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Distribution models of baleen whale species in the Irish Exclusive Economic Zone to inform management and conservation

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ABSTRACT

Irish waters are under increasing pressure from anthropogenic sources including the development of offshore renewable energy, vessel traffic and fishing activity. Spatial planning requires robust datasets on species distribution and the identification of important habitats to inform the planning process. Despite limited survey effort, long-term citizen science data on whale presence are available and provide an opportunity to fill information gaps. Using presence-only data as well as a variety of environmental variables, we constructed seasonal ensemble species distribution models based on five different algorithms for minke whales, fin whales, humpback whales, sei whales, and blue whales. The models predicted that the coastal waters off the south and west of Ireland are particularly suitable for minke, fin and humpback whales. Offshore waters in the Porcupine Seabight area were identified as a relevant habitat for fin whales, sei whales and blue whales. We combined model outputs with data on maritime traffic, fishing activity and offshore wind farms to measure the exposure of all the species to these pressures, identifying areas of concern. This study serves as a baseline for the species presence in Irish waters over the last two decades to help develop appropriate marine spatial plans in the future.

1. Introduction

Irish waters host a diversity of cetaceans (whales, dolphins, and porpoises), with 26 species recorded to date. The Irish Whale and Dolphin Group (IWDG) have been recording and monitoring the presence of cetacean species in Irish waters since the 1990s through a range of observation schemes, mostly based on citizen science backed by a rigorous data validation process (Ryan et al., 2016; Whooley et al., 2011). This long-term effort has led to the construction of extensive datasets which provide an opportunity to help inform future policies and marine spatial planning, especially given the ambitious marine plans the Republic of Ireland has set for the next decade.

In the European Union (EU), member states are required under European law to protect and effectively manage biodiversity and natural resources in the European territory, including marine environments. The Habitats Directive (Directive 92/43/EEC - http://data.europa.eu/eli/dir/1992/43/2013-07-01), the Strategic Environmental Assessment Directive - SEA (Directive, 2001/42/EC - http://data.europa.eu/eli/dir/2001/42/oj), and the Marine Strategy Framework Directive - MSFD (Directive, 2008/56/EC - http://data.europa.eu/eli/dir/2008/56/oj) all require strict protection of cetacean species. These directives are intimately related to spatial planning and policy making within the jurisdictions of EU member states, which must be informed by robust technical and scientific criteria. As an EU member state, the Republic of Ireland is also subject to these obligations. The Republic of Ireland possesses an Exclusive Economic Zone (EEZ) that spans more than 400,000 km^2, seven times its land territory. Under the ambitious EU Biodiversity Strategy (COM/2020/380 final - https://eur-lex.europa.eu/legal-content/EN/ALL/?uri=celex:52020DC0380), the Irish State has committed to protecting 30% of its marine territories as Marine Protected Areas (MPAs) by 2030.

Due to its geographic location off the western seaboard of Europe at intermediate latitudes, Ireland has great potential in renewable energy production based on offshore wind farms (Sustainable Energy Authority of Ireland, SEAI - https://gis.seai.ie/wind/; Global Wind Atlas - https://globalwindatlas.info/en). Following the Climate Action Plan

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2021 and the Marine Area Planning (MAP) Act, the Irish government has committed to significantly increase the country's renewable energy production to 7 GW by 2030 and 20 GW by 2040. Within this framework, the recently presented Offshore Renewable Energy Development Plan II (OREDP II) will seek to map areas most suitable for offshore renewable energy using the latest data available on a range of themes including other maritime activities and marine biodiversity (Government of Ireland - https://www.gov.ie/en/publication/71e36-offshore-renewable-energy-development-plan-ii-oredp-ii/). Currently, six wind farm projects have been awarded with a Marine Area Consent (MAC) enabling their development in Ireland's waters; five in the Irish Sea and one off the west coast of Ireland (approx. 490 km^2 in total). However, other coastal areas are being considered. Under the South Coast Designated Maritime Area Plan (DMAP) proposal (Government of Ireland - https://www.gov.ie/en/consultation/eb17b-south-coast-designated-maritime-area-plan-dmap-proposal/), an area of approximately 8600 square kilometres off the southeast coast of Ireland within which additional offshore renewable energy development may take place in the near future. Marine wind farms may lead to a significant degradation of important habitats for cetaceans. Examples of this degradation may include increased noise levels, risk of collisions and entanglement, changes to benthic and pelagic habitats, alterations to prey availability or distribution, and pollution from increased and/or modified vessel traffic or due to the release of contaminants from seabed sediments (e.g. Gill, 2005; Boehlert and Gill, 2010). Offshore wind farms may also induce changes in prey distribution in form of increased fish biomass around them due to an "artificial reef" effect or through a *de facto* no-take zone where fishing activity is restricted (Inger et al., 2009). Other human activities at sea also pose a threat to cetaceans such as the interaction with fishing gears (entanglements) or those caused by maritime traffic (ship strikes). In Ireland, both activities are economically relevant and their potential impact on marine megafauna has a much larger geographic extent than wind farms. Irish vessels alone landed 156,941 tonnes of fish into Irish ports, worth an estimated €296 million in 2022 (Fisheries Ecosystems Advisory Services - FEAS, 2023). However, most of the fishing activity within the Irish EEZ (64%) is carried out by foreign fleets, with Spain (30%), France (20%) and the UK (11%) as principal actors (Marine Institute - Species Dashboard - https://shiny.marine.ie/speciesdash/). With respect to maritime traffic, most of the shipping routes are located to the east and south of Ireland. Bulk traffic had an all-island volume of more than 25 million tonnes in 2021 (Bailey and Treacy, 2022). Both maritime traffic and fishing activity may not only lead to a decrease in habitat quality, for example in form of underwater noise (Blair et al., 2016; Daly and White, 2021), but may also be a cause of injuries or death of cetaceans in case of direct interaction (Cassoff et al., 2011; Laist et al., 2001). Thus, it is crucial to identify and protect the most relevant areas for marine biodiversity in Irish waters, especially those for highly mobile pelagic megafauna, such as whales and dolphins, to reduce their interaction with these activities as far as possible.

Species distribution models (SDMs) provide one mechanism to inform spatial planning and wildlife conservation. They have been used to identify key habitats for species or populations of interest, and subsequently, to implement measures that promote their conservation. These measures may include the creation of protected areas, the establishment of monitoring programmes, or the identification of risks and threats (Franklin, 2013). SDMs can be built by fitting species presence-absence data and environmental predictor variables using a wide variety of statistical tools or algorithms (Melo-Merino et al., 2020). SDMs have been extensively used in conservation science for a wide range of species, especially in terrestrial environments, including plants (Verspagen and Erkens, 2023), insects (Lobo, 2016), reptiles (Raxworthy et al., 2003) and mammals (Escalante et al., 2013). They are also becoming popular in the study of marine life, including cetaceans (Breen et al., 2016; Melo-Merino et al., 2020; Purdon et al., 2020a; Robinson et al., 2017). Modelling cetacean distribution is a complex task since these animals are usually present in very low density and/or abundance, are highly mobile, and their presence can be easily overlooked if search effort is low. Moreover, the collection of presence data often requires dedicated survey effort and large investment in human, economic and logistic resources, which are typically a limiting factor in data collection. This implies that cetacean presence data can be scarce and sometimes strongly biased, both geographically and temporally, depending on where and when observing effort occurs. The utilisation of datasets collected throughout long periods of time (years, decades), as well as the inclusion of data gathered under different schemes and geographical scales can help mitigate against data scarcity and bias (Breen et al., 2016; Escalante et al., 2013; Pacifici et al., 2016; Purdon et al., 2020a; Waggitt et al., 2020). Data collected by citizen science can provide a valuable source of information on cetacean presence (Derville et al., 2018; Tiago et al., 2017) and complements large broad-scale dedicated surveys such as SCANS-I–II–III-IV (Hammond et al., 2002, 2013, 2021), CODA (Hammond et al., 2007) or ObSERVE (Government of Ireland - https://www.gov.ie/en/publication/12374-observe-programme/#observe-reports). In addition, these large-scale dedicated surveys usually cover shorter periods of time (e.g. only summertime) than well-established citizen science observation schemes.

A wide range of statistical tools have been proposed to create SDMs (Elith et al., 2006). However, it can be challenging to researchers to select the best approach among the variety of analytical options currently available as the selection criteria are also diverse and subject to debate (Melo-Merino et al., 2020). In addition, since the choice of the modelling approach may be an important source of variation in the predicted distribution of a species (Jones-Farrand et al., 2011; Pearson et al., 2006), several studies like Araújo and New (2006), Derville et al. (2018), Heikkinen et al. (2006), Qiao et al. (2015) or Ramirez-Reyes et al. (2021) have recommended the use of several types of SDMs. An alternative way to single-algorithm SDMs is ensemble modelling. Ensemble modelling (Araújo and New, 2006; Ramirez-Reyes et al., 2021) is the integration of different SDMs to generate an ensemble or consensus SDM (ESDM), instead of picking just one of the models used in the study. The major advantage of this method is that it incorporates the variability of the predictions made by different modelling techniques by the creation of a combined SDM that may improve these predictions (Ramirez-Reyes et al., 2021). It also facilitates the direct comparison between the predicted distribution of a species when multiple models are required (e.g. in studies that analyse the distribution of several taxa). Joining long-term datasets gathered under different schemes with ensemble species distribution models constitutes a useful tool to identify the most relevant areas for elusive species like cetaceans. In addition, information provided by ensemble models can be merged with spatial data on different types of human activity (e.g. vessel density, fishing effort, etc.) to measure the exposure of the species to these activities and identify areas of concern (Breen et al., 2016, 2017; Brown et al., 2015).

The aim of this study was to explore the distribution of five large baleen whale species frequently observed in Irish waters to identify areas of interest for their conservation. We used whale presence data from several sources to derive ensemble species distribution models within the Irish EEZ. Results from these models were then used to determine the exposure of these whale species to several human activities (maritime traffic, fishing effort and offshore renewable energy developments). The species included common minke whales (*Balaenoptera acutorostrata*), fin whales (*Balaenoptera physalus*), humpback whales (*Megaptera novaeangliae*), blue whales (*Balaenoptera musculus*) and sei whales (*Balaenoptera borealis*). These species were selected based on 1) the availability of large datasets for robust SDMs, 2) their EU-protected status (Habitats Directive, Annex IV), 3) their wide-ranging migratory behaviour, 4) their overlapping ecological niches and sympatric distribution in Ireland, and 5) their seemingly increasing presence in Irish waters (Berrow et al., 2021; Berrow and Whooley, 2022; Blázquez et al., 2023).

2. Material and methods

2.1. Study area

The study area (57° N - 48° N/16° W - 5° W) was delimited to the Exclusive Economic Zone of the Republic of Ireland although in the interest of ecosystem representation and mapping, large areas of the UK and French EEZs in the Celtic Sea, the Irish Sea and the North Channel were also included in the analysis. This area (approx. 600,000 km^2) encompasses temperate water habitats of the eastern North Atlantic Ocean, including the coastal waters of Ireland, the continental shelf of the western side of the British Isles, as well as continental margins and abyssal plain habitats. Fig. 1 depicts the bathymetry of the study area, along with the Areas of Interest (AoI) proposed by Classen et al. (2022), as well as relevant areas for future wind farm developments.

2.2. Species presence data

We used a large dataset built by the Irish Whale and Dolphin Group, using data mainly obtained on a citizen science basis, as well as data collected by other opportunistic and dedicated surveys, including SCANS-II, CODA and ObSERVE. About 91% of the 8407 verified records of the five species of interest collected between 1999 and 2021 were gathered by the Irish Whale and Dolphin Group. Additional data were provided by surveys funded by the Petroleum Affairs Division, the Department of Communications, Climate Action and Environment, the National Parks and Wildlife Service, the University of Saint Andrews, and the Marine Institute (Table 1). A small part of this dataset (SCANS-II and CODA) was previously used in a study by Breen et al. (2016).

This dataset contained presence-only data. Thus, even if a sighting had associated survey effort available, the effort data were not included. The dataset also included unspecific categories which indicated that an animal had been sighted but the species was not definitely determined. These undefined categories were excluded from the analysis to avoid ambiguous results and confounded conclusions. All the datapoints used for the analysis included, at least, the species identification, date of observation, latitude, longitude, survey ID and observers' name(s). Some more details on part of this dataset can be found in Baines et al. (2017) and Hammond et al. (2007, 2013).

2.3. Environmental data

We selected a series of environmental variables according to their known or potential linkage with baleen whale presence (e.g. Meynecke et al., 2021) and availability for the study area and period. Some of these variables were sampled by satellites through remote sensing technologies, which provided data at various spatial and temporal resolutions and at customizable scales. Firstly, we selected static variables such as bathymetry (m), seafloor slope (°) and distance to the nearest shore (km). We also selected dynamic oceanographic variables including both abiotic: sea surface temperature (SST) and its derived seasonal standard deviation (°C), salinity (PSU), mixed layer thickness (m), northward sea water velocity (Vo, m/s) and eastward seawater velocity (Uo, m/s); and biotic: surface concentration of Chlorophyll-a (Chla) and its derived seasonal standard deviation (mg/m^3). All the dynamic variables were available for the whole study area and period. Original temporal resolution of these variables was one month, all of them were seasonally averaged in ArcGIS (version 3.1.2; Esri, Redlands, CA, USA) over the 1999–2021 period. Seasons were defined according to the astronomical cycle in the northern hemisphere as follows: Winter (January, February,

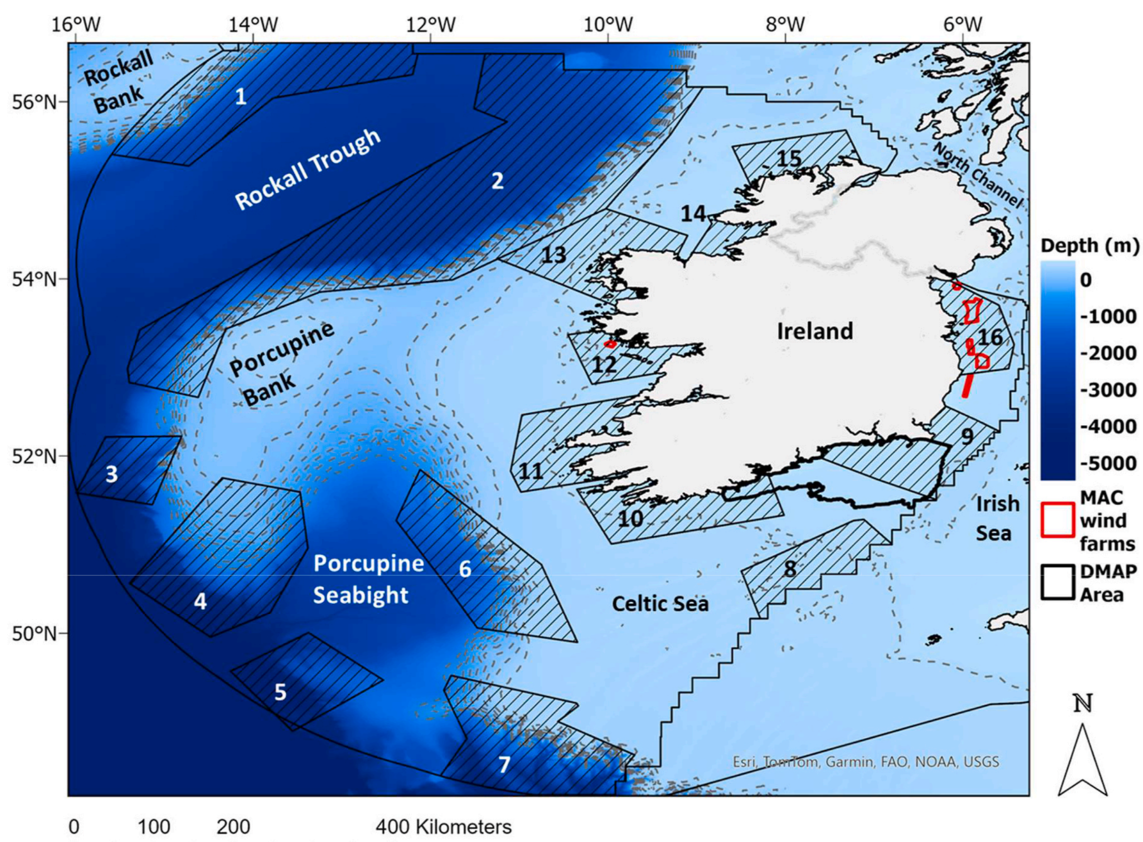


Fig. 1. Irish Exclusive Economic Zone and major oceanographic features. Dashed lines are isobaths between 100 and 1000 m. Colour gradient indicates depth in metres. Red polygons represent currently on-going MAC offshore wind farm projects and the bold black polygon represent the DMAP area of interest for the development of future offshore renewable energy projects. Numbered striped polygons represent Areas of Interest proposed by Classen et al. (2022).

Table 1
Number of records per baleen whale species, season and data source. DCCAE = Department of Communications, Climate Action, and Environment (ObSERVE ship and aerial surveys), IWDG = Irish Whale and Dolphin Group, MI = Marine Institute (ship surveys), NPWS = National Parks and Wildlife Service (ship surveys), PAD = Petroleum Affairs Division (DCCAE; seismic surveys), St. Andrews = University of Saint Andrews (CODA and SCANS-II surveys).

	Minke whale	Fin whale	Humpback whale	Blue whale	Sei whale	Total	%
DCCAE	176	62	2	0	2	242	2.9
IWDG	4376	1948	1298	19	5	7646	90.9
MI	8	4	4	0	0	16	0.2
NPWS	108	19	8	0	0	135	1.6
PAD	51	230	12	14	17	324	3.9
St. Andrews	31	13	0	0	0	44	0.5
Total	**4750**	**2276**	**1324**	**33**	**24**	**8407**	

March), Spring (April, May, June), Summer (July, August, September) and Autumn (October, November, December), similar to Torres et al. (2008) and Wall et al. (2013). We chose to divide the data into seasons to identify possible temporal variability in the predicted species distribution throughout the year, increasing the temporal resolution of our results (Fig. A8).

All variables were resampled to a 0.083° grid (ca. 5 km) using nearest neighbour interpolation, re-projected to the standard WGS84 (EPSG: 4326) geographic projection and clipped to the desired extension in ArcGIS. SDMs were run using the smallest grid size available (0.083°) since it was the lowest spatial resolution of all the raster layers. Finally, multicollinearity (strong correlation between two or more predictor variables) was evaluated pairwise by computing the Variable Inflation Factor (VIF) using the usdm package (version 1.1-8; Naimi and Araújo, 2016) in R (R Development Core Team). When two predictor variables are highly correlated (correlation coefficient is close to ±1), the VIF value will be large. It is generally accepted that VIF = 10 indicates concerning collinearity between two predictor variables although more conservative opinions consider lower values of VIF as an indicator of collinearity (O'Brien, 2007). Therefore, VIF threshold value was set at 5 which resulted in the exclusion of salinity, SST standard deviation, and Chla standard deviation from the final analysis due to the detection of multicollinearity (VIF >5). Details of selected variables are presented in Table 2 and Fig. A1.

2.4. Species distribution modelling

We used the SSDM package (version 0.2.8; Schmitt et al., 2017) implemented in R to create species distribution models (SDMs) for each species and season, using five different algorithms. These algorithms were Generalized Linear Models or GLMs (Lee and Nelder, 2001), Generalized Additive Models or GAMs (Wood, 2017), Multivariate Adaptive Regression Splines or MARS (Friedman, 1991), Random Forests or RFs (Breiman, 2001) and Generalized Boosted Models or GBMs (Elith et al., 2008). Individual SDMs were fitted with default settings. No SDMs were run for blue whales and sei whales in spring, autumn and winter since presence data were insufficient or not available.

Pseudo-absence data were generated at random over the study area. Barbet-Massin et al. (2012) suggest that the number of pseudo-absences affects algorithm performance, and thus, it must be adjusted depending on the algorithm type utilised. By default, the functions integrated in the SSDM package generates the appropriate number of pseudo-absences following Barbet-Massin et al. (2012) recommendations. Moreover, as a considerable proportion of the data were collected opportunistically, the spatial thinning function in the SSDM package was also applied to account spatial bias.

Single-algorithm SDM performance was assessed using the "holdout" cross-validation method and the data were split into training (70%) and evaluation (30%) subsets. Models were then evaluated using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot method (Fielding and Bell, 1997). The AUC relates to the proportions of false positive and false negative classifications made by a model and ranges between 1 (perfect classification) and 0 (reciprocated classification). An AUC value of 0.5 indicates that the model is classifying no better than random (Swets, 1988). Each SDM was run and evaluated six times in total. SDMs were then used to create ensemble species distribution models (ESDMs) for each species and season, using the weighted average of the five SDMs. Only those SDMs which AUC score were at least 0.7 were included in the final ESDMs.

ESDMs variable relative importance was considered as the difference between the full model and one with each predictor variable successively omitted. It was calculated computing the Pearson's correlation (r)

Table 2
Variables selected for species distribution models and anthropogenic pressures geographic datasets.

Variable	Original resolution	Original dataset	Units	Reference
Bathymetry	1/16 arc minute	EMODnet Digital Bathymetry (DTM) - 2022	m	https://emodnet.ec.europa.eu/geoviewer
Seafloor slope	0.083°	Derived from bathymetry raster layer using the slope function (ArcGIS Pro 3.1.2)	°	https://pro.arcgis.com/en/pro-app/latest/help/analysis/raster-functions/slope-function.htm
Distance to shore	0.083°	GMT_intermediate_coast_distance_01 d	km	https://oceancolor.gsfc.nasa.gov
Sea surface temperature	0.083°	GLOBAL_MULTIYEAR_PHY_001_030	°C	https://doi.org/10.48670/moi-00021
Mixed layer thickness	0.083°	GLOBAL_MULTIYEAR_PHY_001_030	m	https://doi.org/10.48670/moi-00021
Northward seawater velocity	0.083°	GLOBAL_MULTIYEAR_PHY_001_030	m/s	https://doi.org/10.48670/moi-00021
Eastward seawater velocity	0.083°	GLOBAL_MULTIYEAR_PHY_001_030	m/s	https://doi.org/10.48670/moi-00021
Chlorophyll-a concentration	4 km	OCEANCOLOUR_GLO_BGC_L4_MY_009_104	mg/m^3	https://doi.org/10.48670/moi-00281
Maritime traffic	1 km	EMODnet_HA_Vessel_Density_all_2017–2022	h/km^2	https://emodnet.ec.europa.eu/en/human-activities
Fishing activity	0.05°	EMODnet_HA_Fisheries_Fishing_Intensity_20230508	mW fishing hours	https://emodnet.ec.europa.eu/en/human-activities

between full model's predictions and the models without the predictor in question, resulting in a final 1-r score. The higher the score, the higher the importance of a given predictor. Final ESDMs also provided habitat suitability maps in which each pixel was classified between 0 (null probability of occurrence) and 1 (maximum probability of occurrence). Uncertainty maps indicating the degree of agreement between SDMs were created to identify areas where model predictions were more dissimilar. The resolution of the final habitat suitability maps was based on the original raster size of the predictor variables.

To describe the relationship between each species presence and each predictor variable, the average response of each species to the range of values of in each predictor variable (partial effects) was computed using the rcurve function available in the sdm package in R (Naimi and Araújo, 2016). Average response curves were also computed for each SDM type (Figs. A5–A7).

2.5. Fishing effort, maritime traffic, and wind farm data analysis

To identify areas where the modelled species distribution coincided with current or planned human activity, we gathered updated spatial data (Table 2, Figs. A2 and A3) on fishing activity, maritime traffic, and offshore wind farm projects within our study area. In line with the environmental data, the original raster layers were clipped to fit our study area, resampled to a 0.083° grid using the nearest neighbour method, and reprojected to the WGS84 geographic coordinate system (EPSG: 4326). We measured the exposure of each whale species to fishing activity and maritime traffic within our study area following methods originally developed by Waugh et al. (2012) to measure susceptibility of seabirds to longlines and further adapted by several studies (Breen et al., 2016, 2017; Brown et al., 2015) for cetacean risk assessment based on Productivity Susceptibility Analysis. We utilised part of this analysis to measure the exposure (*ex*) of our five rorquals to these threats across the study area. For maritime traffic, we calculated the seasonal average vessel density (h/km^2) per grid cell, as we did previously for the environmental data since monthly resolution was available for this dataset between 2017 and 2022. In the case of fishing activity, we calculated the total annual number of mW fishing hours (fishing boats >12 m) per grid cell aggregating all the fishing gears available (beam trawls, bottom otter trawls, bottom seines, dredges, pelagic trawls, and static gears) between 2017 and 2022 (only annual resolution available). Previous authors have reported that large whales are more likely to entangle in some specific fishing gears, particularly static types such as gillnets or pots (Johnson et al., 2005). However, the gear type is unknown in a sizeable proportion of cases, and other types of gear can also cause entanglements (Frisch-Jordán and López-Arzate, 2024; Johnson et al., 2005). Fishing vessel traffic may also be responsible of other kinds of habitat degradation such as underwater noise. Daly and White (2021) suggested that noise produced by bottom trawling is a possible stressor for cetaceans in the Irish continental margins. Thus, we chose to include all the fishing gears available following the precautionary principle.

For each dataset, we calculated the exposure per cell seasonally (traffic) and annually (fishing activity) using the following formula in the raster calculator of ArcGIS:

$$ex_{cell} = \frac{P_{cell}\ x\ activity_{cell}}{P_{area}} \quad (1)$$

Where ex_{cell} is the calculated exposure per grid cell, P_{cell} is the modelled habitat suitability for each species per cell, $activity_{cell}$ is either vessel density in h/km^2 (traffic) or mW fishing hours (fishing activity) per cell, and P_{area} is the average habitat suitability of a species within the study area. For fishing activity, we annually aggregated species presence data and calculated annual average raster layers of the environmental variables to run overall ESDMs (Fig. A9) for each species, as we did for seasonal ESDMs (see above). Resulting habitat suitability maps were then combined with fishing activity data applying formula 1. Monthly fishing effort data was not available for our study area

Then, ex_{cell} was compared to the average exposure for the whole study area following Breen et al. (2016, 2017) and Brown et al. (2015) using the following formula in the raster calculator of ArcGIS:

$$ex_{score} = log_{10}\left(\frac{ex_{cell}}{ex_{mean}}\right) \quad (2)$$

Where ex_{score} is the exposure score for each cell in logarithmic scale, and ex_{mean} is the average exposure for each species to a given threat within the study area. An exposure score >1 (i.e., 10 times mean exposure) was classified as high, while a score < -1 (one tenth of mean exposure) was classified as low. Values between 1 and -1 were, therefore, considered as moderately high (>0) or low (<0), respectively.

To measure the degree of co-occurrence of the species with offshore wind farm areas awarded MACs, we calculated the average habitat suitability of each species within the wind farm polygons (on-going MAC projects and DMAP area separately) and compared it to the average habitat suitability of each species of whale in the whole study area by adapting formula 2, where ex_{cell} was the mean habitat suitability within the wind farm areas and ex_{mean} was the mean habitat suitability of the whole study area.

3. Results

3.1. Species presence data

A total of 8407 verified baleen whale species records collected between 1999 and 2021 were included in the analysis. Most records were collected during the summer months (July to September) but there were also a high number (>2000) collected in spring (April to June) and autumn (October to December). The fewest number of records (467) were collected in winter (January to March).

Minke whales accounted for more than a half (56.5%) of the total number of records, followed by fin whales (27.1%) and humpback whales (15.8%). Blue whales (0.4%) and sei whales (0.3%) were the least reported of the five species (Table 3). Minke whales were the most frequently recorded species during spring and summer, whereas fin whales were the most frequently sighted species in autumn and winter. Minke whales, fin whales, and humpback whales were reported in every single month of the year, whereas blue whales and sei whales were reported only from August to October and June to November, respectively (Table 3; Fig. A8). Minke whales and fin whales were sighted in every year of the study period. Humpback whales were absent in 2000, whereas blue whales and sei whales were recorded more sporadically throughout the study period, with most of the records collected in 2013 (Fig. A8; Baines et al., 2017). Minke whale sightings reached a peak in late spring, with a sharp decline during winter months. Fin whales reached their peak in autumn and their minimum in late winter/early spring. Humpback whales peaked in August and reached their minimum in March. Blue whales were only recorded in summer/early autumn months with a peak in September. Sei whale sightings were recorded from spring to autumn, also peaking in September. From a geographic perspective, minke whales were usually reported in coastal waters all

Table 3
Number of records per baleen whale species and season in the study area between 1999 and 2021.

	Spring	Summer	Autumn	Winter	Total
Minke	1877	1937	801	135	**4750**
Fin	170	832	1011	263	**2276**
Humpback	349	627	279	69	**1324**
Blue	0	30	3	0	**33**
Sei	2	18	4	0	**24**
Total	**2398**	**3444**	**2098**	**467**	**8407**

around Ireland, although the proportion of offshore sightings was larger during winter (Fig. 2). Fin whales usually occurred off the south coast of Ireland with a larger proportion of offshore reports in spring and particularly during the summer. Humpback whale sightings were markedly concentrated in coastal areas, especially off the southwest coasts, although sightings seemingly expanded to northern areas during the summer. Blue whale sightings were only reported offshore, particularly in the Porcupine Seabight area. Sei whales also tended to occupy waters far from the shore, although some isolated sightings occurred during the summer in coastal areas off the south and west coasts of Ireland (Fig. 2).

3.2. Species distribution models

3.2.1. Model performance

Model performance varied across species, seasons, and SDM type (Fig. 3; Table A1). The ensemble species distribution models were outperformed by at least one of the single SDMs in all cases. For minke whales, the best performing models (highest AUC value) were RFs for spring and summer, and MARS and GBMs for autumn and winter models, respectively. RFs were the best SDMs for fin whales during summer, and autumn, whereas MARS was the best in spring and winter. For humpback whale SDMs, RFs performed better in spring and autumn, MARS in summer, and GAMs in winter. The best performing SDMs for sei whales and blue whales were GBMs. On average, AUC value across all the ESDMs was 0.887, SD = 0.054. This value was exceeded, by RFs (0.898, SD = 0.055), MARS (0.895, SD = 0.057), and GAMs (0.893, SD = 0.055). The worst performing SDMs were, on average, GBMs (0.889, SD = 0.061) and GLMs (0.844, SD = 0.091).

3.2.2. Minke whales

According to the ESDMs, the most important variables for minke whales were distance from the shore in spring and summer. However, the most relevant variable in autumn was the depth of the mixed layer (Fig. 5). In winter, when the lowest number of minke whale reports were available, distance to shore and mixed layer thickness had similar relative importance. GLMs, GAMs, MARS and GBMs also followed this trend, but not RFs, which assigned relative importance more evenly across all predictor variables (Figs. A4–A7). Minke whales were more likely to occur in waters <100 km from the nearest coast and when the depth of the mixed layer was <100 m (Fig. 6). Probability maps showed that minke whales occurred in all coastal areas of Ireland, the North Channel and off the west coasts of Scotland and Wales, especially during spring and summer. The probability of occurrence decreased northwards in autumn, with the lowest probability of occurrence happening in winter. Uncertainty was also higher at this time of the year (Fig. 4).

3.2.3. Fin whales

ESDMs indicated that the most important variables that explained fin whale distribution were SST, followed by mixed layer thickness in spring and winter. Mixed layer thickness was the most important variable during the rest of the year, especially in autumn (Fig. 5). In general, SDMs agreed in this regard although some discrepancies were observed. For example, GLMs assigned high relative importance to chlorophyll-a concentration in spring and winter, and eastward seawater velocity, also in winter. GBMs yielded higher relative importance for distance to

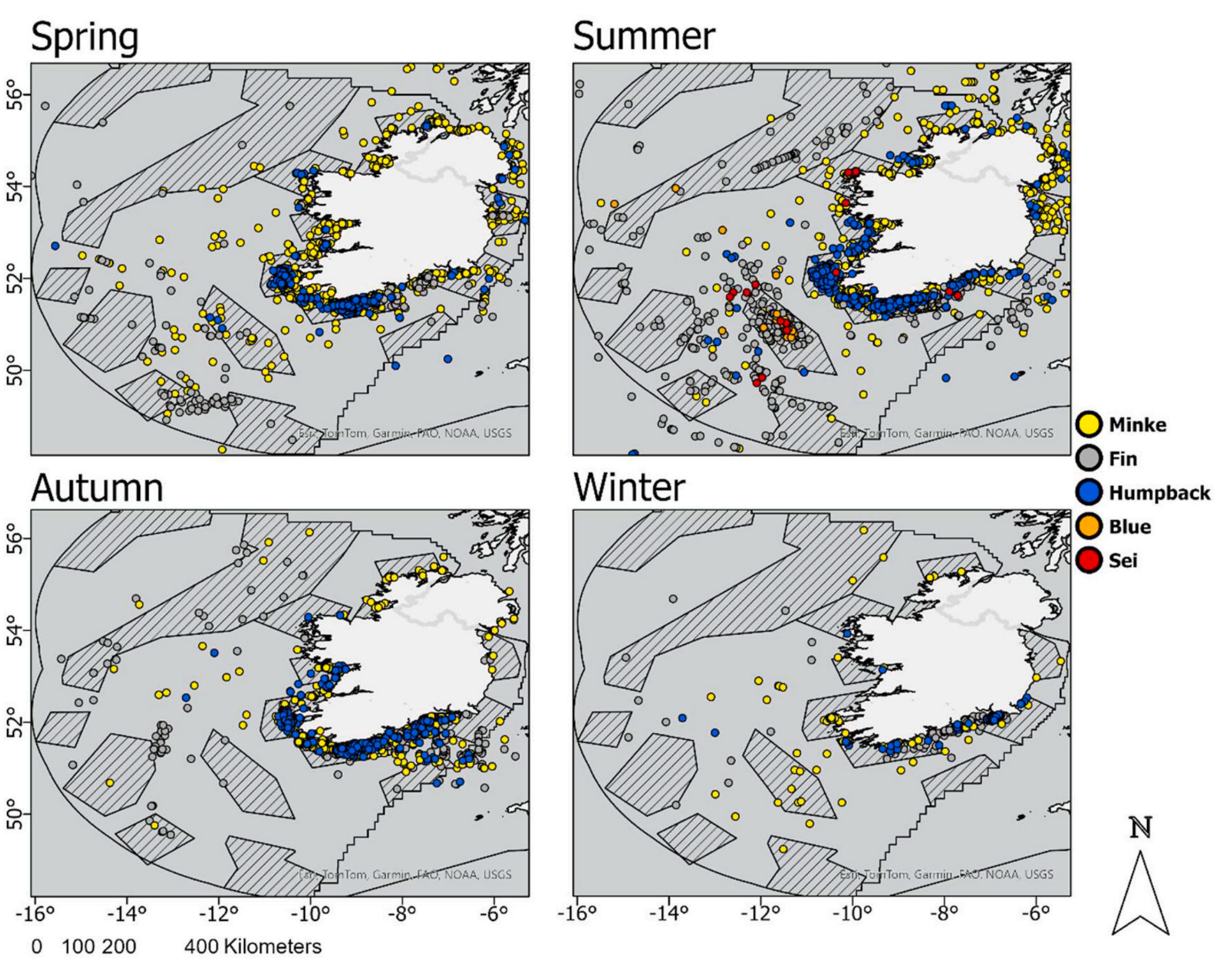


Fig. 2. Seasonal baleen whale species presence data (1999–2021) used to run ESDMs. Striped polygons represent Areas of Interest proposed by Classen et al. (2022).

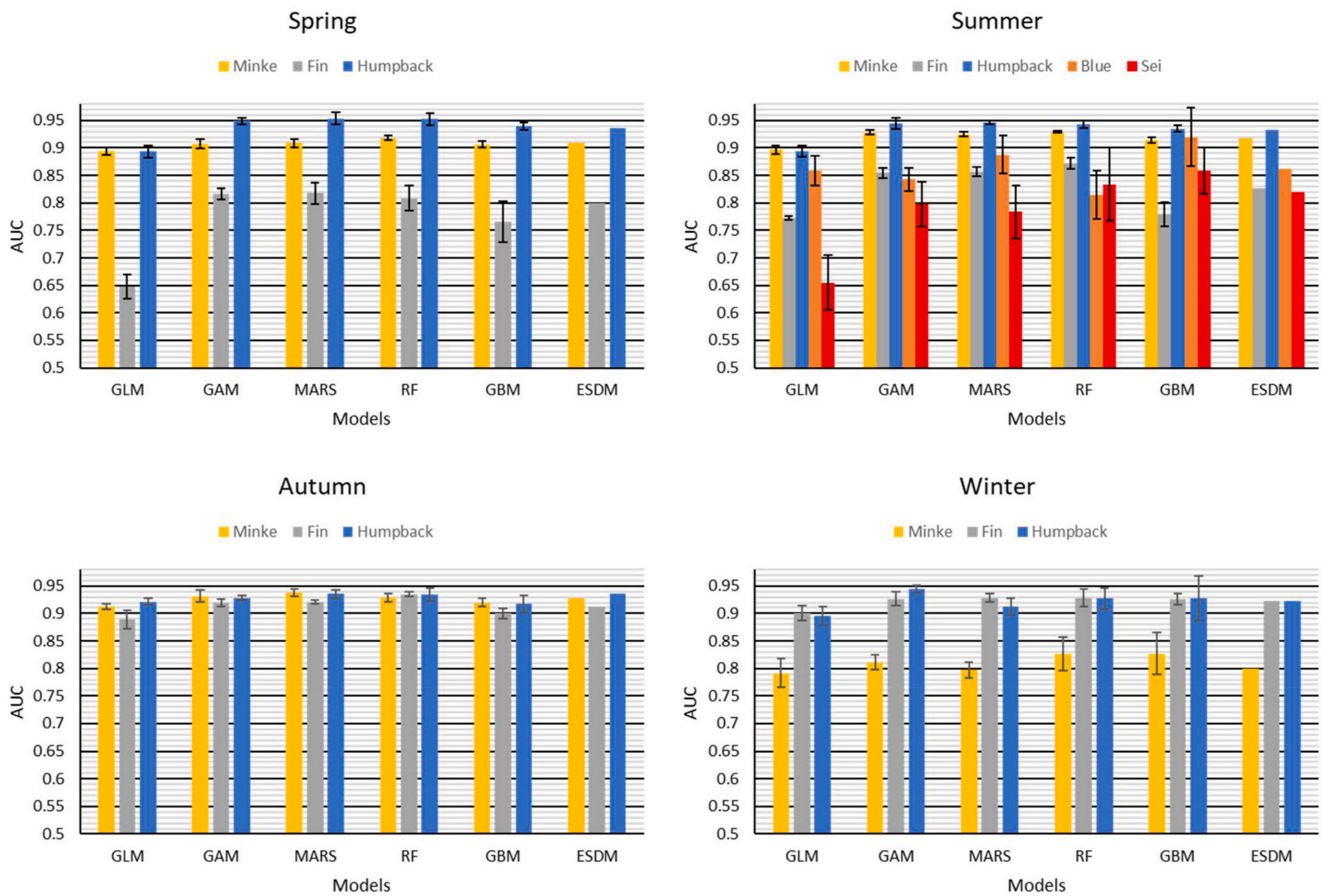


Fig. 3. The Area Under the Curve (AUC) scores of ESDM and individual SDMs for minke whales, fin whales, humpback whales, blue whales and sei whales. GLM = Generalized Linear Models, GAM = Generalized Additive Models, MARS = Multivariate Adaptive Regression Splines, RF = Random Forests, GBM = Generalized Boosted Models. Error bars indicate standard deviation (n = 6).

shore in winter and seafloor slope in summer (Figs. A4–A7). Fin whales were more likely to occur in waters between 9 and 12 °C in winter, and between 10 and 14 °C in spring. The highest probability of occurrence was predicted when the depth of the mixed layer was between 0 and 100 m (Fig. 6). Fin whale predicted distribution was variable and complex from both temporal and geographical perspectives. In spring and summer, higher suitable habitats were predicted off the south coast of Ireland, with relatively suitable areas further offshore in the Porcupine Seabight. In autumn, the highest probability of occurrence was predicted off the south and southwest coasts of Ireland but not further offshore. Similar predictions occurred during winter when the species was less likely to occur than in other seasons (Fig. 4).

3.2.4. Humpback whales

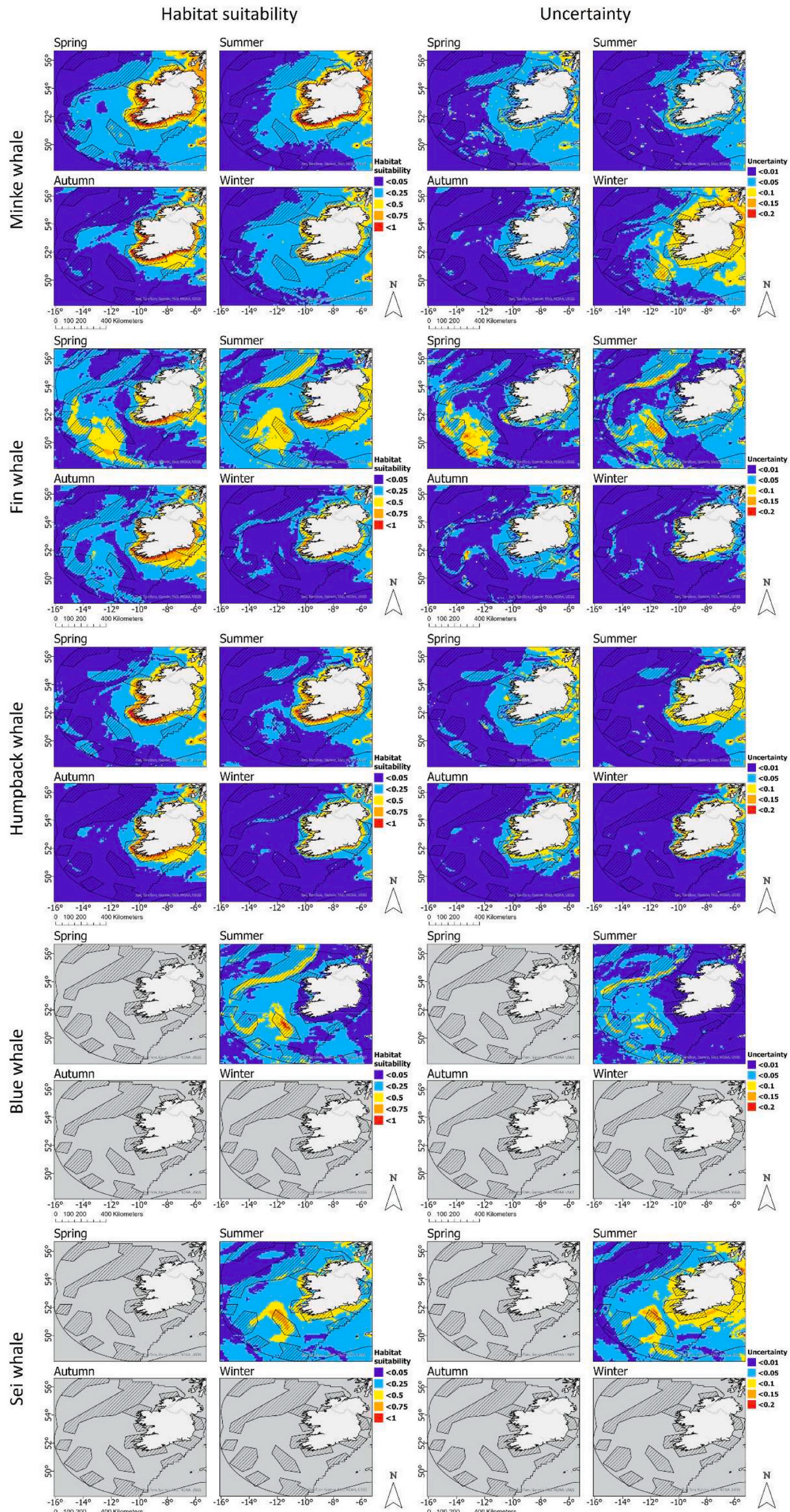
ESDMs indicated that the most important variables influencing humpback whale distribution were distance to shore and SST during spring, distance to shore during summer, and mixed layer thickness during autumn. In winter, the most important variable was chlorophyll-a concentration, followed by mixed layer thickness and eastward seawater velocity (Fig. 5). GAMs, MARS, and RFs also indicated high importance of distance to shore during spring. All SDMs except GLMs also assigned the highest importance to distance to shore in summer. During autumn, all SDMs concurred that the mixed layer thickness was the primary factor influencing the distribution of humpback whales. However, SDMs tended to disagree in winter. The most important variables were eastward seawater velocity and chlorophyll-a concentration for GLMs, mixed layer thickness for GAMs, bathymetry and SST for MARS, distance to shore for RFs, and bathymetry and distance to shore for GBMs (Figs. A4–A7). In every season, humpback whales were more likely to occur in waters less than 50 km from the nearest shore and when the depth of the mixed layer was less than 100 m. In spring, they were more likely to prefer waters at 11–13 °C, while during winter, they preferred waters with 2–3 mg/m^3 of chlorophyll-a (Fig. 6). The presence of humpback whales was more probable in waters close to the shore off the southwest coast of Ireland, especially from west Cork to west Kerry in spring, summer, and autumn. Relatively high habitat suitability was also predicted in some areas off the west coast of Ireland, Irish Sea, North Channel and west coasts of Scotland, Wales, and Cornwall from spring to autumn. The lowest probability of occurrence was predicted during winter months and in offshore waters throughout the entire year (Fig. 4).

3.2.5. Blue whales

Summer ESDM for blue whales predicted that distribution of this species was influenced by the seafloor slope, followed by distance to shore (Fig. 5). GLMs, MARS, RFs and GBMs agreed in this regard, although GLMs and MARS also assigned higher relative importance to distance to shore than the other models. GAMs indicated that the most important variable was SST, followed by slope (Figs. A4–A7). Blue whales were more likely to happen where the seafloor slope was 2° or more, in waters not further than 200 km from the nearest coast (Fig. 6). Probability maps showed that the most suitable habitat for blue whales was an area in the Porcupine Seabight with intermediate probability of occurrence in waters over the continental margins where seafloor slope was steeper. Uncertainty was also higher in these areas (Fig. 4).

3.2.6. Sei whales

The distribution of sei whales was explained by distance to shore and slope of the seafloor, according to the ESDM (Fig. 5). All the SDMs



(caption on next page)

Fig. 4. Ensemble model projections and uncertainty maps for each species and season. For habitat suitability, colours indicate habitat suitability (red = high predicted probability of occurrence, blue = low predicted probability of occurrence). For uncertainty, colours indicate the degree of agreement between SDMs (red = higher disagreement, blue = lower disagreement). Black line indicates the Irish Exclusive Economic Zone and polygons represent the Areas of Interest proposed by Classen et al. (2022) for Irish waters (Fig. 1).

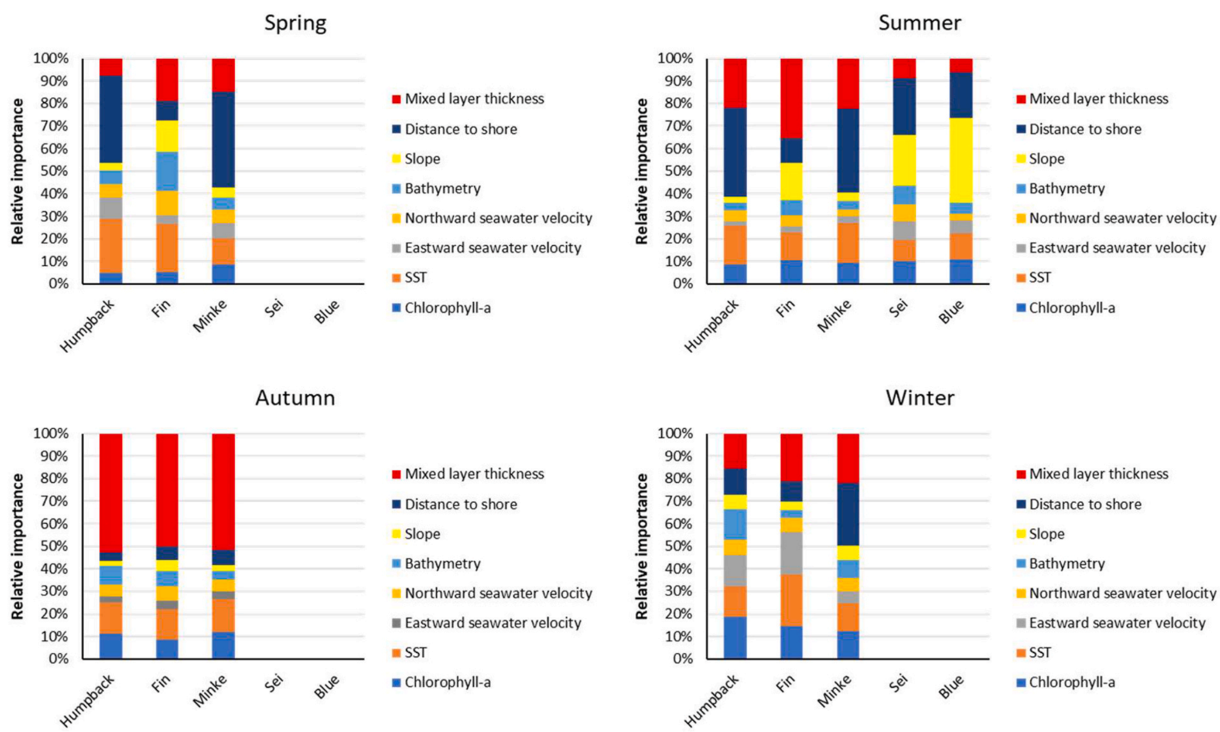


Fig. 5. Relative variable importance of the eight environmental predictors used to run ESDMs per species and season.

tended to agree in this regard with some differences between them. GAMs assigned the highest relative importance to SST, whereas RFs did so with mixed layer thickness. GAMs also yielded relatively high importance to chlorophyll-a concentration (Figs. A4–A7). Sei whales were more likely to occur in areas where the seafloor slope was 1° or higher and no further than 200 km from the nearest shore (Fig. 6). Sei whale presence was more probable in an area within the Porcupine Seabight. The species was also likely to occur in waters over the continental margins and some coastal areas of Ireland, particularly off the south coast and in Broadhaven Bay (Co. Mayo, west coast of Ireland). The highest uncertainty occurred in the Porcupine Seabight and off Northern Ireland, in the North Channel (Fig. 4).

3.3. Maritime traffic, fishing activity and wind farms

3.3.1. Maritime traffic

Limited spatial variability was evident in maritime traffic exposure across species and seasons, probably due to established routes and stable traffic levels throughout the year. Areas of highest exposure included the Irish Sea, the North Channel, and the western English Channel for minke whales, fin whales, humpback whales and sei whales, indicating high traffic density occurring between Ireland, the UK, and the rest of Europe. The eastern half of the study area was classified as moderately high in terms of marine traffic exposure. Certain zones surrounding major ports and harbours of the east and south of Ireland, such as Cork, were classified as highly exposed to traffic for minke whales, fin whales and humpback whales. In contrast, in the western half of the study area, only blue whales and sei whales were highly exposed to traffic in the Porcupine Seabight area, due to the concentration of fishing vessels in that zone (Fig. 7, A2, A3).

3.3.2. Fishing activity

Fishing activity information was only available at an annual resolution and no seasonal maps could be derived. Some geographical differences across species were observed in terms of exposure to fishing effort. High exposure to fishing activity was found between 50 and 100 km off the south coast of Ireland and in the Irish Sea for minke whales, humpback whales, fin whales and sei whales. Some areas further offshore around the shelf edge, the Porcupine Bank, and the Porcupine Seabight were classified as highly exposed to fishing activity for blue whales, sei whales and, to a lesser extent, fin whales. In general, within these waters, along with those off the south of Ireland, all the species were moderately exposed to fishing activity (Fig. 7).

3.3.3. Wind farms

The exposure analysis was adapted to quantify the co-occurrence of each species within potential offshore renewable energy production areas by comparing the mean habitat suitability for each species inside and outside of these areas. In all the cases, scores indicated moderate differences between these values (between −1 and 1). Moreover, those species that were more likely to occur in coastal waters, such as minke whales and humpback whales, yielded the highest scores either within the recent MAC consented wind farm areas in the Irish Sea or in the DMAP area off the southeast coast (Table 4). On the other hand, species that were more likely to occur further offshore (fin whales, sei whales and blue whales) scored lower. Only one species yielded negative scores, the blue whale, indicating this was the only species that, on average, was less likely to occur within wind farm development areas than in the rest of the study area.

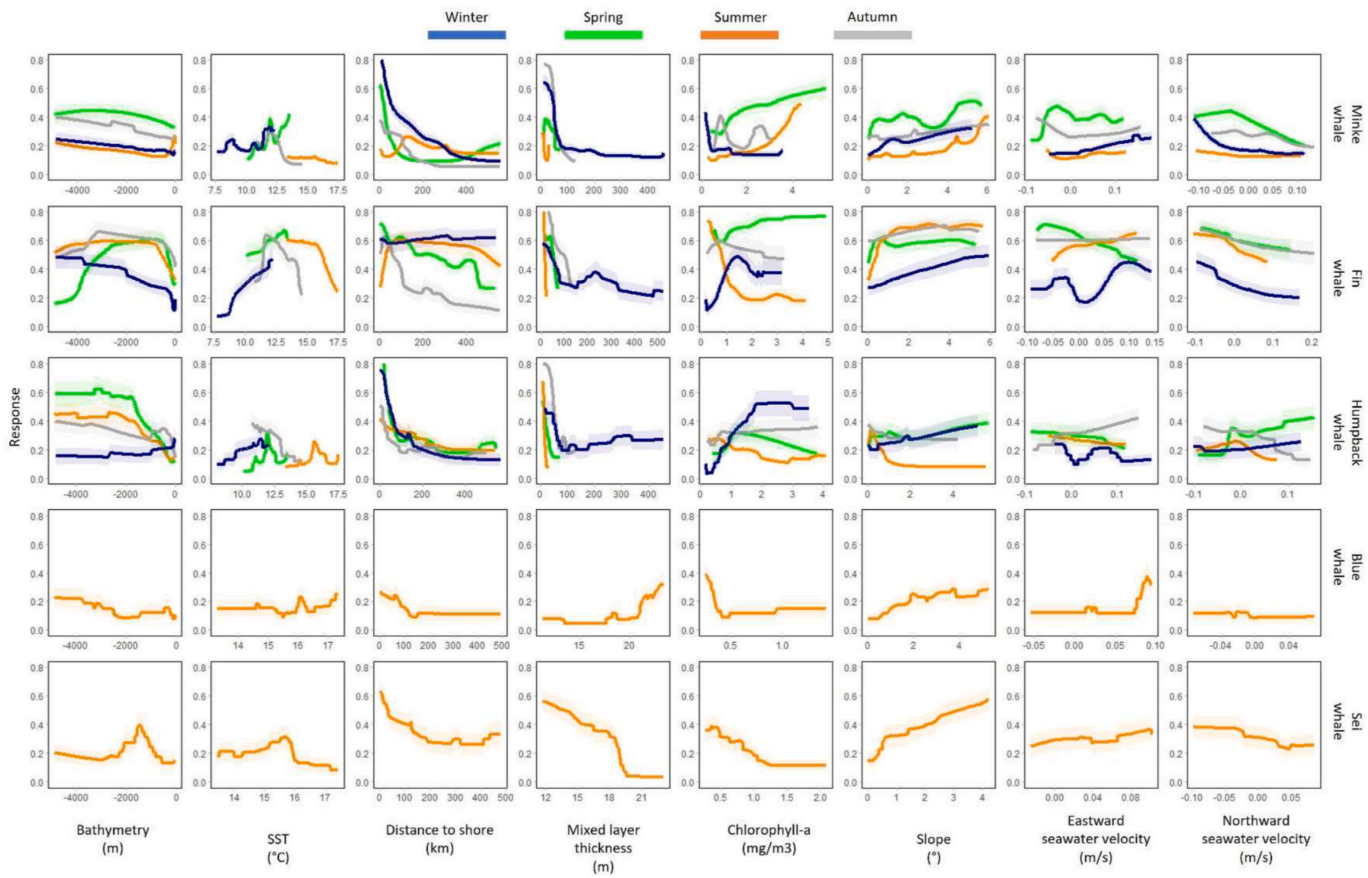


Fig. 6. Average response curves from each SDM for each species and season (n = 30). The y-axis indicates the probability of occurrence of each species along the range of each predictor variable (x-axis). Shadowed areas denote 95% confidence intervals.

4. Discussion

4.1. Data quality and model performance

Data quality and characteristics were diverse as they were gathered under different protocols and scenarios, with most collected through citizen science schemes. Associated effort which determines absence data was not available, which resulted in the generation of pseudo-absence datapoints to compute habitat suitability maps of the study area. Despite its intrinsic constraints, this methodology can be useful to create informative species distribution models and has been previously applied in similar studies involving large cetaceans (Purdon et al., 2020b; Torres et al., 2008). Following these studies and the recommendations from Barbet-Massin et al. (2012), the number of pseudo-absences was generated accordingly to the SDM type that was utilised. Spatial thinning was also applied to reduce to some extent the possible effect of geographic bias in the datasets, contributing to highly performing species distribution models in general terms (Fig. 3). In any case, the possibility of a geographic bias in the data cannot be ruled out in the view of the observed distribution of some species such as the humpback whale (Fig. 2). This may be due to an actual habitat preference of the species but also to data collection limitations, especially those of citizen scientists, who usually observe from the shore or within coastal waters, near to their place of residence.

Although some SDMs outperformed the final ESDMs, other SDMs were under the model selection threshold (AUC $\geq$0.7). None of the ESDMs yielded an AUC value below 0.8, and were, in many cases, above 0.9, which can be considered an excellent model performance (Swets, 1988). Individual SDMs outperforming ESDMs has been reported previously in the literature (Hao et al., 2020; Purdon et al., 2020b). These studies suggested that this may be caused by finely tuned SDMs (in our study SDMs were fitted using default settings) or when ESDMs were used to predict to more geographically distant areas (Hao et al., 2020). On average, RFs, MARS, and GAMs produced higher AUC values than ESDMs, however, overfitting may also be an issue for some individual SDMs. For example, response curves of RFs or GBMs were consistently flatter than those of other SDMs, indicating some degree of overfitting (Derville et al., 2018; Purdon et al., 2020b). Compared to other SDMs, RFs tended to assign similar levels of importance to all predictor variables (Fig. A4), making more difficult to interpret model outcomes in ecological terms. GLMs tended to provide more intuitive results although their performance was usually poorer (Fig. 3, Table A1). GAMs and MARS usually performed well but were not the best performing SDM in all the cases (Fig. 3, Table A1). In addition, SDMs performance seemed to be poorer when the number of datapoints decreased across species and season, and/or when sightings were more evenly distributed over the study area (e.g., minke whale SDMs in winter). This suggests that overfitting and outperforming SDMs may be a consequence of geographical bias in the presence data.

Studies that explored the performance of a range of models using real or virtual species distribution data (Araújo and New, 2006; Derville et al., 2018; Qiao et al., 2015; Purdon et al., 2020b) agreed on the difficulty of selecting an optimal species distribution model. Instead, they suggest that model selection will be dependent on the peculiarities of the data and the questions or goals to be addressed by a given study, implying that the use of multiple modelling techniques is a desirable approach. For our case study, ensemble species distribution modelling represented a robust solution regarding model selection. ESDMs provided a balanced trade-off between model performance and ecologically meaningful results, incorporating the variability in the predictions made

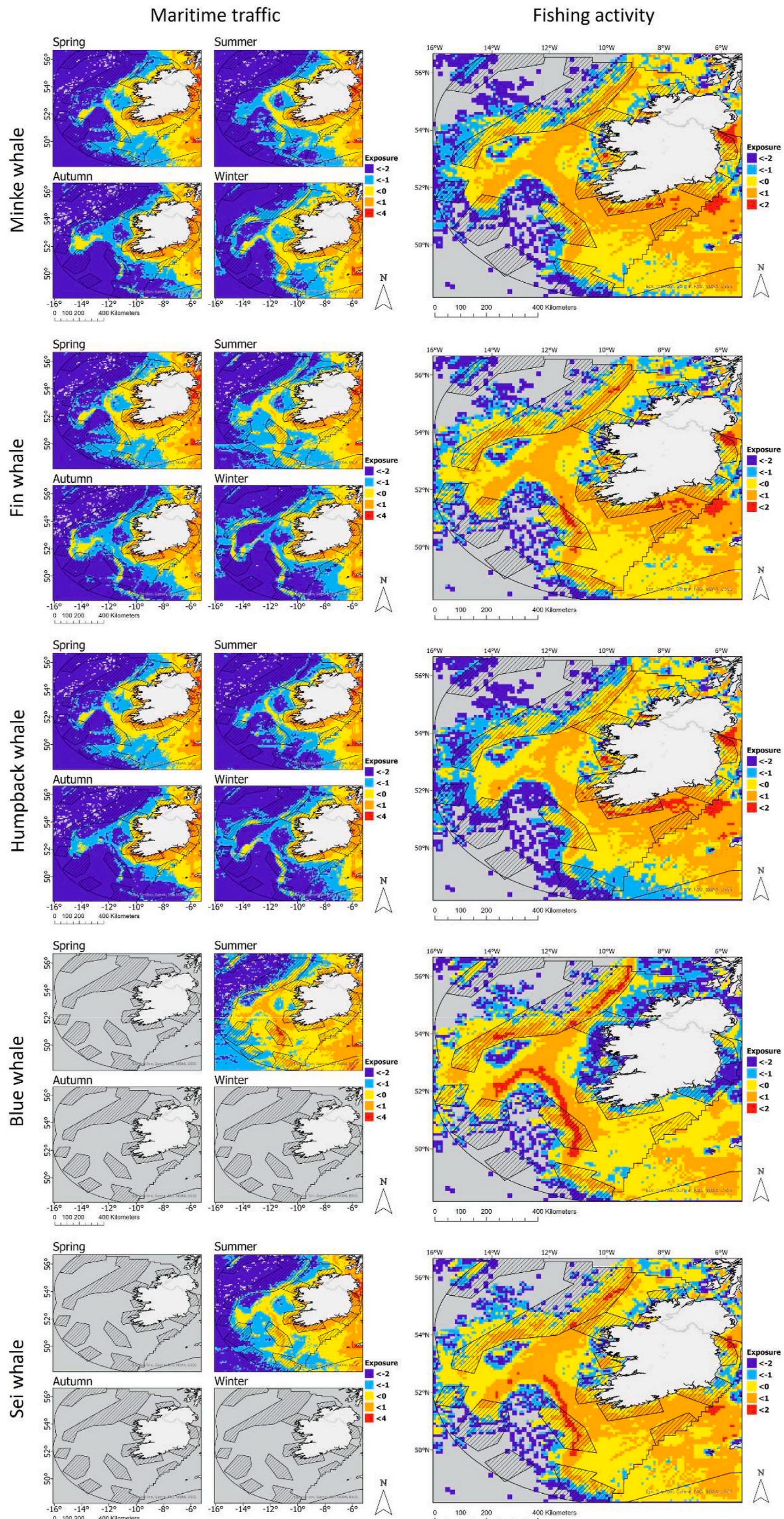


Fig. 7. Classification of the study area according to the exposure of each species to maritime traffic (seasonally) and fishing activity (annually). Red denotes high exposure areas while the rest of the colours indicate moderate to low exposure of a given species to a given activity. Striped polygons represent Areas of Interest proposed by Classen et al. (2022).

Table 4
Average habitat suitability per species and season in the study area, MAC wind farm areas and DMAP area, including exposure scores.

Species	Habitat suitability study area	Habitat suitability MAC wind farms	Habitat suitability DMAP	Score MAC wind farms	Score DMAP	Season
Minke	0.14	0.61	0.50	0.65	0.56	Spring
Humpback	0.10	0.36	0.38	0.57	0.59	
Fin	0.12	0.24	0.50	0.30	0.62	
Minke	0.11	0.63	0.51	0.74	0.65	Summer
Humpback	0.08	0.38	0.42	0.68	0.72	
Fin	0.15	0.26	0.54	0.22	0.54	
Blue	0.10	0.02	0.03	−0.74	−0.57	
Sei	0.13	0.21	0.32	0.21	0.39	
Minke	0.08	0.55	0.49	0.82	0.78	Autumn
Humpback	0.07	0.47	0.51	0.82	0.85	
Fin	0.10	0.55	0.60	0.72	0.76	
Minke	0.11	0.36	0.36	0.52	0.53	Winter
Humpback	0.05	0.32	0.24	0.84	0.72	
Fin	0.05	0.30	0.36	0.75	0.83	

by all the individual SDMs, while also facilitating comparisons across species.

4.2. Baleen whale species distribution in Irish waters

4.2.1. Minke whale

Minke whale sightings were widespread in the coastal waters of Ireland although numbers varied markedly across seasons, with a peak between spring and summer and a decline during autumn and winter (Table 3; Fig. A8). Probability maps computed by ESDMs also supported this distribution with lower habitat suitability and higher uncertainty during winter (Fig. 4). Wall et al. (2013) reported similar seasonal distribution patterns using sighting data between 2005 and 2011. Breen et al. (2016) also used data from SCANS I-II and CODA surveys (part of which are also included in this study), as well as data from the National Biodiversity Data Centre in Ireland to model suitable habitats of a range of cetaceans in Irish waters, including the minke whale. They only used summer data (approx. 50 records) and their models indicated suitable habitats for minke whales in the Irish shelf waters, with higher probability in the North Channel and some coastal areas of the south of Ireland. This contrasts with the low habitat suitability predicted by ESDMs for offshore waters reported here, although we incorporated much larger numbers of minke whale records (4,750) which were proportionally more concentrated in coastal areas.

Despite being the most frequently reported balaenopterid in Irish waters, little is known about the species winter movement patterns outside of Irish coastal waters given the absence of any tracking schemes. However, they are known to also occur far from the coast during summer. Hammond et al. (2007) estimated that almost 7000 (CV = 0.99) minke whales occurred in July 2007 in the offshore waters between NW Scotland and NW Spain. Our ESDMs indicated a clear preference for inshore waters with a marked seasonal variability in species presence, supporting the suggestion by Rogan et al. (2018) of annual movements in and out of the Irish EEZ. This would indicate that minke whales move into Irish coastal areas during spring and summer, with a following migration towards southern breeding grounds during autumn and winter months. This has been supported by acoustic monitoring (Risch et al., 2014). It is also possible that minke whales follow seasonal inshore-offshore movements as suggested by offshore sightings of calves within our study area in autumn and winter (Kavanagh et al., 2018). This was also supported by ObSERVE aerial surveys (Rogan et al., 2018) that recorded minke whale sightings offshore during winter in Irish waters. Additionally, acoustic monitoring stations recorded some isolated minke whale vocalisations in spring and autumn 2015 to the west of the Rockall Trough (Fig. 1). No vocalisations were detected during the summer (Berrow et al., 2018). This evidence, beside the predictions of the presented ESDMs, would support that minke whales migrate into Irish coastal waters to feed during spring and summer, while vacating these inshore waters during winter months. Minke whales are known to feed on schooling fish in our study area (Volkenandt et al., 2016) which indicates its relevance for the species, especially in spring and summer. Photo-identification or tag-based studies would provide further evidence of the movement and residency patterns of the species in these waters, a matter that remains poorly understood due to a lack of comprehensive research effort.

4.2.2. Fin whale

Fin whales were the second most frequently recorded baleen whale species and the one with the most widespread distribution throughout the study area (Table 3 and Fig. 2). ESDMs predicted seasonal variability in their distribution, with higher habitat suitability in offshore waters over the slope during spring and summer, as well as in coastal areas to the south of Ireland (Fig. 4). During their peak occurrence in autumn, ESDMs predicted higher probabilities in coastal waters off the southern half of Ireland. This coastal distribution of fin whales was not reported by Breen et al. (2016), although their models included very few inshore fin whale sightings since most of their data were gathered during offshore surveys. However, they did predict that the summer distribution of fin whales was associated with higher seafloor slope areas. Wall et al. (2013) reported the coastal occurrence of fin whale off the southern shores of Ireland, especially during summer and autumn months. Offshore acoustic detections of fin whales were reported by Berrow et al. (2018) at several locations over the continental margins during 2015 and 2016, with an increase in detections from spring to autumn which supports the results of this study (Fig. A8). The fin whale population structure in the North Atlantic is complex and the subject of debate. Several possible stock structures have been proposed, with Ireland lying between two of these stock subdivisions (International Whaling Commission - IWC, 2009; North Atlantic Marine Mammal Commission - NAMMCO, 2007). The CODA survey (2007) provided a summer abundance estimate for fin whales of approximately 9000 (CV = 0.11) individuals, which included part of our study area. However, the movement patterns of these animals are not completely understood and may be driven by prey availability. Ryan et al. (2013, 2014) confirmed that fin whale diet range may be wider than those of minke whales or humpback whales. This indicates that either fin whales target more diverse feeding webs (krill and clupeids) and/or that fin whale feeding areas were less geographically restricted than those of minke whales or humpback whales. Fariñas-Bermejo et al. (2023) found a positive correlation between fin whale presence and sprat (*Sprattus*) density in the Celtic Sea in autumn, suggesting the relevance of this area as a feeding ground for the species. In addition, the only photo-ID study on fin whales in Ireland by Whooley et al. (2011) indicated some degree of site fidelity to the inshore waters to the south of Ireland. These studies postulated longitudinal movements of individual fin whales within the study area, which would explain ESDMs predictions (see Fig. 4). These movements could imply that fin whales occurring inshore would also feed in offshore waters within the Irish EEZ (Ryan et al., 2014). Other examples of the fin whale complex stock structure and movement patters in the NE Atlantic have been provided by bio-logging studies. A single individual that was tagged off the Faroe Islands in August 2001, migrated into the Bay of Biscay one month later and was finally detected circling around in the south edge of the Rockall Trough (NW Ireland) by October of the same year (Mikkelsen et al., 2007). More recently, Lydersen et al. (2020), also reported southbound movements of fin whales tagged off Svalbard in September. One individual transited southward throughout our study area and spent some time in the southern edge of the Porcupine Seabight by October–November, indicating the existence of a feeding ground in that area. Further development of fin whale photo-identification catalogues (Dudley et al., 2023; Whooley et al., 2011) and the incorporation of drone imagery in this task (Degollada et al., 2023), may provide a cost-effective opportunity to investigate if individual fin whales occur either in coastal and/or offshore waters of Ireland, filling the gaps in our understanding of fin whale ecology and movement patterns within Irish waters and beyond.

4.2.3. Humpback whale

Humpback whales were the third most frequently reported baleen whale species in the Irish EEZ (Table 3). ESDMs predicted the most suitable areas for this species was off the southwest coast of Ireland, with habitat suitability decreasing northeasterly (Fig. 4). Little spatial variability occurred across seasons, although the species was less likely to occur in the study area during winter months. The humpback whale is a migratory species well known to undergo long-range movements between their feeding grounds at high latitudes and their breeding grounds in the tropics. In the North Atlantic, the breeding season occurs during winter months in the Caribbean, including Silver and Navidad Banks in Dominican Republic, Guadeloupe (Clapham and Mead, 1999; Stevick et al., 2018), and in the Cabo Verde archipelago, (West Africa), particularly around the island of Boa Vista (Punt et al., 2006; Wenzel et al., 2020). Humpback whales are also known to regularly visit high latitude feeding grounds in the western (U.S., Gulf of Maine; Eastern Canada including Nova Scotia, Labrador, Newfoundland and Gulf of Saint Lawrence and West Greenland) and eastern (Iceland, Norway, and Svalbard) North Atlantic during the summer (Katona and Beard, 1990; Palsbøll et al., 1997; Stevick et al., 1999). Although sightings have occurred in winter, the low probability of occurrence predicted by the models at that time of the year is consistent with this migratory pattern as mature animals would migrate out of the study area during colder months towards their breeding grounds in the tropics. Thanks to photo-identification, these migratory movements have been demonstrated with humpback whale matches between Ireland, Cabo Verde, the Dominican Republic, and Bermuda with some individuals having also been reported in Iceland and Norway (Berrow et al., 2021).

Humpback whales are known to feed on small schooling fish such as sprat in Irish coastal waters (Fariñas-Bermejo et al., 2023; Ryan et al., 2014), with high resighting rates and residency times of up to 186 days (Berrow et al., 2021; Berrow and Whooley, 2022); suggesting that Irish waters are an important feeding area for the species. The presence of humpback whales in the area also seems to have increased over the last decade (Blázquez et al., 2023). Humpback whale abundance is estimated to be around 10,500 individuals in the North Atlantic (Smith et al., 1999) but the number of individuals occurring in Irish coastal waters appears to be small, with 154 ± 9 individuals estimated to have been present in the area between 1999 and 2022 (Blázquez et al., 2023). These numbers might explain the lack of offshore observations where densities are presumably low, the animals are more mobile, and less likely to be detected by visual offshore surveys such as CODA (Hammond et al., 2007) or ObSERVE (Rogan et al., 2018). Humpback whales have been detected in offshore waters around Britain and Ireland using acoustic monitoring. Charif et al. (2001) reported consistent detections of humpback whale songs between October and March with a south-westerly detection pattern from the Shetland/Faroe Islands along the western margin of Britain and Ireland. Humpback whale songs have also been reported by more recent acoustic projects COMPASS (van Geel et al., 2022) and ObSERVE (Berrow et al., 2018). Vocalisations were detected in spring (April–May) off the west coast of Scotland and Northern Ireland, and in deeper waters around the Porcupine Bank and Seabight. This suggests the existence of migratory corridors further offshore that were not reflected by ESDMs predictions. Given that most of the humpback whale presence data used in the present study were collected under a citizen science scheme, the results may reflect geographic bias due to the inherent data collection limitations of citizen scientists, although it is also plausible that, a sub-group of humpback whales prefer to exploit Ireland's inshore waters as a feeding ground, given the high resighting and site fidelity rates observed by some individuals (Berrow et al., 2021; Blázquez et al., 2023).

4.2.4. Blue whale

Blue whales were very poorly represented in the data (Table 3) and were the only species with no reported coastal sightings (Fig. 2). The most suitable areas were predicted in the Porcupine Seabight, with lower probability of occurrence associated with the northwestern margins of the Irish shelf (Fig. 4). This distribution matches acoustic detections from the ObSERVE project that reported blue whale vocalisations from August to November within our study area (Berrow et al., 2018). Like other rorquals, blue whales are a highly migratory species and undergo long seasonal migrations between high latitude feeding grounds, where the largest aggregations occur during the summer, and low latitude breeding areas in winter. The species was more abundant in the eastern North Atlantic in the past as suggested by whaling records. According to Ryan et al. (2022), 500 blue whales were landed at whaling stations on the west coast of Scotland during the first half of the 20th century. This figure is an order of magnitude greater than the landings of more abundant species nowadays, such as the humpback whale. Similar conclusions were reached by Fairley (1981), recently revised by Ryan (2022), for a whaling station located on the Mullet Peninsula (Co. Mayo, NW Ireland) that captured 126 blue whales and only six humpback whales during its period of activity, although this may be due to whalers' preference towards the larger blue whales (Ryan, 2022). The most recent abundance estimates in the North Atlantic were derived by Pike et al. (2019) within the framework of the North Atlantic Sighting Survey (NASS) in the summer of 2015. They provided an abundance of 3000 (CV = 0.4) individuals for the area between Greenland and Iceland, making the blue whale likely to be the least abundant species of those analysed in this study. This may explain the small number of records of the species in Irish waters, in addition to their consistent offshore distribution in our study area where observation effort is limited. The observations by Baines et al. (2017) during a dedicated survey in the Porcupine Seabight area between the summer and autumn of 2013 added 16 individuals reported during 12 sighting events, exceeding the previously confirmed number of total records for the species in Irish waters. These records were also included in the present study and our ESDM results are like those of Baines et al. (2017), with seafloor rugosity (slope) being an important predictor of whale aggregation size. The results presented here and those from previous studies show that blue whales use offshore Irish waters as a corridor, at least for their seasonal southbound migration (Lesage et al., 2017). Feeding activity of blue whales in these offshore waters has been suggested by visual surveys (Wall et al., 2009). Evidence is not sufficient to identify the Porcupine Seabight as well-established feeding area for this species as current data may just reflect a punctual whale incursion into the area due to transitory high prey densities. Further systematic survey effort is required to better understand the importance of this geographic area for blue whales and other rorqual species.

4.2.5. Sei whale

Sei whales were markedly less frequent in the data than other species (Table 3) and ESDMs could only be run for summer months (Fig. 4 and A8). The most suitable habitats were predicted to be found in waters around the shelf edge in the Porcupine Seabight. A high probability of occurrence was also predicted off northwest Ireland, with intermediate habitat suitability values off the southern coast, due to the existence of a small number of presence records in these areas (Fig. 2). Information regarding sei whale biology and ecology is more limited in the North Atlantic than for other species included in this study. As with other rorquals, they were targeted by industrial whaling operations in the eastern North Atlantic and appeared to occur in low densities in areas covered by dedicated offshore surveys (Prieto et al., 2012). Ryan (2022) reported that 91 sei whales were landed at two whaling stations in northwest Ireland during the first quarter of the 20th Century, being the third most captured species after fin whales and blue whales. More recently, summer abundance estimates have been derived for several regions in the North Atlantic, ranging widely from 71 (CV = 1.01) in the Gulf of Maine in 2002 (Waring et al., 2009) to 10,300 (CV = 0.27) in the Iceland-Denmark Strait in 1989 (Cattanach et al., 1993). The CODA project could not derive an estimate for our study area but provided an abundance of 366 (CV = 0.33) for northwestern Spain. Similarly, ObSERVE visual surveys only reported two sei whale sightings in Irish waters, both during winter 2016–17, although some additional individuals could have been mis-identified as fin whales (Rogan et al., 2018). Sei whales also present a complex stock structure with Ireland falling within the eastern block, which covers all European waters except Iceland (Prieto et al., 2012). According to the same study, sei whale sightings were concentrated in deep waters between Greenland and Iceland, with fewer reports in adjacent areas. In the Bay of Biscay, the species was observed during late summer to early winter, which corresponds with the presence data used in this study. The species was also acoustically detected at the same time of the year by Berrow et al. (2018) along the northwest shelf edge of Ireland. This timing may reflect latitudinal movements throughout the study area between their feeding grounds in colder and temperate waters and their breeding grounds in warmer areas of the North Atlantic (Prieto et al., 2014). Occasional sightings of sei whales feeding in Irish coastal waters have also been documented (Oudejans and Visser, 2010). Most of the sei whale sightings in this study and the most suitable habitats predicted occurred in the Porcupine Seabight during the summer (Fig. 4), which would support the presence of a feeding area for this species (Baines et al., 2017). Available data are sparse, with reduced temporal resolution, and further systematic survey effort is required to investigate if this area is a well-established feeding ground.

4.3. Management implications

The waters around Ireland up to 200 nautical miles offshore were declared a Whale and Dolphin Sanctuary in 1991 (Rogan and Berrow, 1995). Current MPAs barely represent the 8.4% of the area of the Republic of Ireland's EEZ, with limited offshore coverage (Marine Protected Area Advisory Group, 2020). Only two species of cetaceans, namely bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*), are recognised in Annex II of the Habitats Directive as qualifying interests for the designation of marine protected areas in Ireland, specifically Special Areas of Conservation or SACs (Enright, 2021). Currently, these protected sites are relatively small and likely do not cover the whole range of the populations they are aimed to protect (e.g., Levesque et al., 2016). In the case of large baleen whales, a small percentage of their home range falls within protected areas of any kind in Irish waters. Our models show that coastal waters around Ireland provide suitable habitats for minke whales, fin whales and humpback whales. Probability maps showed an overlap between suitable habitats for these species and proposed AoI 9–13 (south and west coasts of Ireland) from spring to autumn. Moreover, the AoI 6, on the eastern side of the Porcupine Seabight overlapped with suitable areas for sei whales, blue whales, and fin whales during the summer. In a more marginal manner, the AoI 2–4 (southeast of the Rockall Trough and Porcupine Bank slopes) overlapped with suitable habitats for the same species during summer months. It is important to consider that the implementation of effective area-based protection measures for the large whales, such as MPAs, is challenging due to the extremely wide ranges and migratory patterns of these animals. However, appropriate management and protection actions at a local level may have a positive impact in the conservation of these species, especially considering the site fidelity that has been observed in some species like humpback whales and fin whales (Berrow et al., 2021; Whooley et al., 2011). They may provide tools to mitigate the impacts generated by disruptive human activities within the study area. Globally, baleen whales still face a wide variety of anthropogenic threats that can compromise the recovery of their populations. Examples of these are the incidental interaction with fishing gear (entanglements), ship strikes, habitat degradation due to chemical or underwater acoustic pollution, prey unavailability or malpractice by the marine ecotourism industry (Thomas et al., 2016). We have made a cursory assessment of some of these potential threats in the present study to identify critical areas within Irish waters and measure the exposure of the species to maritime traffic, fishing activity and offshore renewable energy projects.

The five species were exposed to maritime traffic in the Irish Sea, the North Channel, and the south coast of Ireland. These waters were predicted to be a less suitable habitat for some of the species such as the blue whale. This means that, even in the highly unlikely event of finding a blue whale in those areas, the chances of the species encountering a vessel are high (Breen et al., 2016). Limited spatial variability was observed across seasons for each species, indicating that traffic pressure in the study area is sustained over the year, probably because of the existence of regular shipping routes. Within the Irish EEZ, these higher exposure areas overlap with proposed AoI 9–11 and 16. Despite the high traffic intensity in the Irish Sea between Ireland and the UK, there is little evidence of ship strikes in Irish waters (Parsons et al., 2010; Winkler et al., 2020). This may occur because most of the species, apart from the smaller minke whale, would prefer either coastal waters off the southwest of Ireland or offshore waters further west, where traffic density is much lower than in the eastern half of the study area (Fig. A2). Ship strikes are not the only detrimental effects of vessel traffic on cetaceans. Evidence has shown that underwater noise generated by large ships and powerboats can produce changes in the foraging behaviour of large baleen whales, affecting feeding rates and efficiency (e.g. Blair et al., 2016). Within our study area, highest excess of ship noise has been predicted to occur in the North Channel, Irish Sea, Celtic Sea, and waters over the shelf edge in the Porcupine area in spring and summer (Farcas et al., 2020) which coincides with baleen whale presence peak. How this source of disturbance may potentially affect whales in Ireland remains unknown.

Differences were observed in the exposure to fishing activity across species. Those more likely to occur in coastal waters (minke whales, fin whales and humpback whales) were highly exposed to fishing activity in some areas off the south of Ireland and in the Irish Sea. Those species predicted to prefer offshore areas (blue whales, sei whales and fin whales) were more exposed to this activity in the Porcupine Seabight, Porcupine Bank and the southern slopes of the Rockall Trough (Fig. 7). High exposure to fishing activity overlapped with proposed AoI 2, 6, 9–12 and 16 (Fig. 1), indicating the potential that these areas may have as management tools to protect baleen whale species. Whale entanglements with fishing gear have been documented in Ireland; a humpback whale was observed in Donegal Bay (NW Ireland) in September 2023 with the tail entangled in ropes (K. Smith, pers. comm.). Moreover, eight minke whales and one humpback whale stranded in Ireland between 1990 and 2022 had signs of entanglement on the carcases (Fichefet, 2023). Nevertheless, the fishing activity exposure results presented here must be interpreted cautiously. We included all the fishing effort data available as an aggregation of multiple fishing gears following the precautionary principle. However, static fishing gears such as pots may be more likely to cause entanglements to baleen whales than others (Johnson et al., 2005). In addition, the susceptibility to entanglement may depend on the species or even the individual (body size and strength) that interacts with the fishing gear, as well as the gear's own characteristics such as floatability, strength, length, or soak time (Knowlton et al., 2016). Although we determined areas where fishing effort was more intense, that does not mean necessarily that entanglements would occur in the same location since lost gears may drift with currents and winds. The fishing effort data used in this analysis lacked temporal resolution within a natural year. Given the seasonal nature of fishing activity and the migratory behaviour of the species included in this study, it might be possible that some of the fisheries are less likely to overlap in time with one or several species of whales, and thus, the exposure may be overestimated in some areas. On the other hand, fishing activity data only included fishing vessels larger than 12 m, potentially excluding a significant part of gear that could be involved in entanglements, especially in coastal areas of the southwest of Ireland where most of the species may co-occur with pot-based shellfish fisheries (Fichefet, 2023). In addition, noise produced by bottom trawling has been highlighted as a possible stressor for cetaceans in the Irish continental margins (Daly and White, 2021) where suitable areas for some rorqual species have been highlighted in this study and high exposure to fishing activity has been identified.

With respect to offshore wind farms, only a few projects are currently under development in the Irish sea (mostly within the AoI 16 and on the west coast of Ireland within the area 12). In addition, the proposed southern DMAP area overlaps with AoI 9 and 10, to the south of Ireland. The exposure analysis showed that all the species, except the blue whale, were more likely to occur within these areas of interest for renewable energy production compared to the average habitat suitability of the study area. This would indicate potential interaction between the species and offshore renewable energy developments. Wind farms are usually built between 0 and 30 km from the shore (Bailey et al., 2014). Considering our model results, it can be expected that future wind farm developments in the southwest coast of Ireland may have negative impacts on suitable habitats for minke whales, fin whales and humpback whales. The relevance of these coastal habitats was highlighted by Classen et al. (2022) in the proposal of the AoIs 10 and 11. Offshore renewable energy development within these areas could present a threat to a wide range of other species including seabirds, elasmobranchs (such as the basking shark, *Cetorhinus maximus*), and cetaceans like harbour porpoises, bottlenose dolphins, common dolphins (*Delphinus delphis*) and Risso's dolphins (*Grampus griseus*). This demonstrates the ecological importance of these areas and the need to protect them.

4.4. Conclusions

This study provides novel information on the distribution of the five most common balaenopterid species in Irish waters based on extensive datasets and different modelling approaches. This study improves the existent bibliography on baleen whale distribution in these waters by incorporating wider temporal and spatial scales. Dedicated marine mammal survey effort in Ireland is limited due to the poor weather conditions that usually prevail at these latitudes as well as economic and logistic restrictions. The inclusion of long-term datasets collected on a citizen science basis by the IWDG over the last two decades has helped to fill the information gaps regarding baleen whale presence in Irish waters. We also identified areas where these species may be exposed to anthropogenic pressures such as fishing activity, maritime traffic, and the development of offshore wind farms. The information provided by this study can be used as a baseline to inform the establishment of a comprehensive network of large MPAs in Ireland to protect critical habitats for baleen whales and other species. Along with effective monitoring, management, and stakeholder engagement, these efforts can help sustain healthy local populations by mitigating harmful human activities in key habitats.

CRediT authorship contribution statement

Miguel Blázquez: Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Pádraig Whooley:** Writing – review & editing, Supervision, Data curation. **Nick Massett:** Writing – review & editing, Supervision, Data curation. **Hannah Keogh:** Data curation. **Joanne M. O'Brien:** Writing – review & editing, Validation, Supervision, Conceptualization. **Frederick W. Wenzel:** Writing – review & editing, Validation, Supervision, Conceptualization. **Ian O'Connor:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Simon D. Berrow:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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