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Modelling commercial fish distributions: Prediction and assessment using different approaches

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ABSTRACT

Species distribution models are important tools to explore the effects of future global change on biodiversity. Specifically, AquaMaps, Maxent and the Sea Around Us Project algorithm are three approaches that have been applied to predict distributions of marine fishes and invertebrates. They were designed to cope with issues of data quality and quantity common in species distribution modelling, and especially pertinent to the marine environment. However, the characteristics of model projections for marine species from these different approaches have rarely been compared. Such comparisons provide information about the robustness and uncertainty of the projections, and are thus important for spatial planning and developing management and conservation strategies. Here we apply the three commonly used species distribution modelling methods for commercial fish in the North Sea and North Atlantic, with the aim of drawing comparisons between the approaches. The effect of different assumptions within each approach on the predicted current relative habitat suitability was assessed. Predicted current distributions were tested following data partitioning and selection of pseudoabsences from within a specified distance of occurrence data. As indicated by the test statistics, each modelling method produced plausible predictions of relative habitat suitability for each species, with subsequent incorporation of expert knowledge generally improving predictions. However, because of the differences between modelling algorithms, methodologies and patterns of relative suitability, comparing models using test statistics and selecting a 'best' model are not recommended. We propose that a multi-model approach should be preferred and a suite of possible predictions considered if biases due to uncertainty in data and model formulation are to be minimised.

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1. Introduction

Many pressures are currently affecting the marine environment and driving change in species composition and distribution. Fisheries are removing fishes at a rate considered to be unsustainable (Pauly et al., 2002), while essential habitat is being damaged or destroyed, for example through sand and gravel extraction, or chemically altered through release of endocrine-disrupting substances. Furthermore, concern over the impact of climate change on marine ecosystems is increasing (Root and Rosenzweigk, 2003), with longer term shifts in mean environmental conditions and climatic variability moving outside the bounds within which

adaptations in marine communities have previously been associated (e.g. Beaugrand, 2004; King, 2005). The altered abundances and novel distributions resulting from these ocean-atmospheric changes (e.g. Beaugrand, 2009; Perry et al., 2005; Southward et al., 1995; Stebbing et al., 2002) may severely change the biological and environmental functioning of ecosystems or food webs, the goods and services derived from them, and conservation and resource management.

Species distribution modelling is widely used to study and predict the ecological effects of climate change (e.g. Hijmans and Graham, 2006; Beaumont and Hughes, 2002; Pearson and Dawson, 2003; Thuiller et al., 2008; Cheung et al., 2009). It uses statistically or theoretically derived response surfaces to relate observations of species occurrence or known tolerance limits to environmental predictor variables (Guisan and Zimmermann, 2000), thereby predicting a species' range as the manifestation of habitat characteristics that limit or support its existence at a particular location. It is thus grounded in ecological niche theory. The environmental conditions under which a species can survive and grow and

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which therefore define the ecological properties of a species are described as the fundamental ecological niche (Hutchinson, 1957) or a species' potential distribution. The area within a fundamental niche into which a species is restricted due to the effects of competition and other biotic interactions is described as its realized niche (Austin et al., 1990; Guisan and Zimmermann, 2000), or distribution. To make use of the diversity of available data, a wide range of species distribution models (SDMs) have been proposed [see Guisan and Thuiller (2005) and Franklin (2009) for an overview], approaches varying widely in data requirements, mechanisms used and model performance (Guisan and Zimmermann, 2000; Elith et al., 2006; Austin, 2007; Wisz et al., 2008). The extent to which models are able to capture a species' realized or fundamental niche may thus vary depending on the modelling approach or data requirements.

When choosing and applying an SDM, it is therefore important to understand its performance, assumptions, characteristics and uncertainties, as well as how these might be affected by data availability and quality. Ideally, an SDM is developed from the relationship between direct or indirect environmental predictors and datasets of species presence and absence obtained by targeted surveys. Comprehensive data are, however, seldom available and instead frequently represent a restricted, patchy or biased view of species' distributions, leading to problems when data-driven modelling techniques are used to generate distribution predictions. Furthermore, it has been suggested that presence–absence data attribute superior performance, for example as measured by test statistics, to an SDM and thus a more reliable prediction (Brotons et al., 2004; Hirzel et al., 2001; Martinez-Meyer, 2005; Lobo et al., 2008). This would not be the case, however, if absence at a particular location is caused by factors not included in the model, such as dispersal limitations, biotic interactions or incorrect assessment (Pearson et al., 2007; Pearson and Dawson, 2003). Distributions predicted from recorded species' occurrence (presence) only may thus be more suitable for constructing models of potential habitat. Several studies show that SDM model accuracy decreases and variability in predictive accuracy increases with decreasing size of the species occurrence dataset (Wisz et al., 2008; Hernandez et al., 2006; Kadmon et al., 2003; Stockwell and Peterson, 2002). These issues of data paucity and quality are especially pertinent in the marine environment (Kaschner et al., 2006; MacLeod et al., 2005).

Model complexity is another important factor affecting the performance of SDMs. Complex models are suggested to be more effective (Elith et al., 2006; Tsoar et al., 2007; Wisz et al., 2008) and more accurate at finer resolutions (Kimmins et al., 2008). However, including more parameters or fitting complex response curves may result in a model that generalizes poorly (Drake et al., 2006), becoming less applicable to areas at a broader scale. Greater complexity also often reduces model transparency, which is important for the effective testing and reviewing of model outputs and soliciting additional information to improve model predictions. The complexity and transparency of a selected model may therefore depend not only on its perceived robustness but also on the specific application and the community by which it is being implemented.

Maxent, AquaMaps and the Sea Around Us Project model are three approaches commonly used to model distributions of marine fishes and invertebrates (Kaschner et al., 2008; Ready et al., 2010; Close et al., 2006; Bigg et al., 2008; Cheung et al., 2009). The Maxent software package (Phillips et al., 2006; Phillips and Dudík, 2008) was designed to overcome the problems of small sample sizes in presence-only datasets (Pearson et al., 2007). The AquaMaps procedure, based on a Relative Suitability Model (Kaschner et al., 2006), and the Sea Around Us Project model were also designed to overcome the lack of data and knowledge for many marine species. Generative modelling approaches, such as Maxent, may, however, be more vulnerable to biases from the skewed distribution of sampling effort present in many 'opportunistically' collected datasets, especially those with limited data-points. In these instances, discriminative methods (defined here as distribution models which restrict a species distribution, from a potential extent that encompasses the entire study area, based on a set of filters determined by known parameters or habitat preferences), such as that developed by the Sea Around Us Project (Close et al., 2006), might produce the more valid results. The incorporation of 'expert information' may also overcome this problem (Ready et al., 2010). Expert information may be defined as "habitat use information that is not directly available as raw data; published information about habitat use or preference that is based on quantitative investigations of species occurrence in relation to environmental knowledge" (Ready et al., 2010). It may be incorporated into a modelling procedure in various forms of knowledge such as species' behaviour, known depth range or geographic limits.

This study aims to assess the abilities of three statistical modelling approaches, representing a spectrum of theoretical frameworks and data-requirements, to predict current distributions of a range of marine species. Mentioned above, these are the correlative, presence-only modelling approaches Maxent (Phillips et al., 2004; http://www.cs.princeton.edu/~schapire/maxent) and AquaMaps (Kaschner et al., 2008; Ready et al., 2010; http://www.aquamaps.org), and the discriminative approach developed for the Sea Around Us Project (Close et al., 2006; http://www.seaaroundus.org). The comparison not only focuses on the perceived value of a modelling procedure as indicated by test statistics, but also considers the usability and practical application of the approaches and their results.

2. Methods

2.1. Model construction

2.1.1. Maxent

Maxent (Phillips et al., 2004) uses a generative approach (Phillips et al., 2006) to estimate the environmental co-variates conditioning species presence and bases the final prediction on the principle of maximum entropy. This specifies that the best approximation of an unknown distribution is the probability distribution with maximum entropy, subject to the constraints imposed by the sample of species presence observations (Phillips et al., 2006). Maxent has been shown to compete well with alternative approaches (Pearson et al., 2007; Phillips et al., 2006), perform better than classical presence-only methods (Elith et al., 2006) and perform well with small sample sizes (Pearson et al., 2007). Models were constructed using Maxent (version 3.3.3e) with default parameters for a random seed, regularization parameter (1, included to reduce over-fitting), maximum iterations (500), convergence threshold (0.00001) and maximum number of background points (10,000 points which have not been recorded as present). Selection of environmental features and their relative contribution to each iteration of the model was also carried out automatically.

2.1.2. AquaMaps

The AquaMaps approach to modelling species' distributions was based on a global distribution tool for marine mammals (Kaschner et al., 2006), and has now been applied to a large number of marine fishes (see FishBase, Froese and Pauly, 2011). AquaMaps uses simple, numerical descriptors of species relationships with environmental variables to predict distributions from publically available, global occurrence databases. This methodology does not allow complex, non-linear interactions to be fitted between predictors, but aims for transparency and understanding in the wider, non-modelling, community while also explicitly promoting incorporation of expert judgement.
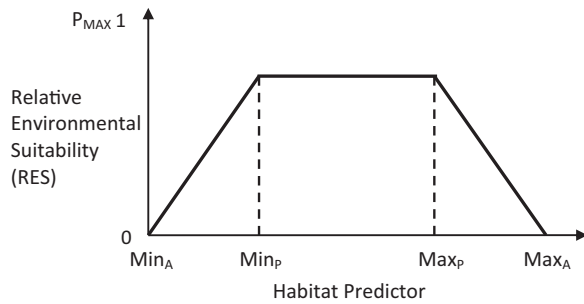
Fig. 1. Trapezoidal species' response curve, showing absolute minimum (Min_A) and maximum (Max_A) and preferred minimum (Min_P) and maximum (Max_P) levels of a habitat predictor, and the relative environmental suitability, the highest obtainable value being 1 (P_{Max}).
(Modified from Kaschner et al. (2006)).

Predicted current distributions are generated multiplicatively from a suite of 'environmental envelopes' over each cell in a study area. This produces a cell value between 0 and 1, representing the relative suitability of that cell for the specified species. The relationship between species occurrence and environmental limits is specified by a trapezoidal distribution (Fig. 1).

The trapezoidal distribution represents a compromise between the likely uni-modal annual distributions exhibited by restricted range species, and the more bi-modal distribution of migratory species. To create environmental envelopes, occurrence data are associated with environmental variables to find absolute and 'preferred' preference ranges and calculated as shown in Table 1.

It is therefore assumed that (relative) environmental suitability is uniformly high throughout the preferred parameter range, with a probability of 1. Those values lying outside the observed minimum or maximum (representing critical predictor limits for a species) are assigned a value of 0, while between these two thresholds relative environmental suitability decreases linearly. Having calculated probability distributions for each predictor, overall habitat suitability can be computed by the geometric mean of all probability distributions, assuming equal influence weighting of predictors.

Expert opinion was incorporated into Maxent and AquaMaps to give refined predictions by eliminating ('clipping') areas that were currently outside known occurrence ranges, including reported occurrence/absence in large ocean basins [delineated by the United Nations' Food and Agricultural Organisation (FAO) statistical area, www.fao.org/fishery/area/search/en] or depth limits reported in FishBase. This avoided over-prediction of relative habitat suitability in areas where species are known not to occur, or which are unsuitable due to depth.

2.1.3. The Sea Around Us Project model

The Sea Around Us Project model (Close et al., 2006, Cheung et al., 2008) was specifically developed to address a need for predicting distribution ranges of commercial fish and invertebrates. The approach employs a discriminative method, applying a set of key environmental predictors, 'filters', to reduce a species' potential range. Firstly, an 'FAO filter' was applied to restrict a species on the basis of its current verified presence in the 18 FAO statistical areas. Subsequently, the distribution was refined by a filter specifying the latitudinal limits of a species' putative 'normal' distribution range. Information for both these filters is available for most fish species on FishBase. The third filter was a 'range-limiting polygon', which was applied to restrict species to a more specific level, thereby preventing occurrence in semi-enclosed seas which are located within specified FAO areas and latitudinal ranges which are unsuitable, for example, due to low salinity values. Data for this filter was obtained from FAO publications (http://www.fao.org/fishery/species/search/en), FishBase (www.FishBase.org), SealifeBase (www.SealifeBase.org (Palomares and Pauly, 2011)) and the Sea Around Us Project database (www.seaaroundus.org). A 'depth range' filter for demersal species was ascertained using the maximum and minimum depth where juvenile and adults are most often found. This range, available from FishBase may be calculated as the range within which approximately 95% of the biomass occurs. Both latitudinal and depth filters were further refined by defining a species' relative occurrence throughout the respective range, assuming a triangular distribution. The model allowed for seasonal differences in the latitudinal centroid of the distribution for migratory pelagic species (Lam et al., 2008). To improve a distribution prediction based on a species' association with different habitats, a habitat preference filter was applied. This assumes that the relative abundance of a taxon within a cell unit is in part determined by a fraction derived from the number of habitats (e.g. coral reefs; seamount; estuaries; see Cheung et al., 2008) it associates with inside that cell, and how far the association effect will extend from that habitat. Extension from a habitat is calculated as a function of a taxon's body size. Finally, an 'equatorial submergence filter' was implemented to account for the tendency for cold-water species to deepen in regions with warm surface waters (Ekman, 1953; Dulvy et al., 2008).

2.1.4. Species data

A set of commercially exploited fish species were chosen, reflecting a diversity of environmental preferences and life history traits. These were as follows: *Molva molva* (Ling); *Merlangius merlangus* (Whiting); *Gadus morhua* (Atlantic cod); *Melanogrammus aeglefinus* (Haddock); *Merluccius merluccius* (European Hake); *Scomber scombrus* (Atlantic mackerel); *Pleuronectes platessa* (European plaice); *Pollachius pollachius* (Pollack); *Pollachius virens* (Saithe); *Psetta maxima* (Turbot); *Solea solea* (Common Sole); *Sardina pilchardus* (European pilchard); *Sprattus sprattus* (European sprat); *Scopthalmus rhombus* (Brill). Species occurrence data were obtained from the three global online databases: the International Council for Exploration of the Sea (ICES) EcoSystemData database (http://ecosystemdata.ices.dk); the Ocean Biogeographic Information System (OBIS) (Vanden Berge, 2007; http://www.iobis.org) and Global Biodiversity Information Facility (GBIF) (http://data.gbif.org), all last accessed in 2010.

Occurrence records were spatially aggregated at the level of 0.5° latitude × 0.5° longitude to give a binary value of presence or absence for each cell. As these data sources are prone to error, for example, due to data being amalgamated from many sources

Table 1
Rules used to compute environmental envelopes (Min_A, Min_P, Max_P, Max_A (Fig. 1)) in AquaMaps (Ready et al., 2010) and its application in calculating cell probability values for a particular environmental variable at a location (×).

Envelope value	Description/calculation
Min_A	Absolute minimum value at which the species is observed OR the 25th percentile of the environmental values − 1.5 × the interquartile range (whichever is lower)
Min_P	Preferred minimum, the 10th percentile of the environmental values
Max_P	Preferred maximum, the 90th percentile of the environmental values
Max_A	Absolute maximum value at which the species is observed OR the 25th percentile + 1.5 × the interquartile range (whichever is greater)

Condition of x	Value/calculation of cell probability value
$x \leq Min_A$	0
$Min_A < x < Min_P$	$(x - Min_A)/(Min_P - Min_A)$
$Min_P \leq x < Max_P$	1
$Max_P \leq x < Max_A$	$(Max_A - x)/(Max_A - Max_P)$
$x \geq Max_A$	0

Table 2
Environmental/oceanographic predictors input into AquaMaps and Maxent.

Variable	Description	Source
Bathymetry	Minimum and maximum depth.	ETOPO2 2 min resolution bathymetry dataset (NOAA, 2006)
Sea surface temperature (SST)	Mean annual sea surface temperature (°C) for the period 1982–1999.	Climatology published by NOAA (2007) produced following methods described by Reynolds and Smith (1995).
Sea bottom temperature (SBT)	Mean annual sea bottom temperature (°C) for the period 1982–1999.	Sea Around Us Project, unpublished data.
Salinity	Mean annual surface salinity for the period 1982–1999.	2001 World Ocean Atlas (Conkright et al., 2002).
Ice	Mean annual proportional ice cover (by area on a scale of 0.00–1.00, for the period 1990–1999. Inverse distance weighted interpolation was performed to fill missing data values in a small number of coastal cells (approximately 1000 cells).	U.S. National Snow and Ice Data Centre (Cavalieri et al., 2006).
Primary productivity	Mean annual primary production in mg Cm^{-2} day^{-1} for the period 1997–2004. Generated from remotely sensed chlorophyll-a concentrations using an approach described in Carr et al. (2006).	European Joint Research Council (http://marine.jrc.ec.europa.eu/ made available by Frédéric Mélin).
Distance to coast	Nearest distance of each cell to the coast.	Sea Around Us Project, unpublished data.

or not being recorded with a date, data were checked and rigorously filtered using further information on species environmental preferences and geographic limits, obtained from FishBase and alternative data sources (Whitehead et al., 1986; Ojaveer et al., 2003; Helcom, 2009; FAO Fact Sheets: www. fao.org). Points were removed if they were: 1. located on land; 2. located outside a verified FAO area (unless contiguous with points lying within a verified FAO area); 3. located outside expert defined geographic range extents (obtainable as latitudinal and longitudinal limits from Fish-Base); 4. located in the Baltic Sea if a species' persistence there was unverifiable (using FishBase, Whitehead et al., 1986; Ojaveer et al., 2003; Helcom, 2009; FAO Fact Sheets: www. fao.org).

2.1.5. Environmental/oceanographic data

Environmental/oceanographic variables were prepared on a 0.5° latitude × 0.5° longitude resolution global grid, comprising 259,200 cells of which 179,904 contain some area of ocean. Data were publicly available and compiled primarily by the Sea Around Us Project (see Table 2). The use of particular environmental variables in the SDM was based on data availability and biological relevance.

2.2. Model evaluation

Model predictions were tested using the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot test statistic. This was implemented using the ROCR package (Sing

et al., 2007, http://rocr.bioinf.mpi-sb.mpg.de), R version 2.10.1, with the ROC curve being plotted as the true positive rate (estimated as the number of true positives/number of positive samples) against the false positive rate (estimated as the number of false positives/number of negative samples). AUC is a widely used test statistic which allows a threshold-independent measure of model performance and can be calculated using pseudoabsences from a random sample of background pixels rather than true absences. It may be interpreted as the probability that a randomly chosen presence site is ranked above a random background site, indicating the quality of site ranking according to suitability (Phillips et al., 2006). A random ranking has on average, AUC = 0.5 and AUC > 0.75 is suggested as providing a useful amount of discrimination between sites where a species is present and those where it is absent (Elith et al., 2006). Due to the lack of independent test datasets, models were assessed internally, by 4-fold cross validation (Fielding and Bell, 1997). Occurrence datasets for Maxent and AquaMaps were thus split into 4 sub-sets, each containing a randomly selected 75% of points for model training, and a corresponding 25% for model testing. As no 'true' absence points were available and using randomly selected points from the entire study areas may artificially inflate the AUC statistic if the geographic area of the study is large (Lobo et al., 2008) or the area of suitable habitat is small relative to the study area, pseudoabsence points were randomly selected from within specified distances of presence points using buffers (Fig. 2). This allowed more valid comparisons between species if AUC values are influenced by relative predicted range area and the distance of pseudo-absence points to presence points. During selection of environmental variables, model runs were tested using global pseudoabsences and those selected from within 2000 km, 1000 km and 500 km buffers whereas only global and 1000 m pseudoabsence points were used in testing final models for all species. Maxent models were further run to perform model cross validation internally, using a random test percentage of 25%. ROC-AUC values were produced for each of 4 subsets of occurrence datapoints by plotting the ROC curve as sensitivity against 1 − specificity (the fraction of the total study area predicted present).

Model assessment was supplemented with the Point Biserial Coefficient (PBC) (Elith et al., 2006; Zheng and Agresti, 2000). PBC was calculated as a Pearson's correlation coefficient between the observation in the occurrence dataset (presence (1) or pseudo-absence (O)) and the prediction and therefore takes into account how far the prediction varies from the observation. This addresses the concern that the AUC test statistic may not always reflect a model's ability to prioritise areas in terms of their habitat suitability relative to alternative models (e.g. Lobo et al., 2008; Austin, 2007). Predictions were further inspected visually and compared to plotted occurrence data in order to assess their plausibility with respect to the known distribution and areas of habitat suitability outside known occurrence range (overprediction).

A subset of species was investigated to undertake a model selection process and determine the sensitivity of predicted species distribution to environmental variables using the Maxent and AquaMaps modelling procedures. These species include the demersal species *P. platessa* and *M. molva* and the pelagic species *S. pilchardus* and *S. scombrus*. Models were run following sequential removal of variables according to the degree of autocorrelation between them, as indicated by Pearson's correlations. They were then evaluated using AUC and PBC test statistics to enable the selection of a final set of input data.

3. Results

3.1. Model selection

Final environmental variables selected for the Maxent and AquaMaps modelling algorithms were as follows: salinity, sea
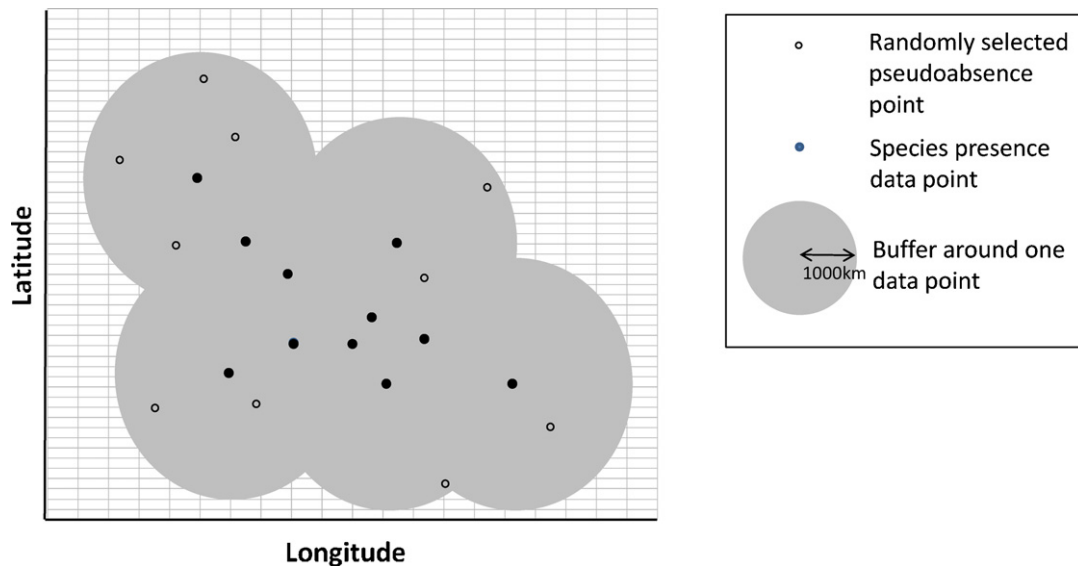
Fig. 2. Diagram representing the selection of pseudoabsence data points from within 1000 m of species occurrence data.

surface temperature, sea bottom temperature, minimum bathymetry, ice concentration and primary productivity. Minimum bathymetry was omitted for pelagic species due to its biological irrelevance and propensity to misleadingly restrict range predictions in these species. It was, however, substituted with distance to coast to account for the fact that many pelagic species are restricted to coastal habitats at certain stages in their life cycle and may not persist in the open ocean despite its seeming environmental suitability.

The AUC values from Aquamaps predictions are above 0.75 and vary over a relatively small range of values (with the exception of *P. pollachius*) (see Supplementary data, Table 1, for a summary of key statistics). Although test statistic values vary with the buffer used to generate pseudo-absences, with a few exceptions, the pattern of difference is similar across buffers for both AUC and PBCs. Pelagic species (*S. rhombus* and *S. pilchardus*) showed less variation in test statistics according to environmental variables included in the AquaMaps models. Maxent models also showed less variation in AUC value with different sets of environmental variables, variation instead mostly resulting from using different sets of pseudoabsences.

3.2. Model comparison

3.2.1. Maxent

Cross-validation using sub-sets of data and Maxent's automated validation test showed relatively little variation in the AUC statistic (e.g. maximum difference in AUC values of 0.01 and 0.009 in *S. rhombus* and *P. pollachius* respectively). The quality of predictions, as indicated by test statistics, was also relatively consistent across species, with the most noticeable deviation in AUC value being shown by *S. scombrus* (AUC = 0.953).

Test statistic values decreased when calculated using pseudoabsences restricted to 1000 m from presence points, although the extent of the difference varied between species and were generally smaller for demersal species (Fig. 3a). While *M. molva*, for example, varied little in model performance (indicated by test statistics) the greatest difference was seen in *S. pilchardus*. AUC value decreased from 0.998 to 0.793 when pseudoabsences from a global and 1000 km buffered distribution were used respectively. PBC values also varied little across species (Fig. 3a), with little

difference between values tested with 'global' and '1000 km buffer' pseudo-negatives other than for the pelagic species *S. pilchardus* and *S. scombrus*.

With the exception of *P. pollachius* and *P. virens*, AUC values generally dropped following clipping by depth in the Maxent refined prediction, when tested using global pseudo-absences (Fig. 3b). The extent of this decrease was slight, although varied between species and fell most for those species restricted to the shallowest depths. Thus while *M. molva* was clipped only to a depth of 1000 m and AUC values decreased slightly by 0.004, *P. maxima* and *S. rhombus*, which were clipped to 70 m and 50 m decreased by 0.101 and 0.193 respectively (using 1000 m buffers). The same was true for PBC values, although frequently the use of a buffer made more difference to this value than the depth clipping of the prediction, for example in *M. merluccius* and *S. solea*.

3.2.2. AquaMaps

The AquaMaps methodology showed a greater response in AUC value to the data subset used in model training and testing. With the exception of a subset of *P. pollachius* (AUC = 0.871) all subsets still obtained high values of 0.944 or greater. This modelling approach also showed greater variation between species, with the most robust, or highest performing, models, as indicated by the test statistics, being obtained for the pelagic species *S. sprattus*. Although another pelagic species (*S. pilchardus*) showed the next highest AUC values, this result was not paralleled by PBC values (Fig. 3c), highlighting the difference in test statistic obtainable when binary presence/absence data are considered as opposed to actual values.

As with Maxent, refinement of predictions by depth clipping produced little difference in PBC and AUC values other than in *P. maxima* (decreases in PBC and AUC of 0.127 and 0.096, respectively) and *S. rhombus*, whereas the reduction in PBC with the 1000 m buffer was more pronounced than in Maxent evaluations and showed wider variation between species. The use of the 1000 m buffer has a less marked effect on test statistics in depth clipped predictions. These patterns are reflected in the high (>0.75) AUC test statistic.

There seemed to be no significant effect on the test statistic of number of occurrence points for either modelling method, although the variation in occurrence dataset size was not great (between 445
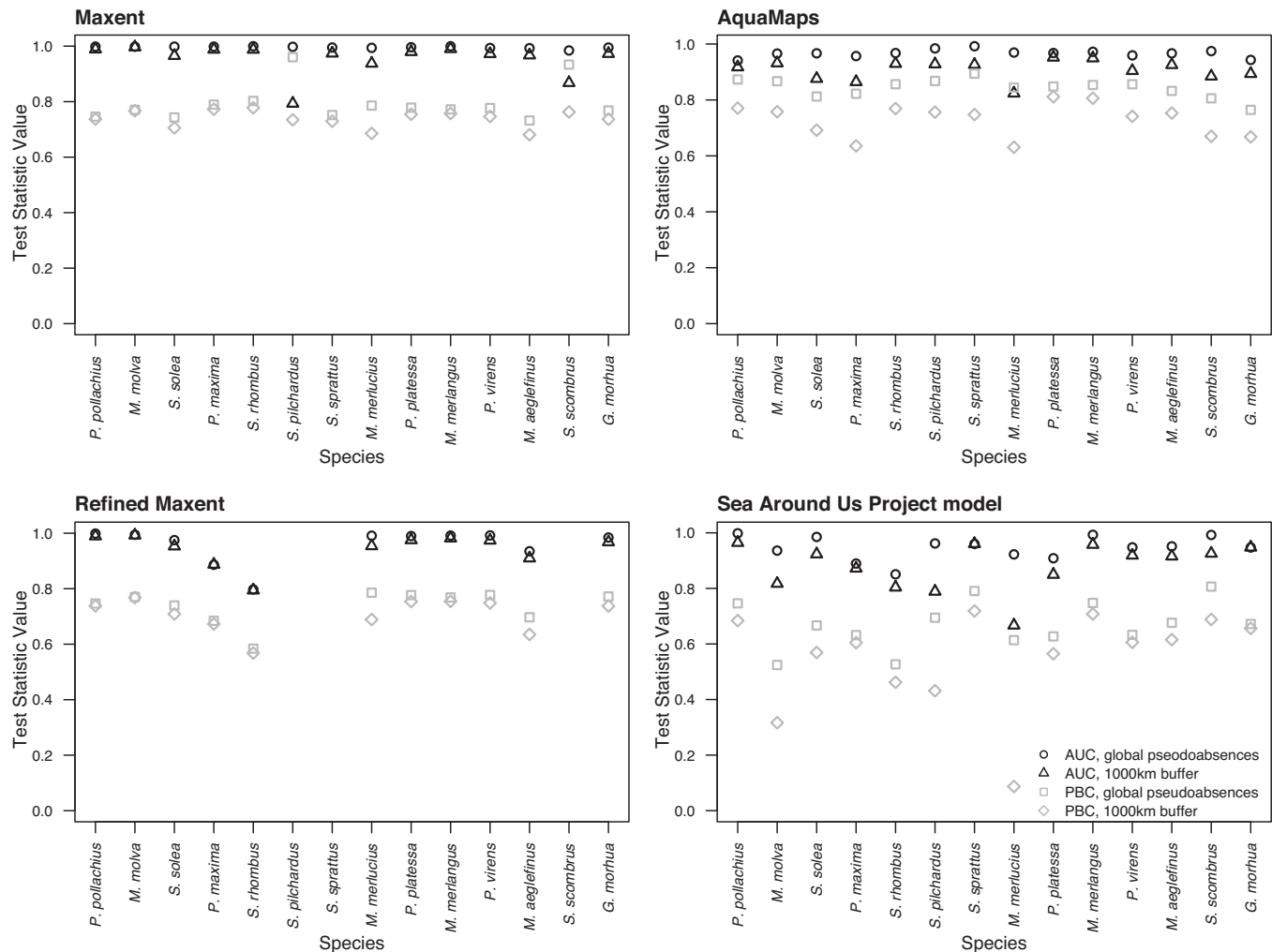
Fig. 3. Test statistic values for all species, calculated using pseudoabsences from within a global distribution or those restricted to within 1000 km of presence points. Test statistic values are calculated as the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot test statistic, and the Point Biserial Coefficient (PBC) for each model (Maxent, Refined Maxent (following clipping of predictions by depth for all species other than pelagic species (*S. pilchardus*, *S. sprattus*, *S. scombrus*), AquaMaps, Sea Around Us Project model.

and 1323 occurrence data points). *P. pollachius*, *M. molva*, *M. merlangus* and *P. platessa* gave consistently high test statistics across AquaMaps, Maxent and their refined models, also when tested with different sets of pseudonegatives. Test statistics for *S. solea* and *M. merluccius* varied most following model clipping by depth and use of a buffer in pseudoabsence selection. Although all achieving AUC > 0.97 using global pseudoabsences, the pelagic species showed large decreases in performance relative to other species following implementation of a buffer, and this was most pronounced in Maxent.

3.2.3. Sea Around Us Project Model

The Sea Around Us Project methodology exhibited greater variation in test statistics than both Maxent and AquaMaps, with the AUC and PBC test statistics showing mostly parallel patterns of change across species (Fig. 3d). Values decreased consistently following implementation of a buffer, with larger decreases in results for *M. merluccius* and *S. pilchardus* compared to other species (AUC decrease = 0.173 and 0.184 respectively, PBC decrease = 0.263 and 0.372 respectively). This reflects a similar pattern of results found in these two species in AquaMaps and, to a lesser extent, Maxent. Some AUC values for predictions for the Sea Around Us Project method compared well to AquaMaps and Maxent (such as

P. pollachius and the pelagic species *S. sprattus*, *S. pilchardus* and *S. scombus*).

Variation was, however, observed in the relative performance of the three models for particular species. In almost all cases, the AquaMaps algorithm produced the least constrained prediction, and thus the greatest distribution ranges, although these were reduced following refinement by depth for demersal species. Maxent occasionally resulted in over-prediction in the Baltic Sea (e.g. *P. pollachius*; *P. virens*) with respect to verified occurrence data and other sources (see Section 2). While *M. merlangus* was predicted consistently well across models, *M. molva* obtained lower test statistics in the Sea Around Us Project model relative to other species, failing to meet the 0.75 threshold AUC and with PBC scores below 0.333.

Overall, although the three models did not vary greatly in the area, or extent of occurrence, predicted for each species, differences lay in the detailed pattern and values of predicted suitability within this area (Figs. 4–6). While Sea Around Us Project predictions were characterised by relatively low levels of suitability, they were contrasted most strongly by AquaMaps, which frequently produced uniformly high predictions across the range, only decreasing in relatively suitability around the periphery of the predicted range, as seen, for example, in *P. platessa* (Fig. 4).
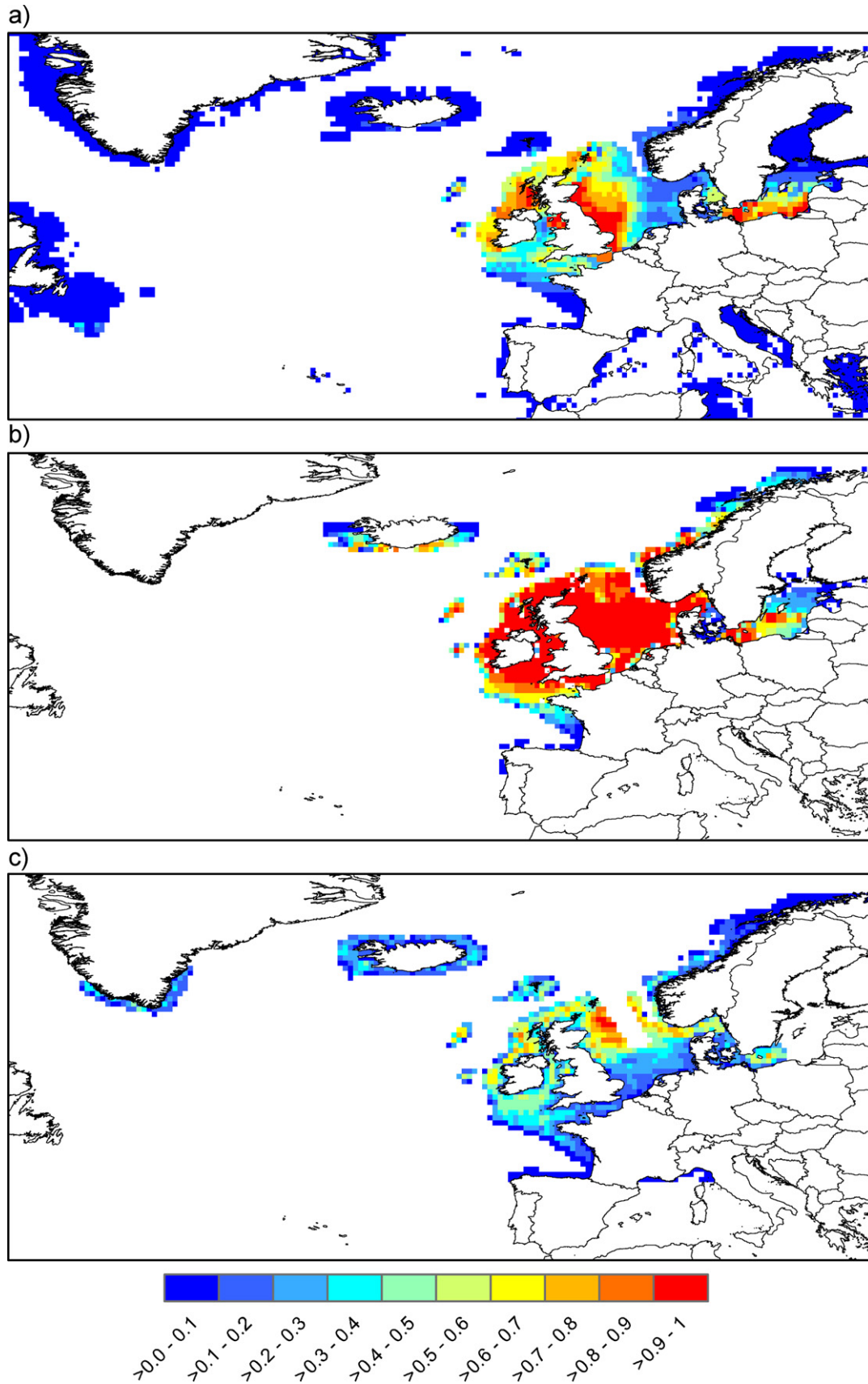
Fig. 4. Predicted distributions of relative habitat suitability (0–1) for *Pleuronectes platessa* using (a) Maxent; (b) AquaMaps; (c) Sea Around Us Project model.

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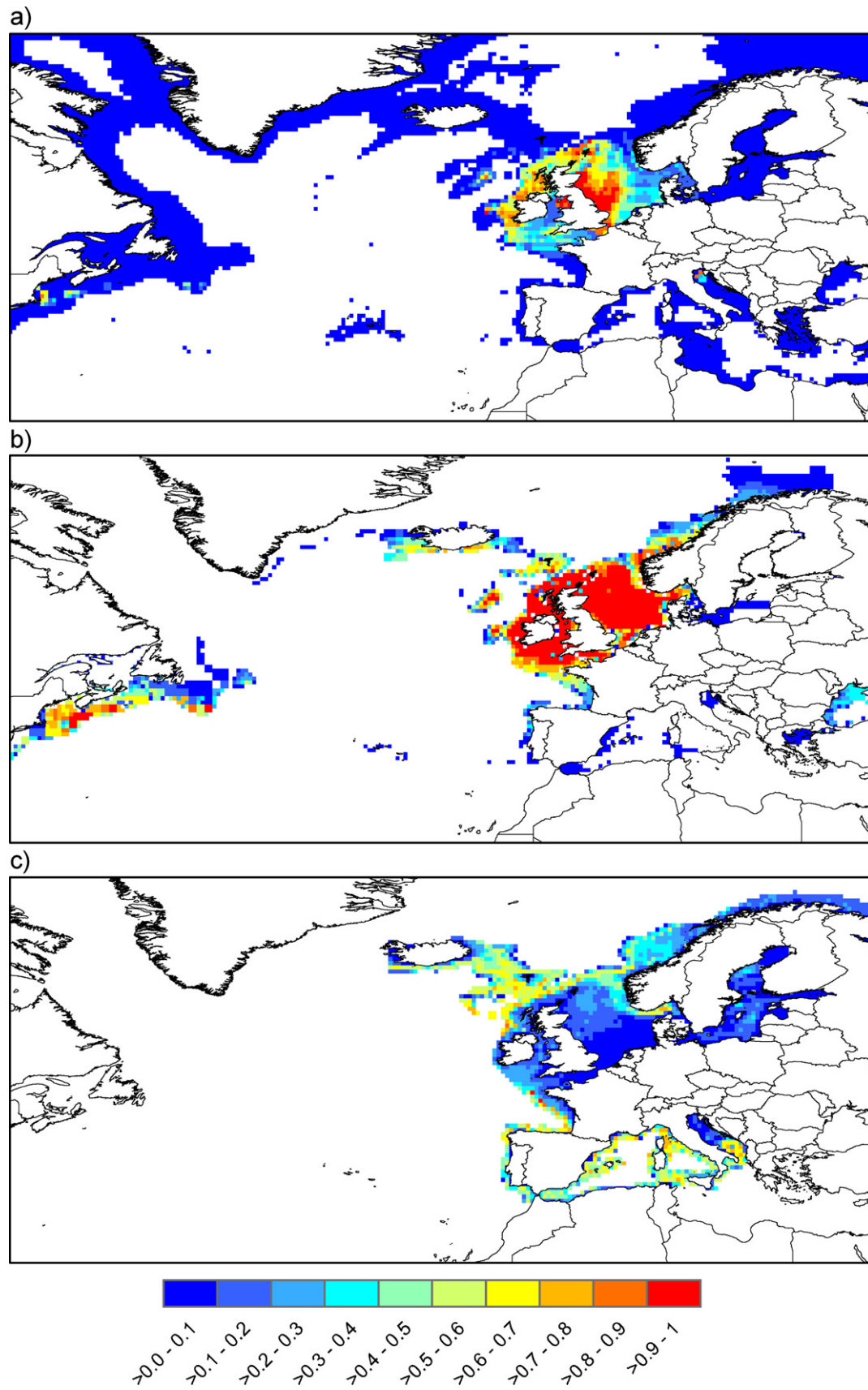

Fig. 5. Predicted distributions of relative habitat suitability (0–1) for *Molva molva* using (a) Maxent; (b) AquaMaps; (c) Sea Around Us Project model.
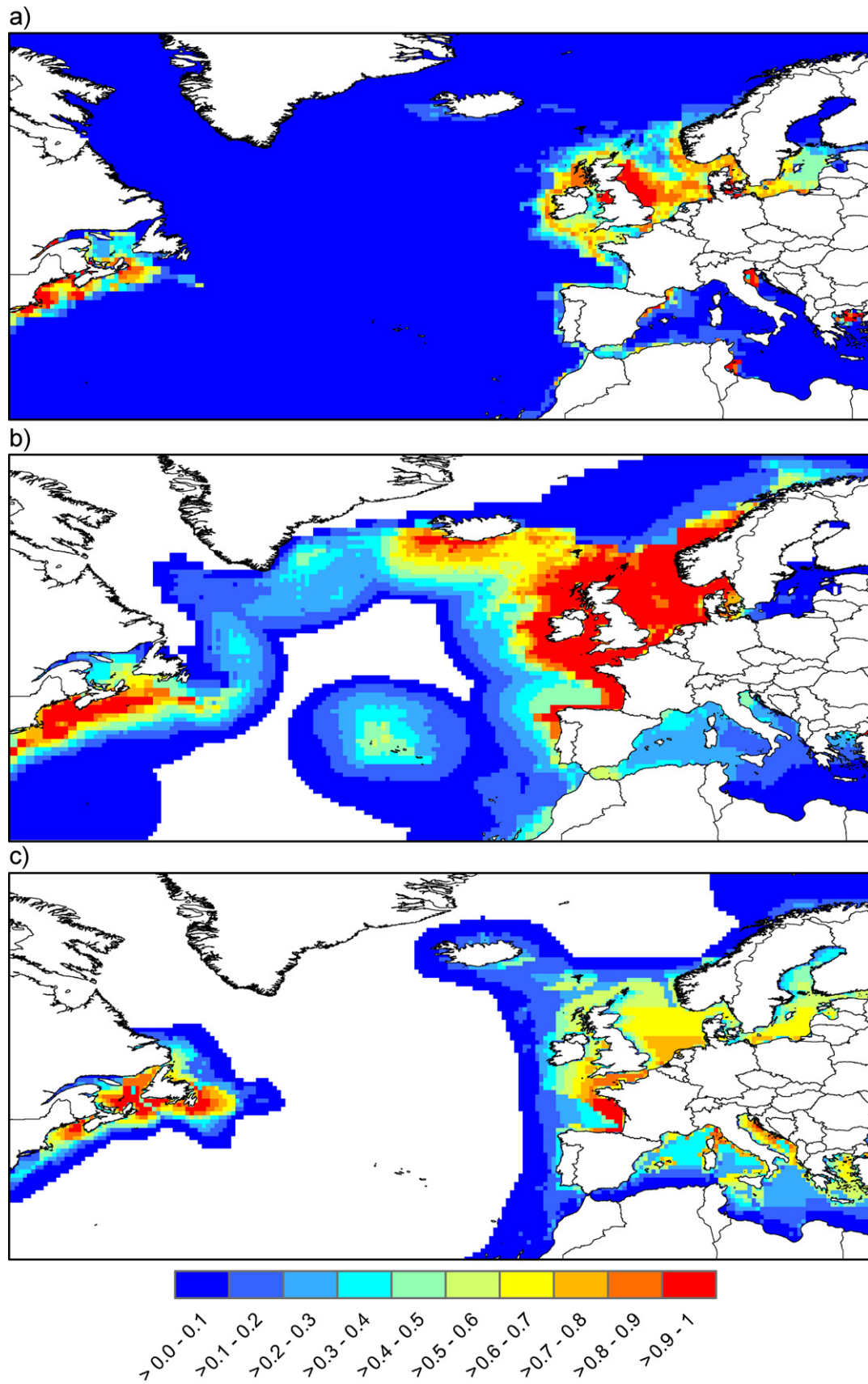
a)

b)

c)

Fig. 6. Predicted distributions of relative habitat suitability (0–1) for *Scomber scombrus* using (a) Maxent; (b) AquaMaps; (c) Sea Around Us Project model.

4. Discussion

4.1. Uncertainties and assumptions

This study aimed to draw comparisons between three commonly used models for obtaining distribution predictions of marine species. Uncertainties are introduced into a multi-model procedure by differences in the data-types used, how the models are parameterized and the actual modelling mechanisms used. Confidence in species occurrence data may, for example, be lowered by sampling bias and taxonomic uncertainty, whereas data on species tolerance limits and expert judgement may be biased by limited experimental data and incomplete or out-dated knowledge. Further uncertainly is caused by inherent assumptions of any species distribution modelling procedure, such as the assumption that a species is in pseudo-equilibrium with its environment (Guisan and Thuiller, 2005). Upholding this assumption ensures that the observed realized distribution used in making predictions or setting environmental filters represents the absolute environmental limits of a species' range, and that true potential range is not underestimated by closely fitted, biased, distribution data (e.g. Svenning and Skov, 2004). The assumption may not be upheld when models fail to take into account biotic interactions that prevent species occupying otherwise seemingly suitable habitat. It has been suggested, however, that many species distributions can be assumed to be in equilibrium with current climate at the macro scale, although the finer details of the distribution may not be identified (Pearson et al., 2002). An attempt to counter this problem was made here by including all occurrence data available rather than restricting points to a specific time period or region. While this may introduce uncertainty as to whether current distributions fail to reflect potential movement of species population due to stock depletion in commercially exploited fisheries, it is hoped that it will contribute to capturing the species true limits of environmental tolerance. It is also assumed that there has been no adaptation towards climatic variation over the period for which data has been amalgamated. Although this might seem reasonable over a short time span, bias may be introduced if, as is frequently the case in compiled online datasets, there is no date associated with a species occurrence record. In this instance, models parameterized on known tolerance limits and expert opinion may be more suitable at depicting current distributions.

4.2. Model characteristics

While predicted distribution ranges from AquaMaps, Maxent and the Sea Around Us Project model show general agreement, there are consistent differences in predictions resulting from differences in input data and model structure (Table 3). Although test results from ROC-AUC and PBC values vary between species, models tested with pseudo-negatives selected from both a global and restricted (1000 m buffer) distribution obtained AUC values indicating performance which is better than random [in all but one case (M. merluccius, Sea Around Us Project)], and may be considered potentially useful (>0.75, Elith et al., 2006).

The generally high test statistic values obtained for Maxent predictions are consistent with its use elsewhere (Elith et al., 2006; Hernandez et al., 2006; Wisz et al., 2008). The lesser variation between test results for partitioned datasets in Maxent than AquaMaps also indicates a greater robustness of this procedure to the particular dataset used and thus to outliers and possibly erroneous datapoints. However, although high model performance suggests accuracy and reliability in predictions of species distribution made by Maxent, it may also be caused by the tendency of Maxent to over-fit the occurrence data of the sample, for which it has been criticised (Jiménez-Valverde et al., 2008). It has also been

suggested that complex models, such as Maxent, are likely to be more accurate at finer resolutions (specificity), but would generalize poorly in predicting potential distributions at large spatial scale (Drake et al., 2006; Jiménez-Valverde et al., 2008) whereas simpler models, such as AquaMaps, will offer useful and parsimonious solutions at a broader scale (generality) (Thuiller et al., 2008). This agrees with the tendency, seen here, of Maxent to produce more constrained predictions than AquaMaps, and indicates that test statistics should not be used as definitive indicators of model performance, but should be assessed together with visual inspection of the distributions and expert knowledge.

Our analysis agrees with Ready et al. (2010) that a 'black-box' use of complex SDM programmes such as Maxent may act as a barrier to users who are not expert, and may also hinder the potential for alteration by experts and thus perhaps their actual practical use and application. Maxent and AquaMaps models were refined by 'expert' review of a distribution map subsequent to a prediction, by 'clipping', and may thus not necessarily involve a detailed knowledge of a modelling procedure. Despite this, the ability to easily investigate and manipulate the environmental envelope for each variable in the AquaMaps approach aids the incorporation of expert judgement and checking for errors caused by potential outlying or erroneous occurrence data points.

The Sea Around Us Project method requires the least amount of point data, and its predicted distributions are generally more restricted relative to those predicted using the other two approaches. However, inherent differences in input data and the way environmental limits and parameters are defined under this approach further seem to prevent the valid comparison of the relative performance of these three models. Thus while the test data subset form a representative sample of the training data used to generate predictions in both Maxent and AquaMaps, a Sea Around Us Project prediction is generated using environmental and geographic limits and thus independently from the occurrence dataset, precluding the selection of the most accurate, reliable 'best' model by direct comparison of test statistics. Particularly, spatial autocorrelation between the presence data for distribution predictions and that for calculation of test statistics may over-estimate the performance of Maxent and AquaMaps relative to the Sea Around Us Project method. For example, in modelling M. molva (Fig. 5) and M. merluccius using the Sea Around Us Project approach, regions were predicted as being unsuitable despite coinciding with species occurrence data points, resulting in the models obtaining low AUC and PBC values (M. molva: AUC = 0.657; PBC = 0.147 with buffer, M. merluccius: AUC = 0.667, PBC = 0.087). This is, however, likely due to the fact that, being tested but not trained on environmental data associated with occurrence points, the minimum depth restriction imposed by the Sea Around Us Project filter excludes areas retained by the other models. The discrepancy presented a valid difference between the two types of data driving the approaches (species occurrence data and tolerance limits) and one that confidence in data quality did not justify eliminating. Minimum depth restrictions were therefore retained in the Sea Around Us Project methodology although that for M. molva was reduced from 100 m due to the presence of immature individuals up to a depth of 15 m (Whitehead et al., 1986). Following this adjustment, the predicted distribution for M. molva has an AUC that is more consistent with other species and methods. Similarly, the differences between datatypes and their effect on test statistics was highlighted following incorporation of expert knowledge in Maxent and AquaMaps predictions for P. maxima and S. rhombus (Fig. 6). The substantial depth restrictions of these species (of 70 m and 50 m respectively) encompassed areas where occurrence data are found and therefore likely result in the relatively low test statistics obtained.

Difficulty therefore lies in the relative confidence in data used for model training and testing. Although occurrence data for S. rhombus

Table 3
Summary of general model characteristics for the original models of Maxent and AquaMaps and the Sea Around Us Project model, inferred from results.

Characteristic	Maxent	AquaMaps	Sea Around Us Project
Relative habitat suitability values	Relatively even allocation from high to low suitability.	Dominated by areas of uniformly high suitability following clipping by depth.	Dominated by area with low suitability values.
Extent of predicted distribution	Intermediate constraint before clipping.	Least constrained before clipping.	Most constrained.
Under-prediction with respect to occurrence data	None pre clipping, some in refined Maxent.	None pre clipping, some in refined AquaMaps.	Some e.g. *M. molva*.
Variation in AUC/PBC value in response to partitioned training/testing data	Low.	Higher.	n/a.
Variation in AUC/PBC value across species	Low.	Intermediate.	High.
Species data (minimum) requirements	Species occurrence points, presence only.	Species occurrence points, presence only.	Knowledge of general geographic range, habitat and depth preferences.
Model complexity	Complex: statistical, generative method enabling predictor variable weighting, modelling of interactions and complex response curves.	Simple: assumes a trapezoidal distribution and equal weighting of predictor variables.	Simple: discriminative approach using a set of key ecological predictors.

indicate its realized niche to be throughout the North Sea, its habit of living on sandy or mixed sea bottoms, only to a depth of 50 m (FishBase), questions its long-term persistence in the deeper areas indicated by occurrence data. If the aim is to model a species' potential niche, where it can reproduce and persist and is not dependent on access to other (shallower) habitats, it may therefore be more suitable to restrict predicted distributions to the more conservative estimate, despite the wider distribution suggested as the observed, realized niche. If projecting predictions in time or space, it does, however, seem wise to take into account both range predictions as containing useful information about the species environmental requirements and tolerances.

Discrepancies between predicted relative suitability in the Baltic Sea further highlight differences in the methodologies and algorithms of the three models. The most accurate predictions for the suitability of the Baltic Sea for particular species, according to verified occurrence data and other sources (see Section 2) were produced by AquaMaps and the Sea Around Us Project model. This likely resulted from the equal weighting given to each environmental variable such that the effect of salinity was considered in equal proportion to other predictors in these two models. As Maxent, by contrast, attributes a low contribution by salinity to the prediction, the suitability of other environmental variables in this area may compensate for an unsuitable salinity value, resulting in predicted distribution in areas where a species is known not to occur. Comparing the two correlative species distribution models used here, AquaMaps is therefore more robust than Maxent to uncertainty in the relative influence of environmental predictor variable due to its simple, multiplicative approach which assigns equal weighting to each predictor.

4.3. Interpretation of test statistics and the problem of model comparison

Further to the problem, mentioned above, of comparing models based on different data sources, in reference to complex SDM techniques such as Maxent, it was suggested that model testing statistics using presence-(pseudo)absence data might produce artificially high values for more restricted distribution predictions as a greater number of absences or 'pseudo-absences' are likely to be predicted as absent. This characteristic would lead to the conclusion that complex techniques are more accurate than simpler ones, precluding any useful comparison between modelling approaches.

Furthermore, although Maxent models generally produce higher AUC values than those produced by AquaMaps, this is seldom the case using the PBC statistic. This disparity raises questions whether either value allows a useful and valid comparison across modelling procedures. Although calculation of AUC scores may be highly influenced by the total modelling area, larger areas increasing the likelihood that pseudoabsences will be more distant in environmental space and decreasing commission error (Lobo et al., 2008), in this case the study area remained consistent. Evaluation of perceived model performance may, however, also be affected by a species' relative occurrence. This is consistent with the observation that the test statistics for AquaMaps fell when all species were tested using pseudoabsences taken from a restricted area (within a buffer of 500 or 1000 m of observed presence points). The decrease in AUC value followed by incorporation of depth limits in the distribution predictions (using Maxent and AquaMaps) do not, however, support the hypothesis that AUC values will increase with decreasing predicted extents of occurrence. This loss of model performance following depth clipping is rarely seen when test statistics are calculated using pseudoabsences restricted to particular distances from presence points, refined models then performing consistently better than the originals. The exceptions to this are shown by *P. maxima* and *S. rhombus*, whose substantial depth restrictions (of 70 m and 50 m respectively) encompass areas where occurrence data-points are found, likely resulting in lower test statistics if presence points from outside these restricted areas are used in their calculation. Results obtained here using global pseudoabsences therefore contrast those obtained by Ready et al. (2010), who found the AquaMaps approach to be generally favourable to the inclusion of expert knowledge in the form of defined depth preferences. It is thus proposed that, in this case, the perceived performance of expert reviewed, or 'refined' predictions may be subject to characteristics of model testing statistics.

As it has been suggested that the focus on predictive performance should be broadened to encompass ecological realism and model credibility to the user community (Franklin, 2009), it is also important not to become over-focused on data errors and model fit. When selecting environmental variables in this study, for example, minimum bathymetry was included although it did not consistently improve test statistics as the vertical (depth) gradients of temperature and oxygen are considered important factors limiting demersal species distributions (Pauly, 2010). A misunderstanding of ecological relevance may thus lead to errors in model specification despite seemingly high test statistic values. Biological relevance should therefore be considered both in model selection and when assessing the applicability of the three models used.

As undertaken here, it is suggested that a range of AUC/PBC statistics should be calculated in order to assess the scope for variation and possibly contrasting results. Although a range of values

may then only allow broad conclusions to be drawn, it is argued that the greater understanding of the model evaluation process and any differences will facilitate reasoned judgement in model evaluation. In conclusion, it is proposed that the refinement of AquaMaps and Maxent predictions by expert opinion do represent more accurate representation of species' distributions, agreeing for the most part with occurrence data and the predictions produced by the Sea Around Us Project model. It should be noted, however, that AUC values are useful in determining the amount of variation in predictions caused by partitioned datasets, emphasising the degree of influence of possible outlying points and the robustness of the model to the occurrence data (Lobo et al., 2008).

5. Conclusions

Uncertainties inherent in both specifying and testing species distribution models indicate that expert review is a vital part of the SDM process. Although the modelling approaches employed here may lose precision in assuming that species distributions are dictated by a general and restricted set of environmental variables, in modelling marine species, for which data and ecological knowledge are frequently scarce, a general approach would seem advisable. Expert review allows models to be refined and developed with increases in knowledge or data, and the ease at which this may be done, by a variety of non-specialist users, will be enhanced by a transparent and intuitive procedure.

The three modelling approaches produced predictions of relative habitat suitability which were plausible given the occurrence data of each species. This analysis does not, however, indicate whether there are differences in the capabilities of each model to portray specific features of the distribution, such as the pattern of relative habitat suitability. In conducting this comparison doubts were raised as to the validity of direct comparisons between models. Striving to find the best model, as indicated by test statistics would therefore risks substantial inaccuracies if wrong selection of alternative data sources or model design are made. Differences between modelling procedures that mask uncertainty as to true suitability values should therefore be retained and used to view the range of plausible predicted distributions for a species. It is proposed that a multi-model ensemble approach is most suitable for investigating distribution ranges, especially in the marine environment where modelling is likely to be hampered by issues of data quality.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2011.11.003.

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