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Modelling climate change effects on benthos: Distributional shifts in the North Sea from 2001 to 2099

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ABSTRACT

In the marine realm, climate change can affect a variety of physico-chemical properties with wide-ranging biological effects, but the knowledge of how climate change affects benthic distributions is limited and mainly restricted to coastal environments. To project the response of benthic species of a shelf sea (North Sea) to the expected climate change, the distributions of 75 marine benthic species were modelled and the spatial changes in distribution were projected for 2099 based on modelled bottom temperature and salinity changes using the IPCC scenario A1B. Mean bottom temperature was projected to increase between 0.15 and 5.4 °C, while mean bottom salinity was projected to moderately increase by 1.7. The spatial changes in species distribution were modelled with Maxent and the direction and extent of these changes were assessed. The results showed a latitudinal northward shift for 64% of the species (maximum 109 km; brittle star *Ophiothrix fragilis*) and a southward shift for 36% (maximum 101 km; hermit crab *Pagurus prideaux* and the associated cloak anemone *Adamsia carciniopados*; 105 km). The relatively low rates of distributional shifts compared to fish or plankton species were probably influenced by the regional topography. The environmental gradients in the central North Sea along the 50 m depth contour might act as a 'barrier', possibly resulting in a compression of distribution range and hampering further shifts to the north. For 49 species this resulted in a habitat loss up to 100%, while only 11 species could benefit from the warming in terms of habitat gain. Particularly the benthic communities of the southern North Sea, where the strongest temperature increase was projected, would be strongly affected by the distributional changes, since key species showed northward shifts and high rates of habitat loss, with potential ramifications for the functioning of the ecosystem.

1. Introduction

In the marine realm, anthropogenically induced global climate change can affect a variety of physico-chemical properties (Hoegh-Guldberg and Bruno, 2010) with potentially wide-ranging biological effects on physiology, phenology, adaption and distribution of species (Brierley and Kingsford, 2009; IPCC, 2014). These processes can result in altered community structures and diversity patterns (Doney et al., 2012), caused by species physiological intolerance to new conditions, altered dispersal patterns, and changes in species interactions.

Globally, climate change has been shown to be one of the key drivers, which causes distributional shifts of species by changing environmental conditions and habitat suitability (Parmesan and Yohe, 2003), with evidence for latitudinal and altitudinal shifts in species distribution (Parmesan and Yohe, 2003; Thuiller, 2004; Lenoir et al., 2008; Chen et al., 2011; Hiddink et al., 2015). Although climate change effects are often assessed on a global scale, regional changes, which are spatially highly heterogeneous, can be more relevant in the context of ecological response of species and communities to climate warming (Walther et al., 2002).

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The water temperature of the northern European shelf seas is increasing more rapidly than the adjacent land masses and the global average (MacKenzie and Schiedek, 2007). For example, the winter bottom temperature in the North Sea has already risen over the second half of the last century (Beare et al., 2002) by 1.6 °C within 25 years (Dulvy et al., 2008; Neumann et al., 2008). Forecasts for the North Sea until 2099 projected the annual volume-averaged temperature to increase by about 1.73 °C (Mathis, 2013), while the increase in bottom temperature range between 0.15 °C in offshore and 5.4 °C in coastal regions.

Due to the increasing water temperatures, distribution shifts in the North Sea were documented for fish (Perry et al., 2005; Ehrich et al., 2007), plankton and benthic species (Beaugrand and Reid, 2003; Hiscock et al., 2004; Rees et al., 2007; Kröncke et al., 2011; Hiddink et al., 2015). For benthic species, distributional shifts were often observed in the transitional region, where Lusitanian and Boreal species co-occur close to their physiological tolerance limits. With increasing water temperatures Lusitanian species showed a range extension to the north, while the distribution of Boreal species showed a general decrease in the south (Mieszkowska et al., 2006; Jansen et al., 2007). Not only the species within the transitional region, also intertidal species, which are assumed to live close to their physiological tolerance limits, can serve as early indicators of climate change effects (Mieszkowska et al., 2006; Wethey and Woodin, 2008).

These observations of benthic species distribution shifts are mainly based on compiled monitoring data and long-term time series (Kröncke et al., 2011, 2013; Birchenough et al., 2015; Hiddink et al., 2015). Both are important to understand and assess how benthic species have responded to anthropogenic impacts and climate warming in the past and present, but are often limited in their spatial and temporal resolution and restricted to more easily accessible coastal ecosystems. Distribution patterns and shifts on large spatial scales can be assessed using Species Distribution Models (SDMs), which are statistical tools that combine observations of species occurrence or abundance with environmental variables (Elith and Leathwick, 2009). The application of SDMs in assessing the distribution of marine species has increased considerably in the last years, not only as a method to better understand species distribution patterns on various spatial scales, but also as a tool for ecosystem management and marine spatial planning (reviewed in Robinson et al., 2011; Reiss et al., 2015). For the North Sea several studies have used SDM to model the distribution of benthic species on a more local scale (Degraer et al., 2007; Meiβner et al., 2008; Willems et al., 2008; Meiβner and Darr, 2009) and for the entire region (Reiss et al., 2011; Neumann et al., 2013). Furthermore, these modelling approaches enable forecasting of distribution shifts in response to climate change by incorporating scenarios of climate driven changes in hydrographic parameters (e.g. sea temperature) into the modelling process. For example, Jones et al. (2013) applied SDMs to assess the distribution of the non-native Pacific oyster in UK waters (North Sea) in the present and in the future based on modelled changes of the sea surface temperature.

The understanding of species distribution patterns and forecasting responses to future climate changes is of fundamental importance for effective management and conservation of biodiversity (Hannah et al., 2002). Although climate change is supposed to severely affect benthic communities in the future, our understanding of distribution shifts and large scale distribution patterns especially of subtidal offshore species is limited (Birchenough et al., 2015).

Bottom temperature and salinity are important hydrographic variables structuring benthic communities (Kröncke et al., 2011). In the marine realm, projected forecasts of environmental variables relevant to subtidal systems are scarce, especially on a large spatial scale. To assess the response of North Sea benthic species to the projected climate change, we modelled and projected for the first time the distribution of 75 selected North Sea invertebrates species in response to projected bottom temperature and salinity increase based on Intergovernmental Panel on Climate Change (IPCC) scenario A1B for the year 2099 (Mathis and Pohlmann, 2014). The A1B scenario is characterised by a future world of very rapid economic growth, global population that peaks in mid-century and declines thereafter, rapid introduction of new and more efficient technologies, and balanced use of fossil and non-fossil energy sources (IPCC, 2007). This scenario thus has been chosen in Mathis and Pohlmann (2014) as well as in our study to represent a moderate emission scenario. The rates of projected changes in water temperature and salinity are similar to the IPCC ensemble means for mid-latitudes of the northern hemisphere and the projected annual volume-average temperature by Mathis and Pohlmann (2014) is similar to field observations in the North Sea.

The objectives of the present study were: i) to project the spatial changes in species distributions, and ii) to determine the direction of distributional shifts and habitat loss or gain in response to climate change.

2. Material and methods

2.1. Study area

The North Sea is a continental shelf sea with increasing depth from south to north. In the northern North Sea, a summer thermocline establishes with relatively stable temperature conditions in the bottom waters (Reid and Valdés, 2011; Fig. 1). Due to decreasing water depth and increased tidal currents in the shallower central and southern North Sea the water column is mostly well mixed resulting in a higher seasonal variability of bottom waters (Reid and Valdés, 2011). Summer stratification occurs only intermittently south and east of the Dogger Bank. The general circulation pattern of the North Sea is influenced by the Gulf Stream. Around 90% of the Atlantic waters enter the North Sea in the north and less than 10% via the English Channel (Dooley, 1974; Turrell, 1992; Otto et al., 1990). The main outflow occurs through the northeastern open boundary via the Norwegian Coastal Current.

2.2. Species data

Benthic species data (presence and background) were extracted from three data sets for the period 1999 to 2004: epifauna data from the EU-Project 'Monitoring biodiversity of epibenthos and demersal fish in the North Sea'; in- and epifauna data from the EU-Project 'Managing Fisheries to Conserve Groundfish and Benthic Invertebrate Species Diversity' (MAFCONS), and infauna data 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). All benthos data were taxonomically checked and harmonised. Detailed information about sampling design and sample processing are given in Greenstreet et al. (2007), Callaway et al. (2007) and Rees et al. (2007), respectively. In total, data from 994 and 624 stations for infauna and epifauna species, respectively, were used for the analyses. In the following we refer to the present day period as '2001', where most of the benthos data were collected, although benthos data were sampled in a period from 1999 to 2004.

The species selection was based on previous studies of North Sea benthos communities (Künitzer et al., 1992; Zühlke et al., 2001; Callaway et al., 2002; Rees et al., 2007; Kröncke et al., 2011) and expert judgment. The criteria for the selection were: (i) species that