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Climate change facilitated range expansion of the non-native angular crab *Goneplax rhomboides* into the North Sea

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ABSTRACT: The angular crab *Goneplax rhomboides* is native to the north-eastern Atlantic and Mediterranean Sea. It has rarely been reported from the North Sea, with no evidence of sustainable populations. Compiled survey data, however, revealed an increasing abundance of this species in the North Sea since 2000. The data were used to (1) describe the range expansion of the angular crab into the North Sea; and (2) to apply species distribution modeling (maximum entropy approach–MAXENT) to predict the potential habitats of this species. Habitats of species with a similar ecology were modeled to analyse habitat overlap and potential competition. The spatial and temporal patterns of records revealed that the expansion of the angular crab into the North Sea is due to natural larval dispersal rather than anthropogenic vectors. Modeled habitats of the angular crab showed a core distribution area along the Scottish coastline and in the southern North Sea. Sea bottom temperatures in February had the highest influence on the model results. We concluded that the angular crab has extended its distribution range from the north-eastern Atlantic to the North Sea, which was facilitated by an increase in water temperature and the prevailing hydrodynamics over the last decade. This was the first time that a benthic range expansion was observed in quasi real time for the North Sea. Habitats of the angular crab overlapped those of possible competitors to a large extent. However, co-existence of the species is expected rather than any negative effects resulting from the range expansion of the angular crab.

KEY WORDS: Temperature · Larvae drift · Currents · Species distribution modeling · SDM · Competition · Norway lobster · *Nephrops norvegicus* · Masked crab · *Corystes cassivelaunus* · Mud shrimp · *Callianassa subterranea*

INTRODUCTION

Range expansions of non-native species provide the opportunity for understanding factors influencing species range and niche dynamics (Alexander & Edwards 2010). The spatial distribution of species is limited by factors influencing positive population growth such as dispersal limitation, unfavorable abiotic conditions beyond the range limit or exclusion through negative interactions with other species. The success of an invasive species, therefore, depends on the colonisation opportunities which allow species to reach new locations, the ecological suitability of the new habitat, overcoming demographic contraints of small population size early in the establishment and the extension across the invaded area (Peterson 2003). It is assumed that climate change is globally one of the major drivers facilitating invasion and distributional shifts of species by changing environmental conditions and habitat suitability (Parmesan &

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Yohe 2003). Distribution shifts within the North Sea due to increasing water temperature are well documented for fish (Perry et al. 2005), as well as for plankton species (Beaugrand & Reid 2003). However, increases in intercontinental shipping and aquaculture activities are considered to be the most important vectors for invaders into the North Sea, and the main reason for non-native species occurring in 'hot spots' such as coastal areas. Prominent examples of the successful establishment of non-native benthic species in North Sea coastal areas are the Pacific oyster *Crassostrea gigas* and the American razor clam *Ensis directus* (Wehrmann et al. 2000, Gollasch 2006, Reise et al. 2006).

The angular crab *Goneplax rhomboides* (Linnaeus, 1758) is a relatively large brachyuran which is native to the north-eastern Atlantic (e.g. Clark 1986, Farina et al. 1997, Trenkel et al. 2007, Skewes 2008) and Mediterranean Sea (Cartes & Sarda 1992, Abello et al. 2002, Fanelli et al. 2007). It has been rarely recorded in the North Sea, with no evidence for sustainable populations. Recently, higher abundances of the angular crab were noted during fisheries surveys in the German Bight including records of juveniles as well as ovigerous females. These observations suggest that the angular crab might already be established in the south-eastern North Sea (Neumann et al. 2010).

We use compiled data from international surveys to reconstruct how the angular crab may have invaded from the north-eastern Atlantic into the North Sea. Species distribution modeling (maximum entropy approach–MAXENT) was applied to predict potential habitats of the angular crab in the North Sea. Species distribution models are empirical models relating present species distribution and environmental predictor variables to describe the potential habitat of a species where conditions are suitable for survival (Guisan & Zimmermann 2000, Elith & Leathwick 2009). They provide a tool to assess invasive potential of a non-native species and to anticipate key routes, arrival sites and initiation points for successful invasions (Peterson 2003). The same approach was used to model the potential habitats of the Norway lobster *Nephrops norvegicus*, the masked crab *Corystes cassivelaunus* and the mud shrimp *Callianassa subterranean*. These species are common in the North Sea and have ecological requirements similar to those of the angular crab, which gives reason to expect competition, especially for space.

We aim to answer the questions (1) how the angular crab reached the North Sea (vector), (2) what makes the North Sea suitable for the survival of this crab (habitat suitability), and (3) to analyse the habitat overlap in the North Sea between the angular crab and 3 common native crustaceans species with a similar ecology to assess potential competition between species.

METHODS

Data and data processing

Species occurrence data were obtained from the ICES co-ordinated International Bottom Trawl Survey (IBTS), the Netherlands Bottom Trawl Survey (BTS) and the German Autumn Survey in the Exclusive Economic Zone (GASEEZ). The survey grid is based on ca. 180 ICES statistical rectangles (1° longitude × 0.5° latitude = ca. 30 × 30 nautical miles) covering the whole North Sea. Twenty-four ICES rectangles in the southern North Sea and ca. 50 rectangles in the southern and central North Sea were annually fished by the German and Dutch IBTS. The Netherlands BTS covers ca. 90 and the GASEEZ covers 14 rectangles in the southern, central and northern North Sea. The angular crab was caught with 2 m (4 mm cod end mesh size), 7 m (20 mm) or 8 m (40 mm) beam trawls, as well as the Grande Ouverture Verticale (GOV; 20 mm). The ICES rectangles were used as a spatial unit to estimate the temporal changes in the geographical spread of the angular crab in the North Sea by summing the number of occupied rectangles per year. Abundance data were taken from the Netherlands Bottom Trawl Survey (BTS) and were given as individuals per 30 min haul duration (ind. 30 min^{-1}). Pearson's correlation was used to analyse linear relationships between years and records, abundance and number of occupied rectangles.

The Federal Maritime and Hydrographic Agency of Germany (BSH) provided weekly sea surface temperature (SST) data from the station White Bank (54° 49.8′ N 5° 32.4′ E)

Species distribution modeling (MAXENT)

The aim of empirical species distribution modeling is to quantify species-environment relationships by predicting environmental suitability for species as a function of the given environmental variables (Phillips et al. 2006). A maximum entropy approach (MAXENT) was used, which is considered to be one of the most effective methods for species distribution modeling (Elith et al. 2006), and was successfully applied to benthic species modeling in the North Sea (Reiss et al. 2011). The MAXENT algorithm uses species presence-only data to find a probability distribution, which is defined over the study area and satisfies a set of constraints derived from the occurrence data. Each constraint requires that the expected value of an environmental variable must be within a confidence interval of its empirical mean (the mean over the presences). Among distributions that satisfy the constraints, MAXENT chooses the one that maximises entropy, that is, the closest to uniform. Entropy, in this context, measures the amount of information that is contained in a random variable or unknown quantity (Phillips et al. 2004, Phillips et al. 2006). The output of the model is a distribution map which shows the probability of occurrence of the angular crab in the North Sea.

The choice of adequate environmental predictors for modeling is an important issue and ideally they should represent 3 main types of influences on species: (1) limiting factors (regulators) that have ecophysiological influence on species; (2) natural and human-induced disturbances and habitat characteristics which might influence species distribution and (3) resources defined as all matter and energy consumed by species (Guisan & Zimmermann 2000, Guisan & Thuiller 2005). Ten environmental variables were selected as predictors which are important factors influencing the spatial variability of epibenthic species in the North Sea (Callaway et al. 2002, Neumann et al. 2009b, Reiss et al. 2010) and representing all 3 kinds of influence on the species distribution mentioned above: bottom temperature in February and June as well as salinity in June (regulators), sediment parameters (mean grain size and mud content), hydrodynamic parameters (tidal stress and stratification) and depth (disturbances and habitat characteristic), annual primary production and chlorophyll *a* (chl *a*) (resources).

Data on bottom temperature and salinity were derived from the hydrodynamic Hamburg Shelf Ocean Model (HAMSOM) (Pohlmann 1996). The model's horizontal resolution is 12 min of latitude and 20 min of longitude with a vertical resolution of 19 layers. Data from the months of February and June 2000 were used for the distribution modelling.

Sediment data were collected during the sampling campaigns of the North Sea Benthos Project 2000 (NSBP 2000) and the MAFCONS project (Managing Fisheries to Conserve Groundfish and Benthic Invertebrate Species Diversity). All sediment data were compiled and interpolated to the entire area by inverse distance weighing.

Annual primary production data of the water column for the year 2000 were based on the ECOlogical North Sea Model HAMburg (ECOHAM1). The horizontal grid size of the numerical model is 20 × 20 km and the vertical resolution is 5 m for the upper 50 m with increasing layer thickness below 50 m up to a maximum of 19 layers.

Depth data were derived from the General Bathymetric Charts of the Oceans (GEBCO) global bathymetry data set from the British Oceanographic Data Centre with a spatial resolution of a 1 arc-minute grid (GEBCO 2003).

Chl *a* pigment concentrations were provided by the Marine and Coastal Information Services (MarCoast) project, based on remote sensing images derived from the Medium Resolution Imaging Spectrometer (MERIS). The concentration of chl *a* was derived from the sea surface between 2 to 15 m water depth, depending on the turbidity of the water. Mean values for the period February to April 2008 and 2009 were used in order to cover the spatial extent of the spring phytoplankton bloom which is characteristic for this region.

Data of peak wave stress and stratification were provided by the Proudman Oceanographic Laboratory (Liverpool, UK) and generated using a 3-dimensional hydrodynamic model (Davies & Aldridge 1993). Peak wave stress was calculated from a 1 yr model run covering the period September 1999 to September 2000, on an approximately 12 km grid. The stratification parameter 'S' was derived from the formulation presented in Pingree and Griffiths (Pingree & Griffiths 1978), using modelled M2 tidal velocities and measured depths.

Model evaluation

The species occurrence data were divided into 2 datasets by randomly selecting 70% of the species records as training data for the calibration of the model and 30% for testing the model. This split-sample approach is a common evaluation tool for datasets, providing a sufficient number of occurrence records which is e.g. >100 (Guisan & Zimmermann 2000). To examine the predictive model performance, receiver operator characteristic (ROC) curves were created and the area under the curve (AUC) was calculated. The AUC is a threshold independent index measuring the ability of a model to discriminate between sites where a species is present versus those where it is absent (Fielding & Bell 1997, Elith et al. 2006). Since the AUC test needs both presence and absence records, MAXENT uses 10 000 random background points in the study area as 'pseudo-absence' records. The AUC ranges from 0.5 for predictive discrimination no better than random to 1.0 for models with perfect predictive ability.

Analysis of variable contribution

The MAXENT program provides several methods to determine which of the predictor variables has the greatest influence on the prediction. Furthermore, MAXENT keeps track of which predictor variable in each iteration of the training algorithm contributes most to the best fit of the model (percent contribution). This measure depends on the path the MAXENT algorithm uses to increase the gain of the model. A path independent measure is the permutation importance. It uses the fitted model and is calculated by randomly permuting the values of a variable among the training presence and background data, and measuring the resulting decrease in training AUC following recalculation of the model. Results of both measures were normalised to percentages. In addition, the MAXENT program provides a jackknife test of variable importance where the model was calculated with only one of each variable and without this variable and just using the remaining ones. The influence of this procedure was tested for the training and test data as well as for the AUC of the test data.

Analysis of habitat overlap

For the analysis of habitat overlap between the angular crab, Norway lobster, masked crab and mud shrimp, pairwise comparison of the predicted habitat distribution was performed. For each species, the number of grid cells for which the predicted occurrence was likely or unlikely was determined. The probability that maximised Cohen's kappa was used as a threshold for each species. Cohen's kappa is an evaluation measure for species distribution models which is often used when a specific threshold level is required (see Fielding & Bell 1997). The percentage of the area with differences in the predictions was then calculated. Thus, the percentage of area disagreement gives the proportion of the area where the probability of occurrence of one species is above its threshold, whereas the probability of the compared model is below its threshold.

RESULTS

Records, abundance and spread of *Goneplax rhomboides*

Since 2000, 1402 angular crabs have been found at 135 locations in the North Sea (Fig. 1). Individuals were found in depths ranging from 25 to 110 m on predominantly muddy sediments. In 2000, the first 2 ind. were caught in the Moray Firth and at the south-western edge of the Fladenground along the 100 m depth contour (north-western North Sea). Subsequent records were predominantly made in the southern North Sea (Oyster Ground) where the angular crab was found for the first time in 2003 (Fig. 1). Both areas were directly influenced by Atlantic water masses entering the North Sea in the north via the Fair Isle current and in the south via the channel. Records ($r = 0.950$; $p < 0.001$) and abundance (ind. 30 min^{-1}) ($r = 0.907$; $p < 0.001$) of the angular crab increased significantly from 2000 to 2009 (Fig. 2A,B). Only few morphometric measurements and sex determinations were carried out during these surveys. However, the German Bight data revealed the regular occurrence of both sexes (21 females; 32 males), juveniles (7 ind.) and ovigerous females (6 ind.). Their carapace width ranged from 9 to 37 mm and their carapace length from 5 to 23 mm. In total, angular crabs were found in 28 ICES-rectangles. The number of occupied rectangles significantly increased from 2000 to 2009 ($r = 0.941$; $p < 0.001$) indicating a continuous spread over the study

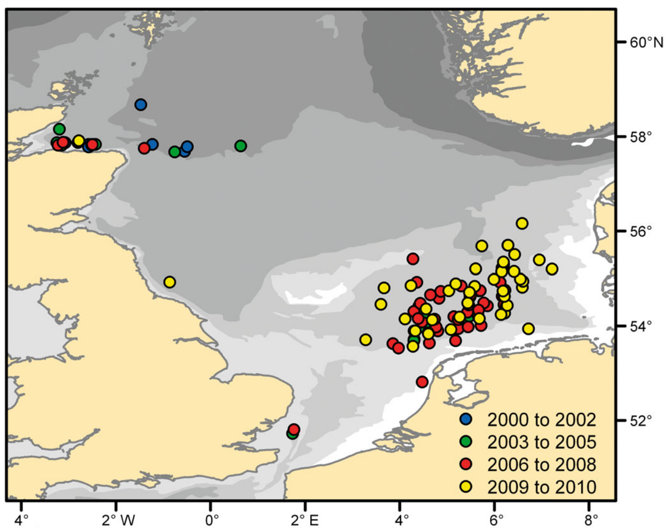

Fig. 1. *Goneplax rhomboides*. Occurrence of *Goneplax rhomboides* in the North Sea from 2000 to 2010. Grey scale: 20, 30, 50, 100, and 200 m depth contours

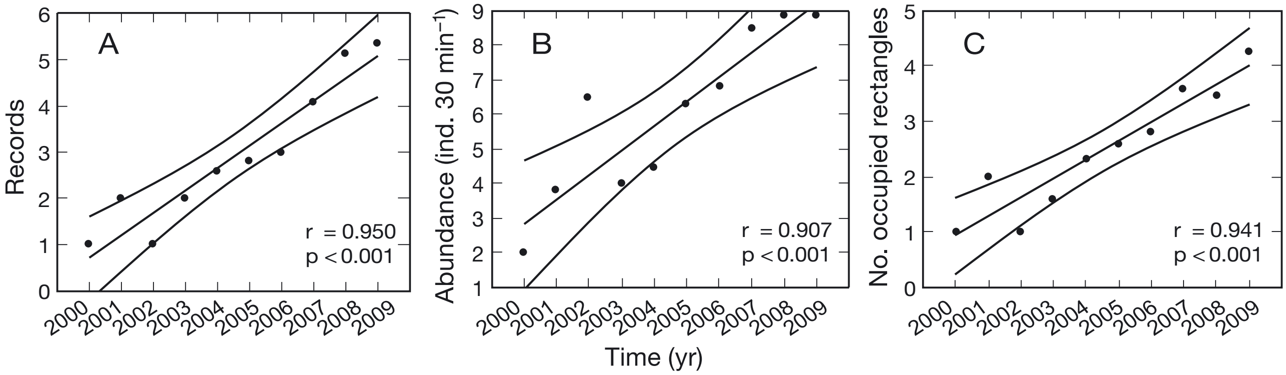

Fig. 2. *Goneplax rhomboides.* Significant linear relationships (Pearson correlation) and 95% confidence interval between time and logtransformed (A) records, (B) abundance per 30 min (8 m beam trawl), and (C) number of occupied ICES rectangles

area (Fig. 2C). This spread was from west to east starting with records at the western Dutch coast in 2003 and ending with records in the eastern parts of the German Bight in 2010 (Fig. 1).

Potential habitats of *Goneplax rhomboides*

Fig. 3 shows the predicted distribution of the potential habitats of the angular crab in the North Sea. AUC scores for training and testing data were 0.950 and 0.937 respectively, indicating very good model performance. A high probability of occurrence is predicted for the Oyster Ground and the Frisian frontal area (southern North Sea), as well as along the Scottish east coast (Moray Firth) up to the south-western edge of the Fladenground (north-western North Sea) along the 100 m depth contour (Fig. 3). Additionally, a high probability of occurrence is predicted for a small area in front of the Thames estuary (Southern Bight). Highest mean probabilities of occurrence (0.72 to 0.78) were found for the Oyster Ground. Analysis of variable contribution revealed that bottom temperature in February has the highest influence on the predicted distribution of the angular crab. Percent contribution was 28.8% and permutation importance 50.1% for bottom temperature in February (Table 1). This was substantiated by the jackknife analysis, which revealed that bottom temperature in February was the predictor variable with the highest gain (training, test and AUC data) when used in isolation as well as the highest decrease of gain when omitted. Mud content of sediments and tidal stress appear to be other important predictor variables with respect to percent contribution and permutation importance (Table 1). In contrast, jackknife analysis revealed lower importance of both variables. The response curve of bottom temperature in February peaked be-

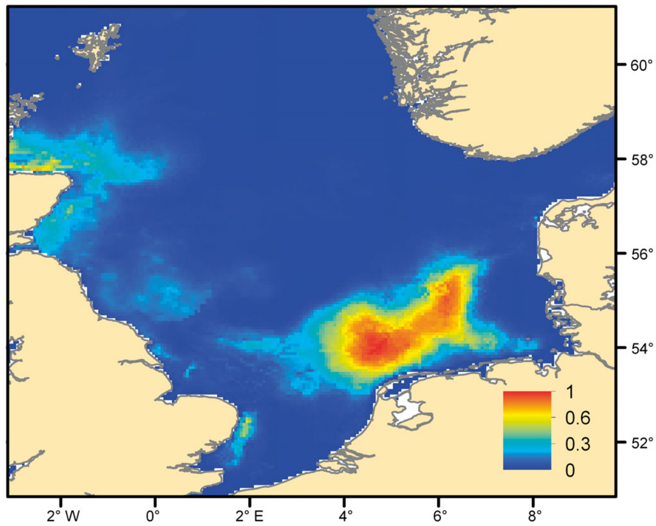

Fig. 3. *Goneplax rhomboides.* Distribution (probability of occurrence) of the crab in the North Sea (area under the curve [AUC] scores training and testing data = 0.950 and 0.937); depth contours are given in Fig. 1

Table 1. Relative contribution and permutation importance of the predictor variable to the MAXENT model

Predictor variable	Percent contribution	Permutation importance (%)
Temperature (February)	28.8	50.1
Mud content	20.2	12.4
Temperature (June)	15.4	0
Tidal stress	14.8	17.3
Depth	9.1	7.3
Primary production	7.8	6.2
Salinity June	2.5	0.6
Chlorophyll	0.8	3.8
Mean grain size	0.5	0.9
Stratification	0.1	1.4

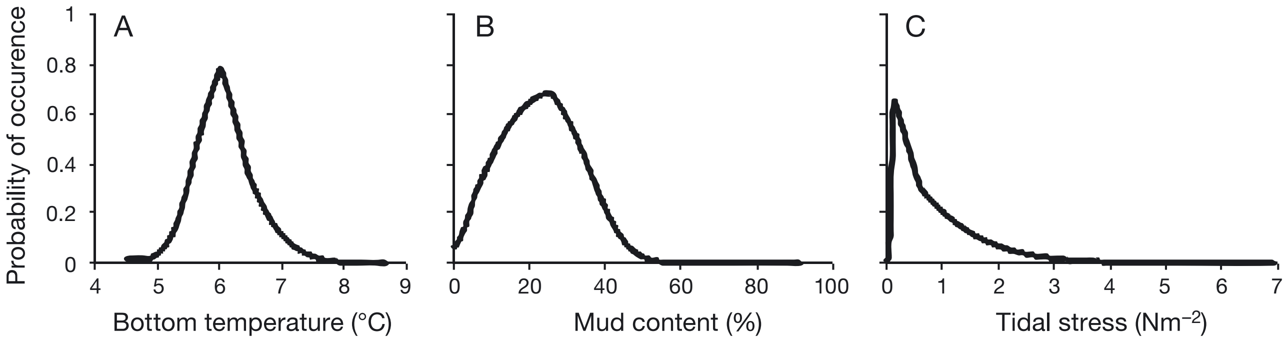

Fig. 4. *Goneplax rhomboides*. Response curves for (A) bottom temperature in February, (B) mud content of sediment and (C) tidal stress derived with MAXENT. Bottom temperature has the highest influence on the model results of the crab

tween 5.6 to 6.0°C giving indications of the preferred temperature range of the angular crab in this month (Fig. 4). Fig. 5 shows the SST in February for the Oyster Ground from 1969 to 2009, which corresponds to bottom temperature in this area due to the well mixed water column in winter. In contrast to previous periods, temperature of the last decade continuously fall within the preferred temperature range of the angular crab.

Analysis of habitat overlap

The MAXENT model performance was very good for the Norway lobster *Nephrops norvegicus*, the masked crab *Corystes cassivelaunus* and the mud shrimp *Callianassa subterranea* with AUC scores for training and testing data ranging from 0.831 to 0.922 (Fig. 6). The potential habitats revealed a wide distribution of the Norway lobster in the North Sea centering on the Fladenground, the Frisian frontal area and parts of the Oyster Ground (Fig. 6). Predicted habitats of the masked crab and the mud shrimp showed a greater restriction to the southern North Sea south of the 50 m depth contour. The masked crab showed a relatively uniform occurrence probability (ca. 0.5) in the southern North Sea while the core distribution area of the mud shrimp was at the Frisian front and in parts of the Oyster Ground with a occurrence probability >0.7 (Fig. 6). Overall, sediment parameters have the highest influence on the predicted distribution of the 3 species, but the analysis of variable contribution was not as clear cut as for the angular crab. Depth and bottom temperature in February (all 3 species) as well as primary production (mud shrimp) were also counted among the important predictor variables of the models. The highest overlap of predicted habitats existed between the angular crab and the mud shrimp. Of the habitats predicted for the angular crab, 90% were occupied by the mud shrimp, which is 48% of the total distribution area of the mud shrimp. The masked crab and the Norway lobster occupied 91 and 69% of the angular crab's habitats respectively, which is a relatively small proportion of the total distribution area of the 2 species (17 and 19% respectively).

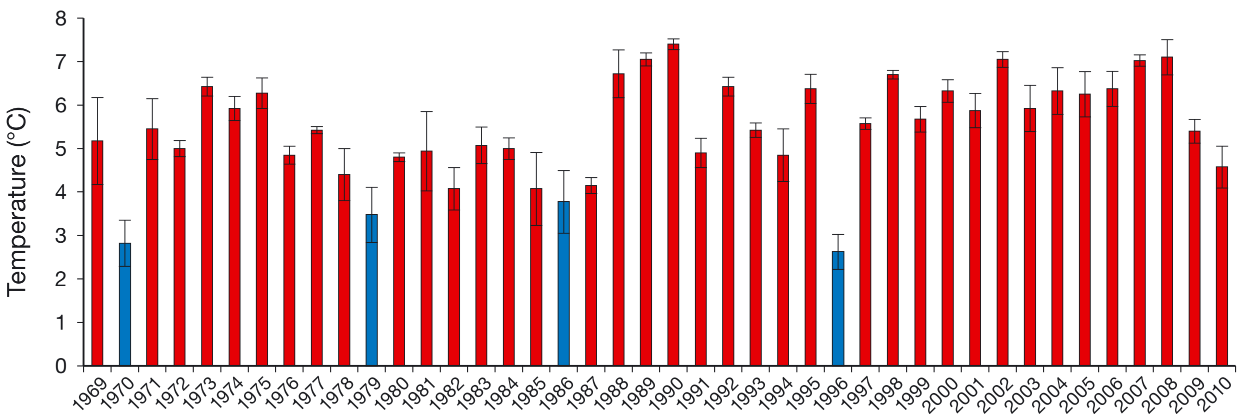

Fig. 5. Sea surface temperature (means ± SD) in February (coldest winter month in the southern North Sea) at the station White Bank (located in the centre of the distribution of the angular crab in the southern North Sea) from 1969 to 2009. Blue bars: exceptional cold winter reported in literature, see e.g. Neumann et al. (2009b)

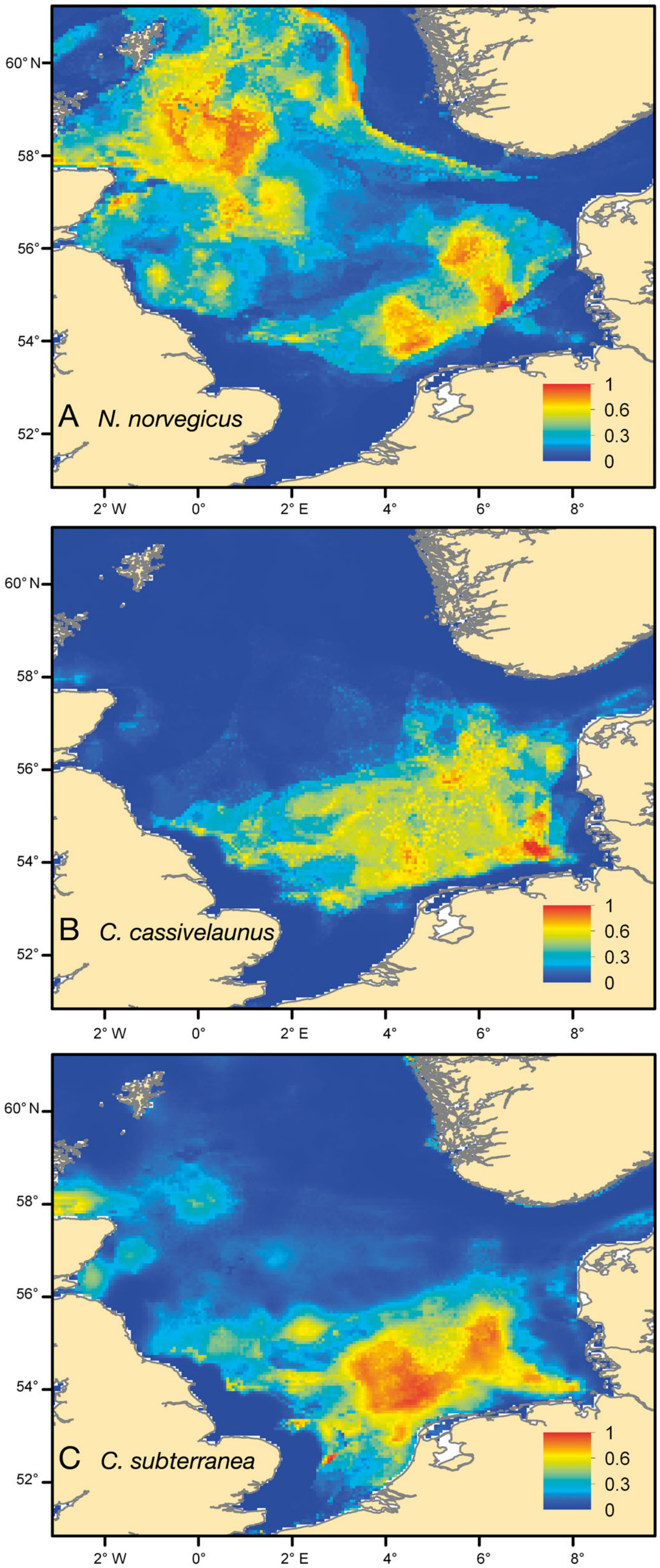

Fig. 6. Distribution map (probability of occurrence) of (A) *Nephrops norvegicus*, (B) *Corystes cassivelaunus* and (C) *Callianassa subterranea* in the North Sea (AUC scores training and testing data between 0.831 and 0.922). Depth contours are given in Fig. 1

DISCUSSION

Understanding how species expand, contract or shift their range is crucial for evaluating biodiversity patterns and how they might change with respect to a changing climate. Biological invasions as well as range expansions of species represent large-scale experiments on the underlying dynamics and evolution of range limits (Alexander & Edwards 2010). Here, *Goneplax rhomboides* extended its distribution from the Atlantic into the North Sea during the last decade. This is evidenced by a significant increase of records and abundance, as well as a significant spread of the angular crab in the North Sea since 2000. Before 2000, only single records of the angular crab in the North Sea exist, e.g. from the Northumberland coast in 1963 and from the Dogger Bank in 1998 (Moore 1987, d'Udekem d'Acoz 2001). However, it is unlikely that sustainable populations of the angular crab were overlooked in the past since the areas of recent findings were intensively monitored and fished for decades, e.g. within the IBTS. It cannot be excluded that abundance of the species was slightly underestimated during recent surveys, due to higher crepuscular activity of the angular crab (Atkinson & Naylor 1973), while sampling took place during the day. Also, the angular crab lives in burrows up to 15 cm beneath the surface (Rice & Chapman 1971) and efficiency of beam trawls is low for burrowing species (Reiss et al. 2006).

Presence as well as the spread of the angular crab indicates the origin and potential arrival pathway of that species into the North Sea. The first individuals of the crab were found in the Moray Firth and in the Fladenground area along the 100 m depth contour (northern North Sea). This area is largely influenced by the Fair Isle current entering the North Sea between Orkney and Shetland and roughly follows the 100 m depth contour to the south (Turrell et al. 1996). The Fair Isle current brings north-east Atlantic water into the North Sea. The water is derived from the Slope current flowing north along the north-west European continental shelf edge (Svendsen et al. 1991), where populations of the angular crab exist (Skewes 2008; R. J. A. Atkinson pers. comm.). The Fair Isle current is a major transport route for fish larvae and was associated with the variability of fish stock recruitment, plankton and epifauna in that area (Svendsen et al. 1991, Turrell 1992, Svendsen et al. 1995, Corten 1999, Neumann et al. 2009a). This suggests that angular crab larvae entered the North Sea via the Fair Isle current originating from populations west of Scotland. Into the southern North Sea larvae might be introduced via the British Channel with an origin in the Bay of Biscay or the Channel itself (Trenkel et al. 2007, Skewes 2008). Angular crab larvae were found for the first time in 2008 in continuous plankton recorder (CPR) samples in the southern North Sea (Lindley et al. 2010, Lindley & Kirby 2010). Inflow of Atlantic water via the Channel brings warm and more saline waters into the North Sea which has a large effect on temperature and salinity distributions in the southern North Sea (Otto et al. 1990, Pingree 2005). Leterme et al. (2008) identified an increased inflow of water masses via the Channel over the last decade as well as an exceptionally high inflow in 2001, 2 yr before the first record of angular crabs from the southern North Sea. The continuously high inflow via the Channel in the last decade may have resulted in a continuous supply of larvae which is critical for new populations to overcome Allee effects (negative population growth rates) in the beginning of their establishment (Dunstan & Bax 2007). Information about the planktonic larval duration or possible dispersal distances of the angular crab is sparse. Larvae of *Nephrops norvegicus* spend ~50 d in the planktonic state before settling and disperse up to 150 km in the Irish Sea (Hill 1990). Larvae of the northern shrimp *Pandalus borealis* can disperse 112 km in 105 d of planktonic larval duration (Siegel et al. 2003). However, these values strongly depend on species properties and the prevailing conditions in their habitat. In general, dispersal range can vary from a few kilometres to 400 km or even 1000 km (Eckman 1996). Thus, it is possible that the North Sea angular crab originated from populations west of Scotland and the Channel.

Larval dispersal is an important factor in defining and shaping species' range limits (Gaylord & Gaines 2000). Larvae have to find suitable habitats for the successful establishment of a population after reaching new locations (Peterson 2003). Our model results revealed that the Oyster Ground and the Scottish East coast are the most suitable areas for the angular crab in the North Sea. Even so, the model possibly underestimated the potential habitats of the angular crab because of the uncertainty of species distribution models when applied to range shifting species that are not in equilibrium with their new environment (Elith et al. 2010). It is likely that the angular crab has not yet reached all suitable habitats in the North Sea; therefore, species records (and model training data) might not be representative. However, we included data from the first 10 yr after the angular crab's arrival in the North Sea, and it is assumed that species records were already reflecting relatively stable relationships with the environment. The analysis of variable importance suggests that bottom temperatures in February were the most important determinant for the distribution of the angular crab in the North Sea. Late winter (January, February) sea temperatures of the North Sea increased markedly during the last decades (Beare et al. 2002, Dulvy et al. 2008), and the first occurrence of the angular crab coincided with an increase of SST anomalies in the Fair Isle region as well as exceptional high SST anomalies in the Oyster Ground (Hughes et al. 2008, Neumann et al. 2009a, Neumann et al. 2009b). In the Oyster Ground, water is coldest in February and March, which is critical for the survival of many benthic species and their larvae. Our results revealed that temperatures in February were within the range preferred by the angular crab for a period of at least 10 yr (Figs. 4 & 5). This suggests that continuous warm water in winter have favoured the survival of the angular crab population in the North Sea, as it was the case for *Crassostrea gigas*, when rising temperatures facilitated the successful reproduction and promoted the colonisation of the entire Wadden Sea (Diederich et al. 2005, Brandt et al. 2008).

When non-native species are introduced into an ecosystem, questions of ecological and possible economic consequences arise. Stomach analysis of fish such as cod, grey gurnard, poor-cod and scaldfish revealed that the angular crab is potentially a considerable additional food resource for North Sea fish (Biagi et al. 1992, Moreno-Amich 1994, Dubuit 1995, Fanelli et al. 2009). Additionally, the angular crab builds extensive burrows which might lead to competition, especially for space, with other burrowing species in the North Sea such as *Nephrops norvegicus*, *Corystes cassivelaunus* or *Callianassa subterranea*. On the other hand, competition for food resources is also conceivable, since all species except for the mud shrimp are opportunistic predators and scavengers feeding on crustaceans, molluscs and polychaetes. Our modeling revealed a spatial habitat overlap between the angular crab and the other 3 species. This overlap is highest between the angular crab and the mud shrimp. However, the MAXENT approach only predicted environmental suitability for species, while biotic interactions between species were not included. The co-existence of the above mentioned species is documented for several regions (e.g. Bay of Biscay; Loch Torridon, Scotland; Fishguard harbour, South Wales) and even interspecific connections between burrows are known, e.g. between the angular crab and the mud shrimp (Atkinson et al. 1977) or the angular crab and the Norway lobster (Atkinson 1974). Trenkel et al. (2007) found that direct competition between the angular crab and the Norway lobster seems to be reduced by different diurnal activity patterns in the Bay of Biscay. Moreover, habitats of both species seem to be separated on a small scale in the Irish Sea due to different demands on mud content (R.J.A. Atkinson pers. comm.). In general, the potential for competition between the different species in the North Sea is considered low, although a spatial niche overlap is evident. Long-term studies dealing with major invasions into the North Sea, e.g. in the case of *Crassostrea gigas* or *Ensis directus*, pointed out that neither of these species suppress native species, instead they increase diversity, stabilise the sediment and function as sediment traps for organic matter (Markert et al. 2010, Dannheim & Rumohr 2012). These results are in agreement with global analyses, which found no evidence that invasion resulted in the extinction of native species in the marine realm and that a 3 step process of invasion, accommodation and speciation resulted in an overall increase in biodiversity through invasion without catastrophic consequences (Briggs 2010).

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