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Adaptive management, international co-operation and planning for marine conservation hotspots in a changing climate

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A B S T R A C T

The aim of this study is to predict changes in the distribution and extent of habitat forming species defined as “Priority Marine Habitats” (PMHs) in the North-East (NE) Atlantic under future scenarios of climate-induced environmental change. A Species Distribution Modelling method was used for each PMH to map the potential distribution of “most suitable” habitat. The area and percentage cover was calculated within each country’s Exclusive Economic Zone for the baseline (2009) and the projected (2100) years. In addition, a conservation management score was calculated based on the number of PMHs that co-occur in assessment units. Overall, this study reveals the potential for movement and/or change in the extent of some PMHs across the NE Atlantic and are subject to conservation management (see Section 2). Maxent has been used to predict contemporary PMH distributions in the deep sea\textsuperscript{10} and the future UK distribution of the PMH, \textit{Modiolus modiolus} beds\textsuperscript{11} (Table 2).

The aim of this study is to predict climate-related changes in the distribution and extent of habitat-forming (biogenic) species that are PMHs in the NE Atlantic. Predicted changes were used to determine: (a) the extent of “conservation hotspots” (measured as PMHs co-occurring in the same broad areas) under baseline (2009) and a future scenario (increased ocean temperatures by 2100); (b) whether a movement of the PMHs may be seen between member state boundaries; (c) to understand to what extent

1. Introduction

Information on the spatial distribution of species is essential for both protecting biodiversity and setting appropriate conservation priorities\textsuperscript{1} within, for example a transboundary Marine Protected Area (MPA) network. The use of predictive Species Distribution Modelling (SDM) methods, such as Maxent\textsuperscript{2,3} has become prominent within the scientific, policy, and public literature around the potential impacts of climate change\textsuperscript{4}. Maxent models have been successful in addressing sensitivities to environmental change including those involving temperature\textsuperscript{5,6}. There are, however, limitations with the use of SDMs\textsuperscript{4} in that they should not be considered as a complete substitute to gathering primary scientific data\textsuperscript{4}. When used in conjunction with data gathering, SDMs have the potential to highlight theoretical problems and/or help define and influence their theoretical landscape, accepting that the climate change predictions of one model on another can vary,\textsuperscript{6}. However, despite model uncertainties at high resolution, climate related range shifts of 10s to 100s of km have already occurred\textsuperscript{7} and are predicted to continue\textsuperscript{8} and therefore the general implications for management are important.

The Intergovernmental Panel on Climate Change (IPCC) provides scenarios for climate change\textsuperscript{9} with differing likelihoods, partly dependent on future carbon emissions. In a precautionary conservation management context it makes sense to consider a plausible but worst case IPCC scenario to emphasise conservation management and policy issues at regional and international scales.

Priority Marine Habitats (PMHs) are threatened and declining in the NE Atlantic and are subject to conservation management (see Section 2). Maxent has been used to predict contemporary PMH distributions in the deep sea\textsuperscript{10} and the future UK distribution of the PMH, \textit{Modiolus modiolus} beds\textsuperscript{11} (Table 2).

The aim of this study is to predict climate-related changes in the distribution and extent of habitat-forming (biogenic) species that are PMHs in the NE Atlantic. Predicted changes were used to determine: (a) the extent of “conservation hotspots” (measured as PMHs co-occurring in the same broad areas) under baseline (2009) and a future scenario (increased ocean temperatures by 2100); (b) whether a movement of the PMHs may be seen between member state boundaries; (c) to understand to what extent

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modelled PMHs fall within the current MPA network and whether these MPAs accommodate a changing climate (e.g. will the MPAs still protect PMHs in the future?); and (d) what the implications of climate-related change will be for future marine conservation and management planning. This study is concerned with the high-level policy context for the MPAs created by habitat forming (biogenic) species and not small scale habitat prediction; nor habitat PMHs such as seamounts that will physically remain, irrespective of climate-induced environmental change.

2. European marine management strategies

Priority Marine Habitats (PMHS) are determined as “threatened and/or declining” under the OSPAR Convention (The Convention for the Protection of the Marine Environment of the NE Atlantic 1992) and are considered to be of greatest marine nature conservation importance within the NE Atlantic (latterly referred to as the OSPAR marine region). PMHs are used to prioritise marine biodiversity conservation and protection under Annex V of the OSPAR (Oslo-Paris) Convention 1992.[12] The maintenance of PMHs will also contribute to the achievement of ‘Good Environmental Status’ (GES) under the European Union’s (EU) Marine Strategy Framework Directive[2] (MSFD; 2008/56/EC), the environmental pillar of the Integrated European Maritime Policy.[12]. Appropriate area-based management strategies, including an ecologically coherent network of well managed Marine Protected Areas (MPAs) by 2016[13] are being considered under the MSFD with these and other habitats in mind.[14] The OSPAR Commission is the main platform through which coordination of the MSFD implementation will occur. This includes the development of regionally coordinated tools for the implementation of integrated management of human activities and ecosystems, such as Marine Spatial Planning[15], integrated coastal zone management (ICZM) and cumulative impact assessment.

Along with the adoption of the MSFD in 2008 came the introduction of a European wide integrated approach to marine environmental protection.[16]. During the past decade there has been a dramatic rise in the number and size of MPAs being designated as a result of international environmental protection targets[17] and it could be argued that Europe has been the most active in establishing regional management strategies[18]. While nations are understandably concerned with their own marine environment first and foremost, some consideration of the potential future movement, expansion and contraction of habitat types and species of conservation importance (as a result of changing climatic conditions) between different Exclusive Economic Zones (EEZs) is necessary. However, implementing a network of MPAs in Europe, and all the factors that need consideration within that (including climate change), is likely to be challenging because marine conservation governance approaches are often developed at both a European and national level[19].

Integrated marine environmental protection is challenged by a number of factors. There are substantial knowledge gaps regarding the condition of the seas and the effects of anthropogenic pressures. There is also a lack of coordination between community and international measures (including the coordination between neighbouring states), and it is widely acknowledged that conservation measures are often restricted in scope, therefore granting limited environmental protection[20,21].

Collaborative management is a commonly published concept that is employed by governments and local communities to manage and protect natural resources in partnership at a national level[22,23]. In contrast, literature regarding how neighbouring nations, within Europe or globally, will manage adjoining marine areas now or in the future, particularly for those habitats and species requiring protection, is sparse. The European Commission (EC) argues that a regional approach (European within this context) to a marine environmental protection regulatory system is required given that marine ecosystems are transboundary and cannot be adequately governed, managed and protected by separate and fragmented national jurisdictions[20]. It has been acknowledged that through the implementation of the MSFD, enhanced cooperation between neighbouring states may develop[24] and that integration of a cross-sectoral policy under this Directive will strengthen marine protection[16]. It is also noted that, despite this, different approaches to marine management are being implemented by the different nations within Europe[21,24]. Some of the issues of transboundary Marine Spatial Planning (MSP) are being considered between England and Scotland through the MSP encompassing the Solway Firth[25], and between Finland and Sweden in the Bothnian Sea[26]. There are a number of challenges associated with transboundary planning, including: legal and policy frameworks, stakeholder interactions, methods of approach, agreed goals and targets and complications associated with devolved/federal nations (e.g. UK and the United States)[27,28]. The difference in marine management strategies being applied within Europe leads to a number of key questions, notably: Will these management strategies be complementary? How will PMHs that straddle Exclusive Economic Zones (EEZ: Art. 56, UN Convention on Law of the Sea) be managed? What happens if climate change leads to the movement of a PMH into an EEZ where it is currently not protected?

In 2006, the OSPAR contracting parties submitted a summary of the distribution of PMHs, within the OSPAR marine region (Table 1). The data are being continuously updated with the most recent submission in 2012. The 2012 dataset (used here) incorporates new discoveries and excludes previously erroneous submissions. The OSPAR Commission’s 2012 status report[13] states that MPA networks may be designed to be resilient to a changing climate. A lack of data and shortcomings in the understanding of the potential impacts of climate change on the distribution of PMHs and their management has however, led to a requirement for the development of predictive management tools. Consideration therefore needs to be given to the potential extent of PMHs under current and future climate conditions between neighbouring countries and within the present MPA network.

3. Methods

3.1. Priority Marine Habitat occurrence datamarine habitat occurrence data

OSPAR PMHs records were extracted from the OSPAR priority habitats dataset[29]. The geographical coverage of some of the environmental data layers was limited; therefore a number of records were excluded because they did not coincide with one or more of the environmental layers. Sample sizes for each PMH are shown in Table 2. The environmental layers were chosen based on their expected relevance to benthic PMHs and if they were freely and publicly available (to demonstrate cost effectiveness and ready application).
Table 1
Reported priority marine habitats within OSPAR contracting parties.

<table>
<thead>
<tr>
<th>Deep-sea sponge aggregations</th>
<th>Lophelia pertusa reefs</th>
<th>Ostreopsis edulis beds</th>
<th>Seapens &amp; burrowing megafauna communities</th>
<th>Zostera beds</th>
<th>Maeled beds</th>
<th>Modiolus modiolus horse mussel beds</th>
<th>Subellaria spinulosa reefs</th>
<th>Intertidal Mytilus edulis beds on mixed and sandy sediments</th>
<th>Coral gardens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Belgium</td>
<td>✓</td>
<td>✓</td>
<td>✓**</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Denmark</td>
<td>✓</td>
<td>✓</td>
<td>✓**</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
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</tr>
<tr>
<td>France</td>
<td>✓**</td>
<td>✓</td>
<td>✓**</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
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<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Germany</td>
<td>✓**</td>
<td>✓</td>
<td>Ex</td>
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<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
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</tr>
<tr>
<td>Iceland</td>
<td>✓**</td>
<td>✓</td>
<td>✓**</td>
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<tr>
<td>Ireland</td>
<td>✓**</td>
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<td>✓</td>
</tr>
<tr>
<td>Netherlands</td>
<td>✓**</td>
<td>✓</td>
<td>✓**</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Norway</td>
<td>✓**</td>
<td>✓</td>
<td>P**</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Portugal</td>
<td>✓**</td>
<td>✓</td>
<td>✓**</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
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<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Spain</td>
<td>✓**</td>
<td>✓</td>
<td>P**</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Sweden</td>
<td>✓**</td>
<td>✓</td>
<td>P**</td>
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<td>✓</td>
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<tr>
<td>UK</td>
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<td>✓</td>
<td>✓</td>
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<td>✓</td>
<td>✓</td>
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<tr>
<td>High seas</td>
<td>✓</td>
<td>✓</td>
<td>✓**</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
</tbody>
</table>

Key:
- ✓: Data have been supplied for the listed habitat (not necessarily by the respective Contracting Party).
- ✓: The listed habitat has not been reported as being present in the Contracting Parties’ waters or the high seas (either currently or in the past).
- P: The habitat has been reported as being present in the Contracting Parties’ waters but no data have been supplied.
- Ex: Presence data were reported in 2012.

3.2. Environmental data

Data on environmental variables were assigned to a 0.05° grid in Geographical Information System (GIS) software. Depth, slope, sea bottom temperature, sea bottom salinity, current speed and euphotic depth were identified as suitable environmental layers (Table 3) based on the ecological requirements of each PMH (Table 2). The grid size for the environmental variables was selected in order to allow for summary area calculations; data with a coarser resolution has not been interpolated to a finer resolution during this process. Due to the availability of consistent environmental layers, euphotic depth was used in place of water quality. In addition, seabed type/landscapes [30] were not included because available layers had very limited geographic coverage.

The increased ocean temperature scenario was established using the NOAA World Ocean Atlas seabed temperature data [31] for the years 2009 (baseline) and 2100; based on the IPCC scenario A1B (which gives a 4 °C increase in ocean surface temperature by 2100) [9]. A 4 °C increase in ocean bottom temperature was therefore assumed over the entire region along with a uniform increase in temperature throughout the water column [5,11,32].

3.3. Species distribution model

In order to create a theoretical map of the environmental conditions favouring the presence of the PMHs (Table 1) within the OSPAR region, the Species Distribution Modelling method, Maxent [2,3] was used. The method involves using mapped species records coupled with environmental data layers to predict the distribution of suitable habitat over a spatial domain. Species distribution will follow the principle of maximum entropy, that is, the relationship between the distribution of background conditions and distribution of presence conditions [3]. Maxent has been used for this purpose in a number of marine studies, including both modelling of mobile and habitat forming species [6,11,33], and is considered reliable in this context [8].

In the general Maxent approach, temperature can be weighted as a dominant predictor of distribution and is therefore more sensitive to warming than other models [6], therefore making it useful in the context of PMHs where management conclusions that tend towards the worst case scenario are required in a precautionary approach.

The model was run for each individual PMH (see Table 1). The model predictions were tested using the ‘Area Under the Curve’ (AUC) produced by Maxent. The area under the Receiver Operating Characteristic (ROC) curve is a widely used test statistic which measures model performance [6,11]. The AUC varies between 0 and 1, with values above 0.9 indicating excellent prediction, between 0.7 and 0.9 indicating good prediction, below 0.7 indicating poor prediction, and below 0.5 no better than random [8].

The presence data were randomly split into 90% training/10% test datasets using Maxent’s internal random test setting and were then internally cross validated for 10 replicate runs. Ten thousand randomly chosen pseudo-absence/background points were run due to the lack of true absence data [11].

Jack-knife contributions of each variable were measured to test the contribution of each variable to the model. Highest gain indicates the most useful information by itself when determining the location of suitable habitat. Lowest gain indicates the variable with the most information not present in the other variables, when determining the location of suitable habitat.

A previous study [11] carried out various tests in order to establish model suitability and validation of the Maxent model in the context of a PMH (horse mussel (M. modiolus) beds), including: changes to the split of the random test/training datasets; altering method of selection of the random test/training datasets (internal
Environmental variables and data sources.

Table 2
Definitions of Priority Marine Habitats, listed with environmental variables known to be important in determining their distribution. Sources: [71–74] and www.ukmarinesac.org.uk.

<table>
<thead>
<tr>
<th>Priority Marine Habitat</th>
<th>Definition</th>
<th>Environmental requirement – important factors</th>
<th>Study sample size</th>
</tr>
</thead>
</table>
| *Modiolus modiolus* horse mussel beds  | Dense beds of *Modiolus modiolus* at depths up to 70 m on a range of substratum. Communities associated with these beds are diverse. Patches extending over > 10 m² with > 30% cover by mussels should be classed as a "bed". | ● Water movement  
● Temperature  
● Depth  
● Salinity  
● Substratum  
● Water quality | 76                |
| Zostera beds                           | Beds of the seagrass *Zostera marina* or *Zostera noltii*. Plant densities should provide at least 5% cover, but > 30% cover is more typically sought.                                      | ● Depth  
● Substratum                                                                                                     | 109               |
| Maerl beds                             | A collective term for various species of non-jointed coralline red algae (*Corallinaceae*). Extensive beds can be formed, mostly in coarse clean sediments of gravels and clean sands or muddy mixed sediments either on the open coast, in tide-swept channels or in sheltered areas of marine inlets with weak current. | ● Water movement – currents and wave action  
● Interaction effects of depth and water quality.  
● Strongly influenced by the temperature regime. | 184               |
| *Sabellaria spinulosa* reefs           | The tube-dwelling polychaete *Sabellaria spinulosa* can form dense aggregations on mixed substrata and on rocky habitats. The *Sabellaria* covers 30% or more of the substrata and is sufficiently thick and persistent to support an associated epibiont community, distinct from surrounding habitats. | ● Depth  
● Suspended sediment  
● Water movement  
● Substratum  
● Salinity                                                                                                           | 149               |
| Intertidal *Mytilus edulis* beds on mixed and sandy sediments | Sediment shores characterised by beds of mussel *Mytilus edulis* occur on mid and lower shore mixed substrata. In high densities (> 30% cover) the mussels bind the sediment and provide a habitat for infaunal and epifaunal species. | ● Temperature  
● Substratum  
● Vertical distribution/depth                                                                                         | 63                |
| *Ostreia edulis* beds                  | occurring at densities of 5 or more per m² on shallow mostly sheltered sediments (typically 0–10 m depth, but occasionally down to 30 m)                                                                 | ● Substratum  
● Depth  
● Temperature                                                                                                             | 5                 |
| Deep-sea sponge aggregations           | Aggregations of deep-sea sponges extending over at least 25 m² that are principally composed of sponges from two classes: *Hexactinellida* and *Demospongia*. | ● Substratum  
● Depth  
● Temperature                                                                                                             | 61                |
| Coral gardens                          | A relatively dense aggregation extending over at least 25 m² of colonies or individuals of one or more coral species, such as leather corals (*Alcyonacea*), gorgonians (*Gorgonacea*), sea pens (*Pennatulacea*), black corals (*Antipatharia*), hard corals (*Scleractinia*) and, in some places, stony hydroids (*lace or hydrocorals: Stylasteridae*). | ● Substratum  
● Depth  
● Temperature  
● Water quality                                                                                                          | 58                |
| *Lophelia pertusa* reefs               | Reefs of the coral *Lophelia pertusa* extending over at least 25 m².                                                                                                                                  | ● Substratum  
● Depth  
● Temperature                                                                                                             | 586               |
| Sea-pen and burrowing megafauna communities | plains of fine mud, extending over an area of at least 25 m² and at water depths ranging from 15–200 m or more, which are heavily bioturbated by burrowing megafauna, with burrows and mounds typically forming a prominent feature of the sediment surface, and which may include conspicuous populations of sea-pens, typically *Virgularia mirabilis* and *Pennatula phosphorea* | ● Substratum                                                                                                                | 1976              |

Table 3
Environmental variables and data sources.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Source</th>
<th>Resolution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bathymetry: depth (m)</td>
<td>GEBCO_08 30-second arc Bathymetry resolution [75]</td>
<td>30°</td>
</tr>
<tr>
<td>Slope: percentage gradient of the seabed (%)</td>
<td>Adapted in ArcGIS 9.3 from: GEBCO_08 30-second arc Bathymetry resolution [75]</td>
<td>30°</td>
</tr>
<tr>
<td>Sea bottom temperature: climatological annual mean sea bottom temperature (°C). Adapted from NOAA depth interval data</td>
<td>NOAA World Ocean Atlas [28]</td>
<td>0.25°</td>
</tr>
<tr>
<td>Bottom salinity: climatological annual mean sea bottom salinity (PSU). Adapted from NOAA depth interval data</td>
<td>NOAA World Ocean Atlas [76]</td>
<td>0.25°</td>
</tr>
<tr>
<td>Current speed: average spring current speed (ms⁻¹)</td>
<td>[77,78]</td>
<td>4 km</td>
</tr>
<tr>
<td>Euphotic depth: (m)</td>
<td>NASA Giovanni portal: <a href="http://disc.sci.gsfc.nasa.gov/giovanni">http://disc.sci.gsfc.nasa.gov/giovanni</a></td>
<td>4 km</td>
</tr>
</tbody>
</table>
vs. external selection); testing the influence of certain environmental variables (Jack-knife contributions); testing the idea that selecting the background points from the whole study area may artificially inflate the AUC value; and carrying out a visual and overlap inspection of results against a uniquely designed environmental envelope analysis (EEA) model. The comparative model and EEA results from the study [11] showed that the two models (EEA vs. Maxent) displayed an acceptable degree of overlap. It was therefore assumed that a similar model quality and performance would be expected when the approach is applied to different species (PMHs). Model validation methods used in the present study were identified to be best fit based on these evaluations [11].

Given that the outputs estimated in the Maxent model training and projections ranked probability of occurrence on a scale from 0 to 1 (0 meaning that the PMH is highly likely not to occur and 1 meaning the PMH is highly likely to occur), determining a suitable level by which potential management strategies could be applied in the context of this study was required. The focus of this study was to determine the “most suitable” habitat; therefore representing a distribution probability of > 0.5; as per [11]; where PMHs occurrence probability greater than 0.5 are more likely to occur than those with a probability occurrence less than 0.5 [11].

### 3.4. Conservation management hotspots

#### 3.4.1. Exclusive economic zones and OSPAR marine regions

The “most suitable” habitat for each PMH was further analysed. The area and percentage cover of each PMH’s “most suitable” habitat category were calculated within each member state’s EEZ for the baseline (2009) and the projected (2100) years. Given the extent of the available layers, Spain, Portugal and High Seas EEZs were excluded and not all countries’ EEZs were completely covered by the environmental layers.

#### 3.4.2. Conservation management score

In order to determine where the future focus for conservation management activities would be required, “most suitable” habitat model outputs for all PMHs were overlaid and mapped with each PMH being given a value of 1. These values were then summed, per grid cell, to give a conservation management score (i.e. the number of co-occurring PMHs). The higher the summed value, the more potential PMHs occur in a particular region and the highest scores were considered ‘Conservation Management Hotspots’ (CMHs).

#### 3.4.3. Marine Protected Areas

The currently designated MPAs in the OSPAR marine region were mapped against the “most suitable” PMHs in 2009 and 2100 to determine the extent of potential “most suitable” habitat within the MPA network. The area of “most suitable” habitat (incorporating all PMHs as one entity) within the MPA network in 2009 and 2100 was calculated.

### 4. Results

#### 4.1. Species distribution model

For each PMH the Maxent model was trained using internally selected sub-sets within the Maxent software automated validation test option. The training AUC values, shown in Table 4, ranged from 0.907 to 0.999 indicating excellent model prediction with little variation shown over the 10 replicates. The test AUC values ranged from 0.904 to 0.999 and showed only slightly more variation over the replicated runs.

The AUC values for the final model for all PMHs ranged from 0.907 to 0.999 and generally equalled the average of the replicated models. The high AUC values in Table 4, with low variability between and within training and testing replicate sets, indicate excellent model performance in terms of predicting habitat suitability.

#### 4.2. Conservation management hotspots

##### 4.2.1. Exclusive economic zones and OSPAR marine regions

The area of “most suitable” (MS) habitat within each contracting party’s EEZ was calculated for 2009 and 2100. The 2009 ‘test’ results were directly comparable with the ‘training’ results, showing that the models generally predicted potential habitat presence in the same EEZs as the training model. Due to the limited distribution of PMHs and minimal amount of records, it was not possible to use completely independent datasets for training and testing. For Modiolus beds,

### Table 4

<table>
<thead>
<tr>
<th>Priority Marine Habitat</th>
<th>10 Replicates (90/10) Model</th>
<th>Full Model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Train</td>
<td>Test</td>
</tr>
<tr>
<td></td>
<td>Average AUC</td>
<td>AUC</td>
</tr>
<tr>
<td>Coral gardens</td>
<td>0.987</td>
<td>Min.</td>
</tr>
<tr>
<td>Zostera beds</td>
<td>0.991</td>
<td>Min.</td>
</tr>
<tr>
<td>Deep-sea sponge aggregations</td>
<td>0.96</td>
<td>Min.</td>
</tr>
<tr>
<td>Intertidal Mytilus edulis beds on mixed and sandy sediments</td>
<td>0.996</td>
<td>Min.</td>
</tr>
<tr>
<td>Lophelia pertusa reefs</td>
<td>0.944</td>
<td>Min.</td>
</tr>
<tr>
<td>Mæeri beds</td>
<td>0.989</td>
<td>Min.</td>
</tr>
<tr>
<td>Modiolus modiolus horse mussel beds</td>
<td>0.993</td>
<td>Min.</td>
</tr>
<tr>
<td>Ostrea edulis beds</td>
<td>0.999</td>
<td>Min.</td>
</tr>
<tr>
<td>Sabellaria spinulosa reefs</td>
<td>0.991</td>
<td>Min.</td>
</tr>
<tr>
<td>Sea-pen and burrowing megafauna communities</td>
<td>0.907</td>
<td>Min.</td>
</tr>
</tbody>
</table>
The results for 2009 (Table 7) show loss of, or gain in, the percentage cover of co-occurring, most suitable PMH results indicating an increase in potentially co-occurring PMHs in 2009, occurring in the French and UK EEZs (taking into account the full EEZ area). Three co-occurring MS PMHs were noted for the Greater North Sea region, which face the same amount of loss and few co-occurring PMHs. The largest area of no PMHs (Conservation Cover of co-occurring most suitable PMH) in the area also includes the Greater North Sea and Celtic Seas regions.

The number potential changes for each PMH were calculated over the OSPAR sub-regions (Table 5). Iceland and Portugal may potentially lose the greatest (Fig. 1). Belgium may gain the most Priority Marine Habitats by 2100, while Germany may gain the most by 2100. The change in the distribution and the number of potential suitable habitat for the different EEZs (Table 5). Iceland and Portugal may potentially lose the greatest by 2100. Belgium may gain the most Priority Marine Habitats by 2100, while Germany may gain the most. The number potential changes for each PMH was calculated over the OSPAR sub-regions (Table 5). Iceland and Portugal may potentially lose the greatest by 2100. Belgium may gain the most Priority Marine Habitats by 2100, while Germany may gain the most.

Table 5
Change in “Most Suitable” habitat area within the North-East Atlantic Exclusive Economic Zones zones (OSPAR contracting parties) between 2009 and 2100.

<table>
<thead>
<tr>
<th>EEZ</th>
<th>Area of EEZ (km²)</th>
<th>Area of MPAs Protected</th>
<th>% EEZ Protected</th>
<th>Area of “Most Suitable” Habitat (km²)</th>
<th>No. of gains</th>
<th>No. of losses</th>
<th>Total no. of changes</th>
</tr>
</thead>
</table>
| Belgium | 3480             | 1238                   | 36              | 0.7% Following omission of each environmental variable in turn; this indicates the most suitable habitat for the different EEZs (Table 5). Iceland and Portugal may potentially lose the greatest by 2100. Belgium may gain the most Priority Marine Habitats by 2100, while Germany may gain the most. The number potential changes for each PMH was calculated over the OSPAR sub-regions (Table 5). Iceland and Portugal may potentially lose the greatest by 2100. Belgium may gain the most Priority Marine Habitats by 2100, while Germany may gain the most.

There was a maximum of four co-occurring most suitable PMHs in 2009, occurring in the French and UK EEZs (taking into account the full EEZ area). Three co-occurring MS PMHs were noted for the Greater North Sea region, which face the same amount of loss and few co-occurring PMHs. The largest area of no PMHs (Conservation Cover of co-occurring most suitable PMH) in the area also includes the Greater North Sea and Celtic Seas regions.
PMHs across all EEZs. The biggest observed differences to co-occurring PMHS between 2009 and 2100 occur in Belgium, France, Germany and the Netherlands (Figs. 3 and 4). The extent of CMHs (sea areas with one or more PMHs) in the UK, Norway and Sweden remain relatively unchanged but there is the potential for an increase in the extent of CMHS in the countries at lower latitudes.

4.2.3. Marine Protected Areas

In 2009 a total of 34,148 km² of the most suitable habitat for all PMHs occurred within 19% of the OSPAR MPA network. By 2100, this area is projected to increase by more than double to 70,192 km² representing 39% of the MPA network.

5. Discussion

The aim of this study was to examine the extent of potentially suitable areas for PMHs throughout the OSPAR region (NE Atlantic) and to consider the implications of climate induced losses and gains in the light of national and international MSP policy.
Overall, there is potential for changes in the distribution and/or increase in the extent of some PMHs in the NE Atlantic by 2100 under a plausible, albeit ‘worst case’ increased ocean temperature scenario (4 °C) [9,11]. In light of this precautionary evaluation, countries may wish to consider adapting MPA and MSP strategies to accommodate these changes.

5.1. Species distribution model and climate change

The Maxent SDM used in this study has been widely applied in both marine [6,8,11,33,36] and terrestrial environments [37–42]. It has been considered robust in the context of marine management [33] albeit one of the models more sensitive to temperature change [5]. Within the present study the trained baseline model provided a good overall prediction in relation to all modelled PMHs but the lack of training data from latitudes 4 °C warmer than the study area was an inescapable potential weakness [43] for more southern PMHs.

A number of studies outline the limitations of SDMs with regard to areas of further study [44]; the lessons learned from terrestrial modelling when applied to the marine environment [45]; sample size [46]; the uncertainties of absence records [47]; and the pitfalls associated with their use in conservation and/or climate change planning [46]. A specific difficulty here is that the model [48] lacked continuous environmental data covering the whole geographic region and the potential small scale of the occurrence data. All seabed type or landscape layers (e.g. EUSeaMap: jncc.defra.gov.uk/page-5040, MESH: searchmesh.net or Mareano: mareano.no datasets) cover a very limited area of some EEZs, therefore could not be included in the final model. Previous deep sea work [33] indicates that the potential limitations from the exclusion of seabed type are mitigated by a combination of other layers (possibly slope and depth) that are operating as sufficient proxies at the scale of the present study. However, habitat forming PMHs in most cases modify the seabed, therefore seabed habitats where they are found are unlikely to be good predictors of where they could occur (but do not).

The selected environmental variables in the present study would be expected to be independently acting ecological factors based on prior reviews (Table 2 and references therein). Scope for confounding effects in the projections of this study is therefore likely to be minimal with the possible exception of temperature and depth for deep water PMHs. However, a more parsimonious model accounting for this potential co-linearity would compromise its ability to consider climate projections. Lack of historical distribution data for heavily declined habitats may also have limited the model. For example, PMH data for oyster beds (Ostrea edulis) were extremely scarce because the extent in Europe is poorly known following historic extirpation of wild populations [49]. There is evidence that this habitat was once far more widespread [49,50] and the modelled distribution and extent in the present study is correspondingly far greater than is occupied in the present day. The wider contemporary distribution and expansion of the oyster bed range by 2100 in the model predictions indicate an opportunity for widespread habitat restoration over the next 100 years [51]. Overall, habitats are unlikely to occupy their full potential niche, but for OSPAR PMHs that are threatened or declining, the model will inevitably over-predict the present range and possibly also the range under 2100 projected scenarios if the underlying causes of the decline are not removed. Habitats with fewer training data might also be expected to have more erroneous predicted distributions. For all habitats in the present study the subtleties of range changes are likely to track local climate change velocities [52,53], and these in turn may depend on local topography and tide, etc. [54] not to mention life history characteristics such as dispersal characteristics and body size [55]. Many of these aspects remain poorly known for PMHs and this high resolution aspect of range shift is beyond the scope of the present study.
Small sample sizes pose a number of statistical challenges, and this is no different when considering SDMs, resulting in decreased predictive potential and accuracy [46,56,57]. Generally, as the sample size increases, so therefore should the accuracy, until maximum accuracy reaches an asymptote [56]; although this will also depend on the environmental variables, the specific species and geographic range.

A previous comparative study [56] between different SDM methods with varying sample sizes found Maxent to be the strongest performer of the methods tested. Maxent performed well and remained fairly stable in both prediction accuracy and the total area predicted present across all sample size categories. This indicates that Maxent can in part compensate for incomplete, small species occurrence data sets and perform near maximal accuracy level in these conditions (also reported in [43,58,59]).

Integrating the concept of climate change into policy and management is understandably complicated, and it is hard to see any alternative other than the use of predictive models. The impacts of climate change are still perceived to be distant and generally ignored in developing day-to-day ocean management strategies [60] but the outcomes of the present study indicate that there is an urgency to start to include it.

It is acknowledged that the scale and pace of change in European and national policy presents a number of challenges in managing the marine environment. Consequently, considerable demands are placed on the marine community to work together to
provide the information necessary to fulfill set objectives [61]. These objectives are set against the context that the European marine territory is larger than its land territory and a considerable effort will therefore be required in order to fulfill all the legislative requirements [62]. It has been reported [62] that many institutions throughout Europe are involved in monitoring strategies which would be greatly improved (cost, effectiveness and efficiency) from better coordination, not to mention supporting more robust and coherent management for the marine environment. As a consequence of data generated by the present study it is suggested that imminent climate changes need to be understood in a regional context from data produced by monitoring programmes. Decision makers need access to sound scientific evidence that is targeted to their needs in order to achieve sustainable use and protection of the marine environment now and in the future [61].

This could be partly facilitated in the future through the mechanism provided by EMBRC (European Marine Biological Record Centre) and other European Infrastructures.

5.2. Conservation management score

A robust approach to conservation is to identify “hotspots”, or areas featuring exceptional concentrations of endemic species and experiencing exceptional loss of habitat [63]. In this study, areas are identified within the NE Atlantic, where potential PMH hotspots occur now, and could occur in the future, thus highlighting possible scope for future MPAs.

Further model development would be required in order to ascertain whether the theoretical distribution of certain PMHs is accurate and in any way interdependent, for example, if the retreat

Table 7

<table>
<thead>
<tr>
<th>2100</th>
<th>Area of EEZ (Sq Km)</th>
<th>Area of MPAs (Sq Km)</th>
<th>% EEZ Protected</th>
<th>Hotspot Ranking (0–4) - Area (Sq km)</th>
<th>Total area (Sq Km)</th>
<th>% of EEZ covered in model</th>
<th>Hotspot Ranking (0–4) - Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 (no PMFs)</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4 (4 PMFs co-occur)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Belgium</td>
<td>3269</td>
<td>1238</td>
<td>36</td>
<td>236</td>
<td>351</td>
<td>1915</td>
<td>653</td>
</tr>
<tr>
<td>Denmark</td>
<td>102,290</td>
<td>12,514</td>
<td>12</td>
<td>72,774</td>
<td>13,158</td>
<td>10,800</td>
<td>5456</td>
</tr>
<tr>
<td>France</td>
<td>327,609</td>
<td>29,881</td>
<td>9</td>
<td>293,431</td>
<td>14532</td>
<td>133,277</td>
<td>5369</td>
</tr>
<tr>
<td>Germany</td>
<td>56,640</td>
<td>16,912</td>
<td>30</td>
<td>26,398</td>
<td>5648</td>
<td>19,246</td>
<td>4093</td>
</tr>
<tr>
<td>Iceland</td>
<td>777,510</td>
<td>165</td>
<td>0.02</td>
<td>774,333</td>
<td>1133</td>
<td>1748</td>
<td>296</td>
</tr>
<tr>
<td>Ireland</td>
<td>420,366</td>
<td>4239</td>
<td>1</td>
<td>313,675</td>
<td>91,567</td>
<td>9501</td>
<td>4342</td>
</tr>
<tr>
<td>Netherlands</td>
<td>64,380</td>
<td>8367</td>
<td>14</td>
<td>13,318</td>
<td>23,966</td>
<td>22,058</td>
<td>3443</td>
</tr>
<tr>
<td>Norway</td>
<td>1,749,628</td>
<td>85,725</td>
<td>5</td>
<td>1,734,550</td>
<td>7006</td>
<td>6323</td>
<td>1684</td>
</tr>
<tr>
<td>Sweden</td>
<td>165,650</td>
<td>2,496</td>
<td>2</td>
<td>161,461</td>
<td>1998</td>
<td>1186</td>
<td>1005</td>
</tr>
<tr>
<td>UK</td>
<td>760,424</td>
<td>79,321</td>
<td>10</td>
<td>521,880</td>
<td>126,874</td>
<td>83,798</td>
<td>23,404</td>
</tr>
</tbody>
</table>

Key:

a Habitat loss between 2009 and 2100.

b Habitat gain between 2009 and 2100.

c No change between 2009 and 2100.

Fig. 3. Percentage cover of co occurring PMH’s per country EEZ 2009.
or loss of one keystone species results in the subsequent expansion or contraction of another.

5.3. Co-ordinating management

Systematic conservation planning is a process that combines short-term assessment (identifying priority areas for conservation management) together with a long-term management framework [19] – essentially the process of locating, implementing and maintaining areas that are managed to promote the persistence of biodiversity and other natural values [64]. In practice, conservation planning is rarely systematic, and “ad hoc” implementation has resulted in the management of areas that do not best represent regional biodiversity, with boundaries and management strategies that are often governed by political or economic constraints [64].

In the NE Atlantic, an assessment of the Marine Protected Area network showed that it was substantially uneven in its distribution and does not yet represent all biogeographic regions signed up to the Convention on Biological Diversity (CBD) targets of 10% by 2020 [13]. The present study shows PMHs will potentially increase in extent in Arctic Waters, so it will become increasingly important to increase MPA coverage there, yet in the 2013 OSPAR assessment [13] it was Arctic Waters that had the smallest proportion of MPA coverage (1.55% at end of 2012). There may be a requirement for expansion of MPA development in this region. Other results from the study indicate that changes will occur throughout the Greater North Sea, Celtic Seas and Arctic Waters (Fig. 2), and UK, Norway and Ireland (Fig. 1), but different management priorities are implicated in different sub-regions. MPAs in the Greater North Sea and Celtic Seas cannot be expected to “maintain” PMHs indefinitely and the locations and objectives of MPAs will have to accommodate some flexibility over time [11]. Although there may not be the same motivation to establish new MPAs in the Greater North Sea because it has reached its CBD target of 10% [13], as climate induced changes occur, connectivity and collaborative cross-border management will be of particular importance, especially given the high number of bordering countries. Management initiatives and strategies will need to be put in place in order to accommodate the potential loss and gain of PMHs between regions if the aspirations of OSPAR are to be achieved. For example, a European/NE Atlantic wide working group for marine conservation or environmental protection would allow for synergistic management strategies to be discussed, agreed and initiated; potentially through the involvement of boundary agreements for managed retreat/expansion of PMHs where necessary. In addition, management policy at a national (EEZ) or regional (OSPAR or Europe) level may also need to be considered. Adoption of an EU wide Marine Spatial Plan could potentially ensure some legislative consistency between contracting parties [65,66]. This in turn will accommodate the climate induced issues raised here, and pave the way for similar co-operative approaches for implementation elsewhere in the world.

Overall, the results presented here indicate a potential for the greatest increase in higher ranked conservation hotspots for nations at lower latitudes such as Belgium and Netherlands. In relation to current MPA designation, Belgium for example already has 36% of their coastal waters designated as MPAs [13], but results herein show that they may still have a greater potential conservation management role to play in the future as the niches of PMH habitats move through their coastal waters. In comparison, countries at higher latitudes, e.g. Iceland and Norway currently have lower proportions of their coastal waters in MPAs (“negligible” and ~4% respectively [13]) and consideration of MPA network expansion is needed.

The OSPAR Commission [13] accepted that an analysis of the ecological coherence of the NE Atlantic MPA network is not yet possible due to limited availability of data on the distribution of habitats and species. In the absence of comprehensive survey data, the present study methods offer the best available evaluation of “coherence”: i.e. whether “at least 5%...of all areas in which they [PMHs] occur within each OSPAR Region ...are protected?” [13]. Such an evaluation is, however, beyond the scope of the present work, especially because the models were not parameterised in Areas Beyond National Jurisdiction and could not, for example, cover the Wider Atlantic or deep sea MPAs such as the Charlie-Gibb North High Seas MPA (also an Ecologically or Biologically Sensitive Marine Area; EBSMA). A maximum entropy...
modelling study could however help evaluate OSPAR concepts of “adequacy” or “representation”.

5.4. Habitat loss, fragmentation and stepping stones

Theoretical studies and modelling clearly need to be reinforced by scientific evidence in order to lead to better MPA design. Global climate change has the very real potential to disrupt connectivity [51].

Habitat loss and fragmentation together pose one of the most serious threats to global biodiversity because restricted gene flow between populations combined with limited dispersal ability, can intensify the isolation by distance effect and play an important role in determining population viability within a degraded landscape [67]. Population responses to fragmentation is as much to do with the pattern of habitat loss as it is to do with the total amount destroyed [67]. Connectivity of PMHs and MPAs containing them is therefore of paramount importance. A PMH that becomes disconnected may persist for some time, but may become increasingly susceptible to damage or disease if recruitment is not maintained. Understanding the gene flow and genetic structure of a population is one way of measuring connectivity and contributes to knowledge of which sites are important as sources and sinks of genetic diversity [68].

This is an area with identified research and knowledge gaps. The creation of, for example, a ‘toolbox’ of genetic markers would provide for underlying knowledge of PMH species, and give the first step towards identifying priority connectivity corridors and contributing knowledge applicable to the development of habitat migration planning and restoration methods, in an approach similar to that in terrestrial environments [69,70].

Even more simplistic measures of MPA network coherence have not yet been possible to assess [13].

There is, however a chance, that given the projected length of time for climate change range shifts under the scenario presented here, the PMHs may be capable of adaptation to the warming oceans within that time and in fact spawning and recruitment will not be hindered at all. Further focussed studies are required to quantify the impact of increasing temperatures, and other climate change factors such as pH would have on the PMH species function and viability.

The issue of managed migration (loss or gain of PMHs) links to Descriptor 2 of the MSFD, non-indigenous species [71], because retreat or establishment of PMHs under climate change scenarios could be readily subverted by non-indigenous species if new niches are not occupied soon enough. If this is accounted for within future synergistic strategies (for example by active habitat enhancement) these risks might be mitigated.

For PMHs there is an opportunity for the creation of stepping stone habitat during the development of for example, offshore wind farms. The exclusion of primary pressures such as demersal fisheries [72–74] and the creation of artificial reefs provide additional settlement habitat for reef forming species in de-facto MPAs. These new stepping stone habitats have however, also been implicated in the spread of non-indigenous species [75]. A more active habitat restoration/facilitation approach may therefore be necessary to avoid these invasions of niches.

6. Conclusions

The present study has highlighted the requirement to develop adaptive management strategies for Priority Marine Habitats in the NE Atlantic including an increase in MPAs in some sub-regions. At present, marine management strategies are principally concerned with managing the status quo, but developing Marine Spatial Planning will need to include a horizon that enables management for a changing climate. Changes in the extent and distribution of these PMH biodiversity hotspots will also need to be considered within the assessment of Good Environmental Status (GES) under the MSFD throughout Europe. The changing extent and distribution of PMHs raises the potential for mitigation measures, such as habitat restoration (perhaps within new built structures), as well as the risks posed by non-indigenous species as niches become available, and the disruption to habitat connectivity and the coherence of MPA networks if these habitats become fragmented. These findings and challenges are unlikely to be unique to the NE Atlantic and have varying global application depending on local climate change velocities [52]. Co-operation between contracting parties and marine sub-regions requires enhancement and there will be different future emphases for MSP and MPA initiatives throughout the region as changes occur to PMH distribution.

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References
