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Predicting the distribution of vulnerable marine ecosystems in the deep sea using presence-background models

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Abstract

In 2006 the United Nations called on states to implement measures to prevent significant adverse impacts to vulnerable marine ecosystems (VMEs) in the deep sea. It has been widely recognised that a major limitation to the effective application of these measures to date is uncertainty regarding the distribution of VMEs. Conservationists, researchers, resource managers, and governmental bodies are increasingly turning to predictive species distribution models (SDMs) to identify the potential presence of species in areas that have not been sampled. In particular, the development of robust 'presence-background' model algorithms has accelerated the application of these techniques for working with presence-only species data. This has allowed scientists to exploit the large amounts of species data held in global biogeographic databases. Despite improvements in model algorithms, environmental data and species presences, there are still limitations to the reliability of these techniques, especially in poorly studied areas such as the deep-sea. Recent studies have begun to address a key limitation, the quality of data, by using multibeam echosounder surveys and species data from video surveys to acquire high-resolution data. Whilst these data are often amongst the very best that can be acquired, the surveys are highly localised, often targeted towards known VME-containing areas, are very expensive and time consuming. It is financially prohibitive to survey whole regions or ocean basins using these techniques, so alternative cost-effective approaches are required. Here, we review 'presence-background' SDMs in the context of those studies conducted in the deep sea. The issues of sampling bias, spatial autocorrelation, spatial scale, model evaluation and validation are considered in detail, and reference is made to recent developments in the species distribution modelling literature. Further information is provided on how these approaches are being used to influence ocean management, and best practises are outlined to aid the effective adoption of these techniques in the future.

Keywords

Maxent, Species distribution models, Cold-water corals, Management, Conservation, Biogeography

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Introduction

In recent decades advances in technology have greatly enhanced our ability to explore, observe and exploit the ecosystems and resources existing in the deep-sea. This age of deep-sea discovery has brought with it an awareness of the complex and diverse ecosystems found in deeper waters (i.e. Freiwald et al., 2004; Hogg et al., 2010; Vanreusel et al., 2010), and evidence of the significant threats that they face (Davies et al., 2007; Williams et al., 2010; Ramirez-Llodra et al., 2011). In 2004, recognition of the degradation of ocean conditions and the wide range of threats facing marine ecosystems led to the formation of an intergovernmental mandate of the Convention on Biological Diversity, which aims to identify and preserve a representative selection of high quality marine habitats through the establishment of a coherent network of marine protected areas (Secretariat of the Convention on Biological Diversity, 2004). Similar commitments exist at both national and supranational levels to protect important marine habitats under ecosystem-based management plans.

In 2006 specific recognition of the susceptibility of certain deep-sea species (collectively termed vulnerable marine ecosystems; VMEs) to damage by bottom contact fisheries led to the formulation of the United Nations General Assembly (UNGA) Resolution 61/105 (UNGA, 2007). This Resolution called on regional fisheries management organisations (RFMOs) to identify areas where these species occur, or are likely to occur, based on available scientific information, and to act to prevent significant adverse impacts to these species by activities under their jurisdiction. Following critical review this need for protection was reiterated with increased urgency in 2009, with UNGA Resolution 64/72 that called upon states to implement protective measures immediately, guided by the recommendations of the Food and Agriculture Organisation (FAO; UNGA, 2009). The progress of these measures was further reviewed in 2011. Whilst some RFMOs had taken significant steps, a lack of scientific information on the distribution of VMEs hampered the application of protective measures in the majority of areas (Weaver et al., 2011). As such there is currently an explicit need for the scientific community to collaborate with industry, national and international organisations to gather and develop the information required to inform the conservation and management of deep-sea ecosystems (Clark et al., 2012; Davies et al., 2007; Ramirez-Llodra et al., 2011).

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It is widely acknowledged that the effective management of deep-sea ecosystems will require the implementation of marine spatial planning in the High Seas (i.e. Auster et al., 2011; Clark et al., 2012; O'Leary et al., 2012). To do so robustly requires extensive information on the distribution of biodiversity and species. However, the vast size of the deep-sea floor in tandem with the expense and technological complexity of sampling in deep waters mean that detailed spatial information is lacking for much of the world's oceans (Ardron et al., 2008). Data initiatives such as the Census of Marine Life (CoML) and national science projects have improved this situation considerably through the collation of global-scale biogeographic databases of species data (e.g. Stocks, 2010). The Ocean Biogeographic Information System (OBIS) database is one of the best known. It was initially developed by Rutgers University and extensively upgraded during the CoML project and is currently maintained by the Intergovernmental Oceanographic Commission of UNESCO. OBIS currently represents a data holding of over 30 million records (as of 2012).

As part of an exploratory analysis, we extracted distribution records for several large taxonomic groups of primarily benthic invertebrates from the OBIS web portal (www.iobis.org; see ESM1 for listing of taxonomic groups incorporated). This analysis shows that the majority of species observations originate from well-studied areas such as the North and West Atlantic, Gulf of Mexico, Alaska and shelves around South America and Australia (Figure 1a). Whilst these areas are known to be productive, more studies in these regions have contributed records to OBIS regions than elsewhere (Figure 1b). The clustering of studies on shelves and near developed countries reveal the disparity of survey effort, especially in areas such as the Pacific Ocean, South Atlantic Ocean and Southern Ocean where no records have been submitted to the OBIS database. This disparity in survey effort means that the data available from online data sources contains considerable spatial bias (clustering around certain areas; i.e. Davies and Guinotte, 2011) and substantial omission errors (false absences; Rondinini et al., 2006). In light of this, predictive species distribution models (SDMs; Guisan and Zimmerman, 2000) are increasingly being recognised as an efficient and cost effective means of expanding the coverage of existing information on the distribution of deep-sea species and ecosystems (Clark et al., 2012; Weaver et al., 2011).

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In recent years correlative SDMs have rapidly gained in popularity, and their usage has proliferated to encompass the study of a diverse selection of ecosystems and species across a range of research topics (Franklin and Miller, 2009; Guisan and Thuiller, 2005). Correlative SDMs are empirical models that relate geographically organised data on species occurrence to that of a selection of ecologically relevant environmental or spatial variables, to derive a species environmental response (Guissan and Zimmerman, 2000). This response can then be interpolated or extrapolated geographically into areas where environmental data are available, to predict the potential distribution of a species in unsurveyed locations or times. Correlative SDMs are frequently referred to as ecological niche models, habitat suitability models or predictive habitat models. Their use is increasingly common to inform conservation, management and survey planning (Franklin and Miller, 2009). However, whilst numerous terrestrial examples exist, the adoption of SDMs for use in the marine environment is still comparatively rare (Robinson et al., 2011). With this in mind this manuscript reviews the application of SDMs to the deep-sea, with a focus on those benthic species that typify VMEs. We devote particular attention to the limitations of the currently available data, and the subsequent implications for model predictions. Alongside this we review the current limitations of presence-only data, with the intention of providing an overview of the sources of uncertainty affecting predictions. By doing so we hope to focus future research efforts, and aid the interpretation and utilisation of deep-sea SDMs.

Species distribution modelling in the deep-sea

The application of SDMs to deep-sea species is a relatively new pursuit (see Table 1 for descriptions of currently published studies in peer-reviewed journals). It has coincided with the development of robust models for working with species where only information on species presence is available (i.e. Hirzel et al., 2002; Phillips et al., 2006). SDMs are conventionally fit with information on both the presence and absence of a species. However, in recent years recognition of the large amount of species data held in sources containing no absence information, and the difficulty in obtaining reliable absence information for some species, has driven the development of 'presence-only' model algorithms (Elith et al., 2011). A common technique for working with presence-only species data involves the substitution of absence data for 'background' or 'pseudo-absence' data. This data is used to characterise the background environment, allowing the model to better discriminate between the environmental conditions of

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the study area, and the conditions of those sites where the species is known to occur. It is selected either by the user, or at random, from sites within the study extent containing no information about the species. As such these algorithms are often more suitably referred to as 'presence-background' or 'presence-pseudoabsence'. These discrimination techniques are now widely used as they have been shown to consistently outperform those that rely purely on presence data (Elith et al., 2006).

A number of SDM algorithms have been used to predict the distribution of deep-sea species habitat (see Table 1 for summary). To date, Woodby et al. (2009) have produced the only example trained with presence-absence data. Their method incorporated logistic regression, a generalised linear model (GLM) widely used for SDM (see Guisan et al. 2002), and generalised estimating equations (GEE), an extension of GLMs that are able to accommodate data that is correlated through space or time, through the inclusion of an additional variance component. The remaining studies have focused on the use of presence-background algorithms due to the difficulty in obtaining reliable absence data for deep-sea species. Early applications of presence-background SDMs to deep-sea species relied primarily on Environmental Niche Factor Analysis (ENFA; Hirzel et al., 2002), a statistical method that produces maps of habitat suitability by relating the mean environmental conditions of the sites where a species is known to occur to the range of environmental conditions covered by the background data. This information is used to construct an estimation of the species environmental niche, which can then be extrapolated into unsampled locations (Hirzel et al., 2002). In the deep-sea, several studies have used this approach with success in predicting species habitat. The first published approach appeared in 2005, where Leverette and Metaxas modelled the distribution of two species of octocoral on the Canadian Atlantic shelf and slope. Early adopters largely focussed on local and sub-regional scale areas (i.e. Bryan and Metaxas, 2007; Dolan et al., 2008; Wilson et al., 2007) with global studies emerging as data availability increased (Davies et al., 2008; Tittensor et al., 2009). In a later study Guinan et al. (2008) successfully applied the genetic algorithm for rule-set production (GARP), a generic machine-learning method which has been widely applied to SDMs working with presence-only data (Franklin and Miller, 2009; Stockwell and Noble, 1992). More recently however, the probability density estimation technique Maximum Entropy (MaxEnt; Phillips et al., 2006) has become the preferred modelling method due to observations of improved model

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performance (Elith et al., 2006; Tittensor et al., 2009). Deep-sea studies using MaxEnt have focussed on large spatial scales (i.e. Davies and Guinotte, 2011; Tittensor et al., 2009; Yesson et al., 2012), with studies emerging on smaller spatial scales (i.e. Howell et al., 2011; Guinotte and Davies 2012).

MaxEnt utilises an alternative approach to traditional regression-based methods, in that it models the probability of the environmental variables at a location conditional on species presence, rather than vice-versa. It does so by applying the principle of maximum entropy, whereby the most uniform distribution of predictions is chosen based on constraints derived from the environmental variables. Specifically these constraints are defined by the expected value of the probability distribution, which is estimated from the species presence information used to fit the model. The final output is then an expression of the distribution of maximum entropy amongst all distributions that satisfy these constraints. These results are then provided as a map of habitat suitability values, where the value within each grid cell is a function of the environmental variables at that cell (Elith et al., 2011). Several factors, as well as model performance have driven the adoption of MaxEnt. Its software application is designed specifically with SDM in mind and is implemented accordingly through an accessible interface. It has also been shown to be flexible in its ability to accommodate a wide range of data situations whilst maintaining a high level of predictive performance relative to other methods (Elith et al., 2006; Pearson et al., 2007; Phillips et al., 2006). Whilst MaxEnt is a robust modelling approach and is highly appropriate for many deep-sea studies, it should be acknowledged that other methods such as Boosted Regression Trees (De'Ath, 2007; Elith et al., 2008) and Artificial Neural Networks (Lek et al., 1996; Watts et al., 2011) also have great potential for use in this area.

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Sources of deep-sea data

In the terrestrial environment, developments in satellite remote sensing have long given species distribution modellers access to accurate, high-resolution maps of topography and land cover over broad spatial scales (Franklin and Miller, 2009). In contrast, the limited penetration of light through seawater in tandem with the costs and logistical issues of sampling in deep-waters mean that the deep-sea is a characteristically data-poor environment (van den Hove and Moreau, 2007). As such the recent advances in the application of SDMs to this area have largely been the

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result of advances in remote sensing (Kenny et al., 2003), oceanographic data sources (i.e. World Ocean Databases, Boyer et al., 2006; 2009) and global bathymetric products (Becker et al., 2009).

At broad-scales, studies have made use of the range of large-scale digitised maps of oceanographic data developed by public bodies or academics (i.e. Davies et al., 2008; Davies and Guinotte, 2011; Tittensor et al., 2009, Yesson et al., 2012). The majority of this data is provided as a collection of monthly, seasonally or annually averaged depth-binned layers, such as the World Ocean Atlas, that provides a variety of data including temperature, salinity, oxygen and nutrients which were collated by a CTD system and interpolated over a global 1° grid. Early studies focussed on collating depth layered habitat suitability predictions with information on seamount distributions (Kitchingman and Lai, 2004) to produce global measures of 'seamount suitability' (Clark et al., 2006 later published in Tittensor et al., 2009). Davies et al. (2008) further extended the range of global studies, merging global bathymetry data acquired from the General Bathymetric Chart of the Oceans (GEBCO) with data on a wide range of ecologically relevant variables in order to create a selection of environmental grids representative of conditions at the seafloor. These early attempts to model deep-sea species on global scales made use of coarse (1° or on average 110 km^2 pixel resolution; Figure 2a, or 0.25° or on average 27 km^2 resolution; Figure 2b) environmental data and were consequently limited in their applicability to conservation and management scenarios (Davies et al., 2008; Tittensor et al., 2009). These data limitations have been improved by the development of new methods for identifying seafloor conditions at high resolutions. Of particular note were the releases of GEBCOs most recent 30 arc-second (~1 km^2) resolution dataset and the STRM30 30 arc-second bathymetric dataset (Becker et al., 2009). These data, combined with the approach of Davies et al. (2008) allowed the deep-sea modelling community to make considerable progress towards addressing previous issues of spatial scale (Figure 2c; Davies and Guinotte, 2011). Subsequently, a wide range of benthic environmental data is now available at relatively fine resolutions (~1 km^2) spanning most of the world's oceans.

At fine scales deep-sea SDMs now commonly utilise this high quality remotely sensed data to inform model predictions (Dolan et al., 2008; Guinan et al., 2009; Howell et al., 2011). Modern

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developments in acoustic survey techniques (most recently multibeam echosounders (MBES)) mean that maps of the seafloor are now becoming available at a resolution and quality that are somewhat comparable to those of the terrestrial realm (Brown et al., 2012). Areal coverage of high resolution data is also increasing as interest in the seafloor expands. For example, Ireland mapped their entire Exclusive Economic Zone (EEZ) using MBES under a nationally funded research program. In turn this data has been used to produce SDMs for deep-sea species (Rengstorf et al., In press). Resolutions are also increasing, as developments to MBES have allowed for their attachment to a variety of underwater submersibles, extending their use to depths and sites that were previously inaccessible (Huvenne et al., 2011). The resultant bathymetric grids are ideal for analyses in geographic information software, allowing users to derive a number of benthic terrain attributes which can then be used as effective predictors of benthic species occurrence due to their relation to local current conditions and substratum (Dunn and Halpin, 2009; Wilson et al., 2007). Alongside this technological advancements to remotely operated vehicles (ROVs) have allowed for the collection of accurately georeferenced video data from which records of species occurrence can be compiled (i.e. Bryan and Metaxas, 2007). These data facilitate the production of high-resolution maps of habitat suitability (i.e. Figure 2d), and have also been used to gain insight into the habitat preferences of deep-sea species (i.e. Dolan et al., 2008; Tong et al., 2012). However, the costs and logistical issues of operating vessels and this sophisticated technology offshore mean that this data is expensive and time consuming to collect. Consequently, fine-scale SDMs have been targeted towards areas of known ecological importance, and their coverage is limited accordingly.

Over fine scales, features such as small banks or highs are prevalent which can have a significant influence on how water flows around and over a structure, significantly altering conditions for benthic species (i.e. Davies et al., 2009; Henry et al., 2010). These features are not often observed in broad-scale bathymetries but are in MBES data (i.e. Rengstorf et al., In press). When extracted from MBES bathymetry, terrain variables can represent the seafloor at very high resolutions, sometimes at metre or even sub-metre accuracy leading to enhancement in the quality and accuracy of SDMs (i.e. Dolan et al., 2008; Rengstorf et al., In press). There are several common terrain variables that can be extracted from MBES data and these have been best described in Wilson et al., (2007). Bathymetric position index (BPI) is an approach to

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determine topographical features based on their relative position within a neighbourhood, and can be calculated over fine or broad scales to capture smaller or larger terrain features respectively. This calculation has been packaged into a popular ArcGIS tool by Wright et al. (2005). Calculations for extracting several other terrain variables have been packaged into a useful and easy to use tool produced by Jenness (2012), DEM Tools for ArcGIS and into the open-source software tool the Geospatial Data Abstraction Library (GDAL, 2012). Slope is defined as the gradient in the direction of the maximum slope and aspect is the direction of the maximum slope. These variables are important because currents and physical processes can be affected by how they interact with topography and this leads to controls on species distribution (i.e. Frederiksen et al., 1992). Curvature attempts to describe the prominence of terrain features and may provide an indication of how water would interact with the terrain. Plan and tangential curvature can describe how water would converge or diverge as it flows over relief, whilst profile curvature describes how water would accelerate or decelerate as it flows over relief (Jenness, 2012). Rugosity, terrain ruggedness and roughness generally describe the variability of the relief of the seafloor (Wilson et al., 2007). Rugosity is defined as the ratio of the surface area to the planar area across a neighbourhood of a central pixel (Jenness 2012). Terrain ruggedness index is defined as the mean difference between the depth value of a central pixel and its surrounding cells. Roughness is the largest inter-cell difference of the depth value of a central pixel and its surrounding cells (Wilson et al., 2007). Terrain variables are also useful as proxies for sediment and substrate type (Dunn and Halpin, 2009), substrate can be highly variable over small spatial scales and high resolution sediment data is not available for most regions. As such, terrain variables are often helpful as proxies that capture the variation associated to substrate nature, assisting in the identification of hard substrate areas that can harbour deep-sea communities.

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Error and uncertainty in SDMs

Whilst considerable progress has been made in recent years, the main hindrance to applying SDM predictions to management action has been their inherent uncertainty. The use of uncertain predictive maps may lead to inefficient decision-making, thus it is important that these uncertainties are acknowledged, and quantified where possible to aid the effective interpretation of SDM outputs (Beale and Lennon, 2012). The uncertainties of SDM predictions can be better

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understood by considering the sources of error from which they result. These can be broadly grouped into two categories; process errors which derive primarily from the failure of current SDMs to account for biotic processes such as competition, dispersal and predator-prey interactions (Araújo and Guisan, 2006; Elith and Leathwick, 2009; Guisan and Thuiller, 2005; Hirzel and Le Lay, 2008; Soberón and Nakamura, 2009); and observation errors which derive primarily from shortfalls in the available data, i.e. data sets containing sample selection bias (Araújo & Guisan, 2006; Phillips et al., 2009; Cabral and Schurr, 2010), autocorrelation (Dormann, 2007a; Legendre, 1993; Segurado et al., 2006) and imperfect measurement (Barry and Elith, 2006; Clark, 2005; McInerny and Purves, 2011; Menke et al., 2009). The following sections review a selection of these sources of prediction error, as they relate to past and future attempts to apply SDMs to benthic deep-sea species.

Sample selection bias and presence-only models

The majority of deep-sea SDMs are built with presence-only species data. At broad scales SDMs utilise species data opportunistically collated from a wide range of sources, the majority of which contain only presence information, e.g. biogeographic databases (e.g. OBIS) and museum collections. At fine-scales species data is collected by surveying transects of the seafloor with video equipment attached to a variety of platforms, namely ROVs, drop-down cameras, manned submersibles and autonomous underwater vehicles (AUVs), in such a case it is problematic to propose the complete absence of a species in a grid cell as visibility in deep waters is limited. As a result, absence data is widely unavailable for the deep-sea. A fundamental limitation of presence-only data is that sample selection bias has a far greater effect on presence-background models than on those fitted with both presence and absence data (Elith et al., 2011). A particular issue being that when species data sets containing sample selection bias are used, the resulting predictions may be more representative of the distribution of survey effort, than of the distribution of the species (Lobo and Tognelli, 2011; Phillips et al., 2009; Soberón and Nakamura, 2009). Sample selection bias (sometimes referred to as survey, or collector bias) is a statistical bias that results from the use of a non-random sample of the population for a statistical analysis. It is the product of a flaw in the sampling methodology, whereby a subset of the population is artificially excluded, or underrepresented, due to a particular attribute. This is likely to be an issue in the deep-sea, as biological sampling in deeper waters is a technically complex

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exercise, and the associated costs of operating vessels offshore, coupled with the costs of ROVs and submersibles also make it financially expensive. As a consequence of these limitations, the majority of the species presence data that are available have been collected from areas close to the coasts of developing nations, preferentially at shallower depths, and are clustered within areas of biological interest (Figure 1b; i.e. Davies et al., 2007).

In SDMs sample selection bias is typically characterised by a geographic or spatial bias in sampling. Correlative SDMs relate species samples to environmental data organised in geographical space. This information is used to derive a species response to environmental conditions, with this response approximating some description of the ecological niche of a species (Pulliam, 2000; Soberón and Peterson, 2005). The process of deriving the niche involves transposing this information from geographical space to environmental space, an n-dimensional hypervolume within which each environmental variable represents a dimension, and each combination of environmental variables is represented as a single point in space (Elith and Leathwick, 2009). Sample selection bias in the species presence data subsequently becomes an issue when the spatial bias present in a species data set exhibits a relationship with trends in the environmental data used to fit the model (Phillips et al., 2009). This is likely to be the case for the spatial biases present in deep-sea species data, with depth, distance from shore, and ocean basins all likely to exhibit an influence on the nature of the environmental conditions at a location. The properties of these spatial biases will subsequently translate from geographical space into environmental space, resulting in a biased perception of the species niche, and thus to inaccurate model outputs (Lobo and Tognelli, 2011). The implications of this may be particularly severe if a SDM's predictive output is converted to a binary format through the application of a threshold, as areas of habitat that fall within the species true distribution may be incorrectly predicted as being of low suitability, and thus excluded completely. Similarly if sample selection bias is severe and unknown (e.g. species for which little information are available), then samples may fail to cover the full range of environmental conditions in which a species exists. This will result in a model which fails to accurately describe the species niche, and consequently in an inaccurate prediction of the species potential distribution.

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In an attempt to adjust for the effects of sample selection bias on broad scale SDM predictions for deep-sea soft corals Yesson et al. (2012) incorporated the method of Phillips et al. (2009). Phillips et al. proposed that where this factor was relevant, the predictive accuracy of a SDM could be improved by incorporating the spatial bias of the species data into the background data used by the model to characterise the environmental conditions of the area being investigated. Application of this method, however, was observed to negatively affect model performance (as measured by the area under the receiver operating characteristic (AUC; Swets ,1988)), leading Yesson et al. to suggest that the supposed depth bias may in fact be associated with the species' true environmental preference. Despite this, it should be considered that this supposed drop in performance might in fact be an artifact of the way in which the AUC statistic is calculated. The AUC is a discrimination index that indicates the likelihood that a known presence location will have a higher predicted suitability value than a known absence location, where a value of 1 represents perfect discrimination by the model, and a value of 0.5 represents discrimination no better than random (see Model evaluation; Fielding and Bell, 1997). Its single value is calculated from the area under a curve, which is plotted based on the proportion of correctly predicted presences and absences across all possible thresholds. In the case of presence-background models, background data is used in the place of absence data when calculating the AUC score. Thus when adjusting this background data to match the supposed bias of the species presence data, and using this same dataset for validation, it seems likely that a drop in the AUC score would occur, as those points taken as 'absences' would exhibit conditions more similar to those where the species is known to be present. As a result, the perceived measure of specificity (Sp; absences correctly predicted as absences) used to calculate the AUC plot (x-axis = 1-Sp, i.e. commission error) would be lowered, as these background 'absence' points would be more likely to occur in areas of potential habitat assigned a high suitability value by the model. This would subsequently lead to a misleadingly low AUC score, as the information they contain is false. The inclusion of an unknown quantity of these 'false absences' when calculating the AUC score for models fitted with presence-only data violates AUC theory, and has consequently been shown to lower the maximum AUC value that can be attained. As such the value representative of a model with perfect discrimination no longer corresponds to 1 but to an unknown value < 1 (Jiminez-Valverdez, 2012). Consequently, this supposedly negative effect would occur irrespective of any detrimental effects to a models ability to accurately predict a species distribution. With this in

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mind further consideration is given to the application of this methodology in the following section.

Background data

To date the selection of background data has been given little attention in the deep-sea SDM literature. This may have had a negative impact on the accuracy of past predictions, particularly for those SDMs built with expansive data sets where the majority of environmental conditions fall well beyond the physiological tolerances of the species. The past standard approach used to compile background data when fitting SDMs with MaxEnt involved selecting sites at random from the unoccupied sites present in the environmental data. When using this technique, increasing the size of the area from which background samples are drawn has been shown to inflate both the AUC value (see *Spatial autocorrelation* section below) and the area of the predicted distribution (VanDerWal et al., 2009). Increasing the background area is likely to increase the range of environmental conditions considered by the model. When large areas of clearly unsuitable habitat are included in the background data as a result of this, it will have a detrimental effect on the models ability to detect the specific environmental characteristics of the species niche. Predictions subsequently tend away from the individual species distribution towards the distribution of broad habitat types. This occurs as the inclusion of an unnecessarily wide range of environmental values leads the model to create more generalised, less informative response variables; and consequently results in more generalised predictions (VanDerWal et al., 2009). As the response variable is inaccurate, errors of this nature are likely to propagate into unsampled areas resulting in misleading predictions. Because of this these effects are particularly undesirable in SDMs extrapolating into novel locations. A number of studies have observed significant changes in model behaviour as a result of altering the quantity and location of the background data used to fit SDMs (Barbet-Massin et al., 2012; Lobo and Tognelli, 2011; Phillips et al., 2009). With this in mind we describe below an appropriate technique for selecting the background data for deep-sea SDMs working with broad scale environmental data.

To account for both the spatial bias present in deep-sea species samples, and the loss of accuracy that results from the inclusion of large areas of unsuitable background, we propose a modification of the target group background methodology, as discussed by Phillips et al., (2009).

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Application of this technique has been shown to improve the accuracy of modelled predictions when using species data containing sample selection bias (Mateo et al., 2010; Phillips et al., 2009). The term 'target group' refers to a broader data set containing information on the distribution of samples for all species for which the sampling methodology is consistent, (i.e. they are collected or observed in the same way as the species being modelled). To facilitate the application of this technique, we suggest performing an *a priori* analysis of the spatial bias present in the species data of the appropriate target group. This analysis can provide a measure of the spatial bias in the distribution of survey effort, and the distribution of background samples can be weighted accordingly. Whilst Phillips et al. (2009) propose the direct use of these target group samples as background points, we feel that provided that an adequate number of background samples are used, conducting spatial analysis of the density of survey effort at a relatively coarse grain (e.g. $\geq 1°$) and then distributing the finer grained background samples according to the measured spatial bias should suffice. Doing so avoids incorporating the environmental bias that may be present due to the preferential sampling of emblematic species (e.g. cold-water corals), the properties of which would likely be analogous to the properties of the majority of benthic VMEs true distributions.

Presence-background models are particularly vulnerable to sample selection bias when compared to presence-absence models. This is because the spatial bias resulting from the practical limitations of sampling will not, by default, be present in the background data. The consequence of this is that presence-background models are prone to recognising the environmental characteristics introduced by sample selection bias, as a characteristic of species presence locations. By manipulating the background data to contain the same spatial bias as the presence data MaxEnt can produce models that better match the properties of those fitted with unbiased samples (Dudik et al., 2006). Thus by applying the above methodology, this can be achieved without the need for prior knowledge of how the properties of the sample distribution may differ from those of the species true distribution, and the accuracy of model predictions should be improved (Phillips et al., 2009). Despite this, consideration should still be given to whether species data covers the species full environmental range, and samples should be updated and assessed accordingly when new survey data and biological information become available.

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Spatial autocorrelation

The majority of statistical tests assume that observations within a sample are independent of one another. However, when considering data that is organised geographically this is rarely the case. Spatial autocorrelation (SA) describes the correlation of a variable with itself through space. It can be positive, where the value in one location is more likely to be similar at a certain distance, or negative, where they are more likely to be different (Cliff and Ord, 1973). SA has long been recognised as an inherent feature of biogeographic data, in both ecology and geography, things that are near tend to be similar (Legendre and Fortin, 1989). The exogenous factors influencing species distributions, such as climatic variables, vary along spatial gradients as a result of the physical processes that drive them. On the other hand endogenous factors, both intraspecific (e.g. dispersal) and interspecific (e.g. competition), act to generate spatial patterns in species distributions (Legendre, 1993; Sokal and Oden, 1978). Despite an awareness of the presence of SA in the data used to fit SDMs, a recent meta-analysis found the majority (> 80%) of published SDM studies did not implement methods to account for its effects (Dormann, 2007a), and to date no studies conducted for the deep-sea have explicitly addressed the effects of SA on model predictions. SA may have significant implications for SDMs when species-environment relationships are examined in a non-spatial context. Clustered samples existing within the influence of SA can no longer be considered as independent, and the information contributed by each is effectively reduced. When this is not accounted for the explanatory power of spatially autocorrelated variables may be distorted, leading to the misinterpretation of causal factors (Lennon, 2000) and bias predictions (Dormann, 2007b; Segurado et al., 2006). An awareness of the SA in the environmental data and its potential influence on model behaviour is subsequently important when producing SDMs (Dormann et al., 2007).

It is now widely recognised that the residual SA present in models may inflate the values of the statistics that are commonly used to measure model performance (Araújo et al., 2005; Hijmans, 2012; Segurado et al., 2006; Veloz, 2009). This issue may be particularly relevant in the case of deep-sea modelling studies. To date species presence samples used to construct global models have been collated from opportunistic sources (i.e. Davies and Guinotte, 2011; Yesson et al., 2012). The targeted nature of deep-sea sampling means that these records are often heavily clustered within areas of ecological interest. This, in combination with the SA present in the

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environmental data has a number of significant implications for model validation procedures. When independent species data are unavailable, as is the case for the majority of presence-only studies, validation instead relies on the random partitioning of the original dataset into two independent sets, 'test' for validation and 'training' for model construction (e.g. cross-validation). However, when under the influence of SA, the presence samples of these two groups are not independent from one another. As such there can be significant inflation of the models supposed performance, and the interpretation of model accuracy may be overly optimistic (Veloz, 2009). SA may also influence the variable selection stage of modelling, as spatially autocorrelated variables may appear to be more important, and are thus more likely to be selected for use in the final model (Diniz-Filho et al., 2003; Lennon, 2000; Segurado et al., 2006). Although, more recent studies have found that this may not be applicable to SDMs fit with real environmental data (Hawkins et al., 2007).

Hijmans (2012) explored the use of a spatial null model, where geographic distance to training sites is the only variable considered, to reduce the influence of spatial autocorrelation on model validation statistics, and allow for better cross comparison between models with varying degrees of SA. It is generally expected that training presence sites will be located closer to testing presence sites than they are to testing absence sites. As a consequence of this the environmental conditions between presence sites are likely to be more similar, and a higher AUC value is expected as a result (Elith et al., 2006; Lobo et al., 2007). In order to adjust for this effect, a geographic distance model can be used to evaluate the extent to which the predictive power of a model can be explained by the spatial distribution of presences compared to absences. The AUC value achieved by this null model can then be used to calibrate the AUC of the non-spatial model accordingly. The application of 'pairwise distance sampling' was also found to be effective in removing the influence of spatial sorting bias, yielding AUC values similar to those of the calibrated AUC. This technique filters those sites used for validation, pairing testing-presence sites with those testing-absence sites which are at a similar distance to their nearest training-presence site. These methods offer some improvements over previous cross-validation approaches. However, consideration needs to be given to the fact that a spatial null model may unfairly discriminate against models beyond a certain distance threshold. VanDerWal (2009) noted the trend of increase in the AUC values of models observed when increasing the size of the

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background area was replaced by a slight trend of decline beyond 200 km^2, and this decline would not occur in the spatial null model. Considerable adjustments will likely need to be made before these methods can be effectively applied to broad scale models working with large areas of unsurveyed environment.

Alongside the aforementioned effects on model validation, the inclusion of sub-regions containing clustered samples in SDMs has been observed to introduce bias into model predictions, towards those areas with similar conditions. This implies that spatial autocorrelation within the sampling data may also have significant impacts on a models predictive outputs (Veloz, 2009). The lack of independence between data points distributed amongst spatially autocorrelated variables leads to a falsely inflated perception of sample size (pseudo-replication). This in turn inflates the degrees of freedom with which statistical tests are performed, artificially reducing standard error and consequently inflating the statistical significance of measured relationships. This is likely to influence a models predictive accuracy, and has been shown to reduce the precision of coefficients, introducing bias into the models estimation of the species response (Dormann, 2007b). In practice this has been shown to increase the likelihood of commission errors (false positives) in multiple regressive models using artificial data (Segurado et al., 2006). A simple solution to this issue is to remove the spatial structures present in the sample data *a priori* (Hawkins et al., 2007). This can be achieved by applying some degree of spatial filtering, removing those samples which fall within a predetermined distance of each other. However, in data poor situations this can be less practical than it first appears. Spatial autocorrelation tends to exert an influence over considerable distances for climatic variables, and correcting for its presence may involve discarding a substantial amount of an already sparse data set. With this in mind, future consideration should be given to the diverse array of methods emerging in the SDM literature for observing and adjusting for the effects of spatial autocorrelation, and their suitability for application to deep-sea SDMs should be assessed (Dormann et al., 2007; Franklin and Miller, 2009; Miller et al., 2007).

Issues of scale

Correlative SDMs detect patterns between the distribution of species, and spatial or environmental variables. These relationships can then be expressed as a response surface.

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Examining relationships at inappropriate scales may alter the perception of the patterns and gradients present in both the species and environmental data (Huston, 2002; Levin, 1992; Wiens, 1989), altering the models interpretation of a species response (McInerny and Purves, 2011; Menke et al., 2009). It is these responses that predictive SDMs use to inform their predictions. Modelling at an inappropriate scale will subsequently be detrimental to a model's predictive performance. In ecology the term scale refers to both the extent of the region of study, and the grain size (resolution) at which it is examined.

Grain size refers to the size of a single sampling unit, and as such represents the minimum spatial unit between which changes in environmental conditions are perceptible. The size of this unit also influences the value of variables within that unit. Specifically, heterogeneity occurring at a finer scale than that of the sampling unit is lost and represented by a single more generalised value (i.e. Rengstorf et al., In press). This loss of information is particularly problematic when the grain of the sample unit exceeds the grain at which ecologically relevant variation in environmental predictors occurs (Huston, 2002). For example, early attempts to model the distribution of the cold-water coral species *Lophelia pertusa*, built with coarse environmental data (1 °, ~110 km^2) were found to be unable to resolve fine-scale variations in temperature. This was observed primarily in areas where depth specific differences between adjacent water masses were undetectable, as significant changes in depth occurred at a finer scale than that of the bathymetric data used to extract the temperature data. As a result of this, inconsistencies were observed between those temperature values extracted from the environmental grid and the known thermal tolerance of the species (Davies et al., 2008). Consequently the model was limited in its ability to accurately predict the distribution of the species, as environmental grids were not representative of the true state of environmental conditions.

Coarse environmental data introduces error into predictor variables by precluding the fine-scale heterogeneity that may be present within a cell. By doing so, coarse data introduces a degree of uncertainty into predictors, resulting from the spatial inaccuracy that is inevitable when assigning large areas a single covariate value. This uncertainty is subsequently transferred to the models construction of the species response, which becomes squashed; where a species predicted response to a variable becomes flatter and broader than the true functional response (i.e. more

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general; Frost and Thompson, 2000; Menke et al., 2009), although it has also been observed to become sharper where the opposite occurs (i.e. more specific; Randin et al., 2009). Where this occurs models may still accurately predict species occurrence at that resolution, as the same uncertainty exists in both the environmental data and the response variable (McInerny and Purves, 2011). The large amount of spatial autocorrelation in climatic data, for example, negates much of the effects of coarse data. However, this effect is still undesirable, as uncertainty in the relationship between the environmental data and the species response is likely to introduce an unknown level of commission and/or omission errors into a model's predictive outputs.

In practise this uncertainty in the response variable is likely to lead to commission errors, as generalised variables widen the perception of the species niche, leading to wider predictions of suitability (Menke et al., 2009). Whilst increasing the grain size of environmental layers may increase the area of unsuitable habitat deemed suitable in a model's predictive outputs, as fine-scale habitat features that actually regulate species occurrence are generalised. Seo et al. (2009) investigated the effects of cell resolution on SDMs for a selection of Californian tree species, grouped according to range size (broad, intermediate and narrow). Working at resolutions ranging from 1 to 64 km^2 they observed an approximately three-fold increase in predicted area at the coarsest resolution when compared to the finest, although results varied in magnitude dependent on the species range size. They also noted a marked divergence in models geographic allocations of predictions when grid resolution surpassed 16 km^2 for intermediately and narrowly distributed species, suggesting that the loss of important fine-scale environmental variation may have significantly altered the models interpretation of the species response.

The lack of accurate fine-scale bathymetric data is perhaps the largest limitation of broad scale deep-sea SDMs. Benthic terrain attributes serve as an effective proxy for current conditions and substrata, which are important determinants of sessile benthic species distributions. However, the existing bathymetric datasets available at suitable extents for broad-scale modelling are unable to resolve the fine-scale variations in depth necessary to accurately inform these variables (Rengstorf et al., In press). This may have significant implications for model predictions. For example the use of coarse-grained bathymetric data (4 km^2) was suggested to introduce significant omission errors into broad-scale SDMs constructed for deep-water gorgonian corals,

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as the inability to distinguish ecologically important terrain features led to an inaccurate representation of the species habitat in the environmental data, and subsequently to inaccurate predictions of the species distributions (Etnoyer and Morgan, 2007). Global bathymetric data sets are constructed using quality controlled data acquired from ships soundings, multi- and singlebeam echosounder surveys, and supplemented by modelled data based on information derived from satellite altimetry. Thus in areas where data are lacking, the reliability of these measures varies considerably. Whilst broad scale models constructed with bioclimatic variables are able to make robust predictions of a species potential distribution, they are likely to contain significant commission errors in areas where the presence of suitable habitat is uncertain due to the lack of data at an appropriate resolution to derive terrain attributes (Rengstorf et al., In press). The predictions from these models should thus be used to guide survey effort so that bathymetric data at a scale which is suitable for the derivation of terrain attributes (e.g. < 250 m^2) can be collected in areas that are predicted as climatically suitable habitat.

In practice, choices relating to the spatial scale of predictors are often predetermined by technical considerations of the data that are available and the limitations of available computational power (although recent progress in both of these areas is significant). Furthermore attempts to interpret apparent functional responses can be confounded by the limitations of environmental data, particularly in cases where only distal variables are available, or where multiple, often unidentified factors interact to determine a species range (Elith and Leathwick, 2009). With this in mind it is important that consideration is given to the whether the grain of the data is sufficient to capture variation at the scale at which it exhibits an influence on species occurrence, and thus whether it is suitable for inclusion in the model. A missing predictor may be less detrimental to a models prediction than a distorted predictor containing false information. This is especially relevant in the case of benthic terrain attributes, which have been shown to contain inaccurate information resulting from artifacts of the scale of analysis when derived from coarse bathymetric data (Rengstorf et al., In press).

Model evaluation

SDM evaluation involves the application of one or more statistical methods to calculate some measure indicative of a model's predictive performance. This is typically achieved by evaluating

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the model's ability to correctly predict the presence and absence of the species using an independently collected 'testing' data set, or where independent data are unavailable, a quasi-independent data set created by dividing the available data into two or more partitions (cross-validation). The testing data can then be used to calculate the proportion of correctly predicted presences (sensitivity; Se) and absences (specificity; Sp), and by deduction the proportion of falsely predicted presences (commission error, 1-Sp) and absences (omission error, 1-Se). These values can be arranged to form a 2 by 2 confusion matrix, the information derived from this matrix is then utilised in a range of ways to inform the value of a number of statistical measures (Fielding and Bell, 1997).

Past studies of deep-sea species have made use of Kappa, a popular metric for measuring categorical agreement (e.g. Howell et al. 2011; Woodby et al. 2008). Kappa measures the difference between the agreement of the observed result, and a chance result with determined class proportions (Fielding and Bell, 1997). Its use, however, is complicated by the need to select a threshold for converting the continuous predictions produced by SDMs into a simplified binary format. Recognition of this and the issues it may introduce mean that more recent SDM evaluation has tended towards the use of threshold independent metrics. Past studies have used Spearmans correlation coefficient to validate model performance (e.g. Bryan and Metaxas, 2007). More recently the AUC has emerged as the favoured measure, as its results are easy to interpret, and valid for the cross comparison of models built with different data. The AUC produces a single value measure of model performance. This is calculated from the area under the curve of the receiver operating characteristic plot, that graphs sensitivity against commission error, calculated across all possible thresholds (0 to 1; Fielding and Bell, 1997, Swets, 1988).

The AUC was originally adopted for use with presence-absence modelling methods, and as such it is calculated using information on both the presence and absence of the species (Fielding and Bell, 1997). The use of the AUC with presence-only data is subsequently complicated by the substitution of absence data for uncertain background data (Lobo et al., 2007). When using this metric with presence-only data interpretation of the resultant value is problematic, as these background sites contain no information on species occurrence (Jiminez-Valverdez, 2012). When randomly distributed, these background points instead represent the entirety of the

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environmental data. As such when the proportion of correctly predicted presences is plotted against the proportion of background sites predicted as presence, the resultant value is in part indicative of the models ability to discriminate the species niche from the background environment. A likely artifact of this is that a wider species niche leads to a reduction in the AUC value, as a higher proportion of the background sites will fall into those areas predicted as suitable by the model. With this in mind care should be taken when using the AUC statistic with presence-only data sets. When doing so the underlying theory of the AUC is violated (Jiminez-Valverdez 2012), with the single value instead providing a somewhat jumbled measure combining information on the predicted prevalence of the species relative to the sampled background, and the proportion of correctly predicted presence sites. As previously discussed an implication of this is that enlarging the background area is likely to inflate the AUC value, as the spatial autocorrelation common in biogeographic data means that distance tends to equate to environmental dissimilarity (VanDerWal, 2009). The supposed ability of the model to discriminate sites where the species is present from the background subsequently improves, and the prevalence of the species is reduced in comparison to the total area, thus a higher AUC value is achieved.

There are currently major limitations when using the AUC as a judge of presence-background model performance, and these issues are further complicated when comparing performance across SDMs built with different data. Where reliable absence data are unavailable for validation, future attempts to model the distributions of deep-sea species may benefit by considering the range of presence-only evaluation methods that are emerging in the SDM literature (i.e. Boyce et al., 2002; Hirzel et al., 2006). Such methods may aid cross model comparisons, allowing for a more reasoned evaluation of new approaches and techniques. The AUC is still a useful metric, and future studies should consider using proposed methods for applying this metric to presence-only data (Peterson et al., 2008). Further its use in future studies would benefit greatly from the inclusion of the ROC plot within manuscripts. As this conveys information on the relative occurrence of errors (commission and omission), and as such is of value to those interpreting models for different end use scenarios (Jiminez-Valverdez, 2012).

Validation

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Where deep-sea SDMs are predicting into areas where no biological survey data exist, novel methods of assessing predictions may need to be developed. In this situation maximising the use of available data will aid model validation. Fisheries bycatch data for example, whilst unsuitable for model training due to the positional uncertainty of samples acquired from trawls, may serve to evaluate the reliability of broad-scale bioclimatic models in areas where it is available, by confirming the presence of a species in an otherwise unsampled location. Whilst reasoned partitioning of the available presence information would allow users to validate the ability of models to make predictions into unsampled areas, and provide useful information on regional discrepancies in predictions. Alongside these, future biological survey data will serve to formally evaluate the reliability of predictive SDMs as and when it becomes available. Future studies should also make use of the alternative SDM validation measures, such as measures of presence-only calibration (Phillips and Elith, 2010), and mapped outputs of uncertainty (e.g. Ibáñez et al., 2009). These will provide valuable information to end users when outputs are utilised to inform conservation and management decision making (Beale & Lennon 2012).

Application of SDMs for VME identification and conservation

The recent improvements in the resolution of SDM results at global and regional scales has led to an increasing awareness of their utility for resource managers and conservation groups interested in identifying areas that may harbour vulnerable marine ecosystems, particularly in data poor areas. The CBD (COP10; Conference of the Parties to the Convention on Biological Diversity, 2011) recently initiated a series of regional workshops to facilitate the description of ecologically or biologically significant marine areas (EBSAs). Five of these regional workshops took place in 2011-2012 (e.g. Eastern Temperate and Tropical Pacific, Southern Indian Ocean) and SDM results for predicted cold-water coral habitat (Davies and Guinotte, 2011; Yesson et al., 2012) were incorporated as inputs in this process. Seven additional regional workshops are planned under the CBD and SDM results for cold-water coral habitats will continue to play a role in the CBDs efforts to identify EBSAs in data poor regions. There has also been interest from the FAO and International Seabed Authority in using SDM results to identify VMEs and the overlap of predicted habitats with current and pending mineral leases in the Indian Ocean (J. Ardron, pers. comm.). In addition to these efforts, SDM results for cold water coral habitat were used in a joint

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GOBI-CenSeam workshop to develop a provisional process for selecting High Seas seamounts that meet EBSA criteria and submitting the results via the CBD process (Dunstan et al 2011).

SDM results are also being utilised within countries EEZs to help identify potential habitat for resource managers in regions that are heavily sampled or data poor. The United States' Fishery Management Councils are responsible for identifying and minimising human impacts via fishing gear restrictions on Essential Fish Habitat (EFH) and Habitat Areas of Particular Concern (HAPC) within the U.S. EEZ. The regional councils review their EFH/HAPC through committees every five years to ensure the latest science is incorporated into their protection plans. The scientific data informing the reviews typically are derived from trawl surveys, research cruises using ROV and submersibles, and other field techniques. For the first time, regional SDM results for cold-water coral habitat have been incorporated into the Pacific Fishery Management Council's 2012-2013 EFH/HAPC review for the waters of California, Oregon and Washington (Guinotte and Davies, 2012). In 2012, SDM results for cold-water coral habitat were also provided to the South Atlantic Fishery Management Council to support discussions of management and conservation measures (Kinlan et al., 2012). These results and others from different regions can play an increasingly important role in future EFH/HAPC reviews including the Gulf of Mexico, north-eastern U.S., and Alaska as models are developed, improved, and validated.

To date the use of SDM results for marine resource managers and conservation groups has largely been limited to cold-water coral taxa. This is due in part to the high vulnerability of these habitats to bottom trawling, the enigmatic status of the species forming cold-water coral habitats, and the availability of known coral locations for presence-only model development. However, efforts are underway within the New Zealand EEZ and South Pacific Regional Fishery Management Organization's competence area to model the potential distribution of a variety of taxa identified as vulnerable to bottom trawl fishing in the South Pacific by Parker et al. (2009). Biological data in the SPRFMO Competence Area is limited making SDM results one of the only non-damaging means for identifying where these habitats are located across large spatial scales. Field validation efforts to identify false positives, false negatives, and determine overall model accuracy for applied resource management, conservation, and MPA planning are a high

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priority. In many cases these validation efforts could be conducted as part of existing field sampling and research efforts currently funded by government agencies, NGOs, and private organisations.

In a few cases known to the authors, SDMs have played an active role in directing sampling effort to certain regions. For example, recent SDMs produced by the National Oceanographic and Atmospheric Administration have been used to identify areas of cold-water coral occurrence in the NE US and Alaska's Aleutian Islands. Both of these modelling efforts were followed by research cruises to these areas. Confirmation of the existence of cold-water corals in previously unexplored areas was obtained on the NE US cruise, validation results are pending for the Aleutian cruise. (Kinlan et al., in preparation; Chris Rooper, pers comm). SDMs have also been used to enhance sampling in areas that have been marked for survey. For example, recent analyses of historical sightings of cold-water corals in Mid-Atlantic Canyons were used to create a high-resolution exploratory model that guided subsequent research activity towards specific parts of the canyon (Ross and Brooke, 2012), increasing the chance of locating areas containing target species. In our opinion, SDMs have intrinsic value as part of a workflow for research cruises investigating VMEs as they can be used to broadly identify areas that have not yet been surveyed or can be used to enhance sampling programs in areas where limited data has already been collected.

Final comments

Species distribution models produce predictions based upon statistical analysis of the available information. In data poor areas such as the deep-sea, these predictions are subsequently inherently uncertain, as they are based on imperfect information derived from data samples that are limited by the practicalities of collection. Much of the information used to inform deep-sea SDMs at broad scales is itself modelled to some extent (i.e. Becker et al., 2009; Steinacher et al., 2009) before being adjusted again (i.e. Davies et al., 2008; Davies and Guinotte, 2011). As such, deep-sea SDMs conducted at these scales are based on data sets that contain imperfect measurement. Furthermore, spatial autocorrelation and sample selection bias have the potential to introduce bias into SDM predictions, which will be detrimental to the reliability and accuracy of the resulting predictive maps. It is hoped that this review has illustrated that many of these

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issues can be overcome in part by careful consideration of the data and its limitations and, when appropriate, through the implementation of novel methodologies.

The reliability and quality of the data used to build deep-sea SDMs will continue to improve alongside advances in the fields of remote sensing and oceanography. These advances will in turn lead to improvements in the ability SDMs to make more accurate predictions. At present, the availability of bathymetric data at a resolution sufficient to inform reliable terrain attribute predictors is a major limitation to the ability of deep-sea SDMs to make accurate predictions of the distributions of benthic organisms. However, recognition of this fact and the wider benefits of collecting bathymetric data, alongside an increasing interest in deep-sea ecosystems, mean that such data is progressively expanding in its coverage. Where uncertainties exist in predictions, broad-scale models based on bioclimatic predictors may serve to guide survey effort so that MBES data can be collected in those regions identified as likely to contain high quality habitat.

The fact that the deep-sea is a data poor area both drives and limits the application of SDMs. There is a clear necessity to gain a wider understanding of the distribution of species, ecosystems and biodiversity in the deep-sea (Clark et al., 2012; Weaver et al., 2011). Whilst the aforementioned limitations persist it is important that the outputs of deep-sea SDMs are used carefully, and evaluated based on existing ecological knowledge, expert opinion and according to the results of the variety of methods that exist for assessing model performance (Franklin and Miller, 2009; Hirzel et al., 2006; Phillips and Elith, 2010). Whilst SDM practitioners should strive to acknowledge the sources of uncertainty in the modelling process and, where possible, quantify such uncertainty so that it may be considered accordingly by the end users. Whilst the data situation is improving, progress on this front would accelerate were the large amounts of information held by private parties, such as the bathymetric data collected by commercial fishing vessels, made available to practitioners. There is as such an on-going need to sufficiently address the privacy concerns of these parties, which are currently hindering its provision. To summarise we make the following recommendations for future applications of SDMs to deep-sea species.

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- Deep-sea species data sets are likely to be biased by the limitations of collection, and presence-only model types are particularly sensitive to this. Future models would therefore benefit from implementation of the methods available for working with biased species data.
- Spatial autocorrelation is an inherent trait of biogeographic data and may influence predictive outputs, implementing methods for dealing with the effects of spatial autocorrelation will allow for the production of better calibrated measures of habitat suitability.
- The popular metrics for measuring SDM's predictive performance should be used cautiously when absence data are unavailable, as the results may be misleading. In recognition of this further consideration should be given to the range of presence-only metrics that are available.
- Uncertainty and errors are an inevitable component of SDM predictions. Further, the costs of errors in SDMs are relative to the intended purpose of the end user. It is thus important that future studies strive to quantify and qualify the uncertainty in outputs, so that end users may better interpret them according to their needs.

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Tables and Figures

Figure 1. Distribution of species records from the Ocean Biogeographic Information System throughout the world's oceans grouped within 2-degree cells. a) The total number of records for primarily benthic marine species (see ESM1a for list of taxonomic groups). b) The number of contributing datasets for those records that fall within each 2-degree cell (see ESM1b for data sources used in this figure).

Figure 2. Examples of SDMs developed for cold-water corals in the North East Atlantic at varying resolutions. a) Global scale prediction for *Lophelia pertusa* at 1° cell resolution made using ENFA (Davies et al., 2008, reproduced with permission from Elsevier). b) Regional prediction for *Lophelia pertusa* at 0.25° cell resolution made using ENFA (Davies et al., 2008, reproduced with permission from Elsevier). c) Global prediction for *Lophelia pertusa* at 1 km cell resolution, made using MaxEnt (Davies and Guinotte, 2011). d) Regional prediction for *L. pertusa* and *Madrepora oculata* at 500 m cell resolution, made using MaxEnt (Davies, unpublished). The colour ramp shows increasing habitat suitability values, from blue (unsuitable) to red (highly suitable).

Table 1. Summary of peer-reviewed deep-sea studies utilising species distribution models, / indicates data not provided in the source publication.

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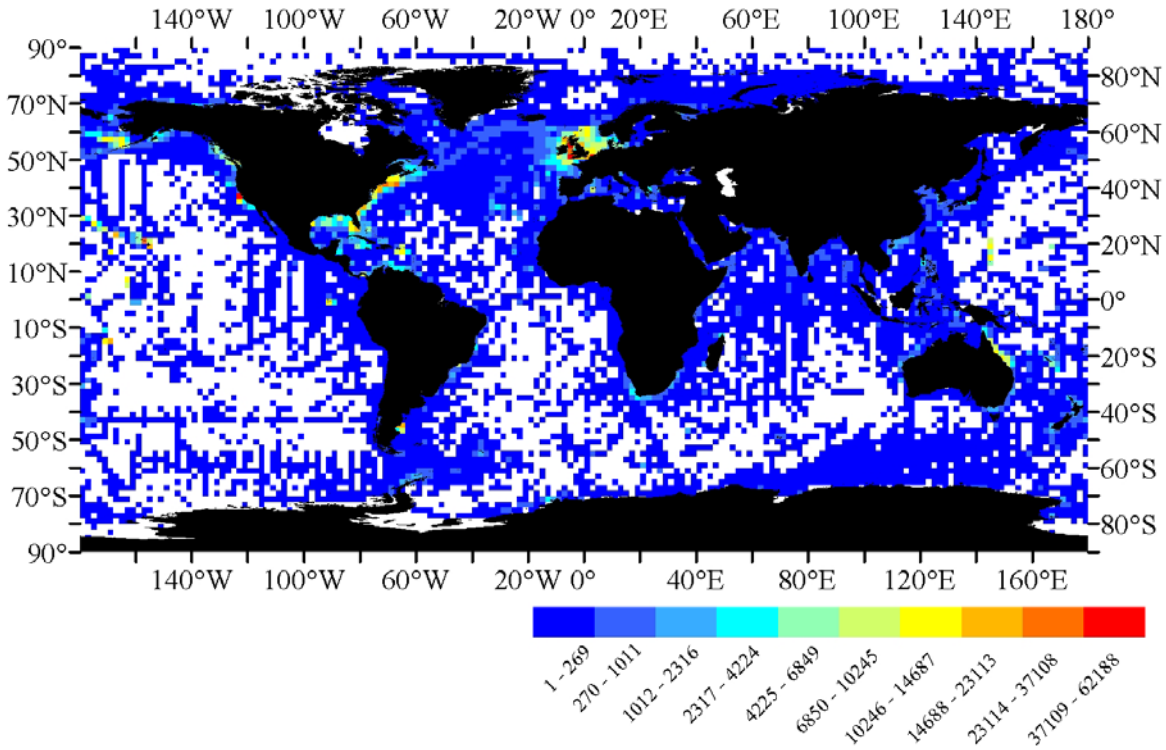
Figure 1

a)


140°W 100°W 60°W 20°W 0° 20°E 60°E 100°E 140°E 180°
90° 70°N 50°N 30°N 10°N 10°S 30°S 50°S 70°S 90°
80°N 60°N 40°N 20°N 0° 20°S 40°S 60°S 80°S
140°W 100°W 60°W 20°W 0° 40°E 80°E 120°E 160°E
1 - 269
270 - 1011
1012 - 2316
2317 - 4224
4225 - 6849
6850 - 10245
10246 - 14687
14688 - 23113
23114 - 37108
37109 - 62188

b)

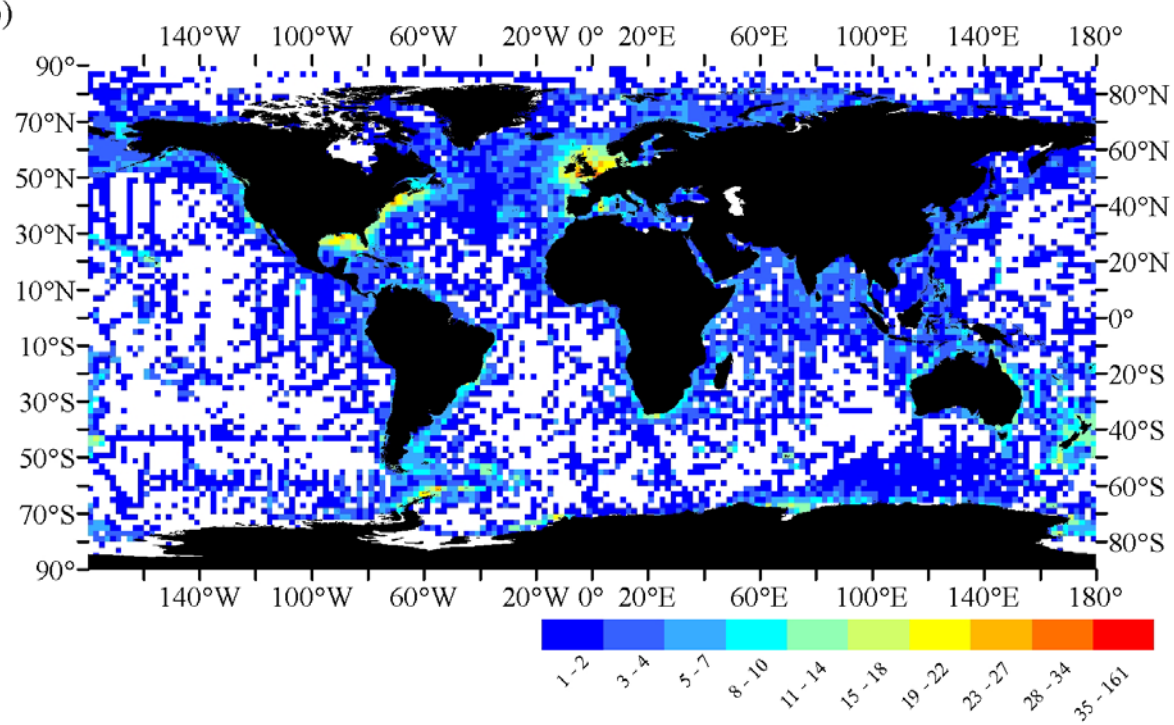

140°W 100°W 60°W 20°W 0° 20°E 60°E 100°E 140°E 180°
90° 70°N 50°N 30°N 10°N 10°S 30°S 50°S 70°S 90°
80°N 60°N 40°N 20°N 0° 20°S 40°S 60°S 80°S
140°W 100°W 60°W 20°W 0° 20°E 60°E 100°E 140°E 180°
1 - 2
3 - 4
5 - 7
8 - 10
11 - 14
15 - 18
19 - 22
23 - 27
28 - 34
35 - 161

Figure 2.

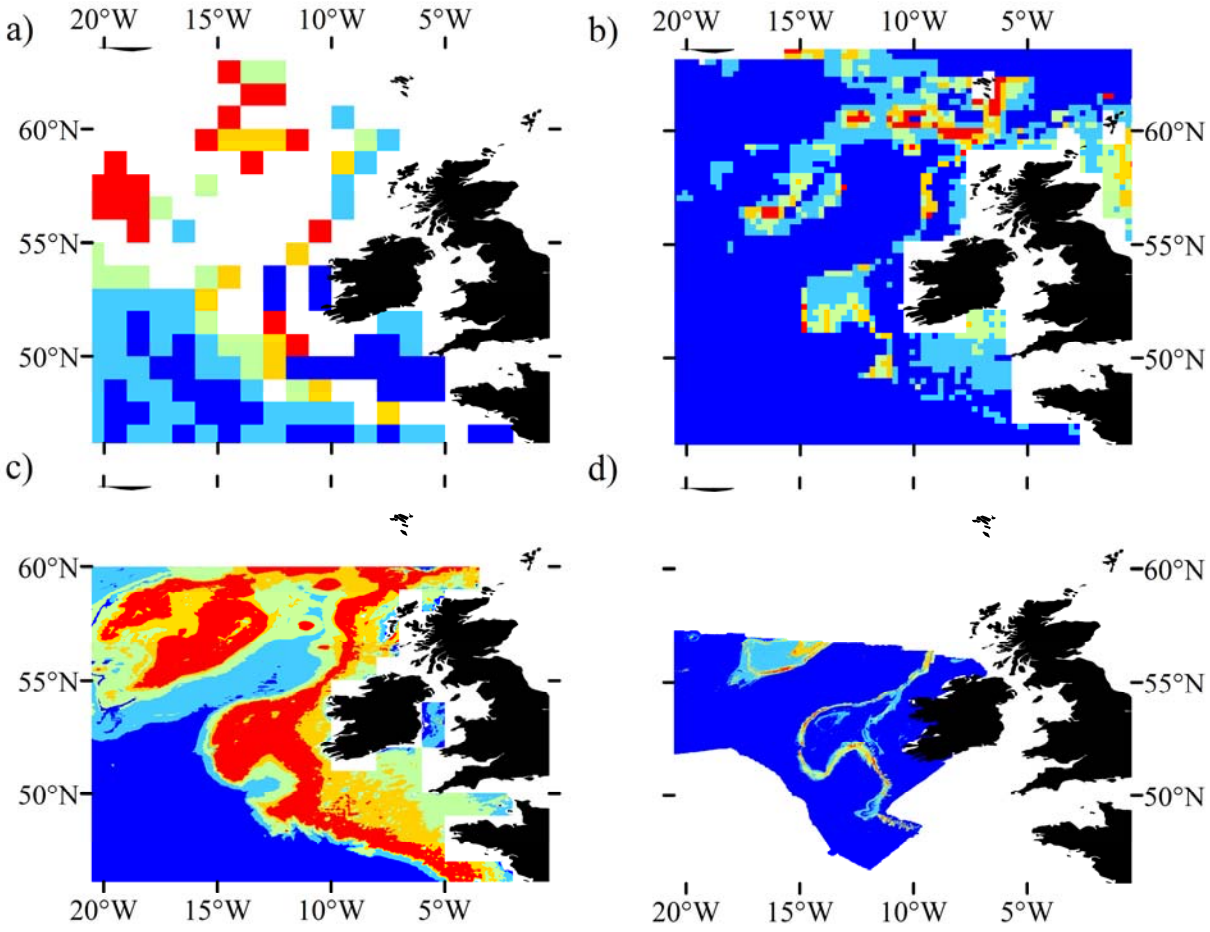


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Table 1

Author(s)	Year	Type	Model	Species	Resolution	Extent
Leverette and Metaxas	2005	Presence	ENFA	*Paragorgia arborea; Primnoa resedaeformis*	9 km^2	800 x 200 km
Clark et al.	2006	Presence	ENFA	Scleractinia	~110 km^2	Global
Bryan & Metaxas	2007	Presence	ENFA	Paragorgiidae, Primoidae	1 km^2; 5 km^2; 9 km^2	900 x 1900 km; 1000 x 1400 km; 300 x 800 km
Davies et al.	2008	Presence	ENFA	*Lophelia pertusa*	~110 km^2; ~27 km^2	Global, regional
Tittensor et al.	2009	Presence	MAXENT; ENFA	Scleractinia	~110 km^2	Global
Tittensor et al.	2010	Presence	MAXENT	*Lophelia pertusa*	~110 km^2	Global
Davies & Guinotte	2011	Presence	MAXENT	Reef-forming scleractinia: *Enallopsammia rostrata, Goniocorella domosa, Lophelia pertusa, Madrepora oculata, Solenosmillia variabilis* .	~1 km^2	Global
Yesson et al.	2012	Presence	MAXENT	Octocorallia: Alcyoniina, Calcaxonia, Holaxonia, Scleraxonia, Sessiliflorae, Stolonifera, Subselliflorae	~1 km^2	Global
Wilson et al.	2007	Presence	ENFA	*Munida* sp.	15 m^2	/
Dolan et al.	2008	Presence	ENFA	*Lophelia pertusa*, *Madrepora oculata*	0.5 m^2	/
Woodby et al.	2008	Presence-absence	Logistic regression, GEE	Composite: Gorgonia, Scleractinia, Stylasteridae,	/	/

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				Isididae		
Guinan et al.	2009	Presence	GARP	*Lophelia pertusa*	30 m^2; 550m^2	/
Howell et al.	2011	Presence	MAXENT	*Lophelia pertusa* (Single; Reef)	200 m^2	~275 x ~350 km
Tong et al.	2012	Presence	ENFA	*Paragorgia arborea; Primnoa resedaeformis*	10 m^2	/
Rengstorf et al.	In press	Presence	MAXENT	*Lophelia pertusa* from Guinan et al. (2009)	50 m^2 to 1 km^2	Regional

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