



## Recurrent seasonal habitat patterns of Mediterranean bottlenose dolphins revealed by long-term monitoring and validated SDMs

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### ARTICLE INFO

#### Keywords:

Species distribution modelling  
Maxent  
Environmental clustering  
Encounter rate  
Common bottlenose dolphin  
Mediterranean

### ABSTRACT

Seasonal environmental variability strongly shapes the spatial distribution of marine megafauna, particularly in semi-enclosed basins such as the Mediterranean Sea, where oceanographic conditions typically follow predictable seasonal patterns. However, resolving recurrent seasonal habitat patterns at basin scale remains challenging because long-term datasets with consistent multi-season coverage are rarely available in marine systems. Here, we analysed 15 years of standardized ferry-based surveys (2008–2024), comprising more than 635,000 km of observation effort and 1020 sightings, to characterize recurrent seasonal habitat configurations of the Mediterranean common bottlenose dolphin (*Tursiops truncatus*) across the western Mediterranean and Adriatic Seas. Using a seasonally structured climatological framework, occurrence records and environmental predictors were aggregated into multi-year climatologies. MaxEnt habitat suitability models were independently validated using external datasets and integrated with encounter rate analyses and environmental clustering to link predicted suitability, observed habitat use, and underlying oceanographic conditions.

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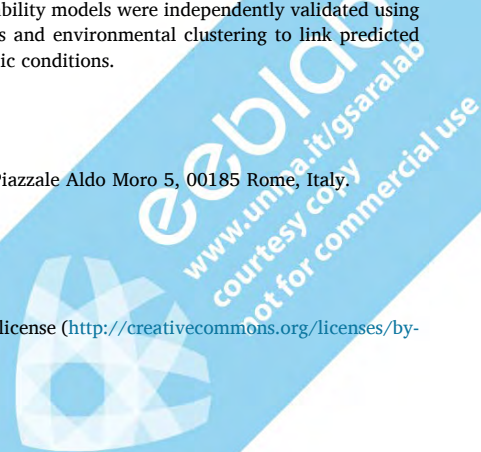
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<https://doi.org/10.1016/j.ecoinf.2026.103859>

Received 24 December 2025; Received in revised form 25 May 2026; Accepted 25 May 2026

Available online 27 May 2026

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Across all analytical components, results revealed a coherent basin-scale seasonal reconfiguration of relative habitat suitability. Winter–spring patterns were dominated by productive coastal and shelf–slope systems, whereas Summer–Autumn showed a marked offshore expansion into pelagic environments and reduced coastal use. These transitions were consistently expressed across major Mediterranean subbasins, indicating a recurrent and structured seasonal habitat cycle. By combining independent validation with complementary distribution metrics and environmental characterization, this study provides the first four-season climatological baseline for Mediterranean bottlenose dolphin seasonal habitat patterns. The framework strengthens the robustness and ecological interpretability of SDMs in seasonally variable marine systems and supports seasonally informed spatial planning and conservation strategies.

## 1. Introduction

Understanding how environmental variability shapes the spatial distribution of highly mobile marine megafauna, including cetaceans, remains a central challenge in marine ecology. This challenge is particularly pronounced in semi-enclosed and data-limited systems, where strong seasonal forcing generates marked but recurrent environmental fluctuations. In the Mediterranean Sea, limited exchange with the open ocean, shallow stratification, and intense atmospheric and riverine forcing drive pronounced seasonal shifts in physical and biogeochemical processes (d'Ortenzio and Ribera d'Alcalà, 2009; Malanotte-Rizzoli et al., 2014). These cyclical dynamics regulate primary productivity and prey availability, ultimately influencing the spatial patterns of top predators (Block et al., 2011; Macias et al., 2018; Scales et al., 2017). Importantly, in such systems seasonal oceanographic regimes typically re-emerge annually, generating recurrent habitat configurations that structure predictable cycles of trophic interactions. Capturing these patterns can be important for distinguishing persistent seasonal habitat structure from short-term variability.

Despite their ecological and management relevance, broad-scale seasonal habitat patterns of highly mobile marine species remain poorly resolved. Obtaining consistent, long-term, multi-season observations in marine environments is logistically demanding and costly, particularly for species that range across both neritic and oceanic habitats (Mannocci et al., 2018; Scales et al., 2017). As a consequence, available datasets are often spatially fragmented, temporally discontinuous, or limited to one or two seasons, constraining robust basin-scale assessments of year-round seasonal habitat patterns.

Long-term ferry-based monitoring programmes offer a rare opportunity to overcome these limitations. In the Mediterranean, the FLT Med Network (since 2007, coordinated by the Italian Institute for Environmental Protection and Research, ISPRA) and the LIFE Conceptu Maris project (2022–2024, LIFE20 NAT/IT/001371) have enabled standardized, effort-controlled surveys along fixed transects across all four seasons. Such sustained monitoring provides extended time series covering large portions of the basin and represents a critical foundation for building robust and transferable species distribution models (SDMs).

SDMs are widely used to link species occurrences with environmental predictors to estimate habitat suitability (Guisan et al., 2017), and are particularly valuable in marine systems where direct, homogeneous sampling coverage is rarely achievable, especially across offshore areas. Among modelling strategies, presence-only approaches such as MaxEnt, when combined with effort-based background correction (Barbet-Massin et al., 2012; Phillips et al., 2009), have proven effective for ferry-based datasets (Arcangeli et al., 2024). Different temporal SDM frameworks can address complementary ecological questions. Time-explicit or temporally matched approaches, in which occurrences are linked to environmental predictors corresponding to the time of observation, are particularly suited for investigating short-term variability and temporally explicit species–environment relationships (Fernandez et al., 2017, 2018). In contrast, climatological approaches based on multi-year seasonal averages emphasize recurring environmental conditions and can provide a baseline for identifying persistent spatial patterns over seasonal scales (e.g., Chandelier and Kiszka, 2026; Redfern

et al., 2017; Waggitt et al., 2020). In semi-enclosed basins characterized by strong recurrent seasonal forcing, such as the Mediterranean, this perspective can be particularly useful for describing broad-scale habitat variability.

Despite their widespread application, SDMs still face two major limitations. First, independent validation remains uncommon, particularly at large spatial and seasonal scales, limiting assessment of transferability and reliability. Second, predicted habitat suitability can be difficult to interpret when considered in isolation, as model outputs do not necessarily reflect observed habitat use intensity or the environmental regimes structuring species occurrence (Mannocci et al., 2018). Integrating SDM outputs with empirical distribution metrics, such as encounter rates (Gnone et al., 2023), and with multivariate environmental characterization (e.g., PCA and clustering; Azzellino et al., 2008) can substantially strengthen ecological interpretation.

Within this context, the common bottlenose dolphin (*Tursiops truncatus*) represents a particularly suitable case study. It is one of the most widespread marine mammals in the Mediterranean, occurring across a wide range of habitats from shallow coastal zones to offshore and island-associated waters (Bearzi et al., 2009; Cañadas et al., 2005; Gnone et al., 2023; Natoli et al., 2021). Although generally considered a coastal species, bottlenose dolphins are also recorded in offshore waters, leading to the hypothesis of distinct coastal and pelagic ecotypes (Gaspari et al., 2015), as described in the North Atlantic (Hoelzel et al., 1998; Natoli et al., 2004). However, in the Mediterranean, such differentiation has not been conclusively demonstrated and remains debated (Bellingeri et al., 2025). Bottlenose dolphins are flexible generalist predators capable of adapting to local environmental conditions (Genov et al., 2025; Giannoulaki et al., 2017; Pace et al., 2024; Pace and Pedrazzi, 2025), including exploitation of anthropogenic resources in some areas (Díaz López, 2012; Labriola et al., 2026; Pace et al., 2022a; Patti et al., 2026; Turchi et al., 2025a, 2025b). This flexibility is also reflected in their acoustic plasticity across environmental and social contexts (Díaz López, 2011; La Manna et al., 2022; Pace et al., 2024).

Mediterranean populations are geographically structured rather than migratory, comprising resident social units with relatively stable home ranges alongside more wide-ranging individuals (Azzellino et al., 2008; Bearzi et al., 2009; Mattiussi et al., 2026; Natoli et al., 2021; Pace et al., 2021). Seasonal shifts in distribution therefore primarily reflect modulation of habitat use rather than basin-scale migrations. While numerous SDMs have been developed at local or subregional scales (e.g., Cafaro et al., 2016; La Manna et al., 2020; Pace et al., 2022b; Panigada et al., 2008; Scuderi et al., 2024), basin-wide analyses remain scarce and are typically limited to one or two seasons (Cañadas et al., 2024; Virgili et al., 2024). Although recurrent hotspots have been identified in several Mediterranean regions, the basin-wide seasonal reorganization of bottlenose dolphin habitat across all four seasons remains poorly understood (Bearzi et al., 2021; Cañadas et al., 2005; Forcada et al., 2004; Gnone et al., 2011).

This study addresses this gap by providing the first basin-scale, four-season assessment of Mediterranean bottlenose dolphin recurrent seasonal habitat patterns integrating long-term standardized survey data with independently validated SDMs.

Using long-term ferry-based data, we develop a four-season

analytical framework combining encounter rate analysis, independently validated MaxEnt-based climatological SDMs, and multivariate environmental analyses (PCA and k-means clustering). This integrated approach allows us to link observed space use, predicted habitat suitability, and the main oceanographic regimes associated with dolphin presence.

Specifically, we address three questions (Q):

- (i) **Observed distribution** – Where and when has the species been recorded within the surveyed effort, and how does its distribution vary across seasons?
- (ii) **Potential distribution** or suitable habitat – How does relative habitat suitability vary across recurrent seasonal environmental conditions at basin scale, including areas not directly surveyed?
- (iii) **Environmental clustering**: Which environmental clusters are associated with dolphin presence, and how does their seasonal use vary?

By explicitly combining long-term monitoring, external validation, and complementary analytical approaches, this study provides a seasonally resolved, basin-scale baseline for characterising bottlenose dolphin seasonal habitat configurations. Beyond the case study, it contributes to improving the robustness and ecological interpretability of SDMs in dynamic marine systems and provides a foundation for seasonally informed conservation and marine spatial planning.

## 2. Materials and methods

To ensure consistency, we clarify how key terms are used in this study. *The observed distribution* refers to areas where dolphins were directly observed, as quantified here as the encounter rate (ER). *Habitat suitability or potential distribution* follows Guisan et al. (2017), i.e. the relative probability of favorable environmental conditions as predicted by Species Distribution Models (SDMs). *Environmental clusters* refers to groups of environmental conditions identified through k-means clustering of oceanographic predictors.

### 2.1. Study area and data collection

The study was carried out in the Western Mediterranean and Adriatic Seas, encompassing both coastal and offshore environments regularly crossed by commercial ferries. Data were collected between 2008 and 2024 through visual surveys conducted by trained observers on large vessels operating along approximately 30 fixed transects. Monitoring was coordinated under the FLT Med Network (since 2007, led by ISPRA) and expanded through the LIFE Conceptu Maris project (2022–2024), both exploiting commercial ferries as cost-effective, long-term observation platforms that ensure broad spatiotemporal coverage, and applying the same standardized survey protocol across all participating institutions and programs.

Surveys followed a standardized, harmonized protocol shared by all participating institutions, ensuring consistency in observer training, sighting recording procedures, and effort definition throughout the study period. Surveys were conducted in all four seasons, with a minimum number of four surveys per season to guarantee seasonal coverage and a representative level of observation effort. Each survey involved at least two observers positioned on both sides of the command bridge, scanning continuously for cetaceans. Each sighting corresponded to a dolphin group observation. For each sighting, time, GPS position, group size, behaviour, and environmental conditions (sea state, visibility, Beaufort Sea State) were recorded. Observation effort was logged as the distance travelled under effective conditions (Beaufort  $\leq 3$ , daylight).

In total, approximately 635,000 km was surveyed during 3161 surveys, with 1020 sightings of bottlenose dolphins distributed across seasons (see Table S1). The sightings were projected in the ETRS89 coordinate system (EPSG:3035) and organized for the entire period and

by season (Winter: Jan–Mar; Spring: Apr–Jun; Summer: Jul–Sep; Autumn: Oct–Dec).

### 2.2. Environmental variables

A common set of environmental predictors was used for both species distribution modelling (Q ii) and environmental clustering (Q iii), selected based on ecological relevance, basin-wide availability, and consistency with previous cetacean habitat studies (e.g., Bearzi et al., 2008b; Cafaro et al., 2016; Correia et al., 2020; Lambert et al., 2017; Maricato et al., 2022; Martino et al., 2021; Tardin et al., 2020).

- **Static variables:** bathymetry, slope, distances to: coastline, seamounts, canyons, shelf.
- **Dynamic variables:** Sea surface temperature (SST, mean and sd), chlorophyll *a* (mean and sd), salinity, sea surface height, mixed layer depth and currents. The derived metrics included the Ekman kinetic energy and thermal gradients.

Static predictors were obtained from GEBCO global bathymetric grid (GEBCO Compilation Group, 2024), EMODnet Geology (EMODnet Geology Consortium, 2025) and Blue Habitats website (<http://www.bluehabitats.org>), and distances were derived using least-cost path analysis considering land barriers. Dynamic predictors were derived from the Copernicus Marine reanalysis (2008–2022) and remote sensing products. Monthly environmental layers were first aggregated into seasonal means for each year, and subsequently averaged across years to obtain multi-year seasonal climatologies. Interannual variability was quantified as the standard deviation of SST and chlorophyll-*a*.

Environmental predictors were therefore structured to represent recurrent seasonal environmental conditions over the study period. Although dynamic environmental data were available for the period 2008–2022, while sighting data extended to 2024, the use of multi-year seasonal climatologies is consistent with the objective of describing recurrent seasonal habitat configurations rather than year-specific conditions. This slight temporal mismatch is therefore unlikely to substantially affect the interpretation of habitat associations at the seasonal climatological scale considered here.

All rasters were resampled to the EEA 5 × 5 km reference grid (ETRS-89, EPSG:3035, European Environment Agency (EEA), 2013). Multicollinearity among environmental predictors was assessed using pairwise Pearson correlation analyses, as highly correlated predictors can inflate parameter uncertainty, obscure variable importance, and reduce ecological interpretability in species distribution models (Guisan et al., 2017). Correlation coefficients were calculated on raster cell values sampled across the study area, and when two predictors were strongly correlated ( $|r| > 0.7$ ), only the variable considered more ecologically meaningful was retained. A complete list of variables, sources, and resolutions is provided in Table 1.

Raster processing, temporal aggregation, and derivation of secondary variables (e.g., thermal gradients and Ekman kinetic energy) were performed in QGIS and R (packages terra and raster). Multicollinearity among predictors was assessed in R using the usdm package, applying the vifcor function (correlation threshold  $|r| > 0.7$ ) and vifstep function (Variance Inflation Factor threshold VIF > 10) to identify and remove highly correlated variables.

### 2.3. Encounter rate (Q i)

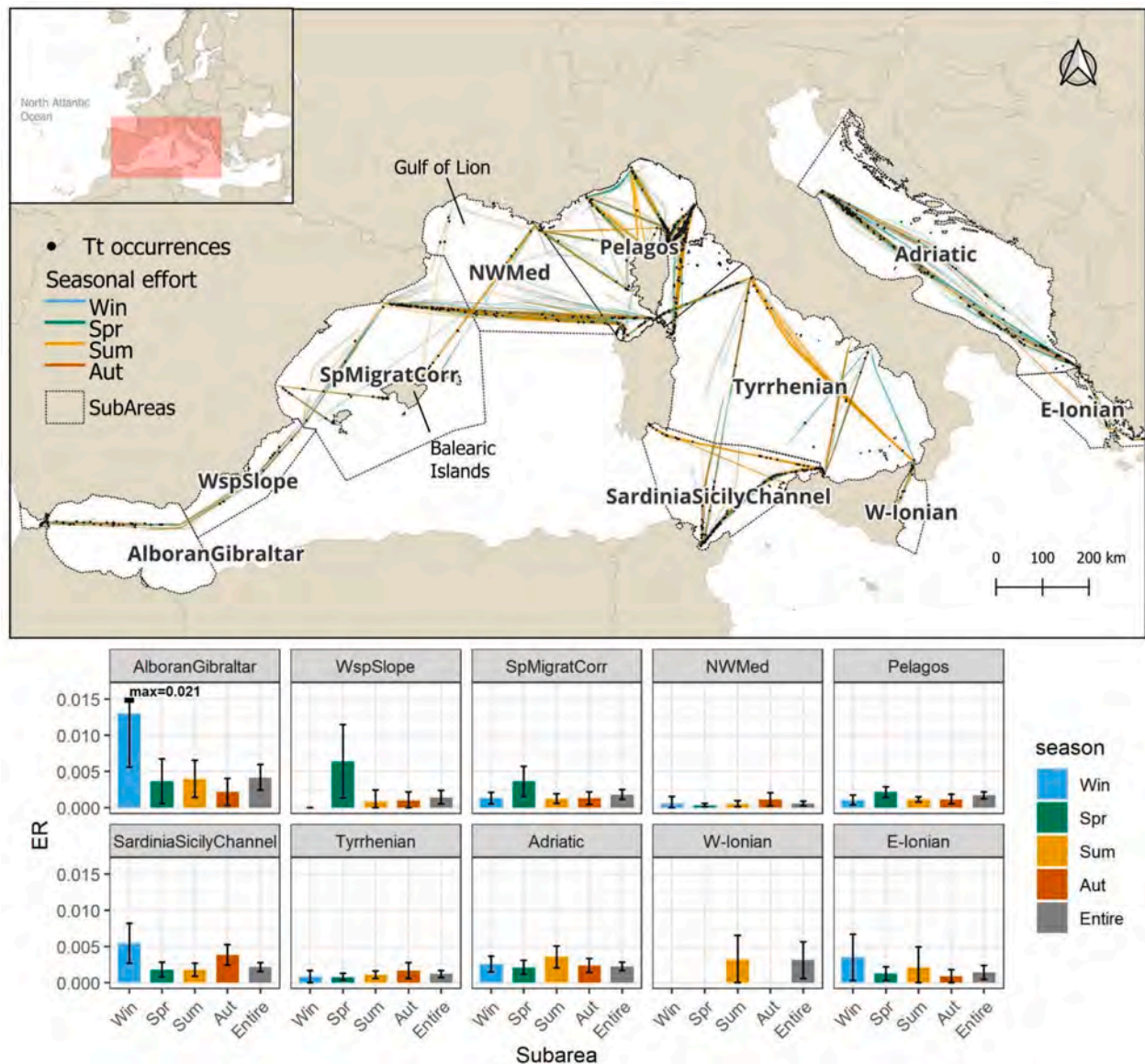
To address the first research question (Q i), Encounter rate (ER) was used as a proxy for the observed distribution. Species occurrence data were projected onto a 5 × 5 km grid (ETRS-89, EPSG:3035). This spatial resolution, consistent with that used for environmental predictors and modelling, was selected based on multiple considerations. First, it matches the native resolution of basin-scale environmental predictors derived from reanalysis and remote sensing products ( $\approx 4$ –5 km).

**Table 1**

Complete list of environmental variables used, with source, temporal and spatial resolution, and derivation method where applicable. Zonal (uo) and meridional (vo) surface current components were used solely to derive Ekman kinetic energy (EKE) and were not included as independent predictors in the final models.

Type	Variable(s)	unit	Temp res	Spat res	Original source
Physical	Surface temperature (thetao)	[degrees_C]	monthly	4.2 km	MEDSEA_MULTITYEAR_PHY_006_004
	Surface temperature dev. (sd_thetao)	[degrees_C]	-	-	Measured across years
	Surface thermal gradient (deltaT)	[degrees_C]	monthly	4.2 km	Derived from temperature
Chemical	Salinity (so)	[PSU]	monthly	4.2 km	MEDSEA_MULTITYEAR_PHY_006_004
	Surface chlorophyll-a (chl-a)	[mg m <sup>-3</sup> ]	monthly	4.2 km	MEDSEA_MULTITYEAR_BGC_006_008
	Surface chlorophyll-a dev. (sd_chl-a)	[mg m <sup>-3</sup> ]	-	-	Measured across years
Hydrodynamic	Surface zonal current speed (uo)	[m/s]	monthly	4.2 km	MEDSEA_MULTITYEAR_PHY_006_004
	Surface meridional current speed (vo)	[m/s]	monthly	4.2 km	MEDSEA_MULTITYEAR_PHY_006_004
	Surface Ekman kinetic energy (EKE)	[m <sup>2</sup> s <sup>-2</sup> ]	monthly	4.2 km	Derived (EKE = 0.5*(U <sup>2</sup> + V <sup>2</sup> ))
	Mixed layer depth (mldst)	[m]	monthly	4.2 km	MEDSEA_MULTITYEAR_PHY_006_004
	Sea surface height (zos)	[m]	monthly	4.2 km	MEDSEA_MULTITYEAR_PHY_006_004
Topographic	Distance to seamount (dist_seamount)	[m]	-	5 km	Derived from EMODNET Geology
	Distance to canyon (dist_canyon)	[m]	-	5 km	Derived from <a href="https://bluehabitats.org">bluehabitats.org</a>
	Depth (depth)	[m]	-	15 arcsec	<a href="https://gebcoscientists.org/">GEBCO Compilation Group, 2024</a>
	Slope (slope)	[°]	-	15 arcsec	Derived from GEBCO 2024
Geographic	Distance to coastline (dist_coast)	[m]	-	15 arcsec	Derived from GEBCO 2024

Second, it corresponds to the EEA 5 × 5 reference grid, widely used in European environmental assessment, thereby facilitating spatial



**Fig. 1.** Top: Map of bottlenose dolphin occurrences used for the analyses. Colored lines represent seasonal survey effort. Bottom: Bar plots showing encounter rate (ER) by subarea and season (mean ± 95% CI). The y-axis is truncated at 0.015 in all panels to facilitate visual comparison among subareas.

interoperability. Third, previous Mediterranean marine habitat studies have adopted similar resolutions for large-scale distribution analyses (e.g., Arcangeli et al., 2017; Mannocci et al., 2018; Scales et al., 2017).

ER was calculated in R by intersecting on-effort tracklines with the grid cells (*sf* package) and converting intersected segment lengths to kilometres. ER was defined as the number of sightings per kilometre of on-effort transect within each cell, comparable to the SPUE index used in other ferry-based monitoring studies (e.g., Arcangeli et al., 2021; Zampollo et al., 2022) or ER used in Gnone et al., 2023. ER spatial layers were produced for the entire study period and separately for each season.

A minimum threshold of 10 km of survey effort per cell was applied to ensure robustness, as ER variability stabilizes beyond this level, reducing the influence of stochastic detections in sparsely sampled cells. To compare relative use at broader ecological scales, ER values were aggregated across ten subregions (Alboran–Gibraltar, Western Spanish Slope, Spanish Migratory Corridor, North-Western Mediterranean, Pelagos Sanctuary, Sardinia and Sicily Channels, Tyrrhenian Sea, Adriatic Sea, Western Ionian, and Eastern Ionian) following Arcangeli et al. (2025). Seasons with fewer than five surveys for each subregion (e.g., Western Ionian; Fig. 1) were excluded to avoid unstable estimates driven by limited sampling effort.

For visualization purposes only, seasonal ER maps were additionally smoothed using kernel density estimation (KDE) in QGIS (v3.38.1; 50 km search radius, 500 m output resolution).

#### 2.4. Species distribution models (Q ii)

To address the second research question (Q ii), SDMs were developed using MaxEnt v3.4.4 (Phillips et al., 2006), widely applied to ferry-based cetacean datasets and shown to provide robust and stable predictions (Arcangeli et al., 2024, 2025).

To correct for spatial sampling bias, effort-based bias files were generated in R by intersecting on-effort tracklines with the EEA 5 × 5 km grid and constraining background sampling to surveyed cells (km > 0). Surveyed cells were assigned a value of 1 and unsurveyed cells set to NoData. Bias layers were produced for the full study period and separately for each season.

Models were fitted for the entire period (2008–2024) and for each season using bootstrap replication (100 runs) with a 70/30 training–testing split, a maximum of 5000 iterations, and 10,000 background points. Logistic output was used and interpreted as relative habitat suitability rather than absolute probability of occurrence. Duplicate presences within the same grid cell were removed to reduce spatial pseudo-replication. Default feature classes (linear, quadratic, hinge, product, and threshold) and the regularization multiplier (RM = 1) were retained to ensure comparability among seasonal models. Parameter tuning was explored in preliminary runs; however, default settings produced stable and ecologically interpretable models and were therefore maintained, consistent with previous studies conducted within the same monitoring framework (Arcangeli et al., 2023). Model reporting follows the transparency guidelines proposed by Zurell et al. (2020).

Model performance was assessed using AUC from bootstrap cross-validation, with values >0.7 considered indicative of acceptable discrimination ability (Swets, 1988). Final habitat suitability maps were obtained by averaging replicate predictions, and uncertainty was quantified as the standard deviation across runs.

Variable importance was evaluated using percent contribution, permutation importance, and jackknife tests. To limit extrapolation, clamping and fade-by-clamping were enabled. Environmental novelty was assessed using both Multivariate Environmental Similarity Surface (MESS) and Mobility-Oriented Parity (MOP) analyses. MOP was implemented in R using the *kuenm* package (Cobos et al., 2019), comparing environmental conditions between calibration (G) and projection (M) regions with 10% trimming of calibration extremes (percent = 10); areas of strict extrapolation were identified as MOP = 0. Raster handling was

performed using the *terra* package.

Core areas were defined by converting continuous suitability maps into binary predictions using the maximum test sensitivity plus specificity threshold, following Arcangeli et al. (2023), and represent areas of highest predicted suitability used for quantitative analyses.

Independent evaluation was conducted using 4499 bottlenose dolphin sightings (1972–2024) from multiple independent sources and platforms, including OBIS (94% of records), the ACCOBAMS Survey Initiative (ASI; 4%), and ORCA (2%) (Panigada et al., 2024; Ocean Biodiversity Information System (OBIS), 2026; ORCA, 2025, see Table S2 for details) covering multiple seasons (Fig. S1). Model performance was evaluated at the basin scale using AUC, precision, sensitivity, specificity, and F1 score, applying the same maximum test sensitivity plus specificity threshold for binarisation. Independent metrics were computed in R using the *pROC* package for AUC calculation and the *caret* package for confusion-matrix-based statistics. In addition to threshold-based core area delineation, broader suitable areas were identified for cartographic purposes using a 12-class Jenks natural breaks classification implemented in R (package *classint*). The breakpoint between the second and third classes was used to approximate the transition from very low to moderate predicted suitability. This classification was applied exclusively for visualization of suitability gradients and did not influence core area definition or model evaluation.

To quantify agreement between predicted suitability and observed distribution, encounter rates (ER) were compared between SDM-derived core and non-core cells using Wilcoxon rank-sum tests (*rstatix*) and Cliff's delta effect sizes (*effsize*).

#### 2.5. Clustering of environmental factors (Q iii)

To address the third research question (Q iii), environmental conditions associated with bottlenose dolphin presence were explored using a multivariate clustering approach conducted after the SDMs analyses. Mean values of environmental predictor aggregated over the study period values were extracted from raster layers for each surveyed cell where the species was recorded (R packages *terra* and *sf*). Predictors were standardized (centered and scaled) and a Principal Component Analysis (PCA) was performed in R using the base *prcomp*. K-means clustering was then applied using the base *kmeans* function (nstart = 25). The number of clusters (K = 3) was selected based on inspection of the elbow method and ecological interpretability. Clusters were subsequently labelled according to their dominant environmental features.

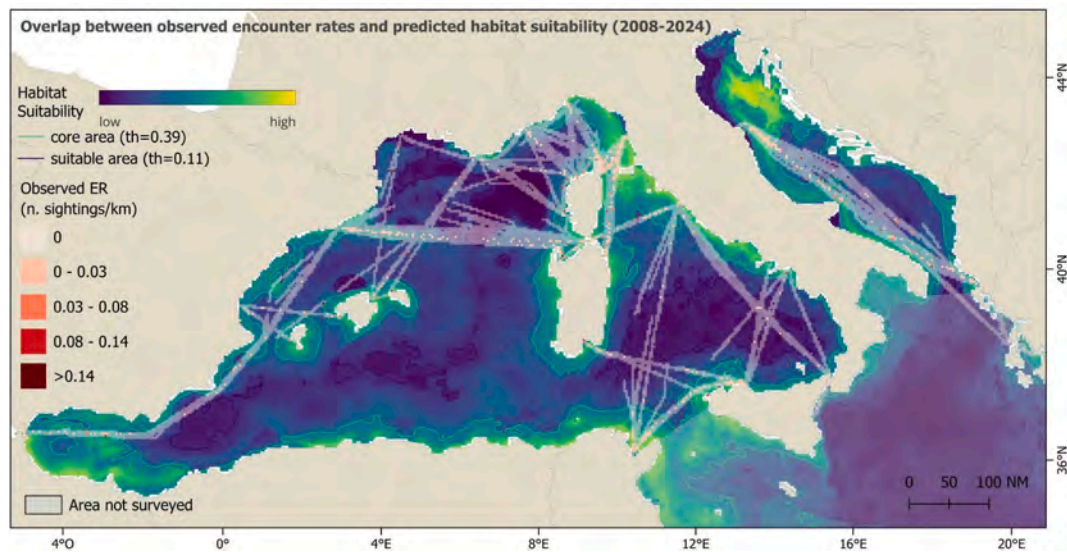
To evaluate how observed distribution varied among environmental clusters, encounter rates (ER) were summarized by cluster for the full period and by season. Differences in ER among clusters and seasons were tested using non-parametric Kruskal–Wallis tests (*stats* package), followed by Dunn's post hoc comparisons with Bonferroni correction implemented in the *FSA* package. All analyses were performed in R (version 4.2.0; R Core Team).

### 3. Results

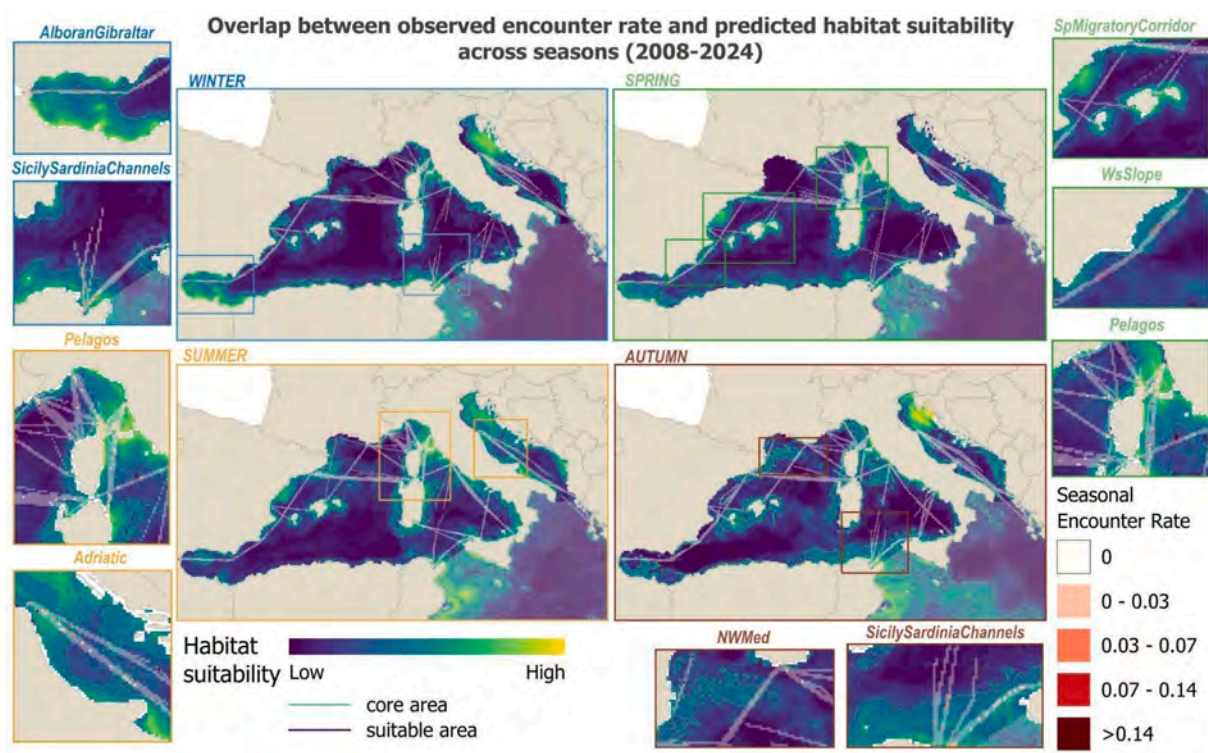
#### 3.1. Observed distribution (ER)

ER analysis revealed marked spatial and seasonal differences in observed distribution across subareas (Figs. 1–3; Table S3). Mean ER values and associated variability among seasons are summarized in Fig. 1, while spatial patterns at grid-cell resolution are shown in Figs. 2–3. Seasonal hotspot configuration is further illustrated through an ER-weighted kernel density representation (Fig. S2), included for visualization purposes to highlight broader spatial gradients in sighting concentration.

The highest ER values were recorded in the Alboran–Gibraltar region, peaking in Winter ( $0.013 \pm 0.033$  sight/km) and declining thereafter. Distinct peaks emerged during spring in the western Spanish slope and Spanish Migratory Corridor (up to  $0.006 \pm 0.023$ ), whereas



**Fig. 2.** Full-period modelled habitat suitability and observed encounter rate (ER) for bottlenose dolphins in the western Mediterranean and Adriatic Seas (2008–2024). ERs represent the observed distribution within the survey effort, while SDM predictions depict potential habitat suitability. Core suitability areas were identified using the maximum test sensitivity plus specificity threshold, while broader suitable zones were delineated using the natural Jenks classification.



**Fig. 3.** Seasonal modelled habitat suitability and observed encounter rate (ER) for bottlenose dolphins in the western Mediterranean and Adriatic Seas (2008–2024). ERs represents the observed seasonal distribution within the survey effort, while SDM predictions depict potential habitat suitability. Core suitability areas were identified using the maximum test sensitivity plus specificity logistic threshold. Zoom panes highlight seasonal hotspots based on ER patterns, providing finer details on local areas of interest.

most other subareas (Northwestern Mediterranean Sea, Pelagos Sanctuary, and Tyrrhenian Sea) showed lower and comparatively stable values across seasons. In the Sardinia–Sicily Channel, ER was higher in Winter (0.005) and Autumn (0.004) compared to Spring and Summer (both 0.002). In the Adriatic Sea, ER peaked in Summer (0.004 ± 0.014). Seasonal comparisons were not possible for the Western Ionian Sea due to sufficient survey effort only in Summer. In contrast, in the Eastern Ionian Sea, ER was higher in Winter (0.003 ± 0.014) and, to a

lesser extent, in Summer (0.002 ± 0.014). Overall, observed use was spatially heterogeneous, with pronounced seasonal peaks in some subareas (e.g., Alboran–Gibraltar, Sardinia–Sicily Channel, Adriatic Sea) and more stable patterns in others, as reflected by both mean ER values and their variability (Fig. 1; Table S3).

### 3.2. Potential distribution across the basin (SDM)

After removing duplicate presence records falling within the same  $5 \times 5$  km grid cell, the final sample size used for modelling was 609 occurrences for the full-period model and ranged from 135 (Winter) to 248 (Summer) for seasonal models (Table 2).

SDMs showed robust predictive performance. Internal validation yielded AUC values between 0.75 (Summer) and 0.89 (Winter), indicating acceptable to excellent discrimination ability (Elith et al., 2011). Independent validation, based on >4000 temporally and spatially independent sightings collected between 1972 and 2025, confirmed model generalizability (Table 3), with AUC values ranging from 0.70 (Autumn) to 0.85 (Summer). Independent AUCs were comparable to, or higher than, internal test values.

Environmental novelty analyses (MESS: Fig. S3; MOP: Fig. S4) indicated that most predicted suitable areas fell within the environmental range represented in the training data. Extrapolation was mainly confined to the south-eastern Mediterranean, with smaller localized areas in the northern Adriatic. Overall environmental similarity was moderate to high (mean MOP  $\approx$  55%), suggesting that projections were largely generated under analogous environmental conditions. Accordingly, interpretation in the main text focuses on well-represented calibration areas (Western Mediterranean and Adriatic), while environmentally dissimilar regions are presented in the Supplementary Material (Figs. S5, S6).

The full-period model identified persistent core areas of high suitability, including the Alboran Sea, Balearic Islands, eastern Pelagos and Tyrrhenian Seas, northern Adriatic, and the Tunisian–Sicilian platform (Fig. 2). Seasonal models (Fig. 3) revealed a coherent temporal pattern. In Winter, suitability was concentrated over continental shelves, particularly in the Alboran basin, Adriatic Sea, and Gulf of Tunis. In Spring, suitable habitat expanded toward slope and deeper environments, with marked hotspots in the Spanish Cetacean Migration Corridor, the eastern Pelagos and the southern Adriatic. Summer predictions showed broader shelf–offshore distribution, notably in the Pelagos Sanctuary, northern Tyrrhenian, and Gulf of Lion. Offshore expansion peaked in Autumn, especially in the Balearic and north-western Mediterranean sectors, corresponding to the widest spatial extent of suitable habitat.

Predicted hotspots consistently overlapped areas of high encounter rates (ER), indicating concordance between modelled suitability and observed habitat use. Across seasons and for the full period, ER values were significantly higher within core suitability areas than in non-core cells (Wilcoxon tests,  $p < 0.001$ ). Although effect sizes were modest (Cliff's  $\delta = 0.17$ – $0.23$ ; Fig. S9), their consistency across temporal scales supports the ecological relevance of the predicted core habitats.

After collinearity screening, all environmental variables were retained as predictors (Table 1). In the full-period model, bathymetry (29%) and distance to coast (12%) were the most influential predictors (Table S3), with thermal variability (Temp\_sd, 9.9%) also contributing substantially. Across seasons, bathymetry remained consistently

**Table 2**

Performance metrics of bottlenose dolphin species distribution models (SDMs) for the entire period (2008–2024) and by season. Final sample size (n; after removing duplicate presences within the same  $5 \times 5$  km cell) and AUC values for training, test (internal validation), and independent datasets (1972–2025) are reported.

Temporal resolution	n.	Internal performance		External validation
		AUC <sub>train</sub>	AUC <sub>test</sub>	AUC <sub>ind</sub>
Entire period	609	0.80	0.76	0.81
Winter	135	0.89	0.81	0.82
Spring	236	0.85	0.78	0.84
Summer	248	0.75	0.75	0.85
Autumn	162	0.88	0.79	0.70

**Table 3**

Validation metrics of *Tursiops truncatus* SDMs (2008–2024) using independent sightings (1972–2025). Results are shown for the full Mediterranean and across different temporal resolutions, using the maximum test sensitivity plus specificity Logistic threshold.

Temporal res.	Threshold	AUC	Precision	F1	Sensitivity	Specificity
Entire period	0.39	0.81	0.79	0.73	0.69	0.81
Winter	0.31	0.82	0.81	0.66	0.56	0.87
Spring	0.34	0.84	0.81	0.61	0.49	0.88
Summer	0.36	0.85	0.81	0.74	0.69	0.84
Autumn	0.30	0.70	0.67	0.59	0.53	0.73

important (up to 29.2% in Summer), while distance to coast peaked in Spring (24.4%). Dynamic variables showed seasonal modulation, with increased importance of chlorophyll variability in Spring (Chl\_sd: 10.3%) and mesoscale circulation (zos) in Autumn (12.8%). Jackknife results were consistent with percent contribution and permutation importance metrics (Fig. S7). Response curves illustrating species–environment relationships are provided in the Supplementary Material (Fig. S8).

### 3.3. Environmental clustering (*k*-means)

Based on PCA scores, the K-means cluster analysis identified three main environmental clusters associated with the presence of dolphins. The first two principal components together explained 50.1% of the total variance (Fig. 4A):

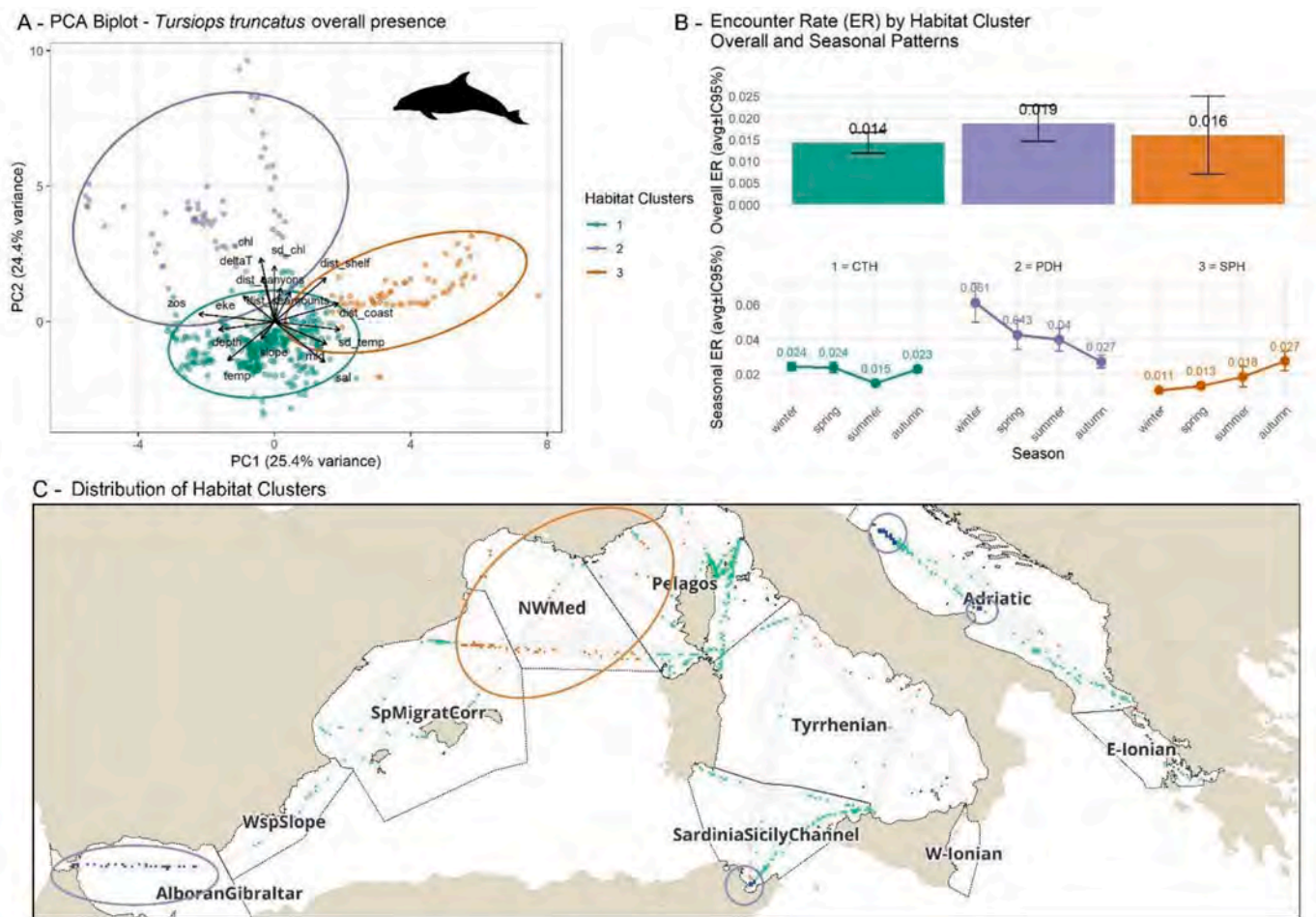
**(Cluster 1) Habitats for coastal topographic structures (CTH):** includes the habitats most influenced by coastal processes, encompassing neritic areas but also extending into open-sea settings shaped by topographic structures such as seamounts and canyons. These areas are characterized by moderate variability in chlorophyll and temperature, reflecting mixed but not highly dynamic conditions.

**(Cluster 2) - Productive-dynamic habitats (PDH):** habitats associated with oceanographic fronts and mixing zones, with stronger thermal gradients and higher chlorophyll variability.

**(Cluster 3) Stable-Pelagic Habitats (SPH):** comprising deep offshore waters with high salinity, moderate productivity, and relatively stable conditions.

Spatially, different regional patterns emerged in association with these three identified clusters (Fig. 4C). Cluster 1 prevailed in the western Spanish slope, the Spanish Cetacean Migratory Corridor, the Tyrrhenian Sea and the Sardinia–Sicily Channel, the Adriatic Sea, while cluster 2 dominated in the Alboran–Gibraltar area and emerged with small spots mainly in the Gulf of Tunis and in the Adriatic. The North-West Mediterranean Sea was dominated by Cluster 3, while Pelagos Sanctuary included features of Clusters 1 and 3. The ERs of bottlenose dolphins differed significantly between environmental clusters (Table S4). Cluster 2 consistently showed the highest ER, with values significantly higher than in both Clusters 1 and 3 (Fig. 4B). On the contrary, Cluster 1, which covered 76% of the cells sampled, had the lowest ER, reflecting widespread but less intense use by dolphins. Cluster 3 showed intermediate ER values, but with higher variability.

Seasonal patterns reinforced these differences (Table S5). Cluster 2 showed significantly higher ER than both cluster 1 and cluster 3 in Winter, Spring and Summer; no significant differences were detected in Autumn. Within the clusters, the seasonal variation was more pronounced in cluster 1, where the ER was significantly lower in Summer than in all other seasons. Cluster 2 showed only a weaker difference (Autumn vs. Winter), and cluster 3 did not exhibit any significant seasonal variation. The violin graphs help characterize these different habitats (Fig. 5).



**Fig. 4.** Clustering of environmental events of bottlenose dolphins. (A) PCA biplot of environmental variables with clustering of  $k$  means, identifying the three environmental clusters; (B) Mean encounter rate (ER  $\pm$  95% CI) per cluster for the entire period (top) and seasonal ER per cluster (bottom), faceted by environmental clusters. (C) Spatial distribution of the three environmental clusters in the Mediterranean Sea. The ellipses highlight areas where each cluster is predominantly represented; 1- CTH = Coastal - Topographic structure cluster (green), 2- PDH = Productive - Dynamic cluster (purple), 3- SPH = Stable - Pelagic cluster (orange). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

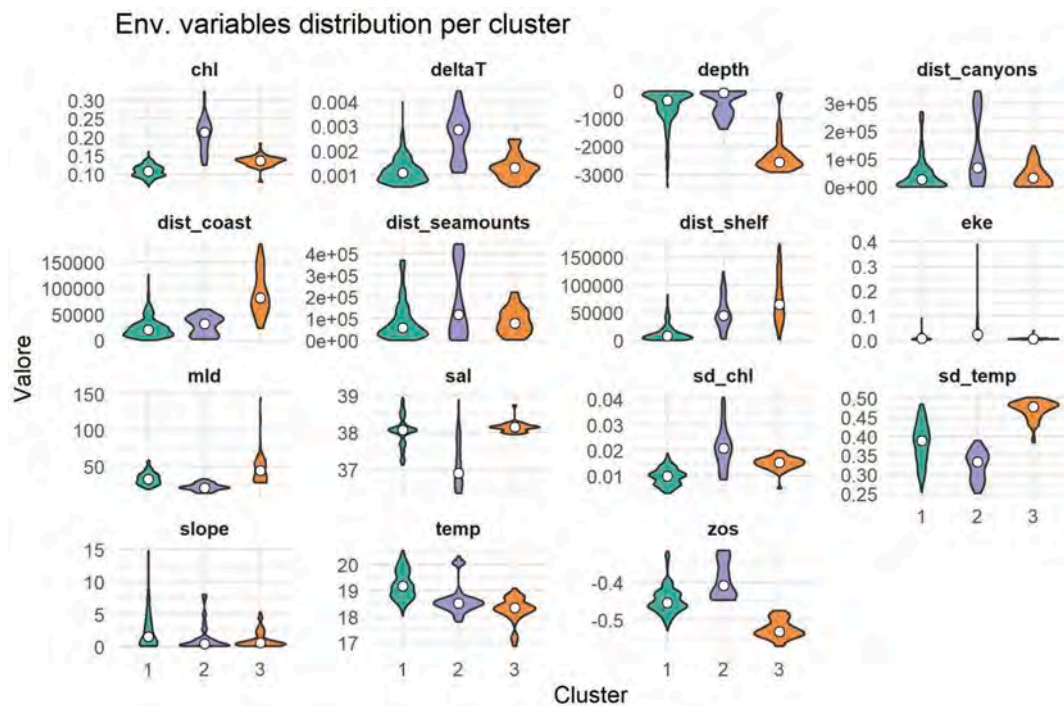
## 4. Discussion

### 4.1. Advantages, reliability and methodological considerations

This study demonstrates the value of a multi-approach analytical workflow centered on species distribution modelling (SDMs) to investigate seasonal habitat patterns in data-limited marine systems. Seasonal models showed robust performance in independent validation ( $AUC > 0.8$  for all seasons except Autumn,  $AUC \approx 0.7$ ), supporting their predictive reliability at basin scale. This performance is grounded in 15 years of standardized ferry-based monitoring, providing consistent multi-season coverage across much of the Mediterranean basin and enabling model calibration while extending inference into offshore areas that are otherwise difficult to cover continuously and at large scale.

SDMs were complemented by encounter rate (ER) analysis and environmental clustering, which together described seasonal habitat patterns from complementary perspectives: SDMs estimated environmental suitability, ER quantified observed habitat use intensity, and clustering characterized underlying environmental regimes. ERs were consistently higher within SDM-derived core areas than in non-core cells across all seasons ( $p < 0.001$ ), with stable, though modest, effect sizes (Cliff's  $\delta = 0.17$ – $0.23$ ), supporting the ecological relevance of predicted core habitats. Seasonal variation in encounter rates across environmental clusters linked predicted suitability and observed use to distinct physical and biogeochemical regimes.

Some methodological considerations should nevertheless be acknowledged when interpreting our results. First, ferry-based sampling follows fixed routes rather than homogeneous survey coverage; however, these routes intercept major environmental gradients across the Mediterranean basin and therefore provide a representative framework for broad-scale habitat modelling (Boye et al., 2024; Pasanisi et al., 2024). Second, environmental predictors were aggregated into multi-year seasonal climatologies, intentionally smoothing short-term temporal variability in order to characterize recurrent seasonal habitat configurations rather than fine-scale dynamics. Third, independent validation and environmental similarity analyses (i.e., MESS and MOP) supported the reliability of model predictions, including in areas beyond the main calibration domain. Nevertheless, to remain highly cautious, interpretation should primarily focus on the Western Mediterranean and Adriatic Seas, where calibration data were concentrated. Moreover, the robustness of the main seasonal configurations emerging from the independently calibrated seasonal models was further supported by the comparison with an alternative pooled MaxEnt framework. This framework was based on a single model calibrated using all occurrences, each associated with predictors from its respective climatological season, and subsequently projected onto seasonal climatologies (Supplementary Material, Table S8, Fig. S11). Results were broadly consistent between frameworks, while highlighting complementary ecological perspectives: the pooled framework prioritizes generalization across seasonal conditions, whereas the season-specific framework better



**Fig. 5.** Violin plots showing the distribution of the main environmental variables across the three habitat clusters (1- CTH = Habitat of Coastal-Topographic structures (green), 2- PDH = Productive-Dynamic Habitat (purple), 3- SPH = Stable-Pelagic Habitat (orange)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

preserves the spatial organization of relative habitat suitability within each season. The season-specific framework was therefore retained because the objective of this study was to characterize how relative habitat suitability is organized under different seasonal environmental conditions.

#### 4.2. Seasonal habitat patterns of Mediterranean bottlenose dolphin

Our results refine current understanding of Mediterranean bottlenose dolphin ecology by showing a coherent seasonal modulation of habitat suitability across previously recognized key areas, including the Alboran Sea, Balearic region, Pelagos Sanctuary, Tyrrhenian Sea, Sicily-Tunisia Channel, and northern Adriatic. Compared with previous basin-wide assessments limited to one or two seasons (e.g., Cañadas et al., 2024; Virgili et al., 2024), our four-season approach reveals a progressive reorganization of suitable habitats across different environmental conditions that would be less evident in full-period or single-season assessments.

A clear seasonal spatial sequence emerged. In Winter higher suitability and encounter rates were largely concentrated over continental shelf systems, including the Alboran basin, Adriatic Sea, Gulf of Tunis and eastern Pelagos. From Spring onward, suitability progressively expanded toward slope and offshore environments, reaching its widest spatial extent in Summer-Autumn. This shelf-to-offshore transition was consistently reflected in both SDM predictions and encounter rate distributions, in agreement with seasonal offshore tendencies previously documented in several Mediterranean sub-basins (Pace et al., 2022b; Virgili et al., 2024).

Environmental clustering helped clarify the ecological gradients underlying these seasonal patterns. Productive-dynamic habitats, typically associated with shelf-slope mixing zones and nutrient inputs, supported the highest encounter rates, particularly in Winter and Spring, consistent with enhanced vertical mixing and prey availability during colder months. This pattern aligns with previous findings linking bottlenose dolphin occurrence to productive frontal systems in areas such as the Alboran Sea and northern Adriatic (Cañadas and Hammond, 2008;

d'Ortenzio and Ribera d'Alcalà, 2009; Virgili et al., 2024). Coastal-topographic habitats, shaped by seabed morphology and nearshore processes, represented the most common cluster across the western Spanish slope, the Spanish migration corridor, eastern Pelagos, Tyrrhenian Sea, Sardinia-Sicily Channel, Adriatic, and Ionian Seas. They showed intermediate but relatively stable encounter rates, except for a Summer decline, consistent with the species' frequent association with coastal waters and structured topographic environments (Bearzi et al., 2008a; Gnone et al., 2022; Labach et al., 2022). In contrast, stable pelagic habitats, representing offshore oligotrophic waters mainly located in the northwestern sector, exhibited stronger seasonal variability, with increased suitability and occurrence during Summer-Autumn. This offshore expansion is consistent with documented mixed neritic-pelagic strategies in the species in the northwestern sector (Arcangeli et al., 2017; Bellingeri et al., 2025; Gnone et al., 2022).

Overall, these environmental contexts indicate a Winter-Spring concentration within productive shelf systems followed by a warm-season expansion toward offshore environments. By Autumn, coastal encounter rates increase again while offshore suitability remains elevated, suggesting a gradual seasonal redistribution of habitat use intensity across coastal and offshore domains rather than abrupt habitat shifts. Although causality cannot be directly tested here, these patterns are consistent with known Mediterranean seasonal environmental processes, including stratification dynamics, mesoscale circulation, and associated changes in productivity and foraging conditions across coastal and offshore environments, as well as seasonal increase in anthropogenic pressures along coastal zones during warmer months (d'Ortenzio and Ribera d'Alcalà, 2009). These mechanisms should therefore be interpreted as plausible contextual drivers rather than demonstrated causal relationships.

Within this seasonal context, the offshore expansion observed during summer may also reflect a redistribution of individuals within the population. Mediterranean bottlenose dolphin populations are often characterized by strong site fidelity to coastal habitats and by spatial structuring linked to habitat specialization (Bearzi et al., 2009; Natoli et al., 2021). Within this framework, more mobile individuals may

expand their foraging range toward offshore environments during summer, whereas coastal areas may remain particularly important for more resident individuals, including females with calves (Gnone et al., 2011; Pace et al., 2021). Such seasonal habitat partitioning may reduce spatial and trophic overlap within the population, especially when individuals differ in mobility, habitat use or foraging specialization (Sprogis et al., 2016; Torres and Read, 2009). In Mediterranean bottlenose dolphins, which are frequently associated with productive coastal habitats (Bearzi et al., 2009; Natoli et al., 2021), this mechanism could help reduce intra-specific competition for locally limited resources. However, testing this hypothesis would require individual-level ecological and behavioural data.

#### 4.2.1. Regional patterns

Although seasonal patterns were coherent at basin scale, their magnitude and timing varied among subregions, reflecting local hydrography, productivity regimes, and anthropogenic pressures. Below, we summarize the main regional expressions of these patterns, structured by environmentally homogeneous areas.

The **Alboran–Gibraltar region** emerged as one of the most important areas for bottlenose dolphins, with the highest encounter rates and consistently high suitability across seasons. Environmental clustering confirmed its role as a productivity and oceanographic hotspot linked to its transitional Atlantic–Mediterranean setting (Cañadas et al., 2005). Dolphins in this region display characteristics typical of Atlantic populations, including pelagic use, large group sizes, and wide-ranging movements (Bellingeri et al., 2025; Gnone et al., 2022; La Manna et al., 2022). Persistent hotspots such as the Gulf of Almería, Seco de los Olivos, and the Alboran Ridge were evident across seasons, consistent with previous studies (Cañadas et al., 2005; Cañadas and Hammond, 2008; Giménez et al., 2018; Sarhan et al., 2000). Seasonal variability reflected the wind-driven upwelling regime, with Winter peaks associated with enhanced mixing and a Summer contraction under reduced upwelling intensity (Sánchez-Garrido and Nadal, 2022). These findings refine earlier two-season assessments by resolving the full annual cycle (Cañadas and Hammond, 2008; Virgili et al., 2024). Lower Summer encounter rates coincide with periods of increased ecological and anthropogenic pressures documented in the region (Arcangeli et al., 2025; Bearzi et al., 2008a; Cañadas et al., 2005; Scuderi et al., 2024).

Along the **Eastern Spanish coast**, suitability and encounter rates peaked in Spring between the Ebro Delta and Alicante, reflecting Winter convection and riverine inputs followed by spring restratification (Vidal et al., 2017). During Summer–Autumn, suitability shifted northward and offshore within the Cetacean Migratory Corridor (Reuelta et al., 2018). In contrast, the **Balearic Islands** retained high suitability and encounter rates year-round, consistent with a resident subpopulation exhibiting strong site fidelity (Brotons et al., 2019; Forcada et al., 2004; Gonzalvo et al., 2014). Seasonal offshore shifts align with documented intra-archipelago movements (Forcada et al., 2004) and may be reinforced by intense Summer coastal activity (i.e., boating and tourism; Gonzalvo et al., 2008).

In the **northern-western Mediterranean** sector (including the NWMed, Pelagos subareas and the northern Tyrrhenian; Fig. 1) two contrasting dynamics emerged. Western pelagic sectors exhibited marked Summer–Autumn increases in suitability and encounter rates, consistent with documented late stratification and secondary productivity peaks (Macias et al., 2018; Vidal et al., 2017), and corroborated by aerial surveys reporting offshore aggregations (Labach et al., 2022; Laran et al., 2017).

Although environmental similarity analyses indicate that parts of the Gulf of Lion fall within the intermediate range of the calibration domain, the lower suitability predicted in spring should be interpreted with caution, as it may partly reflect limited survey coverage in that season. This is supported by the pooled, season-matched framework, which predicted broader spring suitability in the area, likely due to the additional environmental representation provided by records from other

seasons.

In contrast, eastern Pelagos and northern Tyrrhenian sectors showed persistent suitability peaks associated with coastal–topographic habitats and well-documented resident units (Bellingeri et al., 2025; Carnabuci et al., 2016; Gnone et al., 2022; Mattiussi et al., 2026; Pace et al., 2021; Vassallo et al., 2020). These areas coincide with complex bathymetry and localized enrichment processes that may support prey retention (Arcangeli et al., 2021). Additional hotspots near river mouths (e.g., the Tiber) and in northeastern Sardinia may result from combined natural and anthropogenic enrichment, where riverine input enhances productivity and coastal activities (i.e., fisheries) may provide predictable foraging opportunities (Cafaro et al., 2016; Díaz López, 2012; Pace et al., 2021; Labriola et al., 2026).

The **Sicily–Tunisia Channel** is shaped by hydrographic interactions between the Atlantic Ionian Stream, mesoscale eddies and shallow banks, which enhance local productivity (Karaa et al., 2012; Salhi et al., 2018) and support high cetacean diversity (Benmessaoud et al., 2025). The Gulf of Tunis emerged as a Winter hotspot but maintained high suitability year-round, consistent with documented residency along the northeastern Tunisian coast (Benmessaoud et al., 2013). In contrast, model predictions indicate a more dynamic spatial configuration across the broader Strait of Sicily, with habitat suitability expanding offshore from spring to Autumn toward southwestern Sicily, Pantelleria, Lampedusa and Malta, consistent with previous observational data (La Manna et al., 2010; Pace et al., 2012; Pulcini et al., 2014; Soster et al., 2025; Corrias et al., 2024). This seasonal offshore tendency may also reflect the influence of the region's complex bathymetry, where seamounts, banks and steep gradients promote local enrichment and prey aggregation, particularly during Summer stratification when coastal productivity declines. Recent modelling further identifies proximity to these topographic features as a strong predictor of dolphin occurrence (Gregoriotti et al., under review), underscoring the role of bathymetric complexity in sustaining offshore habitat use during the warm season. Population studies from south-western Sicily also report relatively low site fidelity and dynamic association patterns, indicating a mobile population structure consistent with the seasonal habitat patterns observed across the Strait of Sicily (Papale et al., 2017).

The **Adriatic Sea** showed pronounced seasonality under strong continental influence. Winter suitability peaked in the northeastern basin, consistent with wind-driven mixing and dense water formation (Bearzi et al., 2021; Pasarić et al., 2025), whereas Summer suitability expanded toward central offshore sectors under stratified conditions (Fortuna, 2007; Nadal et al., 2024). Most of the basin fell within coastal–topographic habitats, with localized productive areas influenced by major river inputs such as the Po (Campanelli et al., 2011; Russo and Artegiani, 1996). Seasonal patterns broadly mirrored documented prey dynamics, as small pelagic fish and cephalopods show similar productivity-driven aggregations (Coll et al., 2009; Fanelli et al., 2023). The northern Adriatic remains a core area hosting well-studied resident communities (Bearzi et al., 2004; Gaspari et al., 2015), yet evidence also indicates partial transience and basin-wide connectivity: approximately half of dolphins identified in Trieste were recorded only once (Genov et al., 2008), and genetic analyses suggest potential gene flow within the basin (Gaspari et al., 2024). Offshore and central sectors exhibit lower site fidelity (Holcer, 2012; Pleslić et al., 2021), whereas areas such as Kvarnerić host long-term resident groups despite documented temporary emigration (Fortuna, 2007). Although connectivity cannot be inferred directly from our data, marked environmental seasonality aligns with this variability in site fidelity, suggesting that hydrographic dynamics and anthropogenic pressures may jointly shape patterns of residency and movement (Triossi et al., 2013).

#### 4.3. Conservation implications

This study provides the first basin-scale, four-season assessment of bottlenose dolphin habitat patterns in the Mediterranean, highlighting

spatial and seasonal variability. Our results indicate that full-period or single-season assessments may underestimate seasonal habitat configurations, which are important to consider in environmentally dynamic basins such as the Mediterranean Sea, even for species that are not strictly migratory. This information can help improve seasonally explicit spatial conservation planning for bottlenose dolphins and other conservation-priority marine species.

Several seasonally important areas identified here overlap with existing spatial conservation frameworks (e.g., SPAMI, NATURA 2000, IMMAs), supporting their ecological relevance. However, when focusing exclusively on legally binding designations, some recurrent seasonal hotspots remain only partially covered or outside formal protection, including parts of the Alboran Sea, Tyrrhenian coastal sectors, and sections of the Adriatic. A seasonal spatial coherence assessment within the LIFE Conceptu Maris project highlights both alignment and gaps in binding protection (Arcangeli et al., 2025b; Fig. S10). In particular, the Alboran Sea emerged as a recurrent seasonal hotspot of high suitability and encounter rates for bottlenose dolphins. Despite intense maritime traffic and associated pressures, the area remains only partially covered by binding conservation measures, highlighting the need for strengthened protection. Its relatively stable productivity and suitability across seasons further emphasize its ecological importance, particularly under ongoing climate change (Sánchez-Garrido and Nadal, 2022).

These findings emphasize the need to incorporate seasonality and environmental conditions into spatial prioritization, and are consistent with ACCOBAMS conservation objectives aimed at improving the characterisation and monitoring of bottlenose dolphins distribution and habitat use across the Mediterranean (ACCOBAMS, 2023).

More broadly, the framework is transferable to other highly mobile marine species potentially exhibiting seasonal variability. Applied to long-term monitoring data, this integrative approach can improve the robustness and management relevance of SDMs by identifying periods and regions of heightened ecological importance and exposure to human pressures, thereby supporting ecosystem-based and adaptive conservation strategies across marine systems.

#### 4.4. Future perspectives

Looking forward, conservation effectiveness will depend on expanding multiseasonal monitoring in undersurveyed regions such as the Central and Eastern Mediterranean, and on explicitly integrating spatially and seasonally variable anthropogenic pressures into management frameworks. Long-term initiatives such as the FLT Med Network and LIFE Conceptu Maris project will remain essential to support coordinated monitoring and seasonally informed adaptive management in dynamic marine environments. Building on the climatological baseline provided here, future work could implement time-explicit SDMs that temporally match occurrence records with high-resolution environmental predictors, enabling finer-scale resolution of short-term variability and supporting near-real-time and dynamic ocean management applications (e.g., Becker et al., 2016; El-Gabbas et al., 2021; Scales et al., 2017). Such developments would complement the present basin-scale seasonal framework by extending its applicability toward operational forecasting and adaptive management under ongoing environmental change.

#### 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.

#### CRedit authorship contribution statement

**E. Pasanisi:** Writing – original draft, Formal analysis, Data curation, Conceptualization. **M. Gregoriotti:** Writing – review & editing,

Methodology, Data curation. **F. Atzori:** Writing – review & editing, Funding acquisition. **M. Azzolin:** Writing – review & editing, Data curation. **I. Campana:** Writing – review & editing, Data curation. **L. Carosso:** Data curation. **A. Castelli:** Funding acquisition. **M. Costantino:** Writing – review & editing, Data curation. **R. Crosti:** Writing – review & editing, Funding acquisition, Data curation. **L. David:** Writing – review & editing, Funding acquisition, Data curation. **N. Di-Meglio:** Data curation. **M. Farina:** Writing – review & editing, Data curation. **O. Garcia-Garin:** Writing – review & editing, Data curation. **M. Gazo:** Writing – review & editing, Funding acquisition. **F. Grossi:** Writing – review & editing, Data curation. **F. Maffucci:** Writing – review & editing, Funding acquisition. **D.S. Pace:** Writing – review & editing, Supervision. **M. Paraboschi:** Writing – review & editing, Data curation. **M. Pecoraro:** Writing – review & editing, Data curation. **G. Pellegrino:** Writing – review & editing, Data curation. **J.A. Raga:** Writing – review & editing, Funding acquisition. **M. Roul:** Data curation. **G. Sarà:** Writing – review & editing, Funding acquisition. **A. Scuderi:** Writing – review & editing, Data curation. **P. Tepsich:** Writing – review & editing, Data curation. **R. Teti:** Writing – review & editing, Data curation. **M. Vighi:** Writing – review & editing, Data curation. **M. Vitale:** Writing – review & editing. **A. Arcangeli:** Writing – review & editing, Supervision, Funding acquisition, Data curation, Conceptualization.

#### Ethical statement

All data were collected using non-invasive observational methods from ferries operating on fixed routes. No experimental manipulation, handling, or disturbance of animals was involved. Data collection complied with national and international regulations governing marine mammal research. No ethical approval or animal care committee authorisation was required for this type of observational study.

#### Funding statement

This study was supported by the LIFE Conceptu Maris project (LIFE20 NAT/IT/001371) and the FLT Med Network, both coordinated by the Italian Institute for Environmental Protection and Research (ISPRA). The analyses were based on a harmonized dataset covering the period 2008–2024, compiled within the LIFE Conceptu Maris framework. In this project, data collected between 2022 and 2024 within the project were integrated with earlier records (2008–2021) provided by the FLT Med Network. Additional data were contributed by the SICO-MAR PLUS project (INTERREG Italy–France Maritime 2014–2020; data 2018–2020), the Agence Française de la Biodiversité project “Collecte de données scientifiques sur la Mégafaune marine de Méditerranée française (tortues, cétacés, macrodéchets)” (Décision 2018/145; data 2018–2019), and the Monitoring Ferry programs (Convention n°11-011-83,400; n°12-036; n°14-028) funded by the Sanctuaire Pelagos (data 2012 and 2014–2016). Further contributions derived from the ACCOBAMS call for proposals 2012 on cetacean monitoring using ferries as platforms of observation off Tunisia (data 2013), and from the Fondazione Civitavecchia project “Monitoraggio dei cetacei nel mar Tirreno centrale” (data 2009–2012).

#### Acknowledgments

We gratefully acknowledge the collaboration of all the ferry companies that facilitated data collection onboard their vessels, including Grimaldi Lines, Corsica Sardinia Ferries, GNV (Grandi Navi Veloci), Minoan Lines, Tirrenia, and Balearia and all institutions, researchers and citizens involved in the collection, harmonisation, and sharing of these monitoring data, which made this study possible. Finally, we thank the Editor and reviewers for their constructive comments, which helped improve the clarity and robustness of the manuscript.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2026.103859>.

### Data availability

Aggregated occurrence data supporting the findings of this study originate from the LIFE Conceptu Maris project (LIFE20 NAT/IT/001371) and are part of a FAIR data infrastructure currently being finalised within the project framework. These datasets are publicly released through the Conceptu Maris Decision Support System (DSS; <https://conceptumaris-dss.nnb.isprambiente.it/>) and through the Italian National Biodiversity Network (NNB; <https://maps.nnb.isprambiente.it/>). Raw data are also available from the corresponding author upon reasonable request and subject to approval by the data providers. To ensure transparency and reproducibility, all scripts used for data processing, modelling, and analysis are archived in Zenodo and are available at: <https://doi.org/10.5281/zenodo.19048043>.

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