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Predicting habitat suitability for basking sharks (*Cetorhinus maximus*) in UK waters using Ensemble Ecological Niche Modelling

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ABSTRACT

The basking shark (*Cetorhinus maximus*) is an endangered species in the north-east Atlantic, having been historically over exploited. Whilst near-shore aggregation hotspots in the UK have been identified, robust knowledge on species distribution and abundance outside these areas remains limited. Research techniques, such as habitat modelling, could however be used to gain a greater knowledge of the species distribution to inform management plans to aid population recovery. For large mobile species gathering wide-scale distribution data can be financially and logistically challenging. In lieu of conducting a UK-wide expensive strategic survey for basking sharks, we use data from two regional-scale surveys, which were conducted in southwest England and western Scotland, and use an Ensemble Ecological Niche Model (EENM) to produce a spatially explicit map of habitat suitability. When compared against a ~20-year database of public sightings of basking sharks across UK coastal seas (to 6 nautical miles offshore), patterns of habitat suitability yielded a statistically significant agreement with areas known to support basking shark sightings. EENMs could be used to advise Marine Protected Area (MPA) selection, as well as to inform environmental

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impact assessments for offshore developments. The application of EENM outputs could be wide-reaching and benefit not only basking sharks but other large mobile marine species in the north-east Atlantic.

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KEY WORDS

Basking shark, ensemble ecological niche modelling, MPA, habitat suitability, spatial analysis, citizen science, boat transect, public sightings

INTRODUCTION

The global loss of marine biodiversity is of increasing concern, as the rate of population decline accelerates across multiple biota. The north-east Atlantic, for example, has been negatively affected by anthropogenic activities for at least several hundred years [1]. In the UK and Europe, extensive data have been collected on the spatial and temporal distributions of populations of large mobile marine species, in particular cetaceans [2], which can be used to aid effective management of declining and vulnerable marine species.

The basking shark (*Cetorhinus maximus*) is a filter-feeding elasmobranch and the second largest fish species in the world [3]. As a highly mobile species, the basking shark is thought to have a wide global distribution [4]. However, hunting for squalene oil since the 18th century [5], and the lucrative global shark fin trade [6], have caused noticeable population declines, resulting in the species being considered as 'vulnerable' to extinction globally [4], and 'endangered' in the north-east Atlantic [7]. Threats to basking sharks persist in UK waters despite protection in UK law, including incidental bycatch from fisheries, collisions with vessels, and disturbance from recreational craft [8]. The UK is home to several localised basking shark aggregation 'hotspots', where surface sightings are frequent in summer months [9]. These areas include the Sea of the Hebrides [10], the Isle of Man, southwest England, and the west coast of Ireland [9,11,12]. Data have been made available from long-term public sightings schemes for broad, population-level insights [9,13]; boat-based surveys have provided effort-based sightings data in specific areas [10,12] and insights into breaching behaviours [14]; and more recently, real-time satellite tracking has enabled individual movements to be gathered with spatial accuracy of <1 km [15,16].

Ecological Niche Modelling (ENM) makes use of information on species presence and absence and relevant environmental data [17], and has become an important tool for predicting areas of suitable habitat for species distributed over wide spatial areas, positively correlating with abundance data for a variety of taxa [18]. These models provide spatially explicit habitat suitability maps, and can therefore be used to inform management plans [19]. However, one problem is in the selection of appropriate statistical models that best represent the study species from a selection of different models with differing underlying assumptions. 'Ensemble' ecological niche modelling (EENM) has been developed to increase the accuracy and reliability of ecological niche models [20]. By running multiple, carefully selected statistical models multiple times, nuances from each approach can be captured in the final output, and a desired level of model complexity can be reached [21,22]. 'Ensemble' ecological niche modelling of surface distributions has been used for several marine species including the whale shark (*Rhincodon typus*) [23], sperm whale (*Physeter microcephalus*) [24] and marine turtles [25].

The distribution of basking sharks has been shown to be influenced by a range of environmental conditions. Surface sightings of basking sharks are typically reported where sea surface temperatures range

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between 15 and 17.5°C [26,27], where thermal fronts are present [28,29] and where zooplankton, the dominant prey item for the basking shark, is in its greatest abundance [28,30]. Given that basking shark distribution appears to be influenced by such conditions, ecological niche modelling using these environmental variables may provide greater insights into their possible distribution, particularly for areas that are challenging to survey due to logistical and financial constraints (e.g. offshore regions). Wildlife transect surveys, such as by boat and plane, can provide a robust understanding of both true presence and absence at the surface. Presence-absence data are more likely to improve outputs from ecological niche models in comparison to presence-only data (obtainable from public sightings and bycatch records), but can be expensive, time-consuming and logistically challenging to undertake, and their spatial extents rarely match the likely complete distribution of the species of interest. While transect surveys are necessarily spatially constrained, the data they offer to habitat models could be improved by joining data from multiple-spatially explicit surveys sharing similar survey techniques. Resulting data may prove useful for making cost-effective predictions of areas of suitable habitat. Analogous modelling approaches have been developed for basking sharks in Canada [31], the South Atlantic [32], and Scotland's coastal waters, where a single model framework (i.e. Generalised Estimations Equations) was developed for the region [33].

Ensemble ecological niche modelling has not yet, however, been conducted to predict potential areas of suitable surface habitat for basking sharks across the UK seascape. This lack of knowledge is problematic given the need to develop holistic management strategies for marine ecosystems. Here we present an ensemble ecological niche model for basking sharks across UK waters utilising boat-based transect survey data. We suggest that habitat suitability mapping can help inform conservation management planning and direct coastal and offshore development plans. We highlight the future benefit of similar modelling processes for other marine species.

METHODS

Shark survey data

Standardised boat-based line transects (n = 493) recorded basking shark sightings off the southwest peninsula of the UK between the years 2000-2005 (May to June) and 969 transects were conducted in the Sea of the Hebrides, Scotland between the years 2002-2006 and 2011-2014 (July to August). Observations of sharks were made from a sailing vessel platform with low freeboard (observer height above sea level did not exceed 3 metres). Sighting horizontal therefore range did not exceed maximum estimated 3.5 nautical miles (at sea state 0). All transects were timed, with survey duration averaging (mean) 77 minutes, and sightings recorded by observers from Wave Action (http://wave-action.com), with density of animals recorded as sharks per unit hour (SPUE h^{-1}). Only transects conducted in sea state 3 or less were used in this study to minimise detection bias due to changing weather conditions. Spatial adjustments were not applied to sighting locations to account for distance from the survey transect. Boat transect data were converted into a binary presence-absence grid (4 x 4 km cell size) and was used in ensemble ecological niche modelling as the

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species distribution (response) variable. Grid cells through which boat transects were made, but where no sharks were sighted, were assigned zero value (true absence of sharks at the surface), and grid cells in which at least one shark was sighted throughout all survey hours were assigned a value of one (true shark presence). Presence and absence sample size was then matched through random deletion of absence cells (being the most numerous) and then serially decomposed to remove spatial autocorrelation in the resulting model residuals. Autocorrelation was determined using a Moran-I test. The resultant dependent data contained 106 cells (presence, n = 53 cells and absence n = 53).

Environmental data

Within the modelling framework we used environmental data describing seabed depth (m), seabed slope (degrees), Night-Time Sea Surface Temperature (NSST, °C), thermal front activity, and chlorophyll-a concentration (Chl-*a*, mg m^3, a proxy for zooplankton abundance [34]) across the modelling extent. These variables have been identified as influencing the presence of basking sharks at the sea surface [26–29,35]. The number of environmental variables was limited to five key environmental predictors likely to be important describers of presence in order to minimise model over-fitting [21]. The modelling spatial domain encompassed UK waters (N 49°-N 63°, W 11°-E 3°; 988,880 km^2 using projected coordinate system ERTS 1989_LAEA). Environmental data were all sampled at a 4 x 4 km resolution; the coarsest native resolution of data to be used (governed by MODIS NSST and Chl-*a* data) and was used to define the extent and spatial resolution of the basking shark presence/absence data layer. Bathymetry data were obtained from www.gebco.net. All other variables were sourced using the MGETv0.8a43 [36] toolbox in ArcGIS. Mean monthly Chlorophyll-*a* (Chl- *a*; www.oceancolor.gsfc.nasa.gov) and NSST (www.podaac.jpl.nasa.gov, www.noassis.noaa.gov) rasters were extracted and averaged (mean) to produce one layer that encompassed the entire period over which transect data were collected. Thermal front activity was produced using the Cayula and Cornillon Single Image Edge Detection algorithm to detect fronts from NSST data to produce monthly binary grids showing presence/absence of fronts [37], available in MGET. Grids were summed for each year and averaged across years to produce a long-term frontal activity grid for the modelling spatial extent. During EENM development, environmental data on thermal fronts and seabed slope were found to significantly correlate with NSST and seabed depth respectively; as such, thermal front and slope data were excluded from final modelling activities. Depth, NSST and Chl-*a* concentration were therefore the three environmental predictors used in the final EENM framework.

Ensemble ecological niche modelling

Ecological niche modelling was performed in R using Biomod2 [38]. Models were run with a 10-fold cross validation and an 80/20% split of data for calibration, and model testing respectively. The EENM integrated mapped outputs from three statistical approaches; including, Multiple Adaptive Regression Splines

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(MARS), Generalized Linear Models (GLM) and Generalised Boosting Models (GBM). An ensemble approach was adopted to incorporate the strengths of these individual statistical modelling approaches, while simultaneously attempting to constrain modelling uncertainty and the inevitable weaknesses inherent with each statistical modelling approach. MARS can perform well with ecological datasets that can have wide ranging and non-linear relationships between species and the environment [39], GLM is a regression-based modelling approach and can perform well with geographically widely spread data [40], and GBM combines two algorithms; decision trees and boosting. The GBM can be described as a regression model where each term is a tree [41]. Boosted trees model a much smoother gradient, that can handle sharp discontinuities in data [41].

Thirty models were produced from 10 ensemble runs. Each ensemble run (n = 10) considered a single mapped output from each of the statistical algorithms (n = 3). The performance of each model was evaluated using a score based on the Receiver Operating Characteristic (ROC); a frequently used method of determining the accuracy of such models [42]. An ROC score > 0.7 was the threshold above which model performance was deemed suitable for use (a score of 1 suggests a perfect model) [43,44]. The output of the ensemble modelling framework was a mean spatial surface (one for each of the 10 ensemble runs), each being derived across the outputs from the three statistical algorithms (i.e. MARS, GLM and GBM), but only where ROC > 0.7. The mapped EENM output was an unweighted mean of the ensemble model surfaces and represented estimated habitat suitability for basking sharks with values ranging from 0 to 1 (1 being most suitable) with a 4 x 4 km spatial resolution. A mapped coefficient of variation was also calculated across the ensemble surfaces to investigate regions of similarity (low coefficient of variation) and dissimilarity (high coefficient of variation) in predictions of habitat suitability.

Model comparison to public sightings data

Nationwide surface sightings of basking sharks (from the public) collated by the Marine Conservation Society, UK (MCS) [45] were compared with the ensemble model output. Sightings were corrected for duplicates, and data between the years 2000-2006 and 2011-2014 for the months May-August were extracted from the public sightings database. The majority of public sightings occur within 6 nautical miles of the UK coastline [9]; therefore, only sightings within 6 nautical miles of land were used and was expressed as a number of surface sightings records per km^2 for each of 15 coastal regions circumscribing UK coastal seas (coastline to 6 nautical miles offshore). Mean habitat suitability was also determined for each of these coastal regions. A Spearman’s rank test for correlation was then performed to assess the relationship between mean habitat suitability index and surface sighting density of basking sharks from the public sightings data.

Spatial management zone and marine regions

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Mean habitat suitability and the sea surface area of basking shark habitat suitability (≥ 0.5) were calculated for a range of marine spatial management and development zones. Marine spatial management zones included Marine Protected Areas, such as Special Areas of Conservation (SAC), Marine Conservation Zones (MCZ; England and Wales), Nature Conservation Zones (NCZ; Scotland) and Sites of Community Interest (SCI & cSCI; journaled and candidate). MPA data were obtained from the OSPAR MPA database (http://jncc.defra.gov.uk/ProtectedSites/SACselection/gis_data/terms_conditions.asp; data version: May 2018). Coastal zones of the UK to 6 and 12 nm offshore were obtained from the UK Hydrographic Office (http://aws2.caris.com/ukho/mapViewer/map.action; data version: April 2016).

Wind farm development zones in English waters were obtained from The Crown Estate (https://www.thecrownestate.co.uk/en-gb/resources/maps-and-gis-data/; data version: August 2018). Wind farm infrastructure within the waters of Scotland were obtained from Crown Estate Scotland (https://www.crownestatescotland.com/maps-and-publications/download/95; date version: May 2019).

RESULTS

Transect survey data

Between the years 2000-2005, 674 hours of boat-based transect surveys were conducted in the months of May and June off the coast of Cornwall, and 96 sharks were observed on transects (mean 0.14 SPUE h^{-1}). Surface sighting hotspots for basking sharks, where shark densities were >0.5 SPUE h^{-1}, were identified around the Lizard Peninsula, and Porthcurno (Fig. 1A). Between the years 2002-2006 and 2011-2014, 991 hours of line transect surveys were conducted in the months of July and August in Scotland. During this time, 621 sharks were observed on transects (mean 0.63 SPUE h^{-1}). Surface sighting hotspots of basking sharks occurred around Coll and Tiree (Gunna Sound), and the island of Hyskeir (>2 SPUE h^{-1}; Fig. 1B). Autocorrelation was not be observed in the dependent dataset (Global Moran's I; z-score = 1.010195; p = 0.312402).

Ensemble ecological niche modelling

Of the 30 ecological niche models created within biomod2 (i.e. 10 ensemble runs considering model output from each of three statistical approaches, i.e. MARS, GLM and GBM) no model failed to be fitted (Table 1). Fifteen individual models were evaluated with ROC > 0.7; these occurred across seven ensemble runs. In each of these runs at least one model had an ROC > 0.7. The grand mean ensemble model was therefore an unweighted mean from seven ensemble runs. The relative importance of contributing environmental variables within the seven ensembles varied (e.g. depth, night-time sea surface temperature and

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Chl-*a*; Table 2). Depth and NSST were the primary variables in three ensembles each and Chl-*a* was the primary variable in single ensemble output.

Spatial variation was apparent in predicted suitable habitat for surface sightings of basking sharks across the UK seascape (Fig. 2A). Regions of elevated habitat suitability agreed with many geographic areas known to support sightings, including the Sea of the Hebrides (Scotland), the Isle of Man (Irish Sea) and southwest England (Fig. 2; see [13,45]). The grand mean ensemble model also identified regions of suitable habitat (≥ 0.5) but with few historical surface sightings of basking sharks; including, the southern North Sea to the east of the UK, to east of Scotland and to the west of Wales. Coefficient of variation across the ensemble models was low in regions of high relative suitability (Fig. 2B). Highest coefficient of variation occurred in areas off the continental shelf, away from coastal areas and highlighted regions of poor concordance across models.

Within the modelling spatial domain, 15.0% of the grand mean ensemble model surface (147,988 km^2) was rated with a habitat suitability index ≥ 0.5, and 1.6% of the surface was rated with a habitat suitability index ≥ 0.75 (16,076 km^2). Median habitat suitability across the modelling spatial domain was 0.28 (range: 0.05 to 0.9).

Model comparison to public sightings data

The density of public sightings record of basking sharks occurring in the months May to August was significantly positively correlated with mean habitat suitability for coastal regions (Fig. 3C) (n = 15 regions, rho = 0.53, p = 0.04; Fig. S1). Repeating this analysis to include only those coastal regions outside areas of boat-based data collection (i.e. eliminating coastal regions for southwest England and the west coast of Scotland) similarly yielded a significant correlation (n = 13 regions, rho = 0.55; p = 0.05).

Spatial management zones and marine regions

Basking shark habitat suitability, and cumulative surface area of suitability > 0.5, was calculated for a range of spatial management zones and marine regions occurring within UK waters and those of the Isle of Man (Table 1). Grand median habitat suitability within English MCZs was 0.23 (IQR: 0.23) and within designated nearshore and offshore SACs it was 0.31 (IQR: 0.37). Grand median habitat suitability occurring within Scottish NCMPAs was 0.58 (IQR: 0.38). Median habitat suitability for Ramsey Marine Nature Reserve (Isle of Man) was 0.37 (range 0.29 to 0.38). Median habitat suitability of a proposed MPA for basking sharks in the Sea of the Hebrides was 0.47 (range: 0.12 to 0.87). Habitat suitability > 0.5 within this area covered 4,830 km^2, representing 47% of the surface area of the proposed MPA.

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Mean basking shark habitat suitability from the coastline to 6 nm offshore and to 12 nm offshore was 0.44 and 0.42 respectively (Table 1). These marine regions circumscribed a cumulative 43,735 km^2 and 62,186 km^2 respectively of sea area with habitat suitability > 0.5.

Windfarms that are active, undergoing extension, or in pre-planning phase, in the waters of England, predominantly located in the southern North Sea, had a median habitat suitability of 0.45 (IQR: 0.37). In Scotland, of 27 regions associated to wind energy infrastructure (status: lease or agreement / option for release), eight regions exceed areas of 100 km^2, and the grand median habitat suitability for these regions was 0.71 (IQR: 0.12).

DISCUSSION

Coherent information on the spatial distribution of species of conservation concern is an important component in the development and implementation of management measures that seek to maintain and promote population growth and survival. For mobile marine species, data collection by dedicated boat and aerial surveys, and by satellite tagging, can be costly. Thus, in this study, we used ensemble ecological niche modelling to scale up from findings from regional boat-based survey data to determine locations of high relative habitat suitability across nationwide continental shelf waters of the UK. Using public sightings data, we assessed the final ensemble model output within the coastal zone and highlight agreement between the two independent sources. Our study provides a model of habitat suitability that could be used to aid development of spatially-explicit management plans for the species in UK waters, but also serves as an example of how citizen science data and judicious wildlife transect surveys if carefully considered can be used to produce useful scientific output for a relatively low cost. Ensemble ecological niche modelling highlighted several regions of high relative habitat suitability for basking sharks in summer months in UK waters that are worthy of further discussion.

West Scotland

The EENM output highlights several regions throughout the waters west of Scotland with high relative suitability (Fig. 4A-i). While parts of this region, including the Sea of the Hebrides have long been recognised as an important area for basking shark sightings, the model outputs identify other notable areas, including the west of the Outer Hebrides, north of the islands of Jura and the sea area north of the Mull of Kintyre. Spatial patterns of habitat suitability for Scotland from this study, are broadly concordant to that of other efforts using Generalised Estimating Equations to model surface presence likelihood, an alternative modelling approach to EENMs [33], but in that study the modelling domain was set to 12 nautical miles (territorial waters) around Scotland. The absence of habitat suitability (> 0.5) within the Clyde Sea identified by the EENM and by [33] is noteworthy given this region was once abundant with basking sharks. The Sea of

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the Hebrides, at the core of the west coast of Scotland marine area, hosts seasonally resident basking sharks through the summer months and satellite tracked individuals demonstrate interannual site fidelity and subsequent long-range movement [15,16]. Photo-identification in the region also supports intra- and inter-annual site fidelity [46]. The results of our study, which reveal the region supports several large areas of high relative suitability is timely given public consultation is awaiting regards the proposed Sea of the Hebrides Marine Protected Area (Fig. 4B), specifically intended for the protection of basking sharks and minke whales. Our modelling efforts provide useful context in the discussion of the proposed MPA, highlighting the importance of the Sea of the Hebrides for basking sharks regionally and nationally, supporting key areas suitable for basking sharks across the UK seascape. As such, and further supported by modelling efforts here, this region appears important for the species at the local, regional and international scale.

Northern North Sea

The Northern North Sea, on the East coast of Scotland, is an area not previously considered an aggregation hotspot for basking sharks; however, historical sightings have been noted here (C. Speedie, pers. comm.) and more recently sharks have been observed and fidelity confirmed using genetic techniques [47]. The results of the model in this region (Fig 4A-ii) may highlight an area that basking sharks already occupy, but in low numbers, or an area that could be populated in the future as the north-east Atlantic population recovers following historic exploitation across the northern extents of its range. It is therefore important to consider the presence of basking sharks in future environmental impact assessments for offshore activities in this area, including several extant and proposed wind farms. Grand median habitat suitability occurring within windfarm infrastructure, either existing, or in application stage, was particularly high (0.7), potentially indicating the value of surveys for sharks, both at the surface and potentially throughout the water column, for the species.

Irish Sea

The Irish Sea and coastal waters of the Isle of Man are a recognised surface aggregation hotspot for basking sharks [45]. The model outputs further underpin the potential for inter-connectivity between surface aggregation hotspots in the west of Scotland and the Irish Sea, suggesting that predictions on regional scales could play an important role in developing management strategies for such highly mobile marine species (Fig 4A-iii).

Southern North Sea

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The EENM predicted a relatively large novel area of the Southern North Sea with high relative habitat suitability for basking sharks (Fig. 4A-iv). Few public sightings have been reported from this area, potentially because of its distance from shore. As such, the model highlights areas that may be underappreciated at present, or may not yet be occupied by basking sharks, and instead could be populated in the future as basking shark numbers recover. Dedicated boat and aerial surveys in this region would help determine if surfacing basking sharks are present in any appreciable numbers in the region, satellite tracking could also be used to help determine basking shark space-use and eDNA surveillance approaches might also be employed. If basking sharks are routinely present in the Southern North Sea, but away from coastal regions, then appropriate management plans may be required.

Southwest UK

Historically, the southwest UK has supported several isolated aggregation hotspots of basking shark sightings in the late Spring and early Summer months [45]. The EENM highlighted this region as supporting suitable habitat (Fig. 4A-v), although contemporary sightings numbers are reduced substantially compared with previous decades (pers. com. J-L Solandt). The coastal seas of Cornwall, and other areas of England, have seen the introduction of numerous Marine Conservation Zones, predominantly focusing on habitats and benthic species. Whilst the re-designation and adaptation of conservation areas to include mobile marine species has not previously occurred in the UK, evidence as presented here, may suggest that incorporation of these species into planning could further aid protection of basking sharks.

Interpreting model outputs

Care must be taken when interpreting outputs from statistical modelling processes. In our study it should be noted that basking sharks are not explicitly tied to the sea surface, unlike air breathing cetaceans and pinnipeds, and as such the models predict areas of suitable habitat based on surface sightings alone, and so may not highlight areas of suitable habitat where sharks may be present at depth. Basking sharks may also surface more at night in response to zooplankton vertical migration, so areas surveyed during the day may not account for basking shark distribution at night [48]. This may mean, for example, that waters that are not highlighted as of high relative habitat suitability may indeed be suitable at depth, and that sharks may still be present at these locations away from the surface. Future work could integrate three-dimensional habitat suitability modelling with dive information for basking sharks to tackle this challenge.

Boat-based transect data utilised for this study have limitations which may affect model outputs and real-world relevance. For example, not all transect routes were replicated in each year of surveying, and as such our modelling efforts may suffer from over- or under-predictions in certain areas. In addition, we did not undertake corrections for detectability, although we used only those records gathered in sea states ≤ 3, all

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observers were subject to consistent high-quality training and the survey was led by two experienced wildlife biologists for the duration of the study in both Cornwall and Scotland using the same vessel. The ecological niche framework for this study utilised binary response data on the presence/absence of basking sharks, and did not incorporate the intensity of survey effort occurring within each grid cell.

The environmental variables used within the model were selected based on past studies on basking shark habitat preference [26–29,35]. Nevertheless, other environmental drivers exist in the published literature, including tidal energy [33] and Chl-*a* fronts [35]. Thermal stratification of the water column may also influence surfacing behaviours.

Similar modelling approaches could be used to ascertain how suitable areas of habitat change in the UK on an extended temporal basis. This could, for example, indicate whether long-term environmental forcing is likely to influence the distribution of the species such as basking sharks in the area. Sims and Reid [49] found that basking shark catch from Irish fisheries reduced over time from 1948 to 1975 in line with long-term zooplankton decline in the area, with a northward trend in basking shark distribution to more productive areas cited as the reason for fewer catches. If sufficient survey effort could be conducted along consistent transect routes it may become possible to produce annual models; changes in distribution over time could be assessed and changes in environmental variables used within the modelling may be identified as particularly important for basking shark distribution. Models could also be used to forecast the future and predict possible patterns in basking shark distribution under differing scenarios of predicted anthropogenic climate change, though this does increase uncertainties in the model due to the prediction of future environmental variables [50].

No designated management zones currently exist for basking sharks (England, Wales, Scotland and Northern Ireland), however, extant MPAs, including Marine Conservation Zones (England, Wales and Northern Ireland), Special Areas of Conservation (SACs; throughout the UK), and Nature Conservation Marine Protected Areas (NCMPA; in Scotland) may confer a degree protection to basking sharks through management measures typically seeking to establish long-term ecosystem improvement albeit through feature-based conservation management of often non-mobile species.

The modelling efforts presented in this study could contribute evidence for marine protected site proposals and re-designations, and marine spatial planning activities seeking to minimise conflict between species of conservation concern and human activities. They can also be used to highlight key areas where dedicated surveys for basking sharks could be undertaken, as proposed offshore development plans may have the potential to cause disturbance in areas of high basking shark habitat suitability, as in the North and Irish Sea.

CONCLUSIONS

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Predictions of where basking sharks may be found at the surface in summer months across the UK are important for creating a coherent management plan across the entire region, especially as basking sharks are a highly mobile and migratory species [15]. Ensemble ecological niche modelling is becoming a more prominent tool in species ecology to determine areas of suitable habitat and high abundance in a given area and time [22]. By continuing monitoring efforts through dedicated boat transect surveys, public sightings schemes, satellite tracking and emergent eDNA techniques (e.g. [51]) to provide presence/absence or quantitative eDNA timeseries, and by combining these datasets through techniques such as habitat modelling (e.g. EENMs), insights can be revealed regarding basking shark distribution in the seas around the UK to allow for more effective management through MPA placement, disturbance restrictions, and management of fishing and industrial practices.

This study highlights the benefits and practicalities of ensemble ecological niche modelling for increasing spatial and temporal knowledge of the distribution and abundance of basking sharks and other large marine fauna in UK seas.

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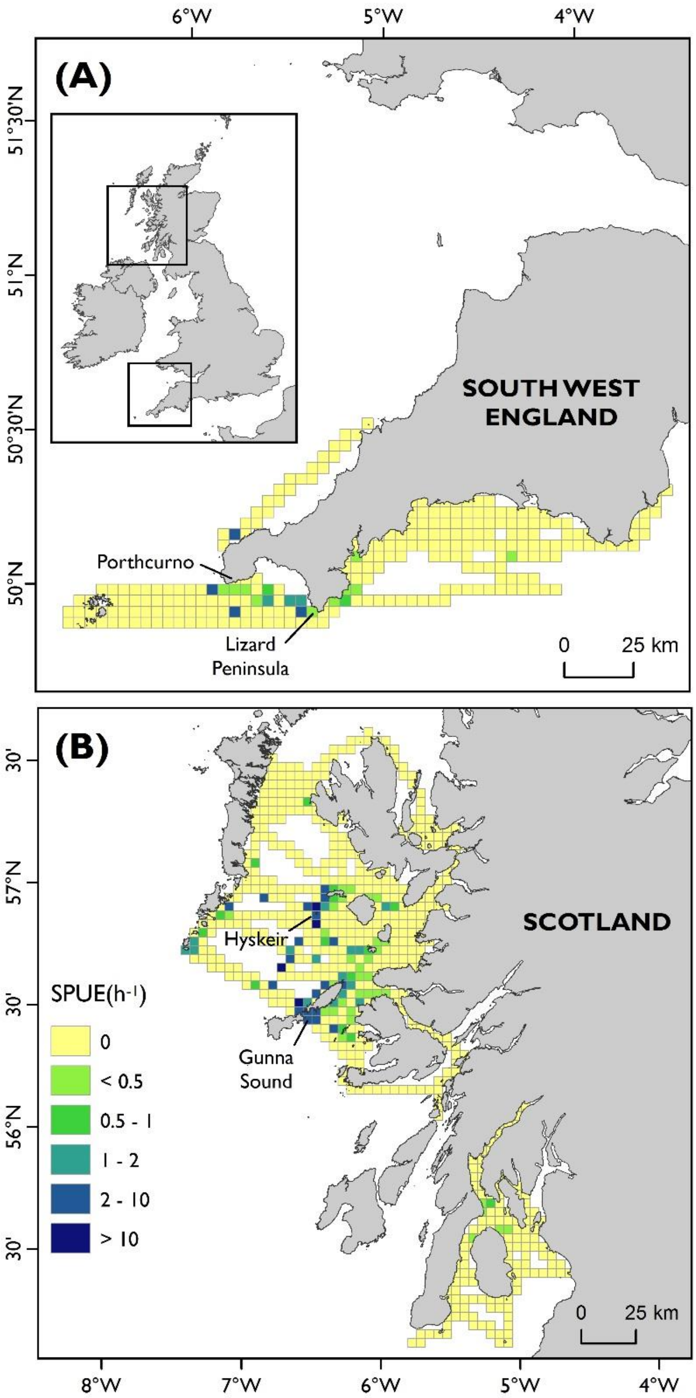

Figure 1. Transect survey data. Gridded density of basking sharks sighted by boat-based transect surveys (4 x 4 km grid; expressed as sharks per unit of survey effort in hours, SPUE h^{-1}) undertaken in **(A)** Southwest England in May and June between 2000-2005 and **(B)** West coast of Scotland in July and August between 2002-2006 and 2011-2014.

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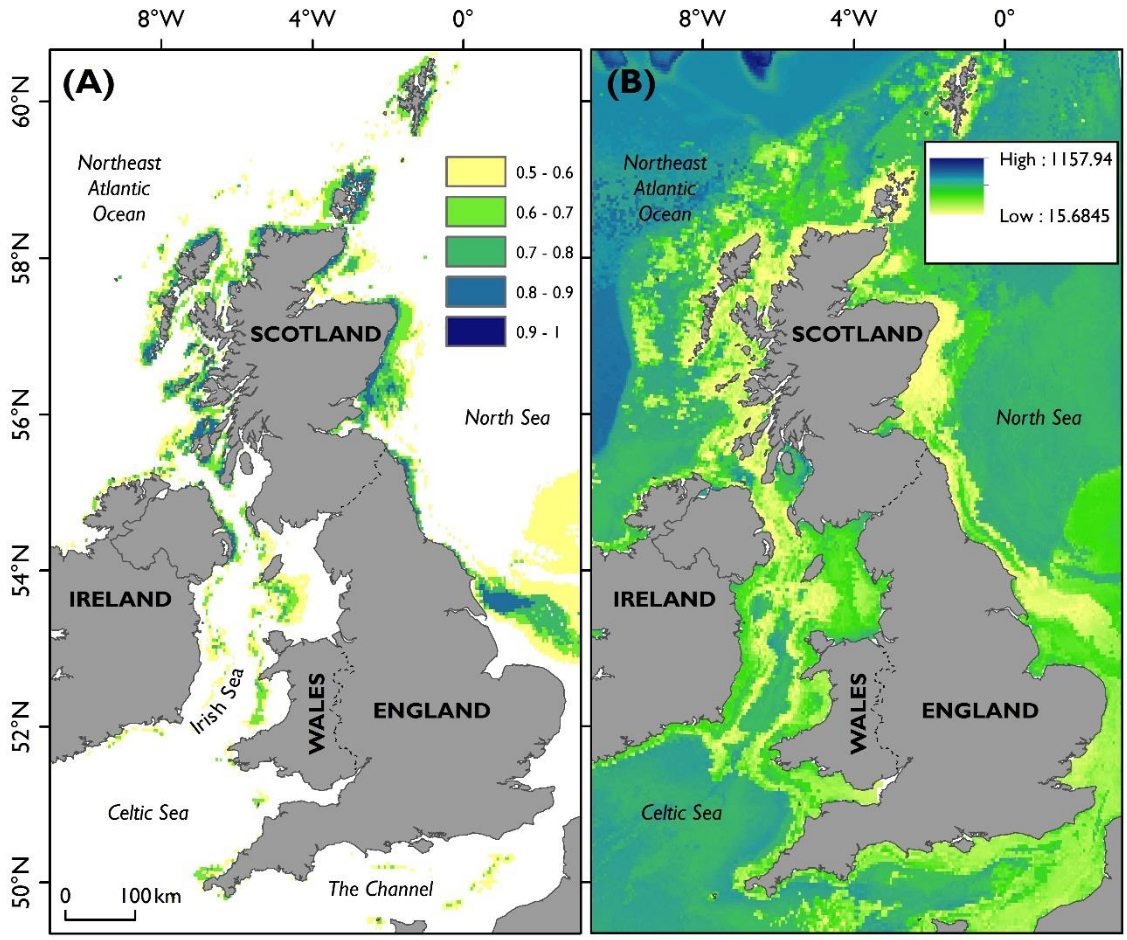

Figure 2. Habitat suitability for basking sharks. (A) Predicted areas of habitat suitability for basking sharks across the UK seascape (grand mean ensemble) using shark presence-absence data gathered by boat-based surveys conducted in Southwest England and Scotland. Higher values indicate areas of more suitable habitat. Habitat suitability <0.5 assigned to white background. (B) Spatial coefficient of variation in model prediction calculated across the seven ensemble models contributing to the grand mean ensemble (part A). Low coefficient of variation indicates agreement across ensembles, and conversely high coefficient of variation indicates a lack of agreement.

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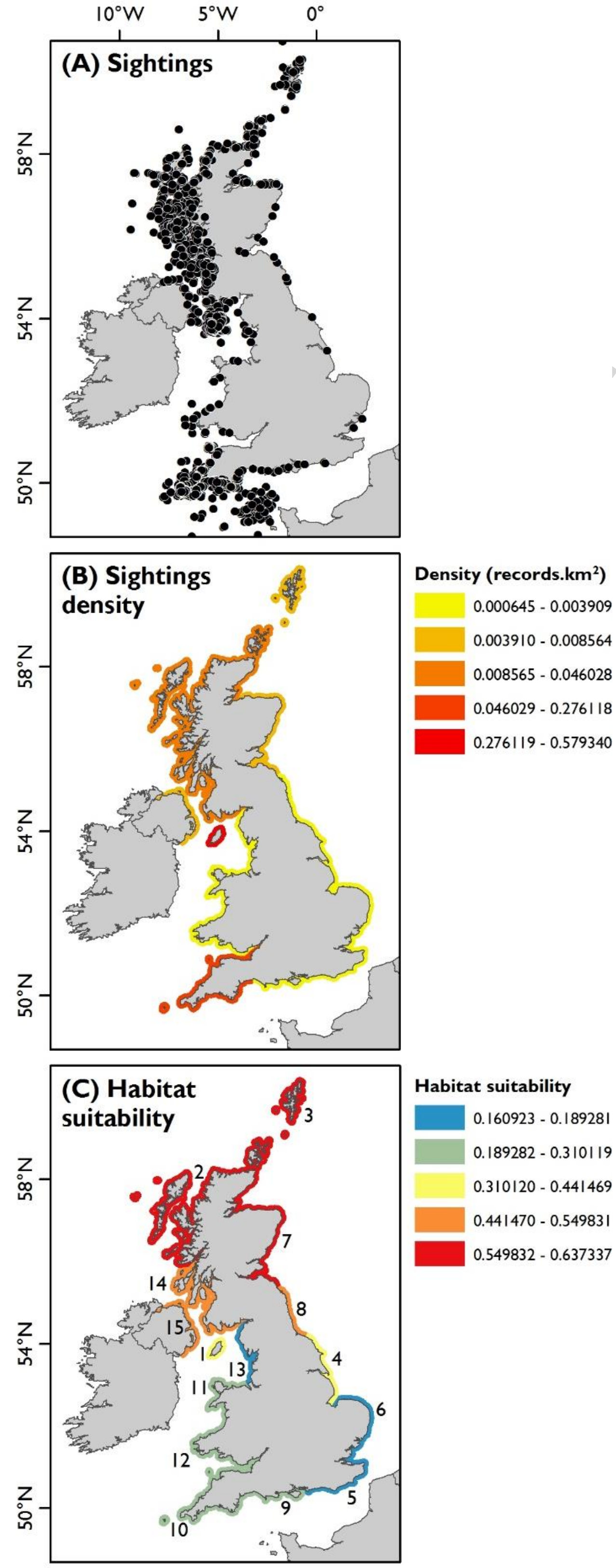

Figure 3. Public sightings data and habitat suitability in coastal regions. (A) public sightings of basking sharks from Witt et al 2012; (B) Density of records occurring within coastal regions and (C) Mean habitat suitability for 15 coastal

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regions of the UK. Regions (Arabic numbers; see Fig. S1). Symbology in parts B and C assigned using Jenks (natural breaks) algorithm in ArcMap 10.5.1 (ESRI).

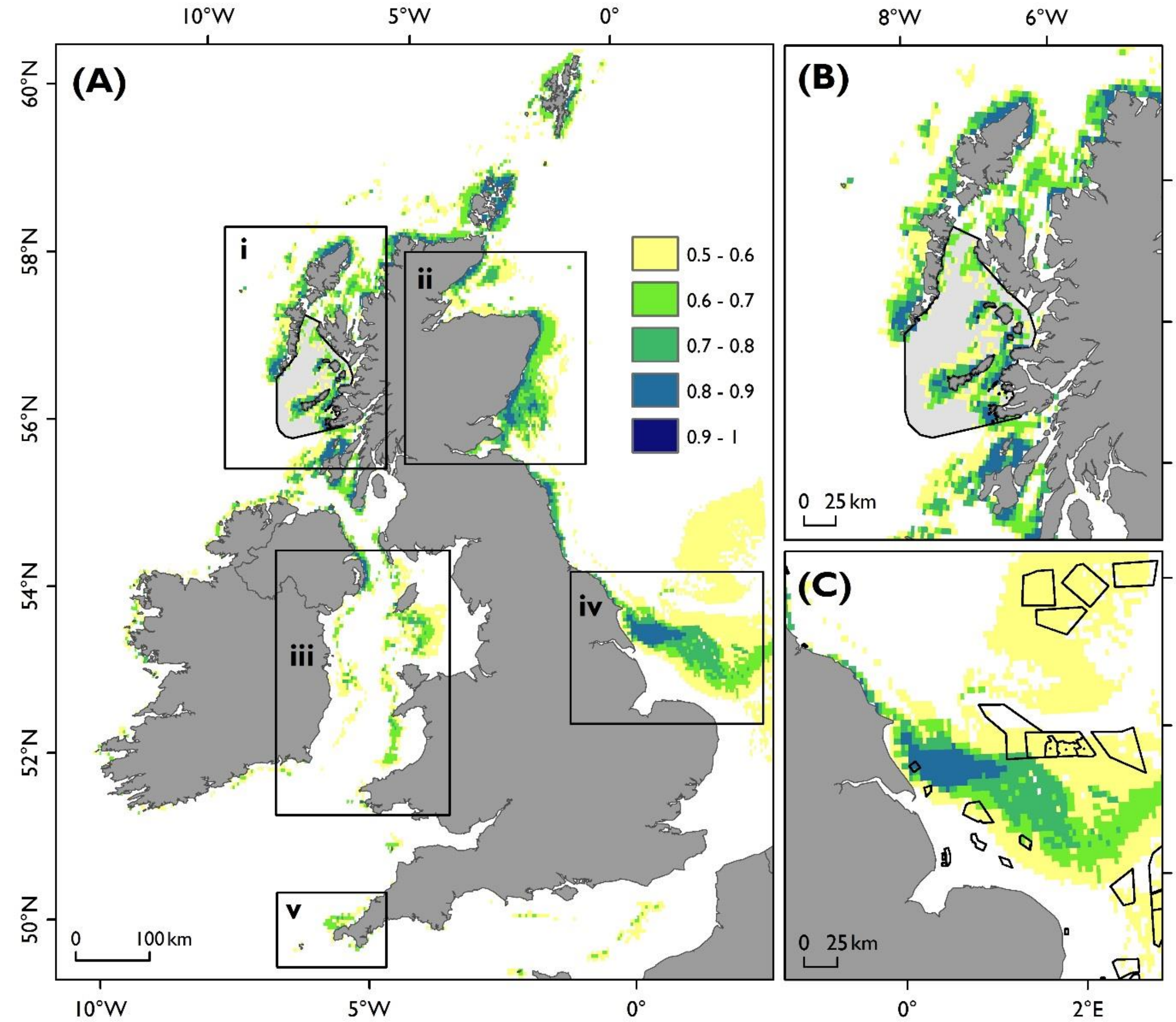

Figure 4. Areas of high relative habitat suitability for basking sharks in UK seas. (A) Five selected areas of high relative suitability; i) west of Scotland, ii) northern North Sea, iii) Irish Sea, iv) southern North Sea, and v) Cornwall. (B) Spatial boundary of a proposed MPA for basking shark and minke whale in the Sea of the Hebrides. (C) Spatial boundaries of proposed and existing wind farms in the Southern North Sea. Habitat suitability <0.5 assigned to white background.

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Table 1. Summary of basking shark habitat suitability by marine management zones and spatial regions

Zone or Region (number of sites; *where applicable*) *Geographic region*	Habitat Suitability	Total area km^2 (area where HS > 0.5; percentage of total area)
Marine Conservation Zones (n=49) *England*	0.23 (0.23) ‡	21,401 (3,915; 18%)
Special Areas of Conservation (n=33) *UK*	0.31 (0.37) ‡	13,992 (1,981; 14%)
Nature Conservation Marine Protected Areas (n=21) *Scotland*	0.58 (0.36) ‡	24,821 (5,177; 21%)
Candidate Special Areas of Conservation and Sites of Community Importance (n=22). *UK*	0.45 (0.32) ‡	10.089 (2,363; 22%)
Ramsey Marine Nature Reserve *Isle of Man*	0.37 (0.29 to 0.38) †	94 (0, 0%)
Sea of Hebrides proposed Marine Protected Area *Scotland*	0.47 (0.12 to 0.87) †	10,309 (4,830, 47%)
Coastal waters to 6nm offshore UK	0.44 (0.08 to 0.90) †	107,981 (43,735, 41%)
Coastal waters to 12nm offshore *UK*	0.42 (0.08 to 0.90) †	165,210 (62,186, 38%)

‡ Grand median of multiple site-level medians and inter-quartile range across site-level medians

† site-level median and range

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SUPPLEMENTAL

Table 1. ROC scores for each model run for each algorithm. Viable ensembles contributed to the grand mean ensemble. Three model runs provided outputs where ROC did not exceed 0.7 for all three statistical approaches and so these outputs did not feature in ensembles contributing to the grand mean ensemble.

Ensemble Run	Failed Models	GLM	GAM	GBM	Viable Ensemble
1	0	0.778	0.756	0.733	Yes
2	0	*0.539*	*0.611*	*0.700*	*No*
3	0	*0.578*	*0.622*	*0.689*	*No*
4	0	*0.444*	*0.567*	*0.572*	*No*
5	0	0.406	0.844	0.856	Yes
6	0	0.706	0.694	0.733	Yes
7	0	0.733	0.778	0.672	Yes
8	0	0.611	0.711	0.544	Yes
9	0	0.622	0.878	0.733	Yes
10	0	0.794	0.889	0.700	Yes

Table 2. Ensemble variable importance. Importance of environmental variables from the seven EENMs contributing to the grand mean ensemble. Environmental variable with greatest importance in each ensemble run is highlighted (bold).

Ensemble Run	Bathymetry	NSST	Chl-*a*
1	**0.464**	0.368	0.172
5	0.209	**0.376**	0.162
6	**0.679**	0.358	0.171
7	0.318	**0.576**	0.035
8	**0.461**	0.370	0.111
9	0.200	**0.496**	0.185
10	0.277	0.205	**0.287**

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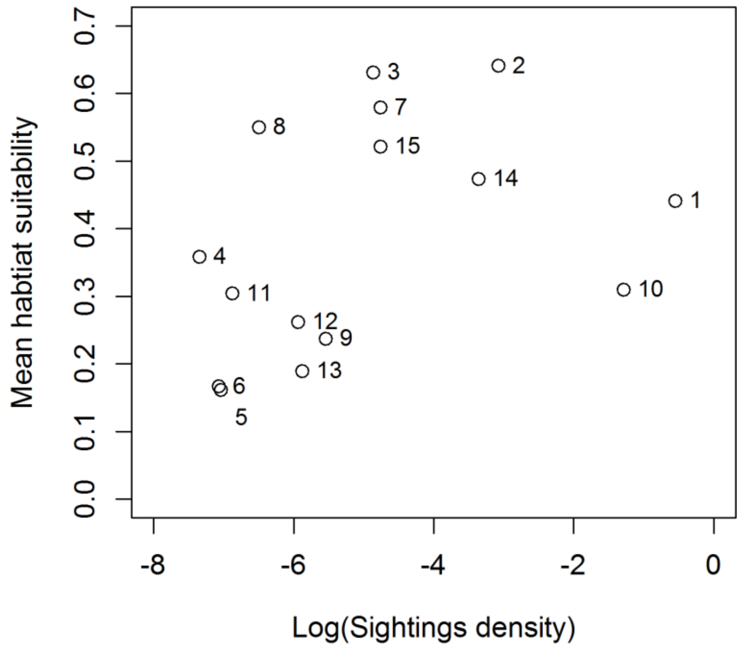

Supplemental Figure 1. Scatterplot of log public sightings density plotted against mean habitat suitability occurring within 15 coastal regions. Arabic numbers indicate region number (see Fig. 3C). A log transformation has been applied to sightings density to aid visual interpretation of the data.

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Highlights

1. We use Ecological Niche Ensemble Models to predict habitat suitability across the UK seascape
2. Areas to known support basking sharks were identified in the resulting habitat suitability model as were novel regions of high relative habitat suitability
3. Public sightings data and habitat suitability strongly correlated in coastal waters
4. EENM shows merits in assisting marine planning and delivering improved conservation outcomes for the species

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