Harmful algal blooms and climate change: exploring future distribution changes

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Harmful algae can cause death in fish, shellfish, marine mammals, and humans, via their toxins or from effects associated with their sheer quantity. There are many species, which cause a variety of problems around north-west Europe, and the frequency and distribution of algal blooms have altered in the recent past. Species distribution modelling was used to understand how harmful algal species may respond in the future to climate change, by considering environmental preferences and how these may shift. Most distribution studies to date use low resolution global model outputs. In this study, high resolution, downscaled shelf seas climate projections for the north-west European shelf were nested within lower resolution global projections, to understand how the distribution of harmful algae may change by the mid to end of century. Projections suggest that the habitat of most species (defined by temperature, salinity, depth, and stratification) will shift north this century, with suitability increasing in the central and northern North Sea. An increase in occurrence here might lead to more frequent detrimental blooms if wind, irradiance and nutrient levels are also suitable. Prioritizing monitoring of species in these susceptible areas could help in establishing early-warning systems for aquaculture and health protection schemes.

Keywords: aquaculture, bioclimatology, dispersal, habitat, impacts, toxicity.

Introduction

Climate change is altering the occurrence of marine species around the world, reorganizing what has historically been considered the native and usual range of species. Marine algae, although underpinning food webs, are sometimes considered a nuisance with implications for society and the economy, especially certain species of diatoms and dinoflagellates. There are approximately 300 harmful algal species (Berdalet et al., 2016) from most phytoplankton groups (Anderson et al., 2015), and some cause toxicity to higher trophic level species, including fish, shellfish, marine mammals, and humans (Wells et al., 2015). Harmful algal blooms (HABs) are occurrences of algal species, which cause toxic effects or otherwise cause harm. Certain algae produce noxious and toxic substances, which accumulate in food chains and cause illness or death in animals and humans (Davidson et al., 2011, 2014). Direct contact with or ingestion of HABs can cause a number of different problems for animals, with knock-on fisheries effects. Some harmful species are retained by filter feeding organisms, such as bivalves, and cause Paralytic and Diarrhetic Shellfish Poisoning (PSP and DSP), or they produce other toxic compounds, which cause health problems and have economic implications for shellfish farms or fisheries (Anderson et al., 2015).

Domoic acid, produced by certain diatoms, causes Amnesic Shellfish Poisoning (ASP), which can cause death in humans as well as marine mammals and sea birds (Tatters et al., 2012). In other cases, high biomass occurrences of non-toxic species can cause negative effects on ecosystems through their sheer quantity, by reducing dissolved oxygen, blocking fish gills, and smothering benthos (Davidson et al., 2014; Anderson et al., 2015; Kudela et al., 2015; Wells et al., 2015). The high biomass of certain algae during a bloom can cause mass decomposition and subsequent reductions in oxygen, resulting in fish kills (Valiela et al., 1997; Kudela et al., 2015) with subsequent ecological problems and economic consequences for fisheries and aquaculture. Economic losses include those to public health, fisheries, and aquaculture closures, and lost recreation (Lewitus et al., 2012; Davidson et al., 2014; Anderson et al., 2015). It has been estimated that HABs cause an annual loss to the European Union of $1billion (Hoagland and Scatasta, 2006). Shellfish harvest can be prevented during blooms, and cause eventual loss of the shellfish if the bloom is prolonged (Cusack et al., 2016). Other consequences include loss of threatened species and changes to ecosystems (Berdalet et al., 2016). Around north-west Europe there are a number of species of algae, which cause economic and human health problems (Table 1). The consequences for food security and safety mean that understanding, predicting and mitigating harmful algal occurrences are a priority for scientists and policy makers (Kudela et al., 2015).

Algal blooms are considered to have increased in frequency and impact around the world in recent decades (Moore et al., 2011; Lewitus et al., 2012; Glibert et al., 2014; Anderson et al., 2015), with global risks to health and economies (Davidson et al., 2014). Human modifications of the environment such as harbour construction, ballast water release, and nutrient enrichment, may

have contributed to these changes (Berdalet et al., 2016). However, species responses have varied and there are many different factors that affect frequency, location, and intensity of bloom formation (Anderson et al., 2015) including upwelling, currents, winds, vertical mixing, surface water temperature, and nutrient supply (Davidson et al., 2014). Shifting climatic regimes and temperature changes can affect these. This could alter the composition of the phytoplankton community, increase or decrease the occurrence and geographic spread of bloom-forming species (Moore et al., 2009; Berdalet et al., 2016; Kudela et al., 2015; Wells et al., 2015), affect the timing of phytoplankton blooms (Henson et al., 2017) and increase the window each year when blooms can develop (Marques et al., 2010; Moore et al. 2011). For example, Karenia mikimotoi blooms are typically associated with high rainfall and subsequent low-salinity events as well as high-nutrient run off from land (Davidson et al., 2009; Barnes et al., 2015). Alexandrium bloom formation occurs only under certain temperature conditions and annually these conditions have persisted for longer in recent years (Moore et al., 2011). Sea surface temperatures in the North Sea have risen more than the global average over the past 50 years (Hobday and Pecl, 2014). In the north-western European shelf seas area, from the end of the 20th century to the end of the 21st there is projected to be a further increase in annual mean sea surface temperature of 2.9°C, and a freshening of 0.41 psu (Tinker et al., 2016). Observed temperature rises in recent decades have coincided with an increase in phytoplankton in the North Sea and north-east Atlantic (Bresnan et al., 2013) and notably diatoms such as Pseudo-nitzschia spp. have increased (Hinder et al., 2012). In recent years K. mikimotoi blooms have been seen further north around the British Isles than in the past, potentially linked to changes in duration of stratification (Davidson et al., 2009;

Table 1. Harmful algal species found around the UK, and the problems caused.

Species	Taxonomy	Distribution	Problems caused
Alexandrium minutum*	Planktonic dinoflagellate	Bloom-forming, coastal regions. Widely distributed.	Paralytic shellfish poisoning (PSP)
Alexandrium ostenfeldii*	Planktonic dinoflagellate	Coastal species along west coast of Europe and Canada. No blooms recorded to date.	PSP
Alexandrium tamarense*	Planktonic dinoflagellate	Bloom-forming. Coastal regions of Europe, Japan, North America.	Produces a number of toxins including PSP. Not all strains toxic.
Dinophysis acuminata*	Planktonic dinoflagellate	Bloom-forming. Coastal waters of North Atlantic and Pacific.	Causes Diarrhetic Shellfish Poisoning (DSP). Can be toxic at low concentrations.
Dinophysis acuta*	Planktonic dinoflagellate	Bloom-forming. Found worldwide.	Produces a number of toxins including DSP
Gymnodinium catenatum*	Planktonic dinoflagellate	Warm, temperate coastal waters	Produces PSP
Karenia mikimotoi△	Planktonic dinoflagellate	Bloom-forming. Worldwide distribution.	Produces brevetoxins, neurotoxic shellfish poisoning (NSP)
Prorocentrum lima*	Benthic dinoflagellate	Estuarine species with world-wide distribution	Produces a number of toxins including DSP
Pseudo-nitzschia australis•	Diatom	Widely distributed in temperate and subtropical waters	Produces domoic and isodomoic acids
Pseudo-nitzschia delicatissima◇	Diatom	Widely distributed in Arctic, temperate, and subtropical waters	Some strains produce domoic acid
Pseudo-nitzschia fraudulenta∧	Diatom	Widely distributed in temperate and subtropical waters	Produces domoic acid
Pseudo-nitzschia seriata°	Diatom	Northern Atlantic and more recently Pacific	Produces domoic acid poisoning in shellfish

Sources: △Woods Hole Oceanographic Institute (2016), *Smithsonian (2015), •WoRMS (2014a), ◇WoRMS (2014b), ∧WoRMS (2014c), and °WoRMS (2014d).

Bresnan *et al.*, 2013). However, certain dinoflagellates in the North Sea such as *Prorocentrum* spp. have decreased in abundance over the last decade, likely as a result of increasing temperatures and windier conditions (Hinder *et al.*, 2012). Shellfish in Scottish waters have witnessed a decline in toxins associated with paralytic shellfish poisoning in the last decade (Bresnan *et al.*, 2013). Nutrient availability has also a large part to play, and in particular affects outbreaks of high biomass HABs (Davidson *et al.*, 2014). These examples show that different species are affected in different ways by changes in environmental conditions.

Integrating knowledge of biogeography into climate change impact studies is fundamental for better understanding the effects of environmental change on biodiversity (Hannah *et al.*, 2002), and modelling is required to turn past observations into future predictions (Anderson *et al.*, 2015). One of the best techniques that can be used to achieve this is species distribution modelling (e.g. Jones *et al.*, 2013; Weinert *et al.*, 2016). By considering the environmental conditions within, which a species lives now, the potential future distribution can be projected based on how the physical environment will change. Such modelling techniques can be used to project how marine species might move in response to climate change, by combining occurrence observations with environmental variables (e.g. Reiss *et al.*, 2015; Rutterford *et al.*, 2015; Barton *et al.*, 2016; Weinert et al., 2016; Townhill *et al.*, 2017). The application to planktonic and algal species is relatively new although such models have been used to provide early warning systems for HABs, and in particular they have been deployed successfully for projecting *Pseudo-nitzschia* spp. distributions on the Pacific and Atlantic coasts of North America (Anderson *et al.*, 2009, 2010). Barton *et al.* (2016) used the maximum entropy model Maxent to assess the future suitability of areas in the North Atlantic for 87 diatom and dinoflagellate species. The authors modelled a north and eastward shift, causing a "shuffle" or redistribution in community composition. To investigate the spread of harmful species in a more focused local area, the use of downscaled climate models is required (Wells *et al.*, 2015), which capture fine-scale dynamics in shelf seas processes including tides (Tinker *et al.*, 2015).

In this study it is not the intention to predict the occurrence and location of an individual bloom event, because these are determined by stochastic processes and discrete weather events. Instead the aim is to provide a broad-brush indication of changing geographic affinity. Outputs from global climate models were combined with those from a dynamically downscaled north-west European shelf model to (i) project how suitable environmental conditions may change in the future, and then to (ii) quantify how the distributions of important HAB species may change and, which species will be more or less problematic in the coming century.

Material and methods
Species occurrence data
Species occurrence data were downloaded from two databases: the Ocean Biogeographic Information System (OBIS) (http://www.iobis.org) and the Global Biodiversity Information Facility (GBIF) (http://data.gbif.org) (see Supplementary Appendix S1 for GBIF citations). Species occurrences from March to October were collated, since these are the most likely to contribute to large algal blooms in the northern hemisphere. In addition, the UK government collects algal data on a regular basis and so data were

also obtained from the Scottish Association for Marine Science (SAMS), the Agri-Food Biosciences Institute (AFBI) in Northern Ireland, and the Centre for the Environment, Fisheries, and Aquaculture Science (Cefas) in England and Wales, with permission granted by the Food Standards Agency. Not all data were recorded to species level, and so only the *Dinophysis acuminata* and *D. acuta* occurrence data from AFBI, and *Prorocentrum lima* from all agencies were included. The data were cleaned to remove duplicates, occurrences outside the known depth ranges and Food and Agriculture Organisation of the United Nations (FAO) regions (taken from OBIS), and to remove those recorded as being on land. The depth limit was rounded up to 100 m to ensure that all plausible occurrences were included. The data were then aggregated to a binary (presence/absence) 0.5° latitude × 0.5° longitude grid.

Nested climate projections
High resolution regional downscaled climate model outputs were nested into global climate model outputs (Townhill *et al.*, 2017), which allowed the whole geographical range of a species' environmental exposure to be incorporated into the habitat suitability function, while also allowing for fine scale local projections in the area of particular interest. All projections were obtained from the UK Met Office Hadley Centre and were for the "medium" emissions climate change scenario (SRES A1B). Global projections from a perturbed physics ensemble (PPE) at a global 1.25 degree resolution (Collins *et al.*, 2011) of the Atmosphere-Ocean Global Climate Model HadCM3 (Gordon *et al.*, 2000; Pope *et al.*, 2000) were used under an SRES A1B business as usual, medium emissions scenario (Tinker *et al.*, 2016). Within this medium emissions scenario, assumptions are made that the world expects rapid economic growth, a peak in population mid-century, followed by the growing use of low carbon technologies (IPCC, 2007). This PPE consisted of the unperturbed (standard) member of the model, with 10 ensemble members, which had atmospheric parameters perturbed to span the uncertainty in climate sensitivity. The unperturbed member is used in this study, which is equivalent to the standard version of HadCM3. The unperturbed member of this ensemble shelf seas model was downscaled using POLCOMS (Proudman Oceanographic Laboratory Coastal Ocean Modelling System; Holt and James, 2001; Holt *et al.*, 2001), which produced a north-west European shelf seas projection. This downscaling resulted in a 12 km resolution (1/9° latitude by 1/6° longitude grid), from 43°N, 63°33′20″N to 18°20′W, 13°E (Figure 1). A 30-year average of 1980–2009 (centred on 1995) annual means was used to represent the present time period, because the majority of the species observations were taken between these dates. The future time horizons to which the models were applied were 2040–2069 (centred on 2055) representing the near future, and 2069–2098 (centred on 2084) representing the end of century. Variables used were those considered to most affect algal occurrence: near bottom and sea surface temperature and salinity, and the differences between the surface and bottom of each (bulk temperature and salinity, which gives an approximation of stratification), and bathymetry. The downscaled shelf seas projections were nested within the driving global projections using Python 2.7 (Python Software Foundation, 2010) (packages "netCDF4" and "numpy") resulting in a dataset with a resolution of 0.5 degrees. The global ocean fields were bi-linearly interpolated from the native 1.25° grid cell resolution to the 0.5°, while the
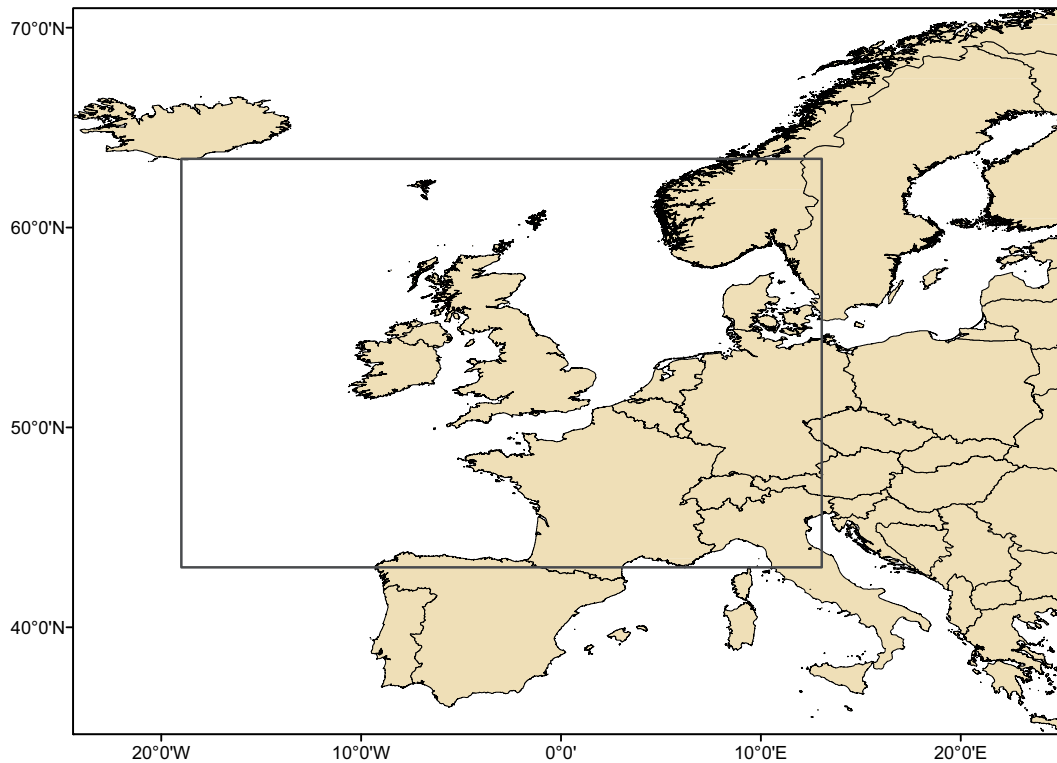
Figure 1. Extent of the north-west Europe shelf seas model.

downscaled regional fields were aggregated up (averaged) from their native $1/6° \times 1/9°$ resolution to the required $0.5°$. These were then copied into the appropriate region within the global model. As the regional data were produced by forcing the global model, the data are consistent and match at the boundary. It was necessary to use a resolution intermediate between the two original models because the local-scale processes are still captured in the shelf seas area, but the global data is not interpolated more than is appropriate. The resulting 0.5 degree grid of environmental parameters was then used to drive the species distribution model.

Species distribution modelling

The Maximum Entropy (Maxent) bioclimate envelope model (Phillips *et al.*, 2006) was used to determine the present day and future habitat suitability of each HAB species. This model is described in Jones *et al.* (2012, 2013) and has performed well in comparison with other models in previous marine studies (Elith *et al.*, 2006; Reiss *et al.*, 2011; Vierod *et al.*, 2014) and for algal species (Barton *et al.*, 2016). Maxent generates habitat suitability by randomly selecting training points and combining presence-only occurrence data with chosen environmental variables, using the rest of the data points to test the model, and then predicting the future habitat suitability by forcing the model based on the same variables. Maxent estimates the probability distribution of the habitat suitability by finding the most uniform distribution (the one with the maximum entropy), within the constraints of incomplete information (Phillips *et al.*, 2006). The term "relative habitat suitability" is used here to describe the bathymetry and hydrographic conditions that the species currently experience. It does not include the bottom substrata or local ecosystem processes such as nutrient availability. Maxent was run for each species in turn using the model interface (version 3.3.3k) downloaded

from http://www.cs.princeton.edu/~schapire/maxent/, for the present day, near future and end of century climate data, giving a habitat suitability score between 0 and 1. "Clamping" was used for model fitting, which ensures that the species' habitat does not get projected outside the suitable environmental conditions and with "jacknife," which checks the importance of each variable. Across the species, the number of training points chosen by the model varied because there was considerable variation in the number of available presence data points. The species with more training samples are likely to present a better fit to reality than others (numbers of presence and training data points are summarized in Table 2). Maxent used the Area under the Curve (AUC) value to test the performance of each model, bounded by 0–1, with 1 being the best fit. A threshold AUC value of 0.8 was considered acceptable, based on Mercks *et al.* (2011), who produced a review of habitat suitability models. This modelling technique is affected by autocorrelation because the species presence sampling is inherently biased. Therefore, the value of >0.8 is used as a guide rather than an absolute measure of robustness.

Latitudinal centroids

The latitudinal centroid for each time period and species was calculated. This gives the centre of the latitudinal range, and can be compared between the present to the future time periods. The centroid (C) was calculated using the equation from Cheung *et al.* (2009):

$$C = \frac{\sum_{i=1}^{n} \text{Lat}_i \cdot \text{Abd}_i}{\sum_{i=1}^{n} \text{Abd}_i},$$

where Lat_i is the central latitude of the spatial cell i, Abd is the predicted relative habitat suitability of the same cell, and n is the

Table 2. Summary of the Maxent model attributes for each species.

Species	AUC value	Number of presence data points	Number of training samples	Two variables with the highest percentage contribution	Percent contribution of those variables
Alexandrium minutum	0.996	51	31	Bathymetry; near bed temperature	70.2; 12.6
Alexandrium ostenfeldii	0.977	68	48	Bathymetry; near bed salinity	55.3; 28.6
Alexandrium tamarense	0.959	88	46	Bathymetry; sea surface salinity	70.8; 22.8
Dinophysis acuminata	0.951	853	640	Near bed temperature; sea surface temperature	54.9; 22.5
Dimophysis acuta	0.950	810	704	Near bed temperature; sea surface salinity	54.6; 28.0
Gymnodinium catenatum	0.982	26	17	Near bed temperature; sea surface temperature	73.1; 14.3
Karenia mikimotoi	0.990	81	56	Bathymetry; near bed temperature	34.7; 33.4
Prorocentrum lima	0.979	241	149	Near bed temperature; sea surface temperature	67.8; 12.8
Pseudo-nitzschia australis	0.994	26	23	Bathymetry; near bed temperature	53.7; 20.2
Pseudo-nitzschia fraudulenta	0.991	17	10	Bathymetry; near bed temperature	61.6; 21.8

total number of cells. The distance between the latitudinal centroids in the present and future years was then calculated in kilometres (Cheung *et al.*, 2011):

$$\text{Distance (km)} = (\text{Lat}_m - \text{Lat}_n) \times \frac{\pi}{180} \times 6\ 378.2,$$

where Lat_m and Lat_n are the latitudinal centroids in the present (n) and projected (m) timeslices, and the approximated equatorial radius of the Earth is 6 378.2 km. This gives the latitudinal shift. The latitudinal shift of each species within the UK EEZ was also calculated.

Results

Following preliminary analyses, two species were excluded (*Pseudo-nitzschia delicatissima* and *Pseudo-nitzschia seriata*). Both were so widespread worldwide that Maxent used around 4 000 training samples with resulting AUC values of 0.8. Their current widespread nature likely means that their future habitat suitability will be similarly widespread and so the models yield few additional insights, hence they were excluded from further assessment.

Maxent provided a good fit for the remaining 10 species, with AUC values above 0.9. All species exhibited a change in habitat suitability distribution from the present day to mid and end of century. For all species, the variable with the highest percentage contribution to the model fit was either bathymetry or near bed temperature (model attributes summarized in Table 2).

The majority of the species exhibited a northward shift in shelf seas and UK EEZ habitat suitability from the present day to mid and end of century (Figures 2 and 3, Table 3). All species exhibited a northward global shift. Most of the species had a larger northward shift at the end of the century than mid-century. For the shelf seas area specifically, *D. acuta* and *Gymnodinium catenatum* had the greatest predicted change in habitat suitability for mid and end of century of around 800–100 km. Globally, *G. catenatum* showed the greatest northward shift at more than 700 km by the end of century. Three species showed a shelf seas southward shift however: *Alexandrium ostenfeldii*, *A. minutum*, and *Pseudo-nitzschia australis*, the first two of which had bathymetry as their highest contributing variable.

Looking in detail at the north-western European shelf seas, the habitat suitability for the majority of the species increased further north (as shown in purple in Figure 4). The maps show that the central and northern North Sea in particular witness large increases in habitat suitability, with a decrease in suitability in the Celtic Sea and the English Channel for many species. *Alexandrium minutum* is one species that exhibits a southward latitudinal shift in the shelf seas, and it can be seen in Figure 4 that the suitability has the greatest increase along the shelf edge, reflected in bathymetry being the variable with the highest contribution to the model. Within the UK exclusive economic zone (EEZ), this species shows an overall decrease, especially in the North Sea, but an increase in the far north and north-west. *Dinophysis acuta* shows a strong decrease in suitability in the shelf seas area, and particularly off the north-east coast of Scotland and in the English Channel, while *G. catenatum* has an overall increase within the UK EEZ, especially in the North Sea. *Prorocentrum lima* shows a decrease to the north of Scotland and Ireland and off south-west England, but an increase or no change in much of the rest of the area and the UK EEZ.

Discussion

Our results show that around the north-west European shelf seas the suitable areas for the occurrence of HAB species are likely to change as a result of climate change in the coming century. In the majority of cases, the suitable environmental conditions will be found further north in the shelf seas than under present day conditions. Exceptions to this are *A. minutum* (change to 2084), *A. ostenfeldii* and *P. australis* all of which showed a southward habitat suitability shift. This may be due to the differences between species in their temperature, salinity and bathymetric preferences and the interactions between these variables. For example *A. minutum* exhibited a higher change in habitat suitability along the shelf edge, and the habitat suitability is constrained by depth (and subsequent effects on circulation and oxygenation) more than temperature. This southward shift projected for *Alexandrium* species corresponds with an observed decrease in recent years around Scotland in PSP toxicity associated with *Alexandrium* (Bresnan *et al.*, 2013). Some species, including *Alexandrium* have a benthic cyst stage and thus are affected by both benthic and pelagic conditions.
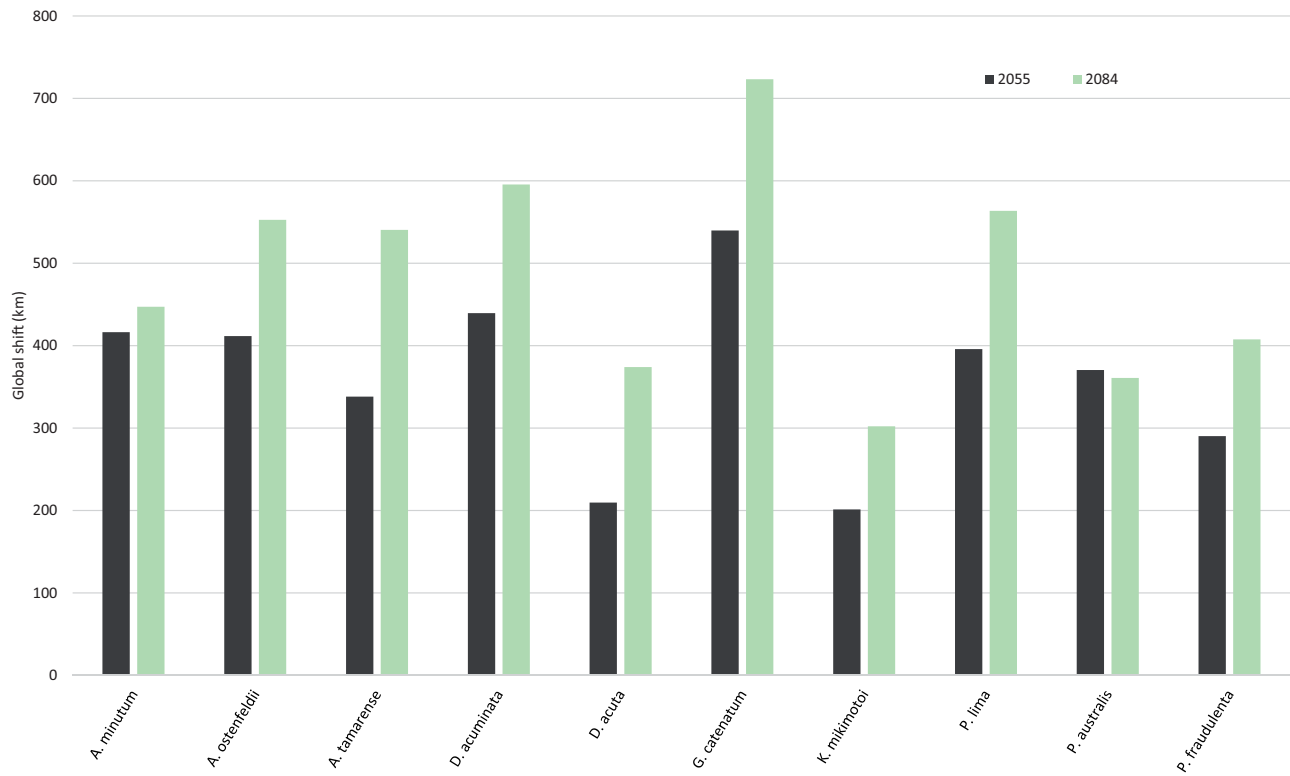
Figure 2. The global poleward shift in the habitat suitability for each species from 1995 to 2055 and to 2084.
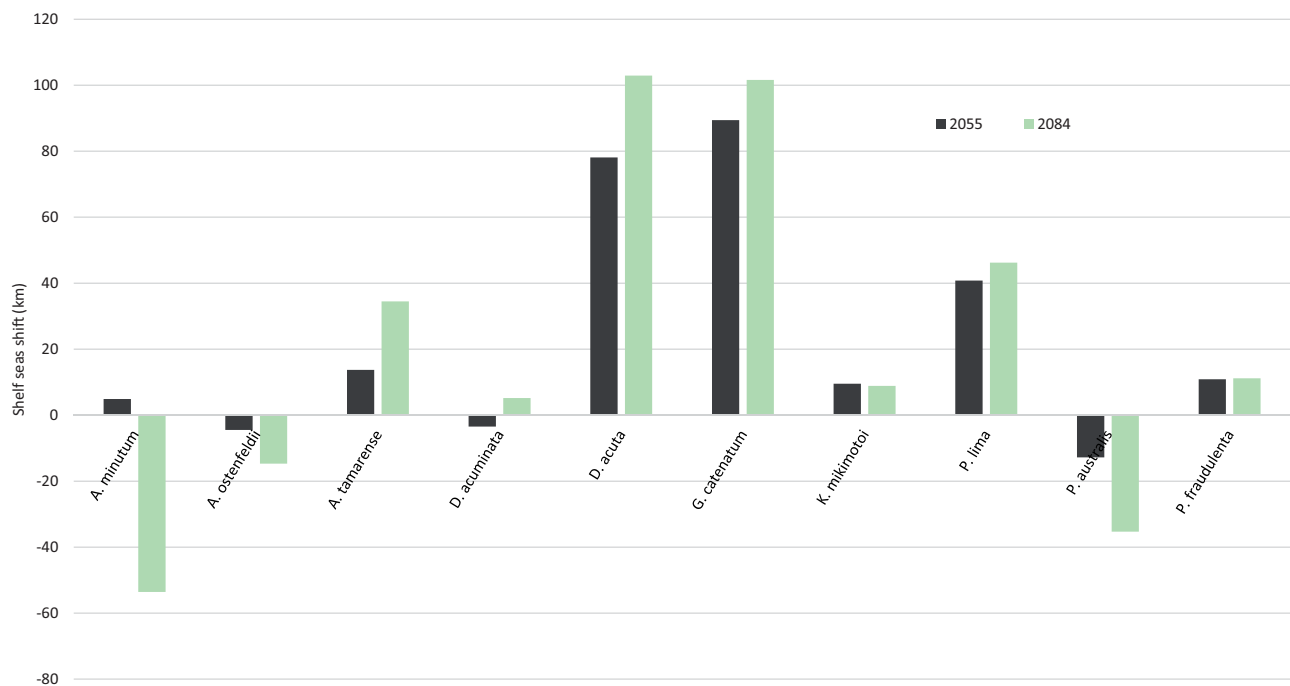

Figure 3. The habitat suitability shift within the north-west European shelf seas area for each species from 1995 to 2055 and to 2084.

The species with the furthest projected northward shift in habitat suitability within the shelf seas were *D. acuta* and *G. catenatum*. These are both planktonic dinoflagellates, which form blooms. *Dinophysis acuta* can cause Diarrhetic Shellfish Poisoning (DSP) and can even be toxic at low concentrations whereas *G. catenatum* can cause Paralytic Shellfish Poisoning (PSP) (Hallegraef *et al.*, 2004). Overall the relative habitat suitability of *D. acuta* is projected to decrease around the UK, with the

Table 3. Habitat suitability latitudinal centroids for the shelf seas area from the present day, near future, and end of century.

| | Latitudinal centroid | | | | | |
| | 1980–2009 | | 2040–2069 | | 2069–2098 | |
Species	Shelf seas	UK EEZ	Shelf seas	UK EEZ	Shelf seas	UK EEZ
Alexandrium minutum	55.25	55.74	55.29	55.78	**54.77**	55.87
Alexandrium ostenfeldii	55.37	56.34	**55.33**	**56.33**	**55.24**	**56.26**
Alexandrium tamarense	55.19	56.23	55.32	56.29	55.50	56.40
Dinophysis acuminata	54.60	56.74	**54.56**	56.91	54.64	**56.86**
Dinophysis acuta	54.47	56.83	55.17	57.21	55.40	57.29
Gymnodinium catenatum	53.65	56.37	54.46	**55.87**	54.57	55.92
Karenia mikimotoi	55.43	56.33	55.51	56.42	55.51	56.45
Prorocentrum lima	54.32	55.73	54.69	55.76	54.73	**55.75**
Pseudo-nitzschia australis	55.34	56.11	**55.22**	**56.02**	**55.02**	**55.83**
Pseudo-nitzschia fraudulenta	55.22	56.38	55.32	56.41	55.32	56.41

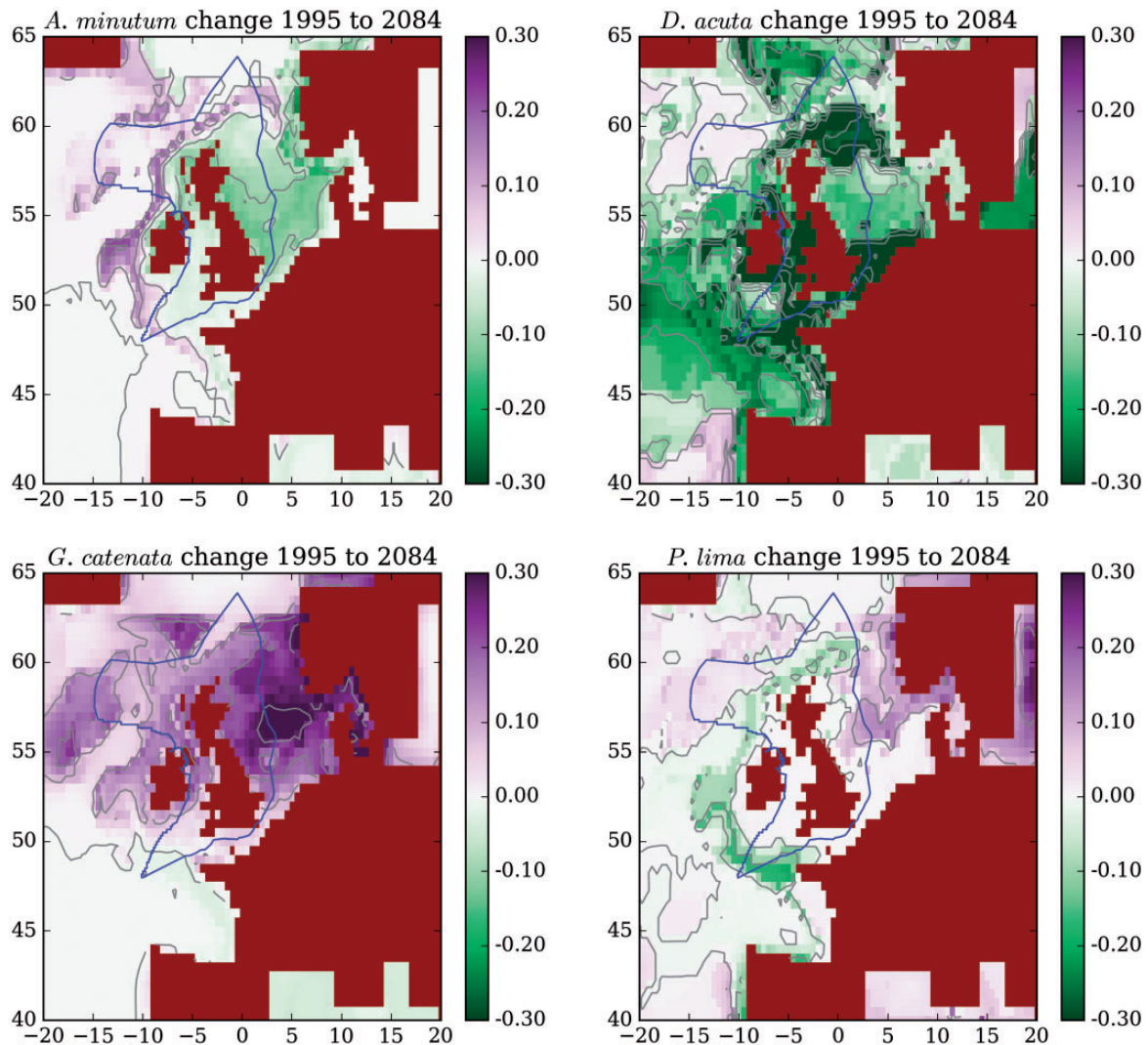Those with southerly shifts in centroid are shown in bold.

Figure 4. The spatial change in habitat suitability (ranging from −1 to 1) for four of the algal species. *Alexandrium minutum* shows a southward shelf seas shift in suitability, while the other three species illustrated are those with the largest northward shift. The UK EEZ is outlined. The outline of the land shows the model resolution.

exception of the north-west of Scotland, but there is a large increase in suitability projected for *G. catenatum*. If this species has a large geographic shift in range, then there may be more occurrences of blooms affecting shellfish fisheries and farms around the north of the UK and in Scandinavia. *Dinophysis acuta* can be retained within shellfish tissue for up to 6 months (Hallegraef et al., 2004), potentially causing huge economic consequences for farmers after a bloom. Incidents of DSP have become more frequent and prolonged across the whole of the UK shelf since it was first recorded in 1997 (Hinder et al., 2011), with 19 incidents between 1999 and 2009. Hinder et al. (2011) report that fisheries have been closed throughout that period for up to 7 months as a result of an outbreak. In 2000–2001, there was the longest closure of a shellfishery ever recorded in the UK, with aquaculture and scallop fisheries being closed throughout the year due to shellfish poisoning events (Hinder et al., 2011), and a facility in Ireland was closed for 48 weeks in 2006 because of *Dinophysis* spp. (Cusack et al., 2016). If *G. catenatum* and other PSP species experience changes in their habitat suitabilities, then farms and fisheries further north may begin to be affected. Mapping the changes in suitability in relation to the UK EEZ shows how UK farmers and fishers may be more affected by some species than others in the near-term and the distant future.

Comparisons with other studies that use alternative models or driving datasets, show that projections tend to point towards a northward shift in HAB occurrence in Europe. A study by Gobler et al. (2017) found that growth rates and days per year of blooms of *D. acuminata* and *Alexandrium fundyense* increased between 1982 and 2016 across the Atlantic. For *D. acuminata* and for *Alexandrium* spp., this study projects a northward shift globally, but less so in the shelf seas. The expectation in this study of a general northward shift for most species in the coming century is similar to that suggested by Barton et al. (2016), who, using similar models, found a north and eastward shift using presence data from the continuous plankton recorder and climate data with a one degree resolution. The authors found that, of the 87 species assessed, most diatoms and dinoflagellates showed this pattern. *Karenia mikimotoi* in particular is one species that is frequently cited as moving further northwards around the UK (Davidson et al., 2009; Bresnan et al., 2013). The results here show that it is likely to exhibit a northwards shift within the shelf seas, and globally, but not to the same extent as most of the other species. *Prorocentrum lima* however does show a much greater latitudinal shift in this study, consistent with Glibert et al. (2014) who found that *Prorocentrum* spp. would have a greater expansion in northern Europe in the future, compared with *Karenina* spp. Glibert et al. (2014) projected changes in pelagic *Prorocentrum* spp. and *Karenia* spp. in north-west Europe, based on climate projections and assumptions of future nutrient inputs, and found that both genera would expand in the region, increasing vulnerability of coastal ecosystems and impacts of HAB events. Comparison of the maps of future suitable area for *Prorocentrum* spp. from this study and Glibert et al. (2014) show that both studies show an increase in suitability in the eastern North Sea towards the end of the century. This study does not show the same increased suitability in the southern North Sea or English Channel as Glibert et al. (2014). This could potentially be owing to the different climate model used in each study, or because the Glibert species were pelagic as opposed to the benthic *P. lima*. Glibert et al. found a smaller increase in *Karenia* spp. suitability in the north east Atlantic compared with *Prorocentrum* spp., consistent

with this study. The changes in suitability found in this study, and these other studies emphasize the importance of regional long- and near-term forecasting and risk assessment in reducing the impacts of these species. The different extents of the expansions and latitudinal shifts for different species found in these studies support the idea of a future "shift and shuffle" in algal communities suggested by Barton et al. (2016).

Species distribution models assume that the tolerances and preferences of species relative to environmental conditions remain the same and do not take into account potential for adaptation. Some HAB species may not be able to adapt to new temperature and stratification regimes or changes in variability, such as *A. fundyense*, which in 2010 in the Gulf of Maine had growth constrained by stratification, causing an early diatom bloom and subsequent nutrient depletion (McGillicuddy et al., 2011). The lack of nutrients meant that the resting cysts from the previous year were unable to grow. However, in laboratory experiments on *A. minutum*, this species was found to physiologically and genetically adapt to changing pH and temperature conditions (Flores-Moya et al., 2012). This example illustrates the complexity of predicting the physiological and adaptation responses to climate change. Experiments can be combined with climate data to investigate how a species would respond to projected future conditions, as was done for dinoflagellate species in the Caribbean region (Kibler et al., 2015). The empirical growth function of *Alexandrium* was determined by Bill et al. (2016) based on temperature and salinity experiments, and historical bloom risk determined. Nearly all historical bloom occurrences occurred within the periods of identified bloom risk. Such experiments can help to determine if the future conditions predicted by a model are really suitable for a bloom or toxin formation.

With HABs, there is not necessarily a strong correlation between species abundance and toxin production (Hinder et al., 2011), but the models in this study are useful in projecting where the species might occur in the future. To predict individual events, local and near-term environmental factors, which are required for a bloom to form must be considered, such as irradiance, cloud cover, precipitation, run-off, and winds (Davidson et al., 2009; Barnes et al., 2015; Wells et al., 2015). Biogeochemical modelling of the North Sea has shown that primary production is expected to increase over the coming century due to climate change, and the annual onset of spring phytoplankton blooms will occur earlier in the year (van der Molen et al., 2013), and may extend for longer periods of time (Marques et al., 2010; Moore et al., 2011). In some areas the duration of stratification and the spring blooms will be extended, while in others they will remain the same, due to local conditions, particularly wind, and current (van der Molen et al., 2013). A measure of stratification was included in this study but further, more detailed, modelling could attempt to incorporate these seasonal meso-scale aspects of wind and rainfall to achieve more specific near-term predictions of bloom formation, as has been attempted for *Pseudo-nitzschia* spp. (Anderson et al., 2009). An increased algal growth rate caused by environmental conditions may result in nutrient limitation for blooms (Hall-Spencer and Allen, 2015), adding a further complication to predictions and long-term projections. Moore et al. (2015) modelled the responses of *Alexandrium* to upwelling winds and circulation in Puget Sound using mechanistic models, and were able to determine the effects of atmospheric heating, river flows and ocean inputs from upwelling on blooms. They concluded that by 2050, global warming

would lead to 30 more days a year with conditions favourable to *Alexandrium* blooms. Another study on *Alexandrium* found that suitable conditions for blooms would occur up to 2 months earlier and finish up to a month later in Puget Sound by the end of century (Moore *et al.*, 2011). Such a longer "window of opportunity" makes understanding, which species are likely to become more or less prevalent vital for monitoring and early warning systems.

Species distribution modelling is a useful tool for understanding the future changes in marine environments, but it is easy to over-interpret the results. Many researchers have been sceptical about the utility of such models (Bell and Schlaepfer, 2016). There are many ecological processes, which are not captured by the model used here, and without consideration of these processes the modelling is oversimplified and measures of fit can be misleading (Bell and Schlaepfer, 2016). It is important that the results of the modelling from this study are taken as relative measures of the suitability of the environment in the broadest sense for a bloom to form, providing all other environmental processes come together at the local scale, and not as a definite prediction of where and when a bloom will form. Knowledge of relative suitability between species, location and time can be used to help us understand, which species might become more problematic in the future, and which to prioritize for monitoring and forecasting. Long-term studies can also be used to pick up species, which may not be of current concern but which may be so in the future. For example, in the west coast of North America previously relatively rare toxic species are being seen more frequently (Lewitus *et al.*, 2012).

In this study, bathymetry and hydrographic variables were used as the key drivers of HAB occurrence. As further climate projections become available, and particularly coupled biogeochemistry models, further variables can be included in distribution models, to investigate the roles for example of oxygen, pH, and nutrients. Reduced pH is known to increase the production of domoic acid in *Pseudo-nitzschia* species, even at levels of pH that can occur today (Tatters *et al.*, 2012). A biogeochemical modelling study of the north-west European shelf projected that in the English Channel and the Irish Sea diatoms would increase in number towards the end of the century, whereas the larger dinoflagellates would decrease because they are outcompeted (Artioli *et al.*, 2014). This work included the projected influences of ocean acidification, which in certain places and at certain times can cancel out the effects of other climatic factors, but in other instances can exacerbate them (Artioli *et al.*, 2014). Such studies could be combined with species distribution modelling to understand the specific requirements of different groups of organisms, along with their potential spatial distribution changes. Large-scale climate patterns, such as the Pacific Decadal Oscillation (PDO) and the North Atlantic Oscillation (NAO), can affect the occurrence of some HABs (Marques *et al.*, 2010) and so distribution modelling could be used to look at different phases of such cycles.

To drive the suitability models, presence records were obtained from global databases, which contain data submitted worldwide. Whilst this data was quality checked to remove anomalies and records unlikely to be correct (such as outside known geographic regions), it is not a perfect database of presence records, and can be biased. The dataset may omit certain regions where no data is collected, or has not been entered into the database, but the use of this data means that general global extents of algal occurrences are captured, and so most of the species' environmental envelope is used within the model. Limiting the model to more detailed data in Europe would mean that climatic conditions, such as temperature, are not captured in the distribution modelling, and so projecting to future warmer conditions is less robust. There are efforts within Europe to coordinate recording of HAB occurrences (such as http://haedat.iode.org/), and so as Europe-wide, species-specific, data are available in the future, and as a longer time series develops, it would be possible to make use of this less biased data in distribution modelling.

This study has shown that harmful algae and HABs are likely to occur further north on average around north-west Europe in the coming century, with some species' habitat suitabilities shifting faster and further than others. Suitability for most species increases in the central and northern North Sea. These changes have implications for aquaculture, recreation, and ecosystems. Understanding which species may become more prevalent in the future is important to marine management as it allows early intervention by implementing surveillance and mitigation measures to reduce the economic and ecological harm of these species, and can also raises awareness around shellfish grounds and among healthcare professionals. Routine recording of these species allows us to further understand the local conditions that cause each species to occur and produce toxins (Hinder *et al.*, 2011), and further records would allow these models to be refined. As more advanced climate modelling and forecasting are developed, this type of modelling output may be useful in marine spatial planning, such as when identifying certain coastlines for aquaculture. Changes to harmful algae occurrence and the nuisance caused is already a feature of a changing marine climate, and it will continue to be so, but studies such as this are highly valuable in anticipating and mitigating their impacts and improving surveillance.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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