

Climate change effects on marine protected areas: Projected decline of benthic species in the North Sea

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ABSTRACT

Climate change is a global threat for marine ecosystems, their biodiversity and consequently ecosystem services. In the marine realm, marine protected areas (MPAs) were designated to counteract regional pressures, but they might be ineffective to protect vulnerable species and habitats, if their distribution is affected by global climate change. We used six Species Distribution Models (GLM, MARS, FDA, RF, GBM, MAXENT) to project changes in the distribution of eight benthic indicator and key species under climate change in the North Sea MPAs for 2050 and 2099. The projected distribution area of most species will be stable or even increase within the MPAs between 2001 and 2050. Thereafter, the distribution area decreased, especially within MPAs in the central North Sea by 2099, and some key species even disappeared from the MPAs. Consequently, the monitoring and protection of benthic species might not be possible within static MPA borders under climate change.

1. Introduction

Anthropogenic climate change is a human-induced indirect pressure for the integrity of marine ecosystems (Doney et al., 2012; Pörtner et al., 2014). Altered environmental conditions (e.g. temperature, salinity, hydrodynamics, ocean acidification) and habitat suitability can affect species distributions, community structures and diversity patterns (Harley et al., 2006; Hoegh-Guldberg and Bruno 2010; Poloczanska et al., 2013; Weinert et al., 2016) as well as ecosystem processes and functioning (Gattuso et al., 2015; Nagelkerken and Connell 2015; Poloczanska et al., 2016). Species distribution shifts during the last decades were documented across oceans and taxonomic groups (Sorte et al., 2010) and were often attributed to seawater temperature increase, one major problem driven by increasing atmospheric greenhouse gas concentrations. Benthic habitats and communities are important indicators of climate change effects, because their species are sessile or have a low mobility and are relatively long-lived. Thus, they integrate changes over time and can be relatively easily monitored (Birchenough et al., 2015). In the North Sea, benthic environments are specifically under climate change pressure, because of a distinct near-bottom

temperature increase between 1980 and 2004 by 1.6 °C (Dulvy et al., 2008) and a sea surface temperature increase from 1985 to 2004 of ~ 0.06 °C yr⁻¹, in comparison with the global warming average of 0.017 ± 0.005 (Good et al., 2007). Hence, the northern European shelf seas can be considered as a “hot spot” of global warming (Holt et al., 2012). For example, a distribution centroid shift between 3.8 and 7.3 km yr⁻¹ towards the north-west was found for 65 benthic species due to temperature changes in the North Sea from 1986 to 2000 (Hiddink et al., 2015). Furthermore, due to the expected water temperature increase until 2099 following SRES emission scenario A1B (Mathis and Pohlmann 2014), the projected distribution of 75 benthic species in the North Sea showed a northward shift for 48 species with mean centroid shifts between 10 and 50 km from 2001 to 2099 for more than half of the species (Weinert et al., 2016). Bottom salinity was observed to be an important parameter as well, structuring the communities of infauna, epifauna and demersal fish (Callaway 2002; Rees et al., 2007; Reiss et al., 2010; Kröncke et al., 2011).

Based on these findings, the question arises to what extent ecosystem management strategies in the North Sea and elsewhere need to adapt to these changes? One central aim of ecosystem management is to reduce

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anthropogenic pressures, ensuring a functional ecosystem with a good environmental status (Directive, 2008/56/EC). Generally, pressures on marine ecosystems can be separated into *endogenic managed pressures* from activities within the system (e.g. fisheries) and *exogenic unmanaged pressures* from forces acting on large scales beyond system boundaries (e.g. climate) (Elliott 2011). While ecosystem management can regulate endogenic pressures to a specific extent, exogenic pressures would not respond on local measures. Thus, the challenge for ecosystem management on mid-term to long-term perspectives will be to assess the impact from both pressure types to better understand and anticipate their consequences (e.g. species distribution shifts), allowing for an effective adjustment of management decisions (Elliott et al., 2015). Marine protected areas (MPAs) have been proven as efficient measures to meet management decisions and ecosystem management aims (Jennings 2009). They are often no-take areas or areas with regulated low disturbance to reduce over-exploitation of marine resources and degradation of marine habitats, and thus, reducing local endogenic pressures. In this way they allow to conserve biodiversity, endangered species and habitat types, and consequently ecosystem functions and services (Agardy et al., 2011; Hopkins et al., 2016).

In the European Union (EU), member states established 1992 an ecological network of protected areas on land and at sea (Natura, 2000) and adopted the Marine Strategy Framework Directive (MSFD) to achieve good environmental status of the EU's marine waters (Directive, 2008/56/EC). So far, about 11% of European seas and almost 27% of the North Sea were designated MPAs by 2016 (EEA 2018; UNEP-WCMC 2020). However, MPAs are relatively static management measures and their boundaries cannot be easily adjusted to a variable environment (Elliott et al., 2015; Maxwell et al., 2015). In addition, exogenic pressures like climate change will probably affect the performance of MPAs independent of their monitoring and management and, in the most extreme case, MPAs could become unsuitable in the light of their initial purpose (e.g. to protect a species) (Côté and Darling 2010; Levy and Ban 2013; Maxwell et al., 2015; Hopkins et al., 2016). For example, Maxwell et al. (2015) suggested a dynamic management that adapts in response to a variable environment through the integration of near real-time data. A simulation of a dynamic management approach with a hypothetical mobile marine species showed that the managed area could be reduced by up to 82%, while keeping the same level of protection efficiency. While these studies exemplify a problem in the current management of MPAs, the question remains, how efficiently MPAs can conserve endangered species and sensitive habitat types, while these species might show distributional shifts under climate change.

Species Distribution Models (SDMs) are useful statistical tools for marine ecosystem management and spatial conservation planning (Reiss et al., 2014; Queirós et al., 2016) that combine observations of species occurrence or abundance with environmental variables, to assess distribution patterns and shifts on large spatial scales (Elith and Leathwick 2009). Furthermore it is an approach to project species distributions in the future by incorporating projections of various environmental parameters in the model. Gormley et al. (2013) projected the distribution of the biogenic bed forming horse mussel *Modiolus modiolus* from 2009 until 2100 around the British Isles and showed a loss of 100% of the "most suitable" habitat by 2080. In contrast, the invasive Pacific oyster (*Crassostrea gigas*) was projected to gain suitable habitat in the northern UK waters and the English Channel by 2050 (Jones et al., 2013b). Nevertheless, the understanding of large scale distribution patterns and shifts, especially of subtidal marine species, in response to climate change is still very limited (Birchenough et al., 2015). Benthic species often play a substantial role in the selection and designation of MPAs as well as in the monitoring of their ecological status (Greathead et al., 2020). Benthic organisms can be target species for protection, because of their vulnerability (e.g. the tube- and reef-building polychaete *Sabellaria spinulosa*) or indicator species for sites with a special conservation value (e.g. the burrowing shrimp *Callinassa subterranea* for muddy bottoms). The assessment of MPAs performance based on benthic monitoring

needs to consider climate change-driven distributional shifts of these species, to avoid misguided management of MPAs.

Therefore, the aim of this study was to assess the response of eight selected benthic key species in North Sea MPAs to projected bottom temperature increase and salinity decrease for the years 2050 and 2099 based on Intergovernmental Panel on Climate Change (IPCC) emission scenario A1B. The main objectives were i) to assess climate-driven distributional changes within MPAs and to discuss methodological consequences for the monitoring and management, in order to support an adaptive MPA management, and ii) to evaluate the robustness and uncertainty of different distribution models using six model algorithms (GLM, MARS, FDA, RF, GBM, MAXENT) and one consensus model.

2. Material and methods

2.1. Study area

For the evaluation of species distributional changes in MPAs, 10 sites in offshore waters and six sites in coastal waters of the Natura 2000 network were selected (Fig. 1, Table 1). They were classified into nine clusters (MPA cluster I-IX) based on the geographical location. All sites were designated as a Special Area of Conservation (SAC) and are either typical sandbanks, mudflats (only parts of MPA IX, Margate and Long Sands) or reefs listed on Annex I of the Habitats Directive. The conservation objectives are to maintain or restore the habitat types (Table 1) and the associated and endangered species (Council-Directive 92/43/EEC). The designated species under the Habitats Directive in these sites are mainly mammals like harbour porpoise, common and grey seal (Natura2000, 2007).

2.2. Species data

The criteria to select the eight benthic key species of the North Sea were (A) threatened species and (B) indicator or monitoring species that are characteristic for a habitat type under protection in the concerning MPAs.

Two species were selected for **group A**: the tube-building polychaete *Sabellaria spinulosa*, which forms reefs and the arctic-boreal bivalve *Arctica islandica*, which declined in the North Sea in the last century. The biogenic reefs of *S. spinulosa* are ecologically significant, because they host a highly diverse associated epibenthic community (Pearce 2014). The species is vulnerable to physical damage (trawling, sediment extraction) and reefs are designated as Special Areas of Conservation (Directive, 2008/56/EC). *Arctica islandica* is also threatened from

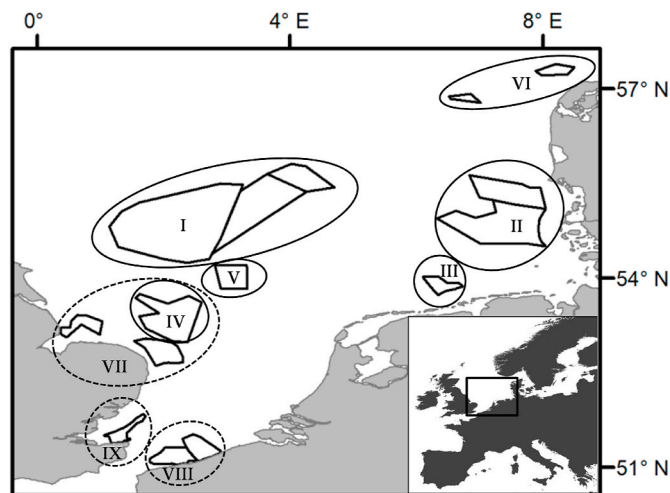


Fig. 1. The North Sea, MPA cluster I - IX in coastal (dashed line) and offshore waters (continuous line), for details see Table 1.

Table 1

Marine protected area clusters in the North Sea (see Fig. 1) showing the protected habitat types, the corresponding site characteristics as well as benthic species in this study, which are relevant monitoring and/or indicator species.

Cluster	Name of MPA	Country	Area [km ²]	Protected habitat	Site characteristics and indicator species
I	Dogger Bank	UK	12340	sandbank	Largest sandbank in UK waters, located in the open sea, exposed to waves, fine sands with shell fragments in shallow areas, muddy sands in deeper regions, depth 13–58m.
I	Dogger Bank	NL	4699	sandbank	Central North Sea, offshore sublittoral zone, mostly fine sands with shell fragments, depth 29–40m, biogeographical border, cold-adapted species in the north, warm-adapted species in the south. <i>Amphiura filiformis</i> , <i>Arctica islandica</i> , <i>Callianassa subterranea</i> , <i>Spisula subtruncata</i>
I	Dogger Bank	GER	1696	sandbank	
II	Sylter Aussenriff	GER	5314	reef, sandbank	South-eastern North Sea, sandbanks (Amrum bank: fine sand to coarse sand and gravel), reefs along the flank of the Elbe glacial valley, depth 8–48m. <i>Amphiura spec.</i> , <i>A. islandica</i> , <i>C. subterranea</i> , <i>S. subtruncata</i> , <i>Upogebia deltaura</i>
II	Sydligge Nordsø	DK	2473	sandbank	Southern North Sea, large sandbank (mostly medium to coarse sand) including patches of reef, depth 18–33m, up to 165 macrozoobenthos species recorded since 1998, several are on the Red List. <i>Lanice conchilega</i>
III	Borkum-Riffgrund	GER	625	reef, sandbank	
IV	North Norfolk Sandbanks and Saturn Reef	UK	3606	reef, sandbank	Ten main sandbanks, fragmented smaller banks, open shelf ridge, not vegetated. <i>A. islandica</i> , <i>Echinocardium cordatum</i> , <i>Sabellaria spinulosa</i>
V	Klaverbank	NL	1240	reef	North-west of Den Helder, gravel (poor in silt) and larger cobbles on the surface, separated by a 60m deep channel (north-west to south-east).
VI	Gule Rev	DK	473	reef	North-west of Denmark, small reefs with rock areas covered partly with stones, sand and gravel, depth 25–60m. <i>A. islandica</i>
VI	Jyske Rev, Lillefiskerbanke	DK	242	reef	Located north-west of Denmark, sandy and rocky habitat, small reefs with relief, depth 30–46m. <i>A. filiformis</i> , <i>A. islandica</i> , <i>U. deltaura</i>
VII	North Norfolk Sandbanks and Saturn Reef	UK	3606	reef, sandbank	Ten main sandbanks, fragmented smaller banks, open shelf ridge, not vegetated. <i>A. islandica</i> , <i>E. cordatum</i> , <i>S. spinulosa</i>
VII	Haisborough, Hammond and Winterton	UK	1469	reef, sandbank	Contains a series of sandbanks, dynamic sediment environments on top, on the flanks sediments tend to be more stable and gravelly. <i>L. conchilega</i> , <i>S. spinulosa</i>
VII	Inner Dowsing, Race Bank and North Ridge	UK	845	reef, sandbank	Several low diverse sandbank types and biogenic reefs, mixed and gravelly sands in the areas between with higher diversity, relatively shallow, mostly less than 30m. <i>L. conchilega</i> , <i>S. spinulosa</i>
VIII	Vlaamse Banken	BEL	1182	reef, sandbank	Located north-east of the Thames Estuary (England), composed of a number of sandbanks, with muddier and more gravelly sediments in the troughs between the banks, tidally influenced, low diversity on tops, higher diversity in the troughs, occurrence of the reef-forming riss worm. <i>S. spinulosa</i>
VIII	Bancs Des Flandres	FRA	1122	sandbank	
IX	Margate and Long Sands	UK	648	sandbank, mudflats and sandflats not covered at low tide	

disturbances to the seabed (e.g. trawling, sand extraction). Both species are listed as decreasing in the IUCN Red List and are described as very seldom (*S. spinulosa*) and seldom (*A. islandica*). *A. islandica* is also under protection in the selected MPAs Dogger Bank and Vlaamse Banken.

For **group B**, six species were chosen: the echinoderms *Amphiura filiformis* and *Echinocardium cordatum*, the ghost shrimps *Callianassa subterranea* and *Upogebia deltaura*, the polychaete *Lanice conchilega* and the bivalve *Spisula subtruncata*. The brittle star *A. filiformis* and the sea urchin *E. cordatum* are characteristic, both reworking the upper sediment layers and feeding on depositional organic matter. *C. subterranea* is a deep burrowing shrimp (approx. 50–80 cm) in soft sediments, while *U. deltaura* inhabits sands and “muddy sands with coarse sands and shell gravel”. The latter four species are indicator species and are important ecosystem engineers (Birchenough et al., 2012; Braeckman et al., 2014). *L. conchilega* is a tube-building polychaete which occurs in dense aggregation (forming biogenic reefs) or patchily distributed mainly in muddy to coarse sand (Van Hoey et al., 2008). *S. subtruncata* is a common bivalve which occurs predominantly in coastal areas in sand and muddy fine sand. The bivalve is of interest for local fisheries.

Species occurrence data were obtained from six data sets for the period 1999 to 2004: from the EU-Projects ‘Monitoring biodiversity of epibenthos and demersal fish in the North Sea’ (Callaway et al., 2007) and ‘Managing Fisheries to Conserve Groundfish and Benthic Invertebrate Species Diversity’ (MAFCONS; Greenstreet et al. (2007)), from the ICES International Bottom Trawl Survey (IBTS; ICES (2012)) and the German Small Scale Bottom Survey (GSBTS; Ehrlich et al. (2007)), the open data infrastructure Global Biodiversity Information Facility (GBIF), and from the database European Ocean Biogeographic Information

System (EurOBIS). The latter is mainly based on the data from the ICES North Sea Benthos Project 2000 (NSBP; Rees et al. (2007)). In the following we refer to the present day period as ‘2001’ although benthos data were sampled in the period from 1999 to 2004.

2.3. Environmental parameters

Six relevant environmental parameters were chosen to model the distribution of the selected species for the present (see below). The correlation coefficient was used to check for collinearity between the environmental parameters. To avoid collinearity, the correlation coefficient threshold indicating collinearity was set to $r > 0.7$ (Dormann et al., 2013). Mean bottom salinity for February showed collinearity with the salinity in June and was therefore omitted. All parameters were rasterized and set to a resolution of 0.06×0.06 decimal degree with an extent of 60.4 north, 50.9 south, 3.1 west and 10.3 east (World Geodetic System, 1984). Raster cells covering land were excluded from the modelling process.

In this study modelled and projected mean bottom temperature and salinity of the simulated years 2001, 2050 and 2099 (Mathis and Pohlmann 2014) were used to address climate change signals in the North Sea for the 21st century. Mathis et al. (2013) and Mathis and Pohlmann (2014) used a global climate projection of the IPCC SRES emission scenario A1B to dynamically downscale it for the North Sea to a meso-scale horizontal resolution of about 3 km. Projections for February and June were used to take seasonality into account and also for the reason that the second quarter of the year was ecologically most affected by previous winter temperatures (Kröncke et al. 1998, 2013). Bottom temperature and salinity for the years 2001, 2050 and 2099 were chosen

to analyse whether projected distributional shifts occur already by mid-century.

Depth data, with a resolution of one arc-minute (1.852 km) were derived from the General Bathymetric Charts of the Oceans (GEBCO) global bathymetry data set from the British Oceanographic Data Centre (GEBCO 2003). Sediment data were collected during research cruises of the North Sea Benthos Project (NSBP, 2000) and the project Managing Fisheries to Conserve Groundfish and Benthic Invertebrate Species Diversity (MAFCONS). The parameters mud content and median grain size were derived from this data set. Data of peak wave stress, with a resolution of about 12 km, were provided by the Proudman Oceanographic Laboratory (Liverpool, UK), generated with the help of a 3-dimensional hydrodynamic model (Davies and Aldridge 1993). Peak wave stress was calculated from a 1 year model run covering the period of September 1999 to September 2000.

A more detailed description of the environmental parameters is given in (Reiss et al., 2011; Mathis and Pohlmann 2014; Weinert et al., 2016). All parameters, except for bottom temperatures and salinity, were kept constant for the period 2001 to 2009 in the modelling process.

2.4. Species Distribution Models

The distribution of benthic species was modelled for the entire North Sea. The R package ‘biomod2’ version 3.1–64 (Thuiller et al. 2009, 2015) was used to generate SDMs for eight benthic species in the North Sea for 2001 and to project potential changes for the year 2050 and 2099 (Table 2). Six algorithms were applied: Generalized Linear Model (GLM) (McCullagh and Nelder 1989), Multiple Adaptive Regression Splines (MARS) (Friedman 1991), Flexible Discriminant Analysis (FDA) (Marmion et al., 2009a), Random Forest (RF) (Breiman 2001; Prasad et al., 2006), Generalized Boosting Model (GBM) (Ridgeway 1999; Elith et al., 2008), and Maximum Entropy (MAXENT) (Phillips et al., 2006; Phillips and Dudík 2008).

The species occurrence data (Table 2) were randomly subsampled with 70% used to calibrate and 30% to evaluate the prediction skill of the models. Species absence data, which would reduce spatial and environmental bias (Phillips et al., 2009) were not available. Therefore 10000 randomly drawn pseudo-absence data were used (Barbet-Massin et al., 2012). For every species 10 replicate runs, with different random subsamples, were performed with each model algorithm to repeat the process of calibration and evaluation. This performance is a relatively robust cross-validation test when independent data are missing (Thuiller et al., 2015). The True Skill statistic (TSS) was used for model evaluation. TSS is defined as the sum of sensitivity (true positive rate) and specificity (true negative rate) minus 1 (Table 2), thus omission and commission errors (false negative rate, false positive rate) were accounted for (Allouche et al., 2006). A threshold of TSS >0.3 was set to discriminate between weak and robust replicate runs (Araujo et al., 2011). Only robust replicate runs were included in further analyses. The robust replicate runs were merged for each model algorithm in an

ensemble model, separately for each species and year (2001, 2050 and 2099). An ensemble model is basically the mean of all projections with a single model algorithm. Thus, for each species analysed, three ensemble models (2001, 2050 and 2099) were generated with each model algorithm. Finally, robust replicate runs of all model algorithms were merged in a consensus model, again separately for each species and year. A consensus model is the mean of the projections carried out with all model algorithms. Weighted averages based on the TSS evaluation scores of single model outputs for each species and model algorithm were used to reduce uncertainty in the ensemble and consensus models (Marmion et al., 2009b). Thus, a good model was given a stronger weight in the ensemble and consensus.

2.5. Analysis of distributional changes within MPAs

Cut-off levels were calculated individually for each species and model algorithm. They were applied to calculate spatial changes of species distribution from 2001 to 2050 and 2099 within the chosen MPA cluster. The applied cut-off levels maximized TSS (Allouche et al., 2006) and produced the most accurate predictions (Jiménez-Valverde and Lobo 2007; Barbet-Massin et al., 2012). They were used to transform the probability distribution of the species occurrence into binary projections whether the species is present or absent. The ‘BIOMOD.RangeSize’ function was applied to calculate absolute numbers and relative frequencies of grid cells occupied by the species within the chosen MPA cluster I-IX.

2.6. Tendency analyses

The projected species distribution tendency (increasing/decreasing area or no change) from 2001 to 2050 and 2099 was compared between the consensus and ensemble models separately for every algorithm across all species. Therefore, the total number of generated consensus models was counted and set to 100%. Then, the number of ensemble models which showed a different tendency was counted and expressed as percentage to quantify uncertainty. Furthermore, the difference between the projected species distribution area (grid cells occupied by the species) of the consensus and each ensemble model for 2099 were calculated for each species to describe the variation in the projections with these approaches. Similarly, the species distribution area of the consensus models was set to 100% and the projected differences of the ensemble models were expressed as percentage relative to the consensus model to better compare the variation in the projections.

2.7. Coefficient of variation

The coefficient of variation (CV) is a measure to describe the variation of data around the mean. It was calculated to evaluate the degree of variation between the projected species distribution area of the six algorithms. The CV is the ratio of the standard deviation to the mean,

Table 2

Results of the projected distributions for the benthic key species showing occurrence data, sensitivity, specificity, the True Skill Statistic (TSS) for model evaluation and the relative importance of environmental parameters (%) in the model (blue = temperature June, red = temperature February, green = salinity June, purple = depth, light brown = median grain size, brown = mud content, light blue = peak wave stress).

Species	occurrence data	sensitivity	specificity	TSS	variable importance [%]
<i>A. filiformis</i>	217	0.83	0.75	0.59	
<i>A. islandica</i>	297	0.89	0.95	0.83	
<i>C. subterranea</i>	111	0.98	0.80	0.78	
<i>E. cordatum</i>	299	0.86	0.82	0.69	
<i>L. conchilega</i>	129	0.89	0.67	0.56	
<i>S. subtruncata</i>	328	0.99	0.87	0.86	
<i>U. deltaura</i>	43	0.98	0.94	0.92	
<i>S. spinulosa</i>	77	1.00	0.96	0.96	

multiplied by 100. Thus, we calculate the CV, of the six projected distribution areas (six algorithms) separately for all species, for each MPA cluster and year.

3. Results

Spatial distributions of eight benthic species were predicted for the North Sea for 2001 and distributional changes within the selected MPAs between 2001 and 2050 as well as 2099 were assessed (Fig. 2). The distributions shown in Fig. 2 represent the results of the consensus model for each species. Only robust replicate runs above a threshold of TSS >0.3 were included with an overall mean TSS of 0.77 ± 0.15 SD.

3.1. Distributional changes within MPAs

Most species showed a more or less stable or even increasing distribution area in the MPAs between 2001 and 2050, which decreased (or even disappeared completely) in some MPAs by 2099 (Table 3). Overall, only the polychaete *L. conchilega* and the bivalve *S. subtruncata* were projected to be found in each MPA cluster (I–VI) between 2001, 2050 and 2099 (Table 3). For *L. conchilega* a distribution decrease was projected for MPA cluster I and III–VI (on the Dogger Bank from 100% to

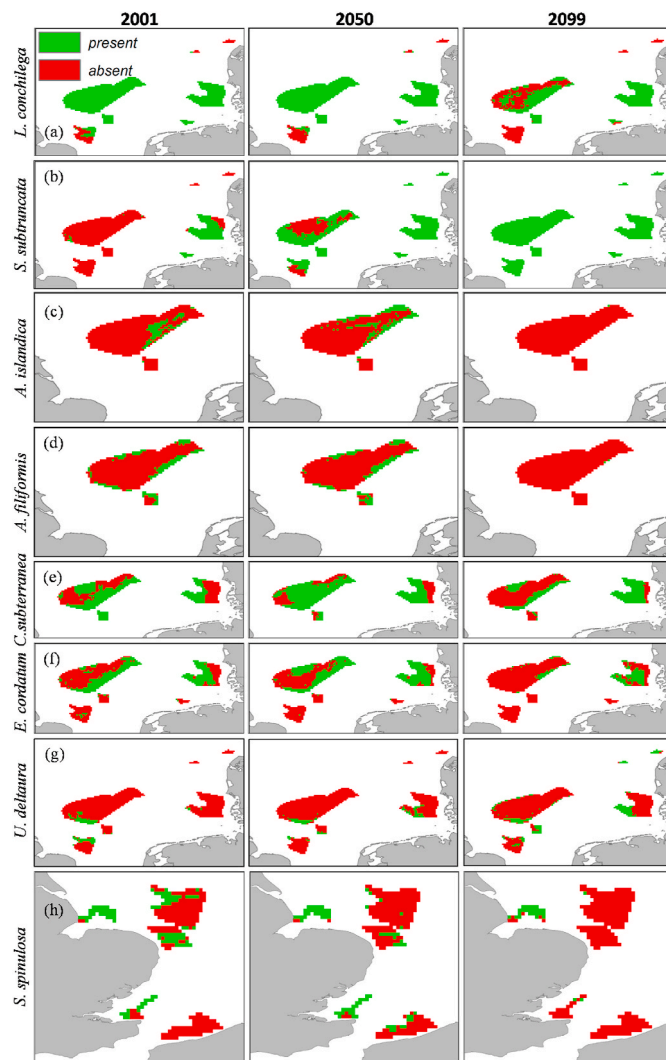


Fig. 2. The maps show the distributional change within the most important analysed MPA cluster for each species (present = green, absent = red) from 2001 to 2050 and 2099. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

51% between 2050 and 2099), whereas for *S. subtruncata* a distribution increase was projected for each MPA cluster with a distribution area of 100% for 2099 (Table 3, Fig. 2a and b). All other species were modelled to occur at least in MPA cluster I and V, as well as II, except for the bivalve *A. islandica*. This bivalve and the brittle star *A. filiformis* showed a constant or slightly increasing distribution between 2001 and 2050 (between 2% and 59%), but were projected to disappear in MPA cluster I and V by 2099 (Fig. 2c and d). For the burrowing shrimp *C. subterranea* a decline of the distribution area was projected for MPA cluster I and V between 2001 and 2099 (from 100% to 20%, MPA cluster V), but vice versa for MPA II, from 49% to 86% (Fig. 2e). Also the sea urchin *E. cordatum* was projected to be affected by a decline of distribution area (from 42% to 8%, MPA I) and even disappeared in MPA V, as well as III and IV by 2099 (Fig. 2f). Three species were projected to be found in MPA VI. Especially the bivalve *S. subtruncata* and the shrimp *U. deltaura* (Fig. 2g) are supposed to colonise this area by 2099 (Table 3). The ross worm *S. spinulosa* (Table 3, Fig. 2h) was projected to occur in all three concerning MPAs (VII, VIII and IX), with a distribution area up to 84% in MPA IX by 2050. However, a decline was projected for MPA VII and IX (to 11% and 8%) and a disappearance for MPA VIII between 2050 and 2099.

3.2. Consensus model tendency and ensemble model variability

Six ensemble SDMs (GLM, MARS, FDA, RF, GBM, MAXENT) were used to generate a final consensus model to project the distribution area of the species within the MPA cluster I – IX between 2001 and 2050 as well as 2099. Overall, 35 consensus models were generated. In some cases, the projected species distribution tendency (increasing/decreasing area or no change) of the ensemble models for the year 2099 was different from the consensus models. Random Forest showed the highest ratio, a different tendency in 21 (60%) cases. In contrast, MAXENT and GBM were the models with the lowest ratio, 5 (14%) and 6 (17%) cases, respectively. The other models showed a ratio from 9 (26%) to 11 (31%) cases. Although different tendencies were projected, the absolute values of the species distribution area of the ensemble and consensus models for 2099 do not necessarily differ to a great extent. Ensemble models generated with RF projected a species distribution area in a range of $\geq 23\% \leq 150\%$ (with an outlier of 3645%), MAXENT in a range of $\geq 43\% \leq 350\%$ and GBM in a range of $\geq 0\% \leq 158\%$ compared to the projected species distribution area of the respective consensus model. Furthermore, differences among the tendency of ensemble model projections did not necessarily result in a high variability of the projected species distribution area. A high or low variability is expressed by the coefficient of variation (CV, Table 4). Generally, moderate CVs were calculated for the projected species distribution area for the years 2001 and 2050, high CVs in particular for the year 2099. Exceptions were the bivalve *Spisula subtruncata* and the burrowing shrimp *Upogebia deltaura* (Table 4). Especially for the bivalve *S. subtruncata*, high CVs were calculated for the year 2001 and rather low to moderate CVs for the years 2050 and 2099.

4. Discussion

In the marine realm, MPAs are designated to counteract regional endogenic pressures and to protect vulnerable species and rare habitats with ‘vulnerable or fundamental features’ (EEA 2015; OSPAR 2015). Nevertheless, under climate change, which is an exogenic pressure, MPAs might lose their effectiveness to fulfill these objectives, because the concerning species might leave their habitats. Therefore, we projected the distribution of eight benthic key species in the North Sea under climate change (projected bottom water temperature and salinity) to assess the effects of distributional changes within MPAs and to evaluate the applicability of ensemble and consensus models to assess these changes. The results showed that the projected distribution area were stable or even increased within the MPAs for most of the species between

2001 and 2050. Thereafter distribution areas decreased and some species were projected to even disappear by 2099 (e.g. *A. filiformis*, *A. islandica*). This is most likely caused by the warming of bottom water temperature specifically in summer, which was projected to be most pronounced in the second half of the 21st century (Mathis and Pohlmann 2014). Consequently, the distribution of the selected benthic species also changed most drastically after 2050, resulting in a projected decline and local disappearance of several benthic species. Thus, the MPAs in the North Sea might not cover the preferred habitat ranges of these indicator or protected species under climate change any longer.

These climate-driven distributional changes can be estimated by using SDMs, although the applied model algorithms showed partly a high variability in the projected results, especially for 2099. We considered the consensus model to be an appropriate tool to reduce uncertainty in the projections so that more robust results can support ecosystem management decisions (Araujo and New 2007) and conservation planning under climate change.

4.1. Distributional changes and MPA assessment

For the majority of species the distributions were projected to be most affected in MPA cluster I (Dogger Bank) and partly V (Klaverbank), both situated in the central North Sea, as well as VII to IX around the British Isles in the south-east and north-west and west of Belgium and France, respectively. Especially the distribution of the indicator species (*C. subterranea*, *A. filiformis*, *E. cordatum*) as well as the threatened bivalve *A. islandica* and biogenic reefs of the ross worm *S. spinulosa* were affected and showed a substantial decline within the protected areas by 2099. In general, climate-induced distributional shifts in combination with expansion or contraction of the distribution were monitored and projected for both, terrestrial and marine species (Markovic et al., 2014; Birchenough et al., 2015; Poloczanska et al., 2016; Pecl et al., 2017). In the North Sea, distributional shifts were for example observed for fish with an average distance change of 172.3 ± 98.8 km ($n = 15$) over 25 years (Perry et al., 2005) and for most benthic invertebrate species ($n = 65$) with an interquartile range (i.e. range between 75th and 25th percentiles) of 3.8–7.3 km per year (Hiddink et al., 2015). Projections of North Sea benthic species ($n = 75$) showed a northward shift for 48

Table 3

Distribution area in per cent based on the consensus model for every species and MPA cluster for the years 2001, 2050 and 2099. Low and high distribution probabilities were projected for the beginning as well as for the end of the analysed period.

	year	MPA I	MPA II	MPA III	MPA IV	MPA V	MPA VI
		habitat [%]	habitat [%]	habitat [%]	habitat [%]	habitat [%]	habitat [%]
<i>A. filiformis</i>	2001	17	13			50	
	2050	17	13			59	
	2099	0	3			0	
<i>A. islandica</i>	2001	13				2	
	2050	21				7	
	2099	0				0	
<i>C. subterranea</i>	2001	55	49	13	30	100	
	2050	79	71	17	15	61	
	2099	28	86	22	14	20	
<i>E. cordatum</i>	2001	42	66	9	8	13	
	2050	49	78	4	1	4	
	2099	8	54	0	0	0	
<i>L. conchilega</i>	2001	100	100	100	36	100	8
	2050	100	100	100	20	100	8
	2099	51	100	70	0	98	0
<i>S. subtruncata</i>	2001	2	85	100	0	0	0
	2050	62	100	100	60	100	100
	2099	100	100	100	100	100	100
<i>U. deltaura</i>	2001	8	2		32	4	
	2050	6	16		7	22	
	2099	10	25		16	65	85
<i>S. spinulosa</i>		MPA VII	MPA VIII	MPA IX			
	year	habitat [%]	habitat [%]	habitat [%]			
	2001	39	0	64			
	2050	21	18	84			
2099	11	0	8				

(64%) species and a southward shift for 27 (36%) between 2001 and 2099, which resulted in a habitat loss up to 100% for more than 60% of the projected species (Weinert et al., 2016). These observed and projected species distributional shifts can, of course, also lead to habitat loss for species in specifically delineated MPAs and potentially to ineffective management and conservation of species and habitat types (Araujo et al., 2011; Gormley et al., 2013; Avalos and Hernández 2015). For example, protected areas for European plant and vertebrate species were projected to be partly unsuitable for about 60% of the species by 2080 (Araujo et al., 2011). In the North-East Atlantic, bed forming species, determined as threatened and/or declining Priority Marine Habitats (PMHs) were projected to shift and/or change the extent under climate projections by 2100 (Gormley et al., 2015). In the North Sea, loss of the

“most suitable” habitat was projected for the biogenic bed forming bivalve *Modiolus modiolus* with 100% by 2080 (Gormley et al., 2013). Furthermore, northward shifts were projected between 1985 and 2050 for seven threatened and nine commercially exploited fish species in the North Sea at an average rate of 27 km per decade (Jones et al., 2013a), which confirmed observed rates of distributional shifts for fish in the North Sea (Perry et al., 2005). Nevertheless, Jones et al. (2013a) did not suggest that the adverse effect on the habitat suitability of protected areas is huge, because of the large variation in the projections between model combinations (Jones et al., 2013a). Variations between projected results of applied model algorithms were also obtained in this study (see below).

However, our results showed the largest change in the distribution of

Table 4

The coefficient of variation (CV) in per cent based on the modelled distribution area of the ensemble models for every species and MPA cluster for the years 2001, 2050 and 2099.

	year	MPA I	MPA II	MPA III	MPA IV	MPA V	MPA VI
		CV [%]	CV [%]	CV [%]	CV [%]	CV [%]	CV [%]
<i>A. filiformis</i>	2001	49	50			50	
	2050	27	24			40	
	2099	111	104			110	
<i>A. islandica</i>	2001	75				76	
	2050	59				137	
	2099	209					
<i>C. subterranea</i>	2001	58	60	122	47	78	
	2050	82	30	99	96	112	
	2099	154	70	187	125	153	
<i>E. cordatum</i>	2001	46	37	91	66	57	
	2050	43	27	88	97	82	
	2099	80	39	137	168	117	
<i>L. conchilega</i>	2001	33	21	26	61	48	125
	2050	48	1	5	120	65	158
	2099	87	12	79	132	78	122
<i>S. subtruncata</i>	2001	160	52	64	245		
	2050	94	46	49	81	77	49
	2099	37	21	59	34	5	26
<i>U. deltaura</i>	2001	108	139	180	67	112	103
	2050	107	124	158	104	91	80
	2099	100	91	112	88	81	57
<i>S. spinulosa</i>		MPA VII	MPA VIII	MPA IX			
	year	CV [%]	CV [%]	CV [%]			
	2001	72	81	76			
	2050	82	89	67			
2099	139	245	96				

the analysed species in the projections between 2050 and 2099. As mentioned before, the applied climate parameters show high rates of change especially in the second half of the 21st century (Mathis and Pohlmann 2014), as also reflected by the IPCC ensemble means for mid-latitudes of the northern hemisphere. While across the entire North Sea mean winter bottom temperature (February) increased at similar rates until 2099 (0.7 until 2050 and 0.6 °C until 2099), mean bottom summer temperatures (June) increased predominantly in the second half of the 21st century (0.1 and 2.1 °C). The strong decrease during the second half of the 21st century of the sea urchin *E. cordatum* and the disappearance of *A. filiformis* and *A. islandica* in the MPAs of the central North Sea (Doggerbank, Klaverbank), where the temperature increase is specifically pronounced, suggests that increasing maximum summer temperatures lead to local conditions that are beyond the range of acclimatisation for these species. That could have consequences such as fitness decrease, which goes along with population decline or even a local species extinction (Hoegh-Guldberg and Bruno 2010).

As mentioned above, especially the analysed ecosystem engineers, which play an important role in ecosystem functioning, and threatened species were projected to be affected by 2099. Ecosystem engineers are defined as organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic material (Jones et al., 1994) and have thus, a specifically important role within MPAs. Typical allogenic engineers like the brittle star *A. filiformis*, the sea urchin *E. cordatum* or the burrowing shrimp *C. subterranea* are important bioturbators that redistribute organic matter in soft sediments (Wenzhöfer and Glud 2004; Braeckman et al. 2010, 2014; Birchenough et al., 2012; Oehler et al., 2015). Whereas autogenic engineers, like the tube- and reef-building polychaete *S. spinulosa*, and the tube-building polychaete *L. conchilega* (Van Hoey et al., 2008), directly modulate the environment through the construction of physical structures, affecting hydrodynamics near the sea floor with potential ecological effects on other ecosystem processes and functions (Braeckman et al., 2014). Consequently, the projected changes in distribution of these engineering species can have repercussions on several other associated species and even the entire benthic community. Besides these climate driven changes, some species such as *S. spinulosa* and the associated reefs are under additional threat and/or decline due to physical damage from exogenic pressures such as fishing (OSPAR 2013). While our projections showed that the distribution of *S. spinulosa* will decrease or even disappear in MPAs around the British Isles, endogenic and exogenic pressures might act synergistically, which could lead to even faster local decline or disappearance. Gormley et al. (2015) projected a loss of the most suitable habitat in the Greater North Sea for *S. spinulosa* (723 km²) with only 3% between 2009 and 2100 based on the same climate scenario A1B, but with the assumption of a uniform temperature increase from the surface to the bottom by 4 °C for the whole area and the use of MAXENT as single species distribution model. In contrast, we applied a consensus model approach and used bottom temperature, which was projected to increase locally up to 5.4 °C until 2099, which has probably led to the projected drastic decline within the protected areas by 2099 found in this study.

Another threatened species in the Greater North Sea is the bivalve *A. islandica*, which is under protection on the Dogger Bank. It was projected to occur with only 21% on the Dogger Bank by 2050 and to disappear in all analysed MPAs by 2099. Thus, based on our results local management measures such as MPAs might not be an efficient tool to protect this species on a long term. However, *A. islandica* is mainly distributed in the northern North Sea (Fladen Ground) and in the deeper Oyster Ground (Witbaard and Bergman 2003; OSPAR 2009), but the species declined in the North Sea in the last century (Witbaard and Bergman 2003; Rees et al., 2007). The species is also abundant in adjacent seas such as the Baltic Sea and northern Norway though, which might function as source populations for the declining North Sea population through relatively long pelagic larval stages (OSPAR 2009).

Although a decline or even disappearance was projected for the

majority of the analysed species by 2099, a stable or increasing distribution was projected for the bivalve *S. subtruncata* and the polychaete *L. conchilega* (Table 3, Fig. 1). These species seem to be less sensitive to temperature increase and their distribution is primarily determined by primary production, sediment type and hydrodynamics (Van Hoey et al., 2008; Wakelin et al., 2015). Thus, changes in these species over time might indicate more accurately local environmental changes driven by endogenic pressures, which can be directly addressed by MPA management measures. This could be reached through more adaptive management, which could probably better control and minimize the consequences of anthropogenic uses in dynamic marine systems.

4.2. Species distribution models - tendency and variability

Distribution models in general were found to be useful tools for ecosystem management and might substantially improve adaptive management approaches (Reiss et al., 2014) and references therein, if the uncertainty of model results can be adequately assessed. Thus, we compared the projected species distribution tendency (increasing/decreasing distribution area or no change) between 2001 and 2099 of the ensemble and consensus models. The ensemble models of the applied machine-learning methods (MAXENT, GBM, RF) showed both, low and high deviations from the consensus model for different species. Therefore, the tendency analyses of the ensemble models resulted in contrary projection in some cases. However, the projected absolute values of the species distribution area generated with those machine-learning methods showed variations in a more or less similar ratio, expressed by the CV. The calculated CV increased for most species from 2001 to 2050 and to 2099. The increasing variation between the projected results are inevitably associated with modelling uncertainties, which can be categorized into four groups a) structural (model) uncertainty, b) initialisation uncertainty and internal variability, c) parametric uncertainty and d) scenario uncertainty (Hawkins and Sutton 2009; Cheung et al., 2016; Payne et al., 2016). Structural uncertainty as well as initialisation uncertainty and internal variability have the greatest impact at smaller spatial scales and shorter periods, e.g. in seasonal and decadal projections, whereas scenario uncertainty dominates in projections for the far future (Hawkins and Sutton 2009; Payne et al., 2016). For the methodological approach in this study various measures in biomod2 were applied to reduce model uncertainty (Thuiller et al. 2009, 2015), but the increase of CV over time for most algorithms indicate that the results of the projected distributions for 2099 has to be interpreted with care.

Ensemble and consensus models were previously used in the marine environment for fish (Albouy et al., 2012; Jones et al., 2013a) and benthos (Jones et al., 2013b; Weinert et al., 2016; Singer et al., 2017) to detect species and areas vulnerable to climate change and important for protection. In comparative studies (Reiss et al., 2011; Aguirre-Gutierrez et al., 2013; Valle et al., 2013) machine learning methods (e.g. MAXENT, GBM, RF) as well as the consensus model approach showed a better performance than regression-based models (e.g. GLM, MARS), based upon the applied evaluation method. In particular consensus models enable the application of different model algorithms and settings to produce multiple distribution models, and only those model runs above a predefined threshold of TSS are merged into a final consensus model by applying weighted criteria to reduce the uncertainty of the applied single-model algorithms (Araújo et al., 2005; Araujo and New 2007; Brook et al., 2009; Marmion et al., 2009b). The applied model algorithms in this study represent different approaches commonly used (i.e. regression models, classification trees and machine learning models) to avoid a bias towards only one approach and, in addition with applied cross validation (Thuiller et al., 2015), to provide an estimate of robust and reliable distribution (Jones et al. 2012, 2013a; Wisz et al., 2015). Initialisation uncertainty and internal variability reflect complex interactions in the simulated processes such as non-linear dependencies and feedback mechanisms. Small differences in the initial state of the

simulation have the potential to rise quickly, so that the projected results tend to diverge instead of converge (Payne et al., 2016). Hence, an approach to explore and minimize these uncertainties is to run models with different initial conditions (e.g. model algorithms, climate projections) and evaluate the spread of the projections (Cheung et al., 2016). Furthermore, distribution modelling also presupposes decisions on the basis of the available environmental parameters and occurrence data to consider parametric uncertainty. In this study, projected forecasts of bottom temperature and salinity for 2050 and 2099 (Mathis and Pohlmann 2014) were used, but other environmental parameters were kept constant over time, which might not be a realistic scenario. Nevertheless, the exclusion of those parameters would reduce discriminatory ability and hence lead to an overestimation of climate change impacts on the species probability of occurrence (Brook et al., 2009). To account for scenario uncertainty, the climate scenario itself and whether a global climate projection was dynamically downscaled are both important (Payne et al., 2016). In this study climate parameters from Mathis et al. (2013) and Mathis and Pohlmann (2014) were applied. They used the IPCC emission scenario A1B, which represents a greenhouse gas trajectory from a balanced utilization across all energy resources, to dynamically downscale the climatic response for the North Sea. Nevertheless, because only a single global model simulation has been downscaled, we cannot properly account for the scenario and climate model uncertainties in the temperature and salinity parameters used in our SDM approach. Despite these uncertainties, consensus models in combination with the applied model settings seem to be an appropriate approach for projecting benthic species distribution in response to climate change, although results have to be interpreted with care when considering long time scales until 2100. Nevertheless, these results could contribute to an adaptive ecosystem and MPA management.

CRedit authorship contribution statement

Michael Weinert: Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing. **Moritz Mathis:** Data curation, Writing - review & editing. **Ingrid Kröncke:** Conceptualization, Writing - review & editing. **Thomas Pohlmann:** Data curation, Writing - review & editing. **Henning Reiss:** Conceptualization, Writing - review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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