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# Predicting sea pen (Pennatulacea) distribution on the UK continental shelf: evidence of range modification by benthic trawling

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## Abstract

Sea pen communities are Vulnerable Marine Ecosystems (VME) which occur worldwide in soft bottom sediments where trawling often occurs. The ability of marine managers to assess, monitor and mitigate impacts to sea pens at national scales has, however, been constrained by a limited understanding of environmental requirements, geographical distribution, and responses to trawling. In this study we use Random Forest species distribution modelling (SDM) to predict the distribution of suitable habitat for the tall, slender, and phosphorescent sea pens (*Funiculina quadrangularis*, *Virgularia mirabilis* and *Pennatula phosphorea*) on the UK continental shelf, exploring the results relative to the distribution of fishing activity. Occurrence of all three species corresponded to areas of low current and wave velocity, where suspended matter in the water column was also low. However, for *F. quadrangularis*, the largest species, the models indicated substantially different drivers of distribution

between the Greater North Sea and Celtic Seas ICES Ecoregions. This disparity appears to reflect modification to the range and realised niche of this species in the Greater North Sea, due to trawling impacts. *P. phosphorea* and *V. mirabilis* appear to be more resilient to trawling, with no clear negative relationships observed. Our findings illustrate the value of broadscale qualitative comparisons between SDMs and human activity data for insights on pressure-state relationships. When combined with robust distribution maps, this improved understanding of vulnerability will enable marine managers to make ecologically sound, defensible decisions and deliver tangible conservation outcomes for sea pen communities.

## 1 Introduction

Sea pens (Pennatulacea) are globally distributed colonial octocorals that are adapted to inhabit soft muddy or sandy sediments. Standing erect from the seabed, often in dense aggregations or 'fields', they provide structural complexity in otherwise featureless sediments, creating microhabitats, shelter and attachment substrata for sessile and motile fauna (Buhl-Mortensen & Buhl-Mortensen 2014, De Clippele et al. 2015). Such aggregations also function as nursery grounds for commercially important fish (e.g. the redfish genus *Sebastes*; Baillon, 2012) and serve as a food source for a range of invertebrates (García-Matucheski & Muniain 2011, Gale et al. 2013). Despite their wide distribution, high abundance and functional value, sea pens remain poorly studied in comparison to hard corals (Scleractinia).

Sea pens, as relatively slow growing and long-lived organisms, are vulnerable to damage, displacement or removal by demersal fishing activities (Hixon & Tissot 2007, Malecha & Stone 2009, Lauria et al. 2017). As such, their conservation status is acknowledged through various international legislative and policy instruments, with sea pen communities being recognised as Vulnerable Marine Ecosystems (VME) by the United Nations General Assembly (Rogers & Gianni 2010). Conservation measures for VMEs have advanced globally in recent decades (as summarised by Aguilar et al. 2017), with a variety of spatial management measures adopted at national and international scales, including the establishment of Marine Protected Areas (MPAs). Although legislative provisions have improved, functional implementation of spatial measures has been slow; partly due to a poor understanding of environmental requirements and geographical distributions of VMEs (Aguilar et al. 2017). This is particularly relevant at the

scale of individual nations, given the fundamental role of national frameworks in driving spatial conservation measures (Grip 2017). As sea pens are vulnerable to trawling impacts, a clear understanding of their environmental requirements and geographical ranges (both observed and theoretical) is essential to underpin spatial management of fishing activity within and beyond MPAs.

The United Kingdom continental shelf (UKCS) is a good example of a marine region that is extensively and chronically impacted by mobile demersal fishing, resulting in modification of biological assemblages and biogeochemical functions (Tillin et al. 2006, Thurstan et al. 2010, Kröger et al. 2018, Rijnsdorp et al. 2018). Sea pens in this region inhabit mud-rich, depositional habitats (Hill & Wilson 2000, Greathead et al. 2007, 2015), resulting in particular vulnerability to the commercially important *Nephrops norvegicus* (or '*Nephrops*') fishery, which deploys otter trawls on muddy sediments, abrading the seabed surface and penetrating the top few centimetres (Ungfors et al. 2013, Eigaard et al. 2016). UK *Nephrops* landings have risen dramatically over recent decades in comparison to other European countries (Ungfors et al. 2013, Marine Management Organisation 2019), and the targeted muds are reported to be more significantly impacted by trawling, and to take longer to recover, than sand or gravel habitats (Hiddink et al. 2006, Rijnsdorp et al. 2016). Despite the potential threats to sea pen communities from demersal trawling, no studies have yet explored these impacts at the scale of the UKCS.

Sea pen communities on the UKCS comprise the tall sea pen (*Funiculina quadrangularis*), slender sea pen (*Virgularia mirabilis*) and phosphorescent sea pen (*Pennatula phosphorea*), the ecology and ranges of which have been explored in territorial Scottish waters by

Howson et al. (1994) and Greathead et al. (2007, 2015). Due to the relative paucity of research on the responses of these species to trawling abrasion, sensitivity assessments and evaluations of population viability in fished areas largely depend on physiological traits information and studies of analogous species (Hill & Wilson 2000, Ager 2003, Jones 2008), supported by a small number of local-scale trawling impact studies (Howson & Davies 1991, Tuck et al. 1998, Greathead et al. 2005, Murray et al. 2015). The available evidence suggests that the sensitivity of these species to trawling impacts may vary depending on physiology (i.e. flexibility and recovery potential) and retraction ability (Hill et al. 2020). *F. quadrangularis*, the largest and least often recorded of the three species (exceeding 200 cm in length) is considered the most sensitive to trawling impacts given its inability to retract its brittle axial rod beneath the sediment (Greathead et al. 2007) and the slow growth rate of analogous species (Wilson et al. 2002). The smaller and more often encountered *V. mirabilis* and *P. phosphorea* are able to retract into burrows and are generally considered less vulnerable than *F. quadrangularis* (Greathead et al. 2007, Ambroso et al. 2013). There is some evidence to support the lower sensitivity of these two species, although direct impact studies have thus far been confined to the north-western Scottish inshore (Greathead et al., 2005; Tuck et al., 1998).

Species distribution models (SDM) are increasingly used in management of marine habitats, where determining actual species distribution can be logistically and financially challenging. SDMs provide geographically broad spatial predictions of environmental suitability for specified fauna, based on sample data and environmental data layers. The increasing accessibility of remotely sensed environmental data products now allows extrapolation from a limited amount of sample data to much larger areas of seabed (Tyberghein et al. 2012, He

et al. 2015). A number of regional scale studies have applied the SDM approach to predict sea pen distribution (Krigsman et al. 2012, Knudby et al. 2013, Kenchington et al. 2014, Beazley et al. 2016, Murillo et al. 2016, Lauria et al. 2017, Bastari et al. 2018, Kinlan et al. 2020), including a study of the Scottish West Coast, lochs and islands by Greathead et al. (2015). In addition to analysing species environmental requirements and extrapolating their distributions into unsampled areas, SDMs can also be used to shed light on external factors affecting natural distributions. The predicted distributions reflect the input data, and models using data from impacted populations will predict impacted distributions, allowing comparison to natural distributions. These predicted distributions can then be evaluated relative to the known distribution of anthropogenic pressures, to support marine spatial planning and management (e.g. Marshall et al. 2014, Reiss et al. 2015). This linkage of species observations, environmental parameters and anthropogenic pressures enhances understanding of 'pressure-state' relationships, enabling defensible, evidence-based management decisions, for example; exclusion of human activities from areas of high species vulnerability and establishment (and modification) of ecologically coherent, well-connected MPA networks (e.g. Smith et al., 2009; Sundblad et al., 2011). To this point the majority of SDM studies on sea pens have focused on spatial predictions of environmental suitability and have not linked predicted species distribution to anthropogenic impacts. A synergistic approach combining spatial predictions by SDM and comparison to anthropogenic activity data would improve the ability of marine managers to assess, mitigate and monitor impacts to sea pen communities. Thus far, to our knowledge, this connection has not yet been made at a national scale.

In this study we present the first application of SDM to sea pens at the scale of the UKCS, using Random Forest classification models (Breiman 2001) to investigate environmental drivers of *F. quadrangularis, V. mirabilis and P. phosphorea* distribution and predict their occurrence across the UKCS. Here we use modelled environmental parameters to predict suitable habitat for the three species, training and validating the models using a large legacy trawl and imagery dataset. The predicted distributions are mapped and evaluated in the context of demersal fishing activity data. Finally, we use these results to explore whether anthropogenic pressures may have shaped the observed distribution of sea pens on the UKCS and discuss the implications for sea pen management and conservation.

## 2 Methods

The study area (Figure 1) covers most of the continental shelf inside the UK Exclusive Economic Zone (EEZ). The spatial extent of the study was determined by the extent of the sediment composition layers (Mitchell et al. 2019a, b) used as predictor variables in the models. Consequently, the northernmost tip of the shelf EEZ is excluded due to lack of environmental data coverage. The full study area is hereafter referred to as the UK continental shelf (UKCS). Based on preliminary results indicating differences in modelled sea pen distribution patterns and environmental responses between sea areas, the study area was further divided into two separate oceanographic 'Ecoregions', Celtic Seas (CELS) and Greater North Sea (GRNS), as delineated by the International Council for the Exploration of the Sea (ICES) (ICES 2020). All environmental data and species observations were aligned to a raster grid of the study area with a cell size of 0.002 degrees (~200 metres).

## 2.1 Species presence / absence data

Presence / absence sample data for the tall sea pen (*Funiculina quadrangularis*), slender sea pen (*Virgularia mirabilis*) and phosphorescent sea pen (*Pennatula phosphorea*) were collated from multiple legacy sources, comprising data collected using underwater imagery, dive surveys, benthic trawls and grabs over a period spanning 1961 to 2019. The majority of observations were derived from the publicly available UK Marine Recorder database (Public snapshot v20170825, available from https://jncc.gov.uk/our-work/marine-recorder, downloaded on 01/11/2017). These were supplemented by additional underwater imagery and grab samples collected as part of the UK Marine Protected Areas Programme, as well as Cefas benthic trawl surveys and grab sampling conducted under various research and monitoring programmes.

Presence / absence observations for each of the three sea pen species were reduced to one observation per 0.002 degree (~200 m) raster cell. For trawls and video tows, where co-ordinates were recorded at the beginning and end, the positional midpoint was used as the observation location. The precision of positioning for the observations differed based on both their vintage and sampling method, but this was mitigated by the size of the raster cells and consequently the spatial scale of prediction. Each raster cell with at least one intersecting presence observation was classified as a presence. Absence observations from grab samples were excluded as they are considered to under-sample large, sparsely distributed epifauna such as sea pens. To limit the effects of spatial autocorrelation and redundancy, the data in raster cells were further spatially subsampled to exclude neighbouring points closer than 250 metres. Datasets with very low prevalence lack the ability to adequately represent the nature

of species dependence on environmental conditions (Santika 2011). Hence, a final subsampling step was conducted individually for each species and region to randomly down-sample absence records, achieving a 10% prevalence for each dataset used in models. Table 1 shows the total number of raster cells with a presence / absence record and the number of cells included for modelling in each region.

## 2.2 Environmental predictor layers

The environmental predictor layers included in model development, their units, sources and spatial resolution of the source data are listed in Table 2. All layers were resampled to the native resolution of the bathymetry layer (0.002 degrees, or ~200 m). Where necessary, values were interpolated using the Empirical Bayesian Kriging function in ArcGIS10.5 Geostatistical Analyst (with default settings).

SAGA GIS tools for QGIS (v. 3.2; Conrad et al. 2015) were used to calculate a set of regional terrain variables that, whilst terrestrial in origin, can be used to represent aspects of seabed topography. The regional terrain variables calculated include Channel Network Base Level, Channel Network Distance, Valley Depth, Closed Depressions, Relative Slope Position and Standardised Height (Shaw et al. 2004). The concept of the channel network base level is used to distinguish topographic highs and lows, by using the Digital Elevation Modelling (DEM) to create a channel network. The channel network base level is an interpolated elevation surface connecting the channel elevations. The channel network distance is calculated as the vertical distance between the DEM elevation and the channel network base level elevation. Valley depth is calculated as the vertical distance to the lowest elevation of source flow. Closed

depressions represent sinks in the topography, surrounded on all sides by higher ground, with values increasing with the height difference to the surrounding higher ground. The relative slope position ranges from 0-1 as an index of location along the entire length of a slope. Standardised height is the product of normalised height (value ranging from 0-1 from the lowest to the highest position within a respective reference) multiplied by absolute height, relating a location to its wider surrounding topology (Shaw et al. 2004).

Layers used for current and wave velocity at the seafloor, winter suspended particulate matter, sand, mud and gravel fractions, as well as sand to gravel log ratio and mud to gravel log ratio are those produced by Mitchell et al. (2019c), available for download through the Cefas Data Hub (Mitchell et al. 2019a,b; Table 2). Mean, maximum and minimum bottom temperatures, along with the mean and maximum annual temperature ranges for 2017-2019, were calculated from daily-mean seabed temperatures (C°), obtained from a high resolution North-West European Shelf forecasting ocean assimilation model, downloaded from http://marine.copernicus.eu/ (Table 2). Seasonal averages for spring (March, April, May), summer (June, July, August) and autumn (September, October, November) of chlorophyll-a concentrations (mg $m^{-3}$) and net primary productivity of carbon (mg $m^{-3}$ $day^{-1}$) between 2017-2019 were computed from monthly composites of ESA Ocean Colour CCI Remote Sensing Reflectance data and the UK Met Office Operational Suite Atlantic Margin Model FOAM output downloaded from http://marine.copernicus.eu/ (Table 2).

Vector layers of ICES Ecoregions (ICES, 2015) and ICES Statistical Areas (ICES, 2005) were rasterised and included as factor variables acting as proxies for biogeographical attributes and oceanographic conditions in the various sea areas surrounding the UK.

## 2.3 Model training and validation

Originating from the field of machine learning, the Random Forest method is increasingly used by ecologists due to its high classification accuracy and ability to characterize complex interactions between variables (Prasad et al. 2006, Cutler et al. 2007). Three Random Forest distribution models (Breiman 2001) were built for each sea pen species; 1) a full model trained using data from the entire study area (hereafter referred to as the UKCS model), 2) a model trained using only data from the Greater North Sea (hereafter referred to as the GRNS model) and 3) a model trained using only data from the Celtic Seas (hereafter referred to as the CELS model). Each model was used to predict the distribution onto the entire study area (UKCS). Transferability of models between the two Ecoregions was tested by calculating model performance statistics on test data separately for each. In the case of the UKCS model, accuracy was tested for the full UKCS test dataset and for each Ecoregion.

All analyses were run using the R statistical computing software (vs. 3.5.1, R Core Team 2018). Pre-selection of predictor variables was conducted using the *Boruta* algorithm in the 'Boruta' R package (Kursa & Rudnicki 2010), to reduce the number of variables included in the model for ease of interpretation and to allow comparison between species. The algorithm compares the importance of a variable calculated by a Random Forest model to the importance of a random permutation of the same variables over several iterations. Variables with higher than random importance for a least one species were considered for inclusion in the final predictor variable set. Of the correlated predictor variables (correlation coefficient > 0.6), the variable with the highest average importance across all three species (calculated by *Boruta*) was selected to be included in the final set of variables. The UKCS model also included Ecoregion

as a factor variable. The final set of predictor variables included in models is indicated in Table 2.

As our dataset was compiled from multiple sources, consideration was given to retaining one or more of the datasets for independent validation. However, combinations of all the component datasets were required to achieve full geographical coverage of the study area for both training and testing the models. Consequently, a multi-run cross-validation on the full dataset was determined to be the more appropriate validation strategy, affording the most comprehensive training and test datasets, together with an approximation of model stability over multiple subsets of data. The 'biomod2' package (vs. 3.4.6, Thuiller et al. 2009, 2020) was used to train and test 10 cross-validation (CV) runs of each model to control for any artefacts resulting from a single split of the data into training and test data sets by random selection. The 10 training and test data splits were created by assigning two five-fold cross-validation sets with equal numbers of presences included in each for balance, resulting in an 80/20 split into training/testing data.

Random Forest models were built using 500 trees and five variables randomly sampled as candidates at each split. Variable importance statistics and partial response curves were extracted from each cross-validation run. Predictions from each CV run were dichotomized into presence / absence using a threshold that optimizes the True Skill Statistic (TSS; Allouche et al. 2006). TSS was selected based on its insensitivity to prevalence and its equal weighting of sensitivity and specificity, avoiding pitfalls of both the Kappa statistic and 'area under the receiver operating characteristic curve' (AUC) highlighted in numerous studies (including Manel et al. 2001, Lobo et al. 2008, Jiménez-Valverde 2012). The final predicted distribution

layer from each model combined the dichotomized outputs from all 10 CV runs, classified into three categories; 1) absence, 2) low likelihood of presence (1-5 CV runs predict presence) and high likelihood of presence (> 5 CV runs predict presence).

The accuracy of predicted presences / absences were examined using the 'PresenceAbsence' package (Freeman & Moisen 2008). Specificity, sensitivity (Fielding & Bell 1997), the Kappa statistic and TSS were calculated for the corresponding test data in each cross-validation run. For the UKCS model separate statistics were calculated by filtering the test data by each Ecoregion in turn. For testing the transferability of the model trained on data from one Ecoregion to the other, the test data from the corresponding cross-validation run from the other Ecoregion were used.

### 2.4 Overlap with demersal fisheries

The potential contribution of bottom contact fishing impacts to the observed difference in environmental preferences of *F. quadrangularis* between the two Ecoregions was investigated further. Spatial fishing intensity data were overlain with presence as predicted by the CELS model, and the ratio of observed absences in impacted to unimpacted sample locations was compared in areas where presence was predicted.

The spatial distribution of potential impacts from fishing activity was determined by combining information on bottom contact fishing from two sources. The spatial distribution of offshore physical disturbance by mobile bottom contacting fishing gears was derived from gridded Vessel Monitoring Systems data (VMS) (ICES 2019), acquired from vessels ≥12m in length. The gridded VMS layer was created by calculating the mean value of the average swept area ratios (SAR) for 2009-2017 from annual 5 km resolution 'OSPAR Bottom Fishing Intensity – Surface' data layers, downloaded from the OSPAR Data and Information System

(ODIMS, https://odims.ospar.org/odims_data_files/). For inshore waters an additional layer was obtained, representing the number of small (<15 m) fishing vessels using bottom contacting gears operating in coastal areas (Kafas et al. 2014). This layer was produced by adding the number of vessels for scallop dredgers, *Nephrops* trawlers and other bottom trawlers, as reported by the ScotMap Inshore Fisheries Mapping Project (2007-2011; downloaded from the Marine Scotland Data portal, https://dx.doi.org/10.7489/1554-1).

The fishing intensity layers ('Mean SAR' / 'no. vessels') were intersected with sample points for *F. quadrangularis*. Histograms of presence observations across increasing fishing intensity (both layers) were used to determine cut-off values for fishing intensity where *F. quadrangularis* was less numerous, inferring a negative impact on this species. The cut-off values were applied to each fishing intensity layer and both were combined into one layer delineating the areas where fishing is likely to impact *F. quadrangularis*.

The number of absence observations from areas with a predicted high likelihood of presence (>5 CV runs predict presence), low likelihood of presence (1-5 CV runs predict a presence) and absence were examined to compare the fraction of absences in 'impacted' vs. 'unimpacted' areas in both Ecoregions.

# 3 Results

## 3.1 Model performance and transferability

The UKCS models for all three sea pen species showed good performance (Table 3). *F. quadrangularis* was modelled with the highest overall accuracy (TSS = 0.90), followed by *P. phosphorea* (TSS = 0.85), then *V. mirabilis* (TSS = 0.77). Inclusion of Ecoregion as a predictor variable in the UKCS models resulted in accurate predictions in both the CELS and GRNS areas.

For *P. phosphorea* and *V. mirabilis* the UKCS model showed fractionally higher sensitivity and overall performance in the Greater North Sea (GRNS) than the Celtic Sea (CELS) (Table 3). *F. quadrangularis* models trained on data from one Ecoregion did not transfer well to the other. The transferred models severely underpredicted presence, with very low sensitivity (0.04 and 0.12 GRNS to CELS and CELS to GRNS, respectively) and consequently poor overall performance in the opposite region (GRNS to CELS TSS = 0.02, CELS to GRNS TSS = 0.04). For *P. phosphorea* and *V. mirabilis* transferability was much better from the CELS model to the Greater North Sea region than from the GRNS model to the Celtic Seas, with an equal or better ability to predict presences and only a marginally poorer specificity (Table 3). The poorer sensitivity and specificity in the *P. phosphorea* and *V. mirabilis* GRNS models transferred to the Celtic Seas, indicating that presence was underpredicted in some areas of this Ecoregion and overpredicted in others, suggesting poor specification of the species niche by the models (Table 3).

### 3.2 Factors driving sea pen distributions

*F. quadrangularis*, *V. mirabilis* and *P. phosphorea* all display broadly similar environmental requirements when modelled and tested using the full dataset (including both ICES Ecoregions). The most important predictor variables for all three species include mean bottom temperature, wave and current velocities, and the concentration of winter suspended particulate matter in the water column. Primary productivity is also a notable contributor to the *P. phosphorea* and *V. mirabilis* models. The topographic and sediment variables contribute to a lesser degree, but all increase model performance when included. However, the order of importance differs between the Ecoregions. The GRNS models are all strongly driven by temperature, whilst the CELS models on the other hand are more influenced by

suspended matter and current and / or wave velocities. Sand and mud content are also more influential in the CELS models than the GRNS models (Figure 2).

All species in both Ecoregions are more likely to occur in low current and wave velocities, where concentration of suspended matter in the water column is low. *F. quadrangularis* and *P. phosphorea* show a preference for current and wave velocities up to 0.3 m $s^{-1}$ and 0.5 m $s^{-1}$, respectively, and suspended matter at less than 2 g $m^{-3}$, with 95% of all presences occurring in these conditions. *V. mirabilis* shows a somewhat higher tolerance of wave conditions and turbidity, up to 1.1 m $s^{-1}$ for wave velocity and 5.5 g $m^{-3}$ for suspended matter. The relationship with primary productivity is more complicated. *P. phosphorea* is more likely to occur in areas with low primary productivity, whereas *V. mirabilis* shows a positive association in the CELS model but a negative one in the GRNS model. Responses to bottom temperature and sediment, and in the case of *F. quadrangularis* to bottom topography, differ between the Ecoregions. All species temperature ranges are similar (7.8-12.9 $^{o}$C) but extend into much warmer mean temperatures in the Celtic Seas than in the Greater North Sea. The clearest difference is seen in *F. quadrangularis*, which in the North Sea is most likely to occur between 8-9$^{o}$C, whilst in the Celtic Seas this extends to ~10.5 $^{o}$C (Figure 3).

*P. phosphorea* and *V. mirabilis* consistently occur in areas with sheltered concave topography with increased 'enclosedness', represented by higher values of valley depth and closed depressions along with low standardised height. *F. quadrangularis* follows these trends in the Celtic Seas, but in the Greater North Sea it occurs almost exclusively offshore, and on flat or slightly elevated ground (Figure 3).

Although the effect of mud and sand content is much lower in the GRNS models, the presence probability for all species, and in both Ecoregions, is increased by higher mud content. The

CELS models show higher probability of presence for all species with lower sand content, whilst in the GRNS models a slight increase is seen with high sand content. The mud to gravel ratio also shows an opposite trend of influence between the Ecoregions. Whilst presences are more likely with a high mud to gravel ratio in the GRNS, the opposite is true of CELS. The differences are most pronounced for *F. quadrangularis* (Figure 3).

The predicted distributions of *F. quadrangularis* across the UKCS by the CELS and GRNS models are almost entirely different (Figure 4). The GRNS model does not predict the presences observed in the warmer inshore bottom temperatures of the CELS, instead predicting presences further offshore in cooler areas with higher sand content. The CELS model, on the other hand, predicts into muddy basins in a wide temperature range, but fails to predict most of the presences in the North Sea that occur in patches of sandier sediments.

### 3.3 Predicted distributions of sea pens on the UK continental shelf

The UKCS models indicate a largely overlapping distribution, with the main habitat for each species occurring in North Atlantic waters off the coast of Scotland and in the northern half of the North Sea. In terms of spatial extent, the area of predicted distribution was greatest for *P. phosphorea*, followed by *V. mirabilis* and *F. quadrangularis*. *F. quadrangularis* has the most restricted distribution, being confined to the northern waters and, in the south, the shelf edge where canyon heads cut into the shelf break. A small suitable patch is also predicted in the Western English Channel. *P. phosphorea* is also predicted to occur in pockets of suitable habitat in the Western English Channel and southern Celtic Sea towards the shelf edge. *V. mirabilis* habitat has the widest geographical distribution, with predicted patches in all sea areas excluding the Eastern English Channel and Southern North Sea (Figure 5).

### 3.4 The role of bottom contact fishing impacts in the observed distribution of *Funiculina quadrangularis*

Comparison of the CELS and GRNS modelled presence distributions and the fishing impact layers revealed spatial trends which related to the Ecoregion model disparities observed for *F. quadrangularis*. *F. quadrangularis* is notably absent from the area predicted as suitable habitat by the CELS model (Figure 6a). The CELS model, therefore, fails to accurately describe the observed distribution of *F. quadrangularis* in the Greater North Sea, despite encompassing the range of environmental conditions existing within it. A large proportion (71%) of the muddier seabed in the Greater North Sea, predicted as suitable *F. quadrangularis* habitat by the CELS model, is impacted by benthic trawling by vessels ≥12 m in length, in comparison with only 39% in the Celtic Seas (Table 4). An additional 5% of the Greater North Sea and 15% of the Celtic Seas Ecoregions, is covered by grid cells where inshore fisheries vessels (<15 m in length) are known to operate. Where presences are observed in areas predicted as suitable by the CELS model, they occur outside of the mapped extent of fishing impact (Figure 6a(i)). *F. quadrangularis* are also observed on sandier ground adjacent to the edges of the mud basins predicted as suitable habitat by the CELS model. This effect is exemplified in Figure 6a(ii), which shows the presence of *F. quadrangularis* in patches of sandier and mixed sediments in one of the large mud basins in the Fladen Ground. In contrast, *P. phosphorea*, which has a very similar predicted distribution, does occur widely across the areas predicted as suitable for *F. quadrangularis*, where *F. quadrangularis* is absent (Figure 6b). An example of *F. quadrangularis* on the sandy mixed ground patches in Figure 6a(ii) is shown in Figure 7.

Figure 8 shows presences of *F. quadrangularis* across the whole study area are highly skewed towards areas of low fishing impact. Presences are overwhelmingly observed where no fishing occurs according to SAR from VMS data (Figure 8a). Similarly, in the inshore region, the majority of presences are observed in areas where less than four inshore vessels (<15 m) are known to regularly fish using bottom contacting gear (Figure 8b). The majority of absences of *F. quadrangularis* observed where the CELS model indicates a high likelihood of presence are from areas impacted by bottom contact fisheries (70% and 60% in the North Sea and Celtic Seas, although these values are likely to be inflated to some degree due to a greater area of predicted suitable habitat being trawled in the North Sea than the Celtic Seas). The comparable values where the model predicts absence are only 24% and 20% (Figure 8c).

## 4 Discussion

The Random Forest models were highly effective in predicting occurrences of *Funiculina quadrangularis*, *Virgularia mirabilis* and *Pennatula phosphorea* on the UKCS. *F. quadrangularis* was predicted with the highest accuracy, followed by *P. phosphorea* and *V. mirabilis*. Preliminary investigations, however, indicated disparities in the responses of sea pens to environmental parameters between the Celtic Seas and Greater North Sea ICES Ecoregions, particularly for *F. quadrangularis* (the species most sensitive to physical disturbance). This was corroborated by models trained on data from one ICES Ecoregion only, which showed different partial responses to environmental variables in each Ecoregion. A formal assessment testing the accuracy of a model trained on data from one ICES Ecoregion using the independent data from the other Ecoregion confirmed the poor transferability of models between Ecoregions. Further qualitative examination of the predicted and observed distributions, in conjunction with fishing data, revealed that these differences are likely to

reflect the modification of sea pen communities by demersal trawling. *F. quandrangularis* appeared to be largely absent from its expected range in the Greater North Sea, whilst *P. phosphorea* and *V. mirabilis* appeared less vulnerable to trawling impacts.

The broadscale geographical distributions predicted by the full UKCS model (using data from both Ecoregions) are largely consistent with sea pen observation data held by the Ocean Biogeographic Information System (OBIS 2020) and the UK National Biodiversity Network (NBN) Atlas (NBN 2020). This is unsurprising given the inclusion of NBN data in the model, however there were some inconsistencies in predicted and observed distributions. All three sea pens (particularly *F. quadrangularis*) are predicted to occur at the shelf break at the extreme south-western tip of the UK EEZ, but are not represented by direct observations in this particular dataset. Fields of *F. quadrangularis* were observed on the shelf break in this region during the Flanders Research Foundation funded MINIMOUNDS project (2013-2016; Howell, unpublished). This provides an example of the efficacy of the model, even where direct observations are absent. The model also predicts all three sea pen species at limited patches in the Western Channel. *P. phosphorea* and *V. mirabilis* are both recorded in this area from NBN and Cefas data, however *F. quadrangularis* are not (also being absent from the OBIS data). It remains unclear whether this absence is due to overprediction by the model (which in this area has been assigned low confidence), a sparse distribution leading to a low probability of encounter, or absence due to human impacts. The different time periods covered by the sea pen observation data (1961 to 2019) and environmental data, such as temperature and primary productivity (2017-2019), add a potential source of error where the conditions may have been different at the time the samples were collected.

The sea pen distributions observed for all three species are strongly influenced by lower seabed temperatures, low wave and current velocities, and low levels of suspended particulate matter, confirming a requirement for deep, depositional environments. Somewhat surprisingly, sediment composition was determined to be less important. This is likely due to sediment composition being equally driven by the more influential variables (e.g. in a negative correlation between wave and current velocities and fine sediments). All three species did, however, display a strong affinity for muds and muddy sands. Primary productivity, which was influential in the models for *P. phosphorea*, and *V. mirabilis,* is likely to act as a proxy for coastal and enclosed water bodies. The varying responses to primary productivity in the two Ecoregions may result from the inshore / offshore balance of sample locations between the regions. A high number of samples in otherwise suitable habitat in the Celtic Seas Ecoregion are from inlets and lochs with corresponding high primary productivity. On the other hand, the deeper mud basins are associated with lower primary productivity in the Greater North Sea, being located offshore in non-photic waters.

Despite the similarities in habitat requirements, the three species displayed some divergence in niche breadth, with *V. mirabilis* and *P. phosphorea* tolerating a wider range of environmental conditions than *F. quadrangularis*, reflected in superior model accuracy for the latter species. *V. mirabilis* and *P. phosphorea* were more tolerant of increased sand fractions, and slightly higher current velocities. *V. mirabilis* showed the greatest tolerance to increased wave velocities and concentration of particulate matter in the water column. This explains its distribution, which extends further inshore in the North Sea than that of *P. phosphorea*, and its presence in the Celtic and Irish Seas, which have higher suspended sediment loads. These findings are supported by those of Greathead et al. (2015), who noted that *V. mirabilis*

showed the widest tolerance of a broader range of environmental conditions in Scottish inshore waters, and that *F. quadrangularis* occupied the narrowest niche. It must, however, be noted that we are only discussing the distribution of these species on the continental shelf. *F. quadrangularis* is a cosmopolitan species that, although most commonly reported on the continental shelf and at the top of continental slopes, has been recorded as deep as 2000 m (De Clippele et al. 2015, Lauria et al. 2017, Bastari et al. 2018). Consequently, the models do not capture the full distribution, which extends to deeper, colder water than the UKCS.

Model transferability between Ecoregions was exceptionally poor for *F. quadrangularis*, with almost no overlap in the observed conditions in which this species was predicted. The Greater North Sea model predicted *F. quadrangularis* in topographically elevated areas of sediment with higher sand content. This result entirely contradicts the Celtic Seas model and the findings of previous Scottish inshore studies (Greathead et al. 2007, 2015), which predicted *F. quadrangularis* in topographically concave muddy basins such as inshore lochs and straits. The apparent 'preference' of *F. quadrangularis* for sandy elevated sediments in the Greater North Sea is therefore thought to reflect artefactual variation in the sea pen dataset. Such a striking disparity in agreement points towards the depletion of *F. quadrangularis* within its natural range in the Greater North Sea (and possibly in the Western Channel, where it has been predicted but not observed), caused by a strongly influential factor which is not accounted for by the environmental layers, and which varies in intensity and spatial distribution between the two Ecoregions.

Demersal trawling is widely acknowledged as one of the main pressures on marine benthic ecosystems (Halpern et al. 2008, Hiddink et al. 2017, Rijnsdorp et al. 2018) and is well known

to modify faunal assemblages and affect species distributions (e.g. Tillin et al. 2006, Hinz et al. 2009). Where prevalent, this can result in sensitive species not occupying their full predicted range or being restricted to suboptimal 'edge of niche' habitats (Braunisch et al. 2008). Evidence from the North Sea shows that otter trawlers targeting *Nephrops* and demersal flatfish focus effort in muddy depressions with low bed shear stress (van der Reijden et al. 2018); habitat which is predicted as optimal for sea pens by the Celtic Seas model. The Fladen Grounds is one such area, which has been reported to support the largest *Nephrops* fishery in the world (Ungfors et al. 2013). *F. quadrangularis* were not observed in the muddy depressions of the Fladen Grounds, where gridded VMS data indicate benthic abrasion by trawling (and where the Celtic Seas model predicted their occurrence). This species did, however, occur in patches of interspersed sandier mixed sediment (as confirmed from imagery data; see Figure 7) that do not support *Nephrops* and are therefore unlikely to be targeted by fishers. We therefore hypothesise that *F. quadrangularis*, the most sensitive of the three species (Ager 2003, Greathead et al. 2007), is subject to range modification in the Greater North Sea, with the observed occurrences representing a remnant population occupying the elevated sandy areas with lower disturbance. This finding reflects a significant shift in the niche of *F. quadrangularis* in the Greater North Sea.

Estimating the accurate spatial range and intensity of demersal fishing activities is inherently challenging, often limiting the extent to which pressure-state relationships can be explored at finer spatial scales (Lee et al. 2010, Lambert et al. 2012). In this study we cannot categorically demonstrate cause and effect, given the coarse resolution of the OSPAR VMS data units in relation to the sea pen occurrence data. However, the overwhelming majority of *F. quadrangularis* were observed in grid cells where the swept area ratio was zero,

providing anecdotal support for our hypothesis. This hypothesis is further supported by the findings of Greathead et al. (2005) that the density of *F. quadrangularis* in the Scottish Cuillin Sound (an area of high *Nephrops* trawling intensity), was lower in contrast to the environmentally comparable (but low trawling intensity) Hebridean Sound. Further afield, Pierdomenico et al. (2018) and Fabri et al. (2014) both observed low abundances of *F. quadrangularis* in chronically trawled Mediterranean canyons, whilst Malecha & Stone (2009) found that experimental breakage of the morphologically similar *Halipteris willemoesi* resulted in extremely high mortality rates. Although the available evidence suggests that *F. quadrangularis* is vulnerable to trawling impacts, there is no such indication that creel fishing for *Nephrops* has a negative impact on its distribution. Eno et al. (2001) observed that *F. quadrangularis* was able to re-insert itself into the sediment after uprooting by creel pots. The theory that *F. quadrangularis* is more resilient to creeling impacts is supported by our study, as *F. quadrangularis* was shown to proliferate in Scottish sea lochs where smaller fishing vessels operate; in particular Loch Linnhe, where the *Nephrops* fishery is predominantly creel-based (Berx et al. 2015).

Whilst the high sensitivity of *F. quadrangularis* to trawling appears to severely diminish the transferability of the Celtic Seas and Greater North Sea models, this effect was not as pronounced for *V. mirabilis* and *P. phosphorea*. Actual presences in the North Sea were captured effectively by the Celtic Seas model, although this model tended to overpredict. Conversely the Greater North Sea model underpredicted presences in the Celtic Seas. This trend suggests that the distributions of these species are more limited in the Greater North Sea and perhaps do not cover the entire natural range of environmental variability covered by observations in the Celtic Seas. *V. mirabilis* and *P. phosphorea* both display far broader

geographical ranges than *F. quadrangularis*, being frequent in areas of demersal fishing activity, both in the Celtic Seas and Greater North Sea. There is, therefore, no clear evidence that trawling limits their distribution on the UKCS, corroborating the findings of previous studies that *V. mirabilis* and *P. phosphorea* are less vulnerable to fishing impacts than *F. quadrangularis* (Howson & Davies 1991, Tuck et al. 1998, Greathead et al. 2005). This is likely due to a combination of wider niche breadth, higher abundance, physiological traits (e.g. flexibility) and the ability to withdraw into a burrow (Ambroso et al. 2013, Chimienti et al. 2018).

Previous publications have proposed that sea pen presence and/or abundance could serve as indicators of condition in mud habitats (Greathead et al. 2007, Murray et al. 2015). This study suggests that the presence of *F. quadrangularis* could potentially act as an indicator of healthy, undisturbed conditions, although the absence of this species in suitable habitat should not automatically be assumed to indicate poor habitat condition, as sea pens are known to display patchy or aggregated distributions (Langton et al. 1990, Greathead et al. 2007). Although the predicted distributions of *V. mirabilis* and *P. phosphorea* did not appear to be adversely affected by demersal fishing, it should be noted that these models only reflect presence or absence of sea pens, offering no insight on density or condition. In their 2015 study of the Fladen Grounds, Murray et al. found that the density of *P. phosphorea* decreased along a gradient of increasing trawling pressure, suggesting that density may have potential as an indicator at higher levels of fishing intensity. We suggest that further studies are conducted to explore the relationships between trawling activity and density of *P. phosphorea* and *V. mirabilis*. A greater understanding of these relationships would allow

evaluation of sea pen management measures, in turn enabling ecologically sound management decisions.

A number of UK MPAs have been designated to protect sea pens, however, management measures within MPAs are spatially variable and trawling is not necessarily under active management in areas of suitable habitat. The vast majority of *F. quadrangularis* observations and areas of suitable habitat identified in this study are not currently covered by MPAs designated to protect sea pen communities (particularly in the Greater North Sea; although they are found within those managed for different habitat types and could benefit from management measures in these areas). The predicted distribution models presented in this study (alongside further pressure-state studies on *P. phosphorea* and *V. mirabilis*) could be used to refine management of specific MPA zones and gear types, thus optimising the balance between access to commercially important fishing grounds and protection of sea pen communities.

This study has demonstrated the effectiveness of the Random Forest method for modelling vulnerable species distributions and highlighted the utility of national (and international) data platforms for addressing conservation questions at large scales. Whilst challenges still remain in reconciling the spatial and temporal disparities of sample data, environmental parameters and human pressures, our findings illustrate the value of broadscale qualitative comparisons between SDMs and human activity data for understanding fundamental pressure-state relationships. Benthic trawling is generally accepted as the greatest global threat to marine benthic fauna, yet the increasing accessibility of marine data creates opportunities for informed and targeted mitigation. We anticipate that the approach used in this study could

be widely applied to investigate trawling impacts on sensitive species at large scales, enabling marine spatial planners to make better management decisions and deliver tangible conservation outcomes.

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**Figures**

Figure 1. Map detailing the study area, extent of distribution models, boundaries of the ICES Ecoregions used to delineate the two target regions and the distribution of sea pen presence / absence point observations.

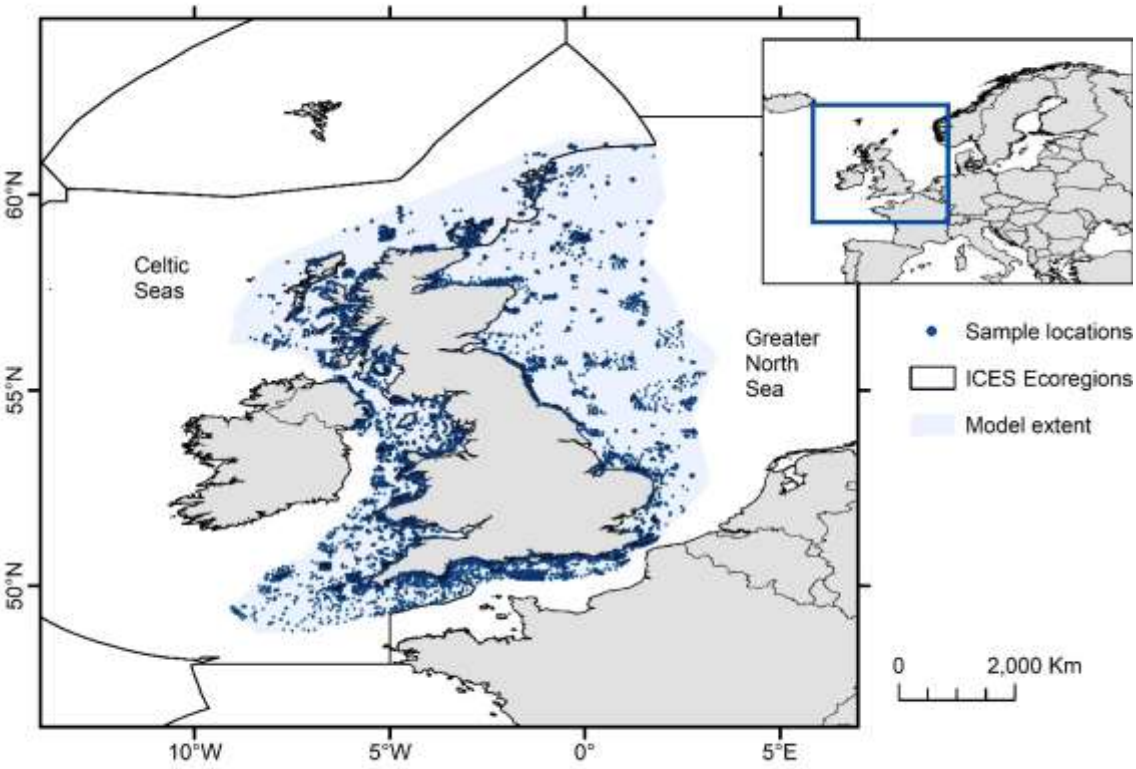


Figure 2. Predictor variable contributions to models by species and regional model. PP = Primary productivity, UKCS = UK continental shelf, CELS = Celtic Seas and GRNS = Greater North Sea. Variable contribution is inferred from a reduction in model accuracy when each predictor variable in turn is randomised. Predictor Importance = 1 minus the correlation coefficient between model accuracies for the full model and the model with the randomised variable.

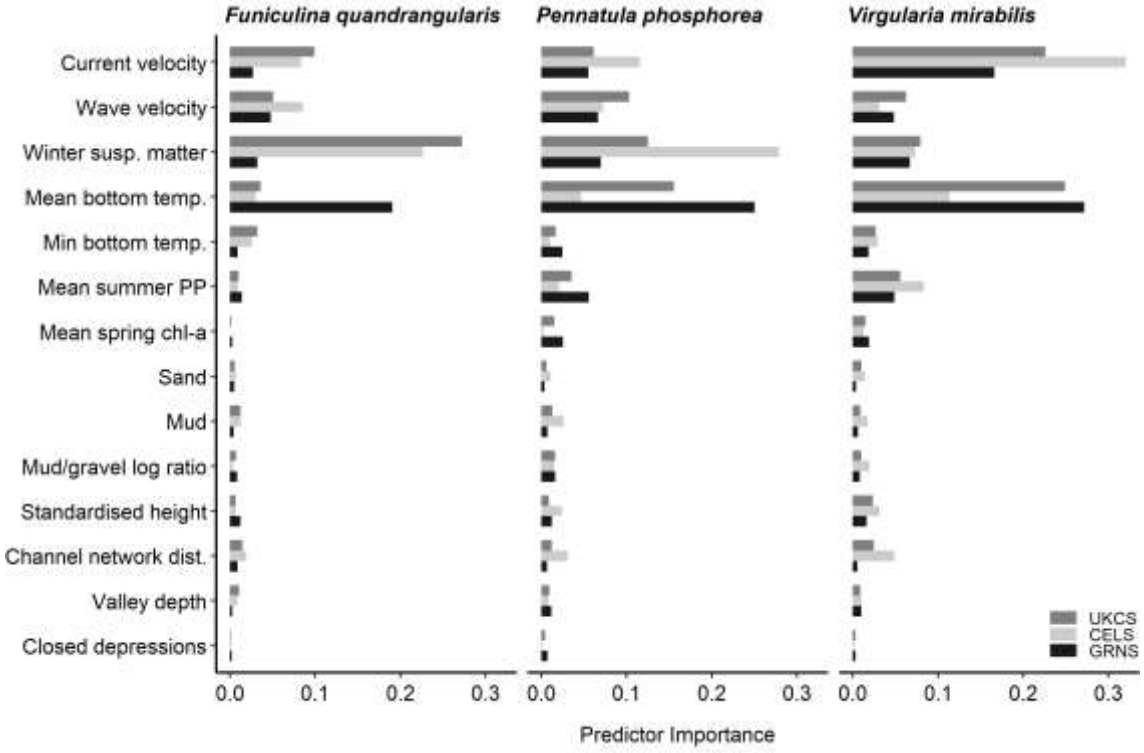


Figure 3. Random Forest model partial response curves illustrating the different response of *Funiculina quadrangularis* presence / absence to substrate and topography variables observed between the Celtic Seas (CELS) and Greater North Sea (GRNS) Ecoregions. The plots show the relative logit contribution of each variable to the probability of presence. The y-axis scale has been log-transformed to allow plotting of curves with a large range of values from both models onto the same axis.

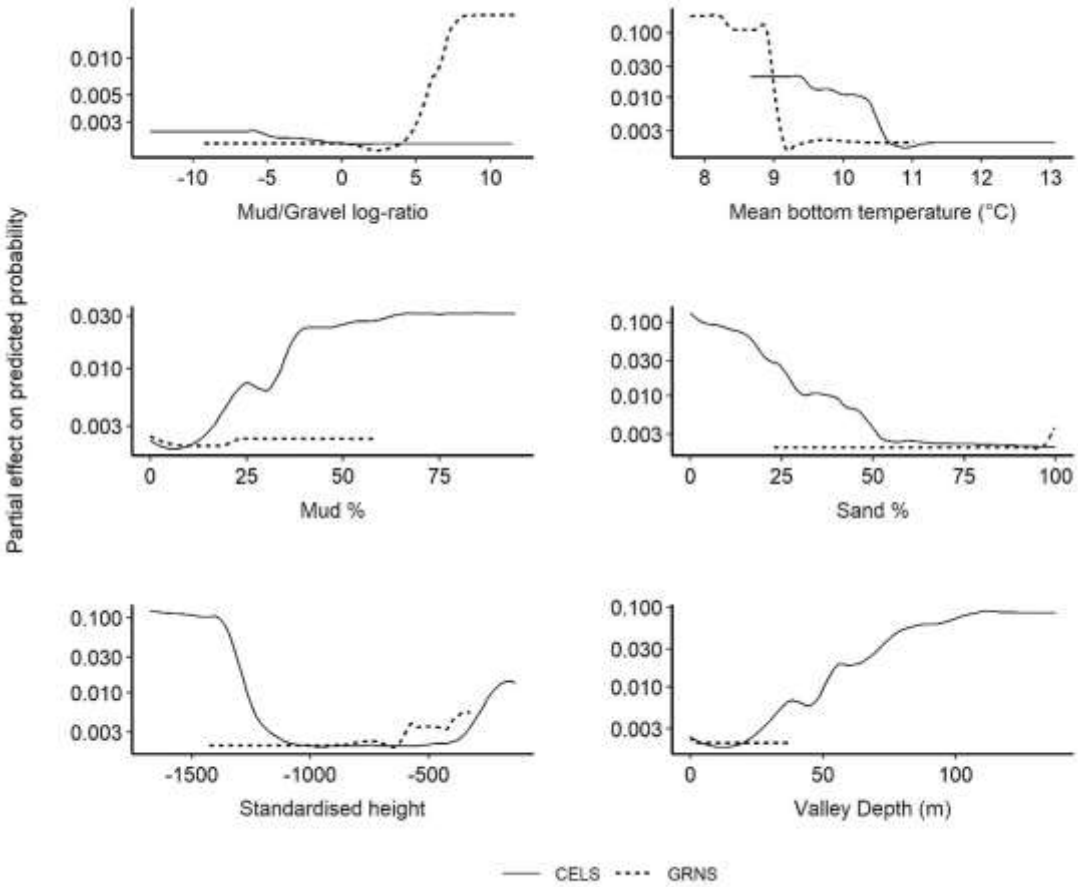


Figure 4. Distribution of *Funiculina quadrangularis* predicted by the CELS (a) and GRNS (b) models, with observed presences. Confidence in the predicted distribution is represented by two categories. Low likelihood of presence is shown where <5 and High likelihood where ≥5 of 10 cross-validation model iterations predicted presence.

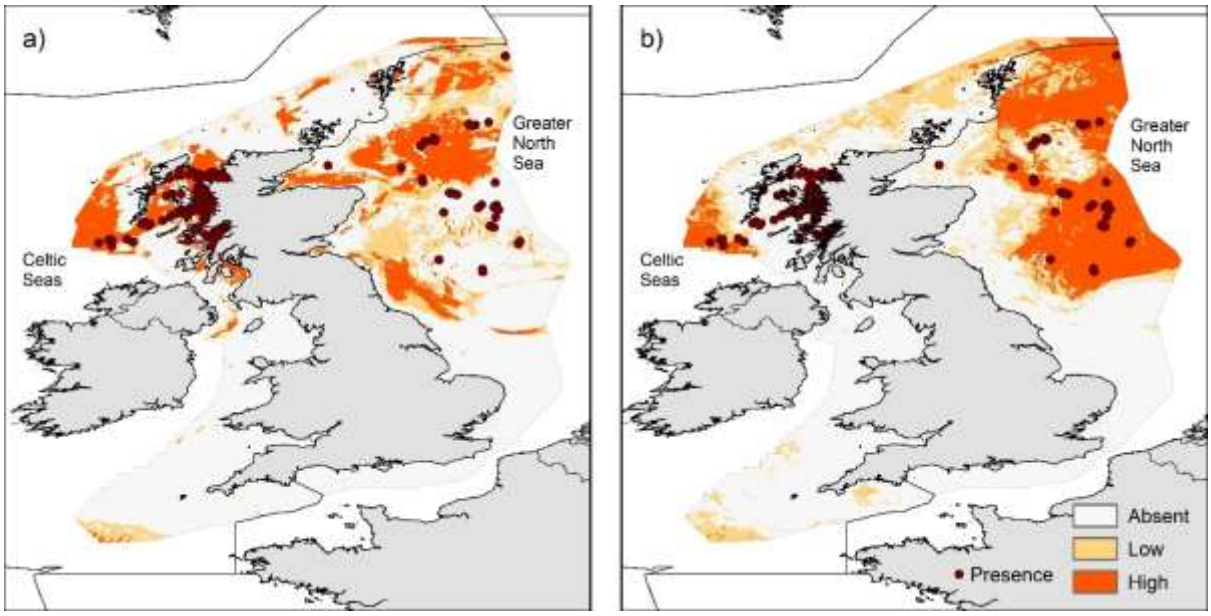



Figure 5. Distributions of (a) *Funiculina quadrangularis,* (b) *Pennatula phosphorea* and (c) *Virgularia mirabilis* predicted by the full UKCS model. Confidence in the predicted distribution is represented by two categories. Low likelihood of presence is shown where <5 and High likelihood where ≥5 of 10 cross-validation model iterations predicted presence.

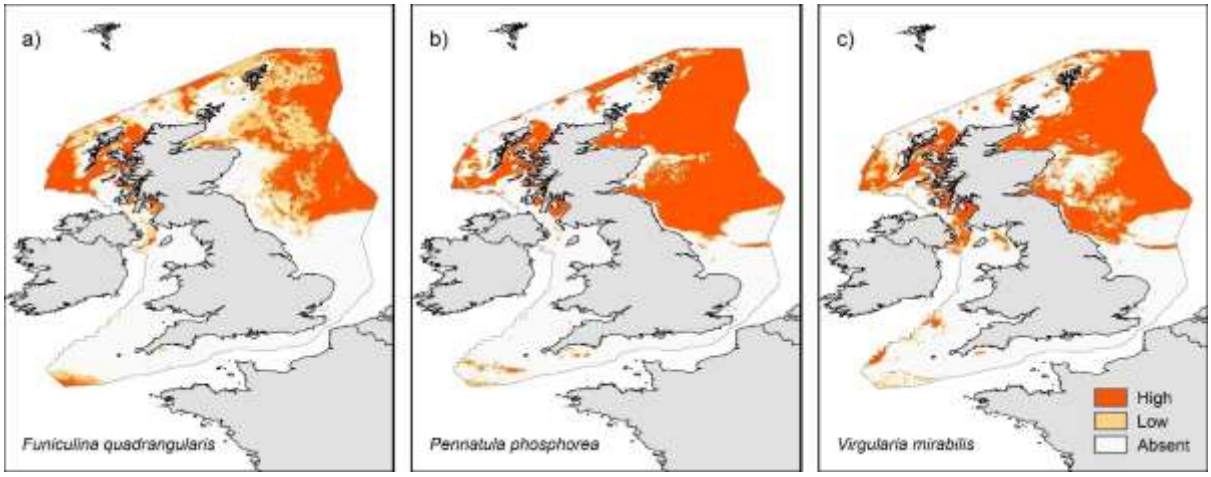


Figure 6. Distribution of *Funiculina quadrangularis* predicted by the CELS model, overlain with the extent of bottom contact fisheries (SAR >0 or >4 vessels reported fishing using bottom contacting gears) and the observed presence / absence of *F. quadrangularis* (a) and *Pennatula phosphorea* (b). Inset (i) in panel (a) shows close-up detail of *F. quadrangularis* presence in areas predicted by the CELS model in the absence of fishing pressure. Inset (ii) in panel (a) shows close-up detail of *F. quadrangularis* presence in sandier patches outside the predicted habitat.

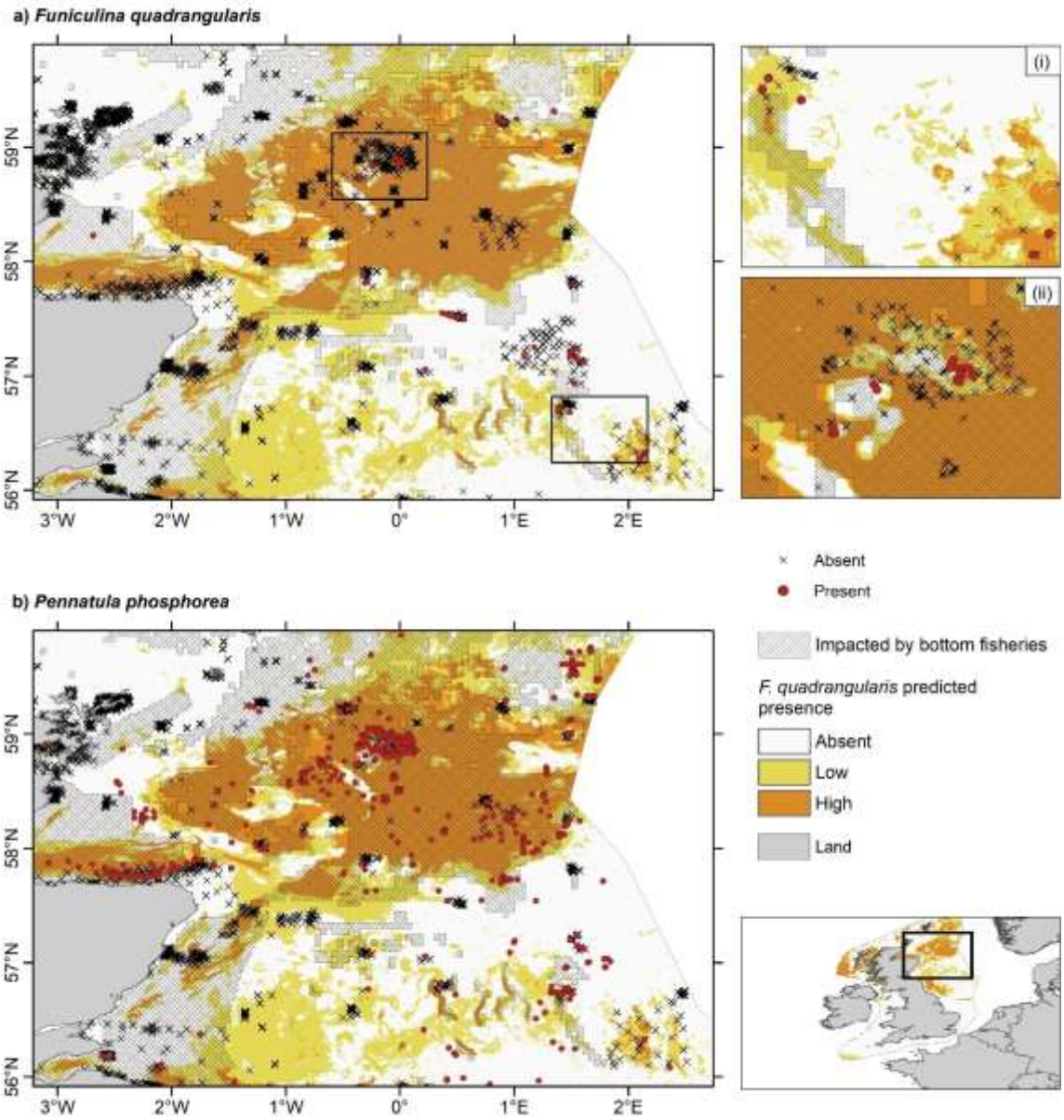


Figure 7. *Funiculina quadrangularis* (and commensal brittlestar *Asteronyx lovenii*)on sandy mixed sediment in the North Sea. Photograph: JNCC & Cefas 2013.

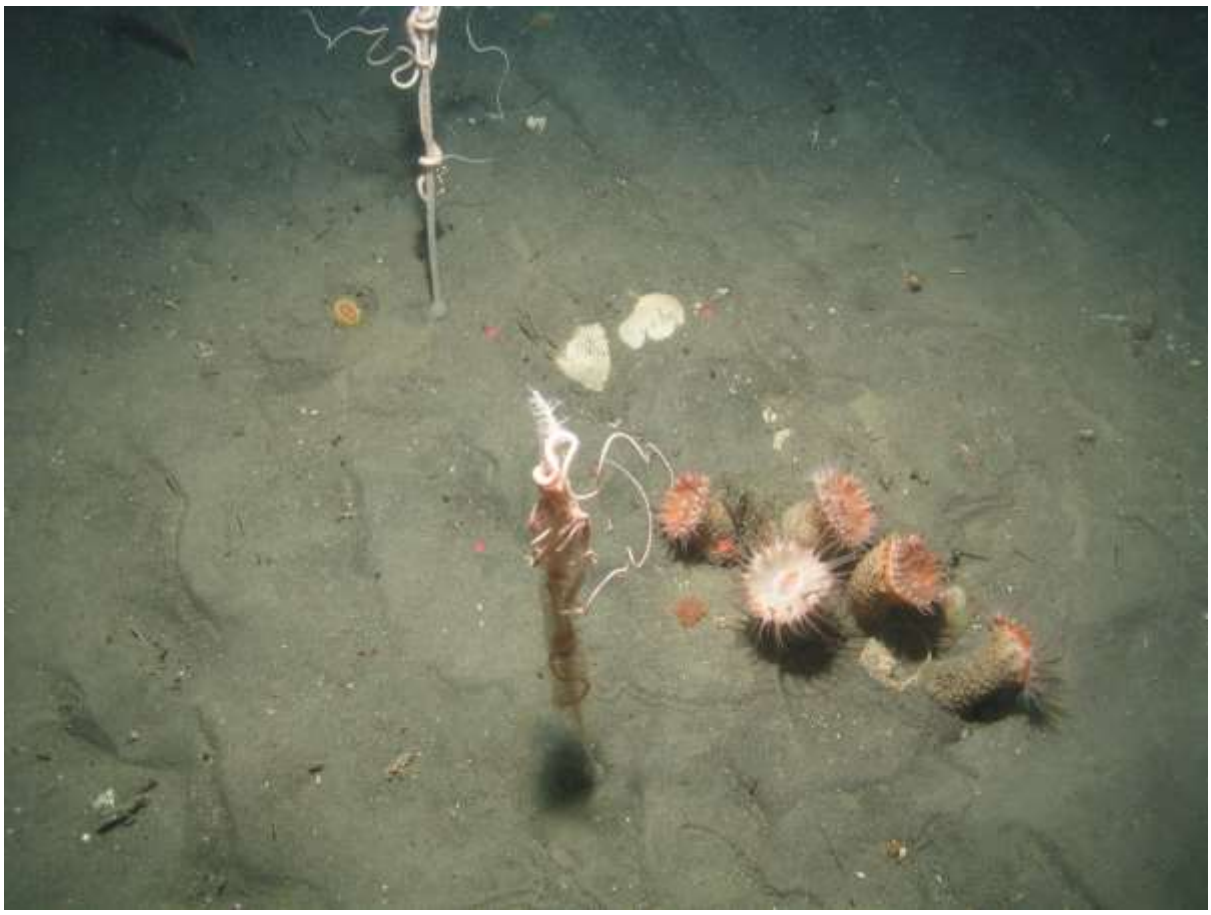
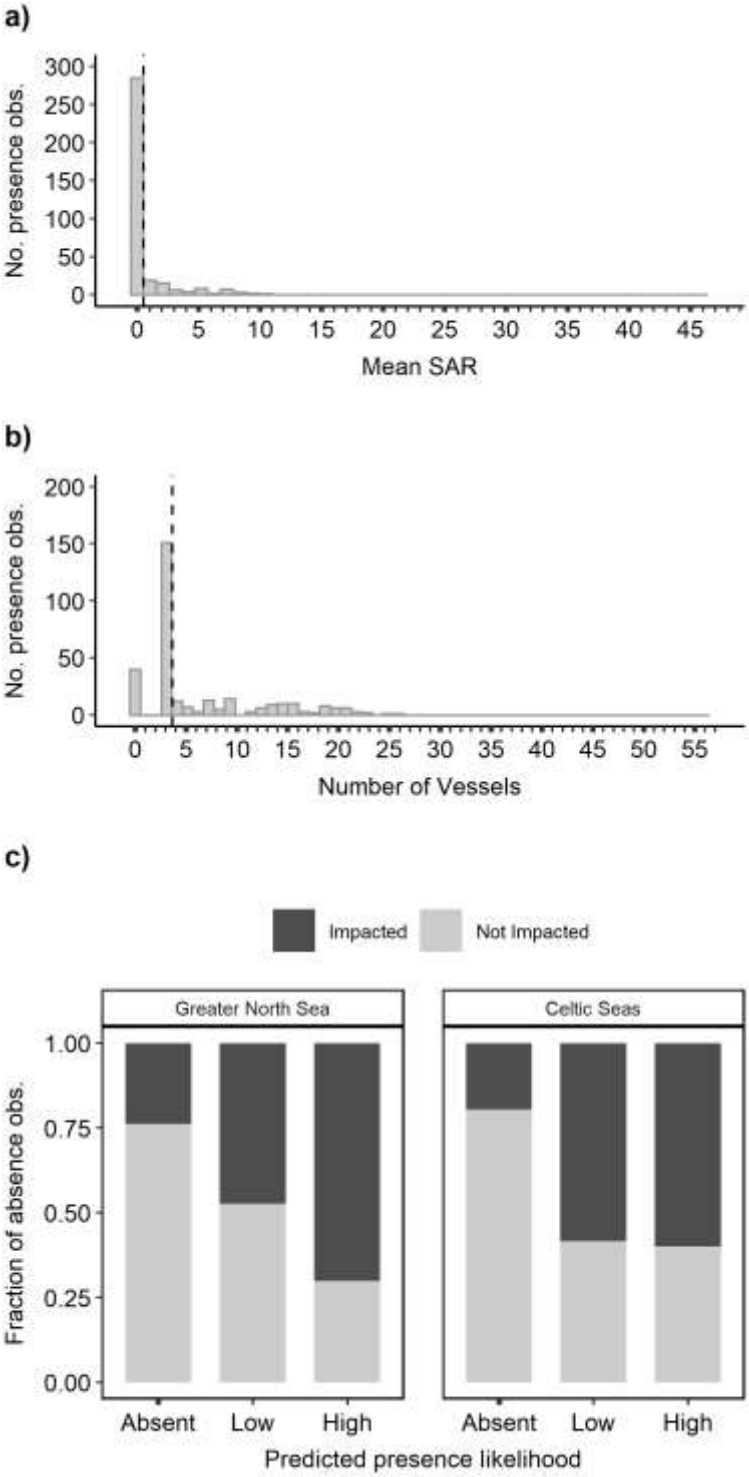


Figure 8. Frequency of *Funiculina quadrangularis* presences across (a) the range of observed swept area ratio (SAR) and (b) number of vessels across the full UKCS study area. Dotted lines indicate the threshold values that were used to split each fishing intensity layer into impacted and non-impacted categories. These were used to plot the fraction of *F. quadrangularis* observed absences in impacted and non-impacted areas (c), where presence was either not predicted, predicted with low likelihood, or predicted with high likelihood.



## Tables

Table 1. Summary of *Funiculina quadrangularis*, *Pennatula phosphorea* and *Virgularia mirabilis* presence / absence records used in the Species Distribution Models (SDMs). Each record corresponds to a raster cell with at least one point observation. The total number of records in the full dataset is given for the whole study extent (UKCS). Number of records in the final datasets subsampled to 10 % prevalence are given for each model region.

| **Species** | **Total number of records (Presences/Absences)** | | | |
|---|---|---|---|---|
| | **All records** | **Subsampled records** | | |
| | **UKCS** | **UKCS** | **GRNS** | **CELS** |
| ***Funiculina quadrangularis*** | 30103 (379/29724) | 3861 (351/3510) | 627 (57/570) | 3234 (294/2940) |
| ***Pennatula phosphorea*** | 30541 (1677/28864) | 11132 (1012/10120) | 7225 (656/6569) | 3267 (297/2970) |
| ***Virgularia mirabilis*** | 30301 (1383/28918) | 9790 (890/8900) | 4884 (444/4440) | 4906 (446/4460) |

Table 2. Environmental layers included in model development. Variables selected for the final models are indicated by a tick mark.

| Variable | Unit | Selected | Source resolution | Source |
|---|---|---|---|---|
| Bathymetry | m | | 0.002 deg | EMODnet Digital Bathymetry (EMODnet 2016) |
| Valley Depth | m | √ | 0.002 deg | Calculated from Bathymetry with SAGA for QGIS – Basic terrain analysis tools |
| Relative Slope Position | 0-1 | | | |
| Distance from Channel Network | m | √ | | |
| Standardised height | m | √ | | |
| Channel Network Baseline | m | | | |
| Closed Depressions | ? | √ | | |
| Current Velocity | m/s | √ | 0.002 deg | Cefas Data Hub, Mitchell et al. (2019a) https://doi.org/10.14466/CefasDataHub.62. |
| Wave velocity | m/s | √ | | |
| Winter suspended particulate matter | g/m3 | √ | | |
| Sand fraction | % | √ | 0.002 deg | Cefas Data Hub, Mitchell et al. (2019b) https://doi.org/10.14466/CefasDataHub.63. |
| Mud fraction | % | √ | | |
| Gravel fraction | % | | | |
| Sand to gravel log ratio | ratio | | | |
| Mud to gravel log ratio | ratio | √ | | |
| ICES Statistical Areas | n/a | | vector | ICES Data Portal (ICES, 2005) |
| ICES Ecoregions | n/a | √ | vector | ICES Data Portal (ICES, 2015) |
| Mean Spring chlorophyll-a concentration (2017-2019) | mg/m3 | √ | 1 km | OCEANCOLOUR_ATL_CHL_L3_NRT_OBSERVATIONS_009_036 from http://marine.copernicus.eu/ |
| Mean Summer chlorophyll-a concentration (2017-2019) | mg/m3 | | 1 km | |
| Mean Autumn chlorophyll-a concentration (2017-2019) | mg/m3 | | 1 km | |
| Mean Spring primary production (2017-2019) | C mg/m3/d | | 7 km | NORTHWESTSHELF_REANALYSIS_BIO_004_011 from http://marine.copernicus.eu/ |
| Mean Summer primary production (2017-2019) | C mg/m3/d | √ | 7 km | |
| Mean Autumn primary production (2017-2019) | C mg/m3/d | | 7 km | |
| Annual Range in Bottom Temperature (2017-2019) | Deg C | | 1.5 km | NORTHWESTSHELF_ANALYSIS_FORECAST_PHY_004_013 from http://marine.copernicus.eu/ |
| Maximum Bottom Temperature (2017-2019) | Deg C | | 1.5 km | |
| Mean Bottom Temperature (2017-2019) | Deg C | √ | 1.5 km | |
| Minimum Bottom Temperature (2017-2019) | Deg C | √ | 1.5 km | |

Table 3. Model validation results (± standard deviation). Results for full models are shown for validation datasets covering the entire UK continental shelf (UKCS) study area, as well as separately for the Greater North Sea (GRNS) and Celtic Seas (CELS). Results for the regional models are shown for both Ecoregions. N = Number of samples included in each training data set, P = Number of presences in each training data set, TSS = True Skill Statistic.

| Model | N | P | Test data | Sensitivity | Specificity | Kappa | TSS |
|---|---|---|---|---|---|---|---|
| ***Funiculina quadrangularis*** | | | | | | | |
| UKCS | 3089 | 281 | UKCS | 0.98 (±0.02) | 0.92 (±0.03) | 0.68 (±0.09) | 0.9 (±0.03) |
| | | | GRNS | 0.91 (±0.09) | 0.93 (±0.04) | 0.53 (±0.14) | 0.84 (±0.08) |
| | | | CELS | 0.98 (±0.02) | 0.92 (±0.03) | 0.72 (±0.08) | 0.9 (±0.03) |
| GRNS | 502 | 46 | GRNS | 0.98 (±0.04) | 0.93 (±0.03) | 0.7 (±0.09) | 0.91 (±0.05) |
| | | | CELS | 0.04 (±0.08) | 0.98 (±0.02) | 0.03 (±0.07) | 0.02 (±0.06) |
| CELS | 2587 | 235 | GRNS | 0.12 (±0.14) | 0.92 (±0.04) | 0.03 (±0.12) | 0.04 (±0.12) |
| | | | CELS | 0.97 (±0.01) | 0.93 (±0.02) | 0.7 (±0.07) | 0.9 (±0.02) |
| ***Pennatula phosphorea*** | | | | | | | |
| UKCS | 8906 | 810 | UKCS | 0.96 (±0.02) | 0.9 (±0.01) | 0.6 (±0.03) | 0.85 (±0.01) |
| | | | GRNS | 0.98 (±0.01) | 0.88 (±0.01) | 0.7 (±0.03) | 0.87 (±0.02) |
| | | | CELS | 0.88 (±0.05) | 0.9 (±0.02) | 0.42 (±0.03) | 0.78 (±0.04) |
| GRNS | 5780 | 525 | GRNS | 0.96 (±0.02) | 0.92 (±0.02) | 0.67 (±0.07) | 0.88 (±0.01) |
| | | | CELS | 0.59 (±0.14) | 0.85 (±0.07) | 0.3 (±0.07) | 0.44 (±0.1) |
| CELS | 2614 | 238 | GRNS | 0.96 (±0.03) | 0.83 (±0.03) | 0.46 (±0.05) | 0.79 (±0.03) |
| | | | CELS | 0.93 (±0.03) | 0.87 (±0.03) | 0.52 (±0.06) | 0.8 (±0.04) |
| ***Virgularia mirabilis*** | | | | | | | |
| UKCS | 7832 | 712 | UKCS | 0.92 (±0.03) | 0.85 (±0.03) | 0.48 (±0.05) | 0.77 (±0.03) |
| | | | GRNS | 0.95 (±0.03) | 0.89 (±0.03) | 0.63 (±0.08) | 0.84 (±0.04) |
| | | | CELS | 0.89 (±0.04) | 0.83 (±0.03) | 0.38 (±0.04) | 0.71 (±0.04) |
| GRNS | 3907 | 355 | GRNS | 0.91 (±0.02) | 0.95 (±0.02) | 0.73 (±0.06) | 0.86 (±0.03) |
| | | | CELS | 0.44 (±0.12) | 0.85 (±0.07) | 0.22 (±0.05) | 0.3 (±0.07) |
| CELS | 3925 | 357 | GRNS | 0.94 (±0.04) | 0.71 (±0.07) | 0.3 (±0.07) | 0.66 (±0.06) |
| | | | CELS | 0.9 (±0.04) | 0.82 (±0.04) | 0.41 (±0.05) | 0.72 (±0.02) |

Table 4. Fraction of the area predicted as suitable habitat by the CELS model (presence in >5 cross-validation iterations) overlapping fished areas. Area fished by offshore vessels comprises the area covered by OSPAR gridded VMS data where swept area ratio (SAR) > 0 (ODIMS, https://odims.ospar.org/odims_data_files/) and inshore vessels the area where > 4 dredgers and trawlers were reported fishing in the ScotMap Inshore Fisheries Mapping Project (Kafas et al. 2014).

| Ecoregion | Fishing Impact | Area (km2) | Percentage of Area |
|---|---|---|---|
| Celtic Seas | Offshore vessels | 10193.192 | 39% |
| | Inshore vessels | 4021.080 | 15% |
| | ***Total Fished*** | ***14214.272*** | ***53%*** |
| | Not fished | 12310.761 | 46% |
| | ***Total*** | ***26525.033*** | ***100%*** |
| North Sea | Offshore vessels | 30388.753 | 71% |
| | Inshore vessels | 2030.666 | 5% |
| | ***Total Fished*** | ***32419.419*** | ***76%*** |
| | Not fished | 10281.401 | 24% |
| | ***Total*** | ***42700.820*** | ***100%*** |