Title

Cetacean range and climate in the eastern North Atlantic: future predictions and implications for conservation.

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Abstract

There is increasing evidence that the global distributions of a large number of species are shifting with global climate change as they track changing surface temperatures that define their thermal niche. Modelling efforts to predict species distributions under future climates have increased with concern about the overall impact of these distribution shifts on species ecology, and especially where barriers to dispersal exist. Here we apply a bio-climatic envelope modelling technique to investigate the impacts of climate change on the geographic range of ten cetacean species in the eastern North Atlantic and to assess how such modelling can be used to inform conservation and management. The modelling process integrates elements of a species' habitat and thermal niche, and employs "hindcasting" of historical distribution changes in order to verify the accuracy of the modelled relationship between temperature and species range. If this ability is not verified, there is a risk that inappropriate or inaccurate models will be used to make future predictions of species distributions. Of the ten species investigated, we found that while the models for nine could successfully explain current spatial distribution, only four had a good ability to predict distribution changes over time in response to changes in water temperature. Applied to future climate scenarios, the four species-specific models with good predictive abilities indicated range expansion in one species and range contraction in three others, including the potential loss of up to 80% of suitable white-beaked dolphin habitat. Model predictions allow identification of affected areas and the likely time-scales over which impacts will occur. Thus, this work provides important information on both our ability to predict how individual species will respond to future climate change and the applicability of predictive distribution models as a tool to help construct viable conservation and management strategies.

Introduction

The potential impact of climate change on the geographic range of cetacean species has important implications for the conservation and management of cetaceans (Simmonds & Isaac 2007; IWC 2009; MacLeod 2009; Lambert *et al.* 2011). Climate is an important contributor to the position of species range boundaries and, as such, the global distribution of a species is often determined by the spatio-temporal distribution of climatic variables that define this 'thermal niche' (Hutchinson 1957, Kearney 2006). There is an increasing consensus and evidence that future increases in water temperature associated with climate change are likely to affect the distribution of many cetacean species to a greater or lesser extent as they track changing surface temperatures that define their thermal niche (e.g. Learmonth *et al.* 2006; MacLeod 2009; Salvadeo *et al.* 2010; Kaschner *et al.* 2011).

Such geographic range shifts are expected to have significant ecological consequences, impacting on species abundance, prey availability, competition, migration and extinction (Thomas 2010), and, in relation to cetaceans, there is considerable concern for those species which are limited in their ability to track temperature changes due to land barriers or habitat preferences, such as the white-beaked dolphin (MacLeod 2009). However, to date there has been little work in relation to cetacean species which allows reliable predictions of future distributions under different climate scenarios, despite the fact that such predictions are important when trying to create conservation and management strategies which will remain applicable in the face of climate change.

For a growing number of taxa, bio-climatic envelope models (also known as ecological niche models or species distribution models) are being used to predict likely range shifts under

3

different climate change scenarios in order to consider potential ecological impacts (e.g. Levinsky *et al.* 2007; Jarnevich & Stohlgren 2009; Rebelo *et al.* 2010; Velásquez-Tibatá *et al.* 2012). This type of modelling can provide an important tool in the development of species management plans (e.g. Dockerty *et al.* 2003; Pyke *et al.* 2005; Morueta-Holme *et al.* 2010; Faleiro *et al.* 2013) however, its application relies on being able to accurately identify the relationships between species distribution and the spatial distribution of key environmental variables. While these relationships can be easily proposed based on ecological theory or empirical analyses of present-day data, assessing whether they are sufficiently persistent, precise and accurate to allow reliable predictions of changes in distribution over time, can prove problematic.

In the present study, we aim to expand our understanding of how cetacean species ranges are related to water temperature and use this information to predict how climate change is likely to affect species occurrence, and the implications for future management strategies. Specifically, we apply a bio-climatic-modelling framework published by Lambert *et al.* (2011) to ten species of cetacean in the eastern North Atlantic. This framework was chosen as it incorporates a direct assessment of a model's ability to predict changes in distribution over time in relation to changes in climate through hindcasting of historical distribution changes. The method also controls for potential effects of habitat niche components on spatial distribution, meaning that any barriers to temperature tracking may be identified within future projections. Using common dolphin data from the eastern North Atlantic, Lambert *et al.* (2011) showed that a bio-climatic envelope model created using data collected since the late 1970s could be used to accurately describe current spatial distribution and predict range boundary changes in relation to changes in water temperature over a substantially longer historic time period.

4

In applying this framework to a further ten species of cetacean we also aim to provide important information on both our ability to predict how individual cetacean species will respond to future climate change and on the applicability of SDMs as a tool to help construct viable conservation and management strategies for cetaceans and other taxa.

Materials and Methods

Cetacean sightings and environmental data

Summer sightings data (recorded between June and September) were obtained from long-term boat-based sightings datasets collected by JNCC (Joint Nature Conservation Committee), IWDG (Irish Whale and Dolphin Group) and Marinelife between 1974 and 2007 (Table S1). The use of these three datasets provided a comprehensive sightings database (N=15,800) obtained from a combination of dedicated and opportunistic boat-based marine mammal surveys.

To generate models of thermal preference, gridded monthly sea surface temperature data (SST) from 1980 to 2007 were obtained from the HadiSST dataset at a 1° resolution. SST data were extracted for all sightings based on the location, the month and the year in which the sighting was recorded. For the habitat niche component, 2.5 x 2.5 km grids of water depth, seabed slope and standard deviation of seabed slope were generated using ESRI ArcMap 9.2, from a combination of ETOP02 and DigiBath 250 water depth datasets. These variables were selected because they are known to be most important for determining topographic habitat preferences of cetaceans in this region (e.g. Kiszka et al. 2007, MacLeod et al. 2007), and were used to model the habitat preferences of all species. However, for

5

bottlenose dolphin, an additional variable, 'distance to coast', was also included to account for the fact that, unlike the other species included in this analysis, this species is primarily recorded only in coastal shelf regions. The grid for this variable was generated using GEBCO (General Bathymetric Chart of the Oceans) coastline data.

Modelling process

The modelling approach used for this study was originally developed by Lambert *et al.* (2011), and consists of six components: 1. The creation of a thermal niche model; 2. The creation of a habitat niche model; 3. Combining the thermal and habitat models to create a predicted distribution for a specific time period. 4. Assessing the ability of the full model to describe the current static distribution; 5. Assessing the ability of the full model to predict changes in distribution over time with changes in local climate; 6. Predicting future distributions under different climate change scenarios for those species for which the model was found to have a good ability to predict both the current spatial distribution and changes in distribution over time. The approach is summarised in Fig. 1, while full details of this framework can be found in Lambert *et al.* (2011).
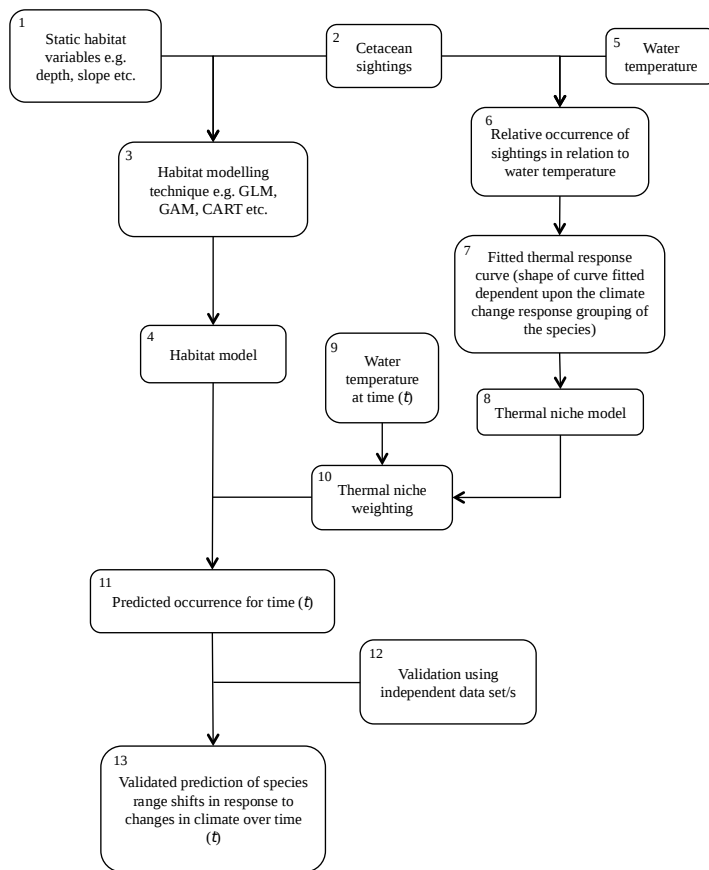
6

Figure 1: Modelling framework used to provide quantitative predictions of how cetacean ranges are likely to respond to temperature changes over time.

Thermal niche component

Individual species were first assigned to one of four climate-change response groupings proposed by MacLeod (2009) in accordance with current knowledge of their distributional range in relation to water temperature within the eastern North Atlantic (Table S1). These groupings are 1) warm water-limited species (lower temperature limit to range), 2) cool water-limited species (upper temperature limit to range), 3) cooler and warmer water-limited species (range limited to intermediate water temperatures), and 4) cosmopolitan species (no temperature limit to range).

A thermal niche model was then empirically derived from the cetacean sightings dataset for six species (white-sided dolphin, bottlenose dolphin, harbour porpoise, minke whale, striped dolphin and white-beaked dolphin) by first calculating the relative occurrence for a particular species in relation to 1°C temperature classes (see Lambert et al. 2011 for details), and then re-classifying it into three categories, equating to unsuitable (proportional occurrence <5%), marginal (proportional occurrence between 5-25%) and core (proportional occurrence >25%) sections of the thermal niche respectively. For each climate-change response grouping a separate response curve and associated equation were applied (Figure S1) and quantified through an iterative process, repeated >20,000 times, to find the most appropriate values to fit the frequency distribution on a least sum of squares basis (see Lambert *et al.* 2011 for full details).

For four further species (Cuvier's beaked whale, long-finned pilot whale, northern bottlenose whale and Risso's dolphin), there were too few sightings data to reliably fit the appropriate response curve to the data. For these species, an 'expert' distribution was created (based on the groupings from MacLeod, 2009, and existing knowledge of the distribution of these species in relation to water temperature in this region summarised by MacLeod *et al.* 2005), and used to calculate the species thermal niche, as described for empirically derived thermal niche models.

Habitat niche model component

The habitat niche model component for each species was created using a classification tree, whereby the sightings of a particular species were classified as presence data, and all sightings of other species were classified as absences of the species in question (see Table S1). This was to ensure that the maximum number of habitat combinations surveyed could be

8

included in the model. While the use of the presence locations of other species as absence locations for the target species can potentially cause biases when modelling species distribution, the model validation procedures (see below) provide a direct assessment of whether this was the case in this study. In order to select the tree size with the smallest estimated error, the initial classification tree was pruned using cross validation.

Combining the thermal and habitat models to create a predicted distribution for a specific time period

Predictions of species range under specific climatic conditions were achieved by creating a 2.5 x 2.5 temperature (*t*) grid for the study area for a specific time period and applying the species-specific thermal niche weighting. The habitat niche model component for the same species was then multiplied by this weighting to produce a likelihood of occurrence that is defined by the interaction between both temperature and habitat preferences.

Assessing the ability to predict current static distribution

In order to assess the ability to predict the current static distribution of each species, a prediction based on the combined model was made for the period 2000-2008 based on water temperature data from the HADiSST data set (see above). This predicted distribution was then compared to the species distribution from the Cetacean Distribution Atlas (Reid *et al.* 2003), which provides an independent and comprehensive analysis of cetacean distribution within the study region, and it is generally taken to represent the accepted current distribution

of individual species in this region. The relationship between predicted and actual occurrence for each species was assessed using a General Additive Model (GAM) with a binomial distribution and logit link function. Two criteria were used to determine whether or not a model was suitably validated. Firstly, a significant positive relationship was required between predicted modelled occurrence (independent variable) and the presence of a species within each grid cell (dependent variable); Secondly, the model fit was graded according to the percentage of deviance explained, whereby a model with an explained deviance of less than 5% was considered a poor fit. Models which explained between 5 and 10% were considered a moderate fit, while those which explained more than 10% were considered a good fit. Only those models with a good or moderate fit were considered good enough to be suitable for continuation onto the next validation step.

Assessing the ability to predict changes in distribution in response to changes in water temperature

The second validation step tested the ability of the combined model to predict changes in the range of each individual species in response to changes in water temperature. Here, historic strandings records from UK and Irish coastlines were compared with predicted occurrence of each species for each decade between 1930 and 2008, a time period beyond that used to build the model (see Lambert *et al*. 2011). Although the presence or absence of a species within the strandings record is likely, in part, to be influenced by reporting effort (which has considerably increased post-1990 in the UK and Ireland), strandings records can still provide a reasonable indicator to identify the presence (or changes in the presence) of a species occurrence within a specific region (e.g. Maldini *et al*. 2005, Jung *et al*. 2009, Pyenson, 2011). However, in order to reduce the impact of increasing strandings effort over time, strandings rate was here measured by the number of strandings per decade of the species of

interest, calculated as a proportion of all species stranded within the same time period. The HadiSST dataset was the source of temperature data for these historical predictions.

The area used for model validation in each species was determined according to where the greatest change in occurrence of that species was predicted to have happened for each species between 1930 and 2008, as it is only in these areas that species' response to changes in temperature at a range boundary could be adequately tested. A Pearson's correlation was used to test for a relationship between average predicted occurrence and (standardised) strandings rate for each decade, within the validation area, between 1930 and 2008. A significant and positive correlation between predicted model occurrence and strandings rate was considered indicative of the model's ability to predict changes in range in response to changes in water temperature over time. Based on the correlation coefficient, this relationship was defined as strong (above 0.5), moderate (between 0.3 and 0.5) or weak (below 0.3) (Cohen 1988).

Predicting future distribution under projected GCC scenarios of sea surface temperature

For those species in which the models were adequate to predict both current range and historic changes in range in response to changes in temperature, predictions of future range were made using 2.5 x 2.5km grids of average projected SST for summer months (June-September) for each of three climate change scenarios and for each decade between 2010 and 2099.

For future projected monthly SST, we used three datasets developed from the A1b (medium greenhouse gas emission), A2 (high GHG emission) and B1 (low GHG emission) Special Report Emission Scenarios (Nakićenović *et al.* 2000). These were generated from the

11

HadCM3 atmosphere-ocean general circulation model (Johns *et al.* 2003) and provided data for between 2010 and 2099 at a 1.25° resolution.

Results

Comparisons between the predictive ability of the models of different species

The models for all species, with the exception of the bottlenose dolphin, were found to have a good ability to describe their current ranges (see supplementary materials for full details). However, only the models for minke whale, northern bottlenose whale, striped dolphin and white-beaked dolphin were also able to accurately predict changes in distribution over time in response to changes in water temperature (Fig. 2, Table 1, Table S2a&b and Figs. S7, S8, S10 & S11). The results for common dolphin from Lambert *et al.* (2011) have been included in Table 1 for comparison.
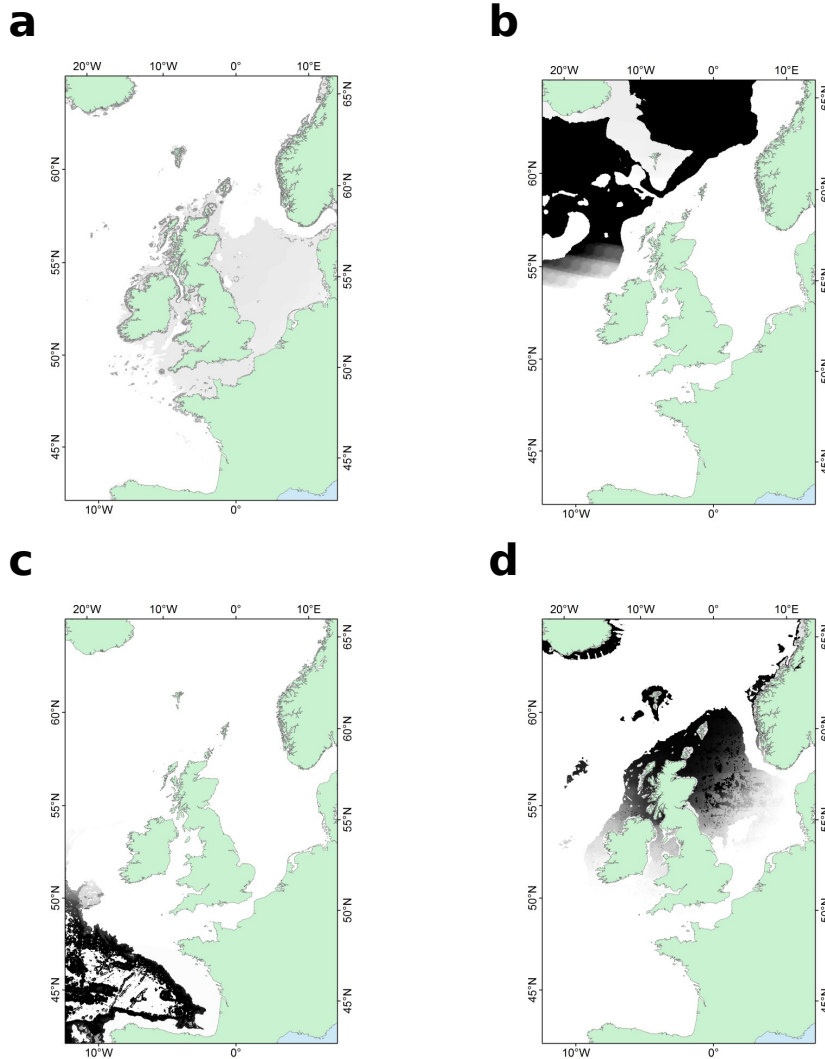
Figure 2: Predicted occurrence of a) minke whale, b) northern bottlenose whale, c) striped dolphin, and d) white-beaked dolphin using combined habitat and thermal niche models for the period 2000-2008. The shading illustrates a scale from most unsuitable habitat (white) to core habitat (black). See Figure S2 for combined models for this period for all other species investigated.

Table 1: Comparative results for each validation step for individual species. A tick for both steps indicates the overall suitability of the species model for predicting changes in range in relation to changes in climate.

Species (climatic response grouping)	Step 1: Validation of ability to predict the current, static, range	Step 2: Validation of ability to predict changes in range in response to changes in climate

13

Species		
Atlantic white-sided dolphin (CWL)	☐	☐
Bottlenose dolphin (WWL)	☐	-
Common dolphin (WWL)	☐	☐
Cuvier's beaked whale (WWL)	☐	☐
Harbour porpoise (CWWL)	☐	☐
Pilot whale (CWWL)	☐	☐
Minke whale (CWL)	☐	☐
Northern bottlenose whale (CWL)	☐	☐
Risso's dolphin (WWL)	☐	☐
Striped dolphin (WWL)	☐	☐
White-beaked dolphin (CWL)	☐	☐

N.B. See Table S2a&b, and Figure S3 for a detailed breakdown of these results.

Predicted distribution of four cetacean species under different climate change scenarios between 2010-2099 in the eastern North Atlantic

For the four species models with a good ability to predict both the current range and changes in the range over time in response to changes in water temperature, predictions of the species range were made for the summer months of each decade between 2010 and 2099 for the eastern North Atlantic. These predictions show an overall northwards range contraction for minke whale, northern bottlenose whale, and white-beaked dolphin (all CWL species), and overall northwards range expansion for striped dolphin (a WWL species), (Fig. 3 and Figs. S7e, S8e, S10e & S10e). The most extensive change in predicted occurrence across this period was for the white-beaked dolphin, with an 80% reduction in relative occurrence

14

following the A2 scenario (Fig. 3 and 4). For all species, the rates of contraction/expansion are greatest for the A1b and A2 scenarios, under which the greatest overall changes in temperature are predicted to occur.
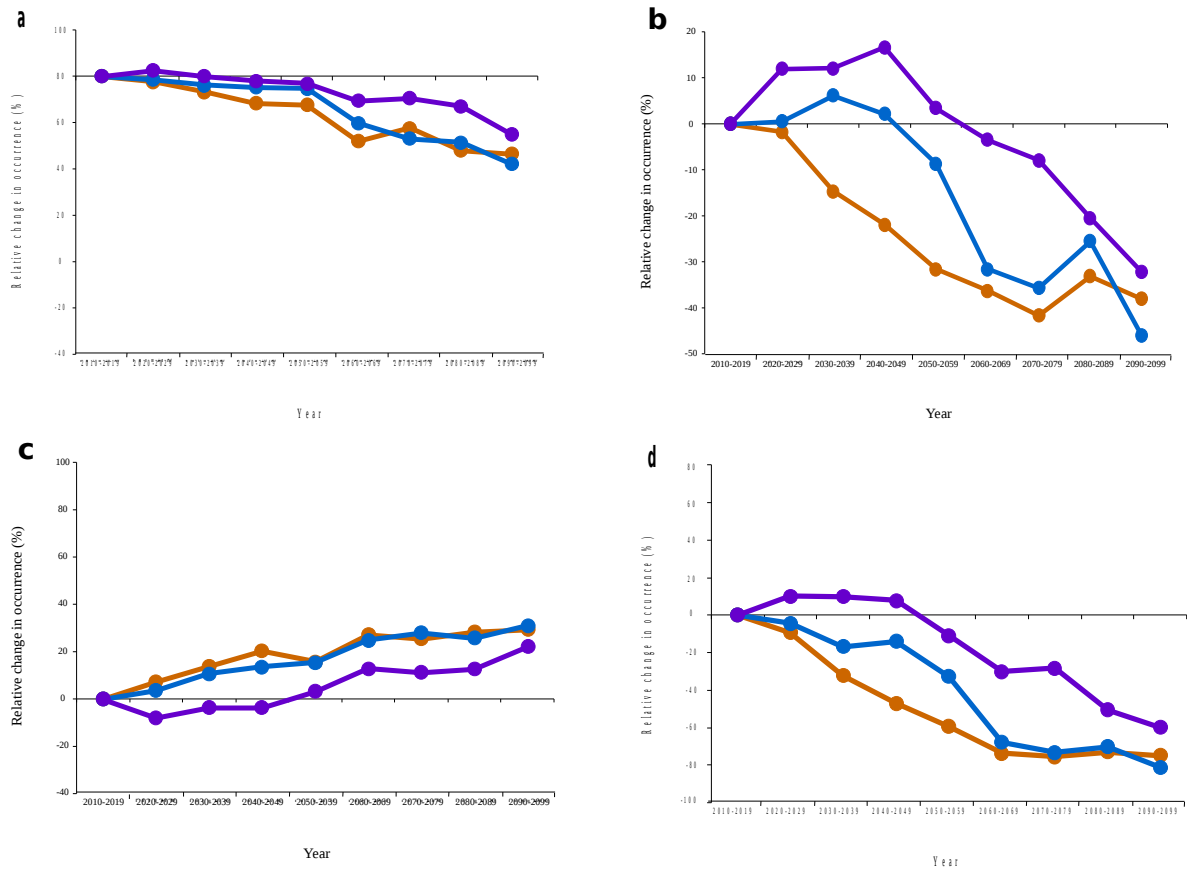

Figure 3: Predicted change in summer occurrence of four cetacean species in the eastern North Atlantic between the 2020s and 2090s in relation to 2019-2019 predictions. A) minke whale, B) northern bottlenose whale, C) striped dolphin, D) white-beaked dolphin. Black and grey = A1b scenario, grey = A2 scenario, black = B1 scenario.
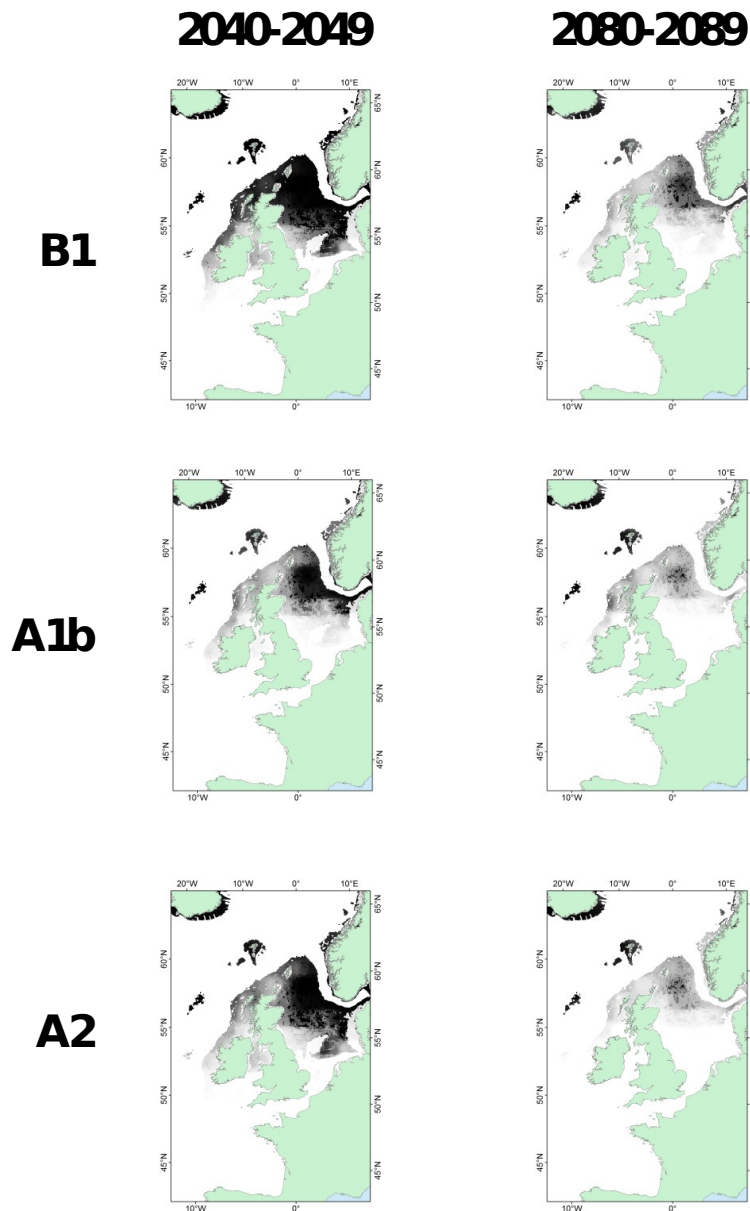
15

2040-2049   **2080-2089**

B1

A1b

A2

Figure 4: Predicted future range of white-beaked dolphin for the periods 2040-2049 and 2080-2089 based on projected A1b, A2 and B1 scenario SST data. The shading illustrates a scale from most unsuitable habitat (white) to core habitat (black). See Fig. S1 for mapped predicted ranges for other species.

Discussion

In this study, we used a bioclimatic envelope model to make a quantitative assessment of how

cetacean ranges are limited by a combination of fixed habitat characteristics and water

16

temperature, and used this information to predict how future changes in climate could affect the geographic distribution of cetacean species in the eastern North Atlantic. Such bioclimatic envelope models have the potential to play an important role in management strategies for species conservation, especially in light of climate change (Martínez-Meyer 2005; Hoegh-Guldberg *et al.* 2007; Faleiro *et al.* 2013). However, distribution models used for this purpose are often validated (if at all) only in terms of their ability to predict the present spatial distribution of a species (e.g. Thomas *et al.* 2004; Bond *et al.* 2011; Kou *et al.* 2011), and while a model may perform well in predicting a species' current distribution in relation to local ocean climate, this does not necessarily mean that it will accurately capture how a species' distribution changes over time in response to changes in climate (Davis *et al.* 1998; Morin & Thuiller 2009; McMahon *et al.* 2011). This has been one of the primary criticisms of the use of bioclimatic envelope models to predict future distributions under climate change (Araújo *et al.* 2005a,b; Guisan & Thuiller 2005), as modelled environmental relationships may turn out to be contingent on values of other variables that were not included in the model or even to be coincidental (Solow, 2002). This is of particular concern when models are built using empirical relationships identified from relatively small datasets (e.g. short time series or small geographic areas).

In order to avoid this potential limitation in the present study, the models for ten different cetacean species were tested to ensure that they could successfully predict both the current spatial distribution and temporal (historical) changes in distribution in relation to changes in water temperature. From this, we concluded that it was appropriate to use the models for four species to make future predictions under different climate change scenarios.

17

Future predictions for species-specific models with a good predictive ability

Predictions of future spatial distribution under climate change show a northwards expansion in the range of a warmer water species (striped dolphin) and a northwards contraction in the range of three cooler water species (minke whale, northern bottlenose whale and white-beaked dolphin), results which are consistent with previously proposed effects of climate change on cetacean species' ranges (MacLeod *et al.* 2005; Learmonth *et al.* 2006; Simmonds & Isaac 2007; MacLeod 2009). These effects raise two potential conservation and management issues.

Firstly, there is predicted to be a marked reduction in the availability of minke whale summer feeding grounds. In particular, a substantial reduction in suitable habitat is predicted within the southern part of minke whale range by the 2080s following the medium and high emission scenarios. Reduced availability of these waters could have important implications for minke whale conservation, given that the shelf waters around the UK and Ireland represent an important summer feeding ground for this eastern North Atlantic population (Born *et al.* 2003; Macleod *et al.* 2004). Reductions in feeding opportunities that may occur with reduced habitat availability could have considerable impacts on food competition and for reproduction and survival of migratory whales (Greene & Pershing 2004; Ainley *et al.* 2012) and could, ultimately, also have wider implications for migration timing and routes and for the location of breeding/feeding grounds (Stafford *et al.* 2007; Kovacs *et al.* 2010; Visser *et al.* 2011). These effects may be compounded by likely shifts in prey distribution with continued changes in climate (see for example Perry *et al.* 2005; Lenoir *et al.* 2011), which should ideally be integrated alongside model predictions within any future conservation strategy for minke whale in this area. Note however that uncertainty about future fishery

exploitation of prey species of minke whales, such as sandeels, herring and sprats makes changes in future food availability more difficult to predict (Pierce *et al.*, 2004).

Secondly, there is predicted to be a dramatic contraction in the range of white-beaked dolphin. For example, following medium and high emission scenarios, available white-beaked dolphin habitat is likely to be greatly reduced post-2040s, with a likely 80% reduction in occurrence by the 2060s within the UK and Irish waters. A similar trend is evident following the low emission scenario, although reductions in occurrence and total range extent are predicted to occur at a slower rate. Given that there is usually a positive relationship between abundance and range extent (Lawton 1993; Thomas *et al.* 2004), such a dramatic reduction in available habitat would very likely present severe conservation implications for the genetically-distinct population of white-beaked dolphin which currently resides in the shallow shelf waters of northwest Europe, and which make up around 20% of the global population of this species.

White-beaked dolphin model predictions therefore support, and more importantly, quantify, previous concerns regarding the potential threat of increasing water temperatures to eastern North Atlantic white-beaked dolphin populations. These concerns are compounded by the fact that climate change impacts are likely to be accentuated by other existing anthropogenic pressures, such as commercial fishing, pollution, shipping and offshore oil, gas and renewable energy activities (Akçakaya *et al.* 2006; Alter *et al.* 2010, Davidson *et al.* 2012). For example, the area covered by predicted critical white-beaked dolphin habitat coincides with one of the areas of highest cumulative human impact in the marine environment (Halpern *et al.* 2008). Consequently, reductions in the abundance of white-beaked dolphin could occur at a greater rate than the rate of range reduction predicted here, and it is therefore

19

essential that consideration of climate change, including any compounding factors, be integrated within species management plans.

Important to achieving this is the re-evaluation of this species' overall conservation status, such as within the ICUN 'Red List', which often forms the basis of much conservation action and policy. To date the 'Red List' does not account for potential climate change impacts in its categorisation of the majority of cetacean species, including the most recent Red List assessment of white-beaked dolphin, a species which is currently classified as of 'Least Concern' (Hammond *et al.* 2008).

While the results presented here are specifically relevant to the eastern North Atlantic population of white-beaked dolphin and do not explicitly equate to predictions of abundance change or extinction risk, the predicted dramatic decline in range size strongly highlights the need for bodies such as the IUCN to consider and integrate climate change impacts into their species assessments. The consideration of climate change within cetacean management strategies would also facilitate the integration of model outputs with the management of a range of marine and maritime sectors of human activity, for example within the general framework of Marine Spatial Planning (Halpern *et al.* 2012, Levy & Ban 2012), where balancing conservation requirements with other management objectives will become increasingly important.

Implications of the species-specific models found to have a poor predictive ability

Despite the application of the same modelling framework and modelling approach, the models for six of the ten species analysed had sufficiently poor predictive ability that it was concluded that they should not be used to make future predictions of likely range shifts in

20

response to changes in climate. This finding presents important implications for the use of bioclimatic envelope models in predicting the future effects of climate change on species range.

Firstly, it highlights that even where the modelling process has been shown to work for a number of species within a specific taxonomic group, that this does not automatically mean that the same modelling process will produce equally good models when applied to other related species, even if they have broadly similar ecologies. Secondly, as noted above, the value of testing a model's temporal (and not just spatial) predictive ability is demonstrated by the failure of five species models to produce accurate predictions of range changes over time, while still having a good ability to predict the current spatial distribution (although see issues with strandings data below). Without this additional validation step, we might have incorrectly concluded that these five models were suitable for predicting the effect of climate change on the ranges of these species when, in fact, they may be unreliable..

Likely reasons why some models were found to have a poor ability to predict changes in occurrence over time include the possibility that the species concerned simply do not respond to climate change as expected or that the historic strandings data available to test the temporal predictions were of insufficient quality. The modelling framework used in this study is based on the assumptions that water temperature is a limiting factor for species range, that these temperature-imposed limits will stay constant as water temperatures change, and that range changes are not influenced by interactions with other species. These assumptions are supported for those models with a good spatial and temporal predictive ability but the poor ability of five models to predict changes over time could be due to one or more of these assumptions not being met for these species. Further research is required to assess whether or

21

not this is correct.

For offshore species such as Atlantic white-sided dolphin and Cuvier's beaked whale, low stranding frequencies make it more difficult to robustly test the models' abilities to test range shifts over time. Not only are offshore species less well represented within the strandings record, but strandings of offshore species are also likely to provide a less accurate indication of occurrence compared to shelf species (see MacLeod *et al.* 2004). We suggest that while strandings data may be sufficiently accurate for assessing the predictive ability of models for species which occur in nearshore environments, independent historic at-sea sightings data (where available) may provide a more accurate and reliable method for testing the temporal predictions of the models of offshore, oceanic cetacean species. .

Conclusions

In order to ensure that any future predictions are likely to be accurate, it is essential that the species distribution models are tested in terms of their ability to predict both current spatial distribution and changes in distribution over time. This is especially important where such predictions are to be used as the basis for conservation and management strategies, for which model predictions with the lowest uncertainty and highest degree of predictive accuracy are essential. For models tested only in relation to a species' current spatial distribution, the risk of incorrectly assigning a model as suitable for making predictions of future distribution is potentially high (up to 50% in this study).

When applied to future climates, the model predictions from this study not only illustrate the potential value and limitation of species distribution models for species management, but they also quantify previous concerns regarding the eastern North Atlantic population of white-beaked dolphin. Alongside predictions for future northern bottlenose whale and minke whale distribution, these models highlight the urgent need for better integration of climate change within species conservation and management strategies. Bioclimatic envelope modelling can also aid in identifying the areas where such strategies should be best targeted, as well as providing a time scale on which management initiatives would be most relevant. How best to deliver effective action at a local scale clearly merits investigation, in addition to the application of a regional circulation model, or at the least, a finer resolution global model, (such as the HadGAM1) in order to improve upon the accuracy of modelling output at finer scales. As such, the most immediate value of these model predictions is in illustrating the need (and means) to better incorporate consideration of climate change within any evaluation of a species' conservation status.

efforts in data collection for these organisations. Additional sightings were provided by the Joint Nature Conservation Committee (JNCC). JNCC delivers the UK and international responsibilities of the Council for Nature Conservation and the Countryside (CNCC), Natural Resources Wales (NRW), Natural England (NE), and Scottish Natural Heritage (SNH). We also gratefully acknowledge the use of sea surface temperature data from the Met Office Hadley Centre (www.metoffice.gov.uk/ hadobs) and the modeling groups, the Program for Climate Model Diagnosis and Intercomparison (PCMDI) and the WCRP's Working Group on Coupled Modelling (WGCM) for their roles in making available the WCRP CMIP3 multi-model dataset. Support of this dataset is provided by the Office of Science, US Department of Energy.

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29

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