (Eds.), Jellyfish Blooms. Springer, Dordrecht, Netherlands, pp. 237–266.

Cantarero-Prados, F.J., de la Fuente Roselló, A.L., 2024. Citizen science as a resource to define threats to bathing on beaches: the case of jellyfish in Malaga. Progress in Industrial Ecology, an International Journal 17 (1–2), 26–39.

Cantarero-Prados, F.J., de la Fuente Roselló, A., López, J.J.B., 2023. El impacto de las medusas en el uso recreativo de las playas. Un enfoque desde la perspectiva del riesgo. Cuadernos Geográficos 62 (1), 300–318.

Castro-Gutiérrez, J., Gutiérrez-Estrada, J.C., Aroba, J., Pulido-Calvo, I., Peregrín, A., Báez, J.C., Bellido, J.C., Souviron-Priego, L., 2022. Estimation of jellyfish abundance in the south-eastern Spanish coastline by using an explainable artificial intelligence model based on fuzzy logic. Estuar. Coast Shelf Sci. 277, 108062.

Castro-Gutiérrez, J., Gutiérrez-Estrada, J.C., Báez, J.C., 2024. Using artificial neural networks and citizen science data to assess jellyfish presence along coastal areas. J. Appl. Ecol. 61 (9), 2244–2257.

Condon, R.H., Graham, W.M., Duarte, C.M., Pitt, K.A., Lucas, C.H., Haddock, S.H., Sutherland, K.R., Robinson, K.L., Dawson, M.N., Decker, M.B., Mills, C.E., Purcell, J. E., Malej, A., Mianzan, H., Uye, S.-I., Gelcich, S., Madin, L.P., 2012. Questioning the rise of gelatinous zooplankton in the world's oceans. Bioscience 62 (2), 160–169.

de la Fuente Roselló, A., Perles Roselló, M.J., Cantarero Prados, F.J., 2024. A Predictive Analysis of Beach Susceptibility to Jellyfish Arrivals in Costa del Sol. J. Mar. Sci. Eng. 12 (12), 2316.

Doyle, T.K., Hays, G.C., Harrod, C., Houghton, J.D.R., 2014. Ecological and societal benefits of jellyfish. In: Pitt, K.A., Lucas, C.H. (Eds.), Jellyfish Blooms. Springer, Dordrecht, Netherlands, pp. 105–127. https://doi.org/10.1007/978-94-007-7015-7_5.

Escudier, R., Clementi, E., Cipollone, A., Pistoia, J., Drudi, M., Grandi, A., Lyubartsev, V., Lecci, R., Aydogdu, A., Delrosso, D., Omar, M., Masina, S., Coppini, G., Pinardi, N., 2021. A high resolution reanalysis for the Mediterranean Sea. Front. Earth Sci. 9, 702285.

Escudier, R., Clementi, E., Omar, M., Cipollone, A., Pistoia, J., Aydogdu, A., Drudi, M., Grandi, A., Lyubartsev, V., Lecci, R., Cretí, S., Masina, S., Coppini, G., Pinardi, N., 2020. Mediterranean Sea physical reanalysis (CMEMS MED-currents) (version 1). Copernicus Monitoring Environment Marine Service (CMEMS). https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1 [Data set].

Fernández-Alías, A., Marcos, C., Pérez-Ruzafa, A., 2024. The unpredictability of scyphozoan jellyfish blooms. Front. Mar. Sci. 11, 1349956.

Forkman, J., Josse, J., Piepho, H.P., 2019. Hypothesis tests for principal component analysis when variables are standardized. J. Agric. Biol. Environ. Stat. 24, 289–308.

García-Lafuente, J., Naranjo, C., Sammartino, S., Sánchez-Garrido, J.C., Delgado, J., 2017. The Mediterranean outflow in the Strait of Gibraltar and its connection with upstream conditions in the Alborán Sea. Ocean Sci. 13 (2), 195–207.

Garcia-Lafuente, J., Sánchez-Garrido, J.C., García, A., Hidalgo, M., Sammartino, S., Laiz, R., et al., 2021. Biophysical processes determining the connectivity of the Alboran Sea fish populations. In: Báez, J.C., Vázquez, J.T., Caminas, J.A., Malouli, M. (Eds.), Alboran Sea – Ecosystems and Marine Resources. Springer, Nature Switzerland AG, pp. 459–487.

Garcia-Soto, C., Seys, J.J.C., Zielinski, O., Busch, J.A., Luna, S.I., Baez, J.C., Domegan, C., Dubsky, K., Kotynska-Zielinska, I., Loubat, P., Malfatti, F., Mannaerts, G., McHugh, P., Monestiez, P., van der Meeren, G.I., Gorsky, G., 2021. Marine citizen science: current state in europe and new technological developments. Front. Mar. Sci. 8, 621472. https://doi.org/10.3389/fmars.2021.621472.
Ghermandi, A., Galil, B., Gowdy, J., Nunes, P.A., 2015. Jellyfish outbreak impacts on recreation in the Mediterranean Sea: welfare estimates from a socioeconomic pilot survey in Israel. Ecosyst. Serv. 11, 140–147.
Graham, W.M., Gelcich, S., Robinson, K.L., Duarte, C.M., Brotz, L., Purcell, J.E., Madin, L.P., Mianzan, H., Sutherland, K.R., Uye, S.-I., Pitt, K.A., Lucas, C.H., Bøgeberg, M., Brodeur, R.D., Condon, R.H., 2014. Linking human well-being and jellyfish: ecosystem services, impacts, and societal responses. Front. Ecol. Environ. 12 (9), 515–523.
Graham, W.M., Pagès, F., Hamner, W.M., 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451 (1–3), 199–212.
Guo, D., Zhang, F., Wang, P., Sun, S., 2023. Distribution patterns of large jellyfish and their effects on the Zooplankton Community in the Northern Chinese Coastal seas during the summer of 2021. Diversity 15 (6), 729.
Gutiérrez-Estrada, J.C., Pulido-Calvo, I., Peregrín, A., García-Gálvez, A., Báez, J.C., Bellido, J.J., Souviron-Priego, L., Sánchez-Laulhé, J.M., López, J.A., 2021. Integrating local environmental data and information from non-driven citizen science to estimate jellyfish abundance in Costa del Sol (southern Spain). Estuar. Coast Shelf Sci. 249, 107112.
Gutiérrez-Hernández, O., Rubio-Gómez, A., 2023. Jellyfish distribution and abundance on the southern coast of the iberian peninsula. In: De Lázaro Torres, M.L., De Miguel González, R. (Eds.), Sustainable Development Goals in Europe. Key Challenges in Geography. Springer, Cham. https://doi.org/10.1007/978-3-031-21614-5_14.
Hamel, H., Lhoumeau, S., Wahlberg, M., Javidpour, J., 2021. Using drones to measure jellyfish density in shallow estuaries. J. Mar. Sci. Eng. 9 (6), 659. https://doi.org/10.3390/jmse9060659.
Jolliffe, I.T., 2002. Choosing a subset of principal components or variables. Principal component analysis 111–149.
Long, A.P., Bastian, T., Haberlin, D., Stokes, D., Lyashevska, O., Brophy, D., et al., 2024. Regular widespread aggregations of the oceanic jellyfish *Pelagia noctiluca* in the northeast Atlantic over 11 years. Estuar. Coast Shelf Sci., 108805
Lucas, C.H., Graham, W.M., Widmer, C., 2012. Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. Adv. Mar. Biol. 63, 133–196.
Macías, D., Prieto, L., García-Gorriz, E., 2021. A model-based management tool to predict the spread of Physalia physalis in the Mediterranean Sea. Minimizing risks for coastal activities. Ocean Coast Manag. 212, 105810.
Marambio, M., Canepa, A., Lòpez, L., Gauci, A.A., Gueroun, S.K., Zampardi, S., Boero, S., Yahia, O.K.D., Yahia, M.N.D., Fuentes, V., Piraino, S., Deidun, A., 2021. Unfolding jellyfish bloom dynamics along the Mediterranean basin by transnational citizen science initiatives. Diversity 13 (6), 274.
Messié, M., Chavez, F.P., 2017. Nutrient supply, surface currents, and plankton dynamics predict zooplankton hotspots in coastal upwelling systems. Geophys. Res. Lett. 44 (17), 8979–8986.
Mghili, B.A., Analla, M., Aksissou, M., 2020a. Temporal dynamics of jellyfish *Pelagia noctiluca* stranded on the mediterranean coast of Morocco. Turk. J. Fish. Aquat. Sci. 21 (2), 87–94.
Mghili, B.A., Analla, M., Aksissou, M., 2020b. First records of the jellyfish *Physalia physalis* (Linnaeus, 1758) on the Mediterranean coast of Morocco. Cah. Biol. Mar. 61, 263–269.
Mghili, B.A., Analla, M., Aksissou, M., 2020c. Epidemiology of the cnidarian *Pelagia noctiluca* stings on Moroccan Mediterranean beaches. Trop. Doct. 1–4.
Mghili, B., Benyoub, B., Lamine, I., Aksissou, M., 2024. Biodiversity and conservation of Cnidarians along the Moroccan Mediterranean, with an updated species checklist. Regional Studies in Marine Science 74.
Mghili, B., Analla, M., Aksissou, M., 2022. Estimating the economic damage caused by jellyfish to fisheries in Morocco. Afr. J. Mar. Sci. 44 (3), 271–277.
Molinero, J.C., Ibanez, F., Nival, P., Buecher, E., Souissi, S., 2005. North Atlantic climate and northwestern Mediterranean plankton variability. Limnol. Oceanogr. 50 (4), 1213–1220.
Nigam, T., Escudier, R., Pistoia, J., Aydogdu, A., Omar, M., Clementi, E., Cipollone, A., Drudi, M., Grandi, A., Mariani, A., Lyubartsev, V., Lecci, R., Cretí, S., Masina, S., Coppini, G., Pinardi, N., 2021. Mediterranean Sea physical reanalysis INTERIM (CMEMS MED-currents, E3R1i system) (version 1). Copernicus Monitoring Environment Marine Service (CMEMS). https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1I [Data set].
O'Brien, R.M., 2007. A caution regarding rules of thumb for variance inflation factors. Qual. Quantity 41, 673–690.
Olivero, J., Toxopeus, A.G., Skidmore, A.K., Real, R., 2016. Testing the efficacy of downscaling in species distribution modelling: a comparison between MaxEnt and favourability function models. Anim. Biodivers. Conserv. 39 (1), 99–114. https://doi.org/10.32800/abc.2016.39.0099.
Ottmann, D., Álvarez-Berastegui, D., Prieto, L., Balbín, R., Alemany, F., Fiksen, Ø., Gordoa, A., Reglero, P., 2021. Abundance of *Pelagia noctiluca* early life stages in the western Mediterranean Sea scales with surface chlorophyll. Mar. Ecol. Prog. Ser. 658, 75–88.
Pantiukhin, D., Verhaegen, G., Havermans, C., 2024. Pan-Arctic distribution modeling reveals climate-change-driven poleward shifts of major gelatinous zooplankton species. Limnol. Oceanogr. 69 (6), 1316–1334.
Pérez-Portela, R., Wangensteen, O.S., Garcia-Cisneros, A., Valero-Jiménez, C., Palacín, C., Turon, X., 2019. Spatio-temporal patterns of genetic variation in Arbacia lixula, a thermophilous sea urchin in expansion in the Mediterranean. Heredity 122 (2), 244–259.
Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. Ecography 40 (7), 887–893.
Piraino, S., Deidun, A., Fuentes, V., Daly Yahia, M.N., Daly Yahia, O., Marambio, M., Canepa, A., Olariaga, A., Gueroun, S., Aissi, M., Aglieri, G., Milisenda, G., Purcell, J., 2016. Are anti-jellyfish nets a useful mitigation tool for coastal tourism? Hindsight from the MED-JELLYRISK experience. In: 5th International Jellyfish Bloom Symposium in Barcelona. May 30-June 3, 16.
Pitt, K.A., Lucas, C.H., Condon, R.H., Duarte, C.M., Stewart-Koster, B., 2018. Claims that anthropogenic stressors facilitate jellyfish blooms have been amplified beyond the available evidence: a systematic review. Front. Mar. Sci. 5, 451.
Purcell, J.E., 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. J. Mar. Biol. Assoc. U. K. 85 (3), 461–476.
Purcell, J.E., Uye, S.-I., Lo, W.T., 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar. Ecol. Prog. Ser. 350, 153–174.
Record, N.R., Tupper, B., Pershing, A.J., 2018. The jelly report: forecasting jellyfish using email and social media. Anthropocene Coasts 1 (1), 34–43.
Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol. Evol. 24 (6), 312–322. https://doi.org/10.1016/j.tree.2009.01.010.
Rosa, S., Pansera, M., Granata, A., Guglielmo, L., 2013. Interannual variability, growth, reproduction and feeding of *Pelagia noctiluca* (Cnidaria: scyphozoa) in the straits of messina (central Mediterranean Sea): linkages with temperature and diet. J. Mar. Syst. 111, 97–107.
Rubio-Gómez, A., Gutiérrez-Hernández, O., 2020. Impacto de las medusas en el litoral andaluz. Implicaciones para el turismo de Sol y Playa. Estud. Geográficos 81 (288) e038-e038.
Ruiz-Frau, A., 2023. Impacts of jellyfish presence on tourists' holiday destination choices and their willingness to pay for mitigation measures. J. Environ. Plann. Manag. 66 (10), 2107–2125.
Sanchez-Garrido, J.C., Nadal, I., 2022. The Alboran Sea circulation and its biological response: a review. Front. Mar. Sci. 9, 933390.
Sánchez-Garrido, J.C., Lafuente, J.G., Fanjul, E.Á., Sotillo, M.G., de los Santos, F.J., 2013. What does cause the collapse of the Western Alboran Gyre? Results of an operational ocean model. Prog. Oceanogr. 116, 142–153.
Sanz-Martín, M., Pitt, K.A., Condon, R.H., Lucas, C.H., Novaes de Santana, C., Duarte, C. M., 2016. Flawed citation practices facilitate the unsubstantiated perception of a global trend toward increased jellyfish blooms. Global Ecol. Biogeogr. 25 (9), 1039–1049.
Souviron-Priego, L., Bellido-López, J.J., López-Jaime, J.A., Castro-Gutiérrez, J., Gutiérrez-Estrada, J.C., Báez-Barrionuevo, J.C., 2024. Data from: using artificial neural networks and citizen science data to assess jellyfish presence along coastal areas. Zenodo. https://doi.org/10.5281/zenodo.12732089 [Data set].
Tegaccia, N., 1983. Condizioni idrologiche collegate alla presenza di *Pelagia noctiluca* in Adriatico. Nova Thalassia 84 (6), 59–64.
Teruzzi, A., Di Biagio, V., Feudale, L., Bolzon, G., Lazzari, P., Salon, S., Coidessa, G., Cossarini, G., 2021a. Mediterranean Sea biogeochemical reanalysis (CMEMS MED-biogeochemistry, MedBFM3 system) (version 1). Copernicus Monitoring Environment Marine Service (CMEMS). https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_BGC_006_008_MEDBFM3 [Data set].
Teruzzi, A., Feudale, L., Bolzon, G., Lazzari, P., Salon, S., Di Biagio, V., Coidessa, G., Cossarini, G., 2021b. Mediterranean Sea biogeochemical reanalysis INTERIM (CMEMS MED-biogeochemistry, MedBFM3i system) (version 1). Copernicus Monitoring Environment Marine Service (CMEMS). https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_BGC_006_008_MEDBFM3I [Data set].
Tugcu, C.T., 2014. Tourism and economic growth nexus revisited: a panel causality analysis for the case of the Mediterranean Region. Tour. Manag. 42, 207–212.
Vargas-Yáñez, M., García-Martínez, M.C., Moya, F., Balbín, R., López-Jurado, J.L., 2021. The oceanographic and climatic context. In: Báez, J.C., Vázquez, J.T., Caminas, J.A., Malouli, M. (Eds.), Alboran Sea – Ecosystems and Marine Resources. Springer, Nature Switzerland AG, pp. 85–109.
Wang, L., Kerr, L.A., Record, N.R., Bridger, E., Tupper, B., Mills, K.E., Armstrong, E.M., Pershing, A.J., 2018. Modeling marine pelagic fish species spatiotemporal distributions utilizing a maximum entropy approach. Fish. Oceanogr. 27 (6), 571–586.
Wihsgott, J.U., Sharples, J., Hopkins, J.E., Woodward, E.M.S., Hull, T., Greenwood, N., Sivyer, D.B., 2019. Observations of vertical mixing in autumn and its effect on the autumn phytoplankton bloom. Prog. Oceanogr. 177, 102059.
Zavodnik, D.J.M.B., 1987. Spatial aggregations of the swarming jellyfish *Pelagia noctiluca* (Scyphozoa). Mar. Biol. 94 (2), 265–269.