Small-scale benthos distribution modelling in a North Sea tidal basin in response to climatic and environmental changes (1970s–2009)

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ABSTRACT: We used small-scale species distribution models to predict the past and present spatial distribution of 7 characteristic macrofauna species in response to climatic and environmental changes that have been recorded for the Jade Bay (German Wadden Sea) over the last 4 decades (1970s to 2009). Four presence–absence modelling algorithms (RF, MARS, GLM, GBM) were merged within the ensemble forecasting platform 'biomod2'. The present spatial distribution (representing 2009) was modelled based on statistical relationships between species presences, true species absences and 7 high-resolution (5 m) environmental grids. The past spatial distribution (representing the 1970s) was then hindcast in response to climate change-induced (1) sea-level rise, (2) water temperature increase and (3) seagrass recovery due to de-eutrophication. The past distribution scenario was evaluated using independent historical macrofauna data from the 1970s. Present ensemble prediction maps accurately captured the potential ecological niches of the modelled species throughout Jade Bay (i.e. good to excellent true skill statistic [TSS] and area under the receiver operating characteristic curve [AUC] evaluation measures). The predicted present macrofauna distribution correlated most significantly with hydrodynamic conditions (submergence time, shear stress) and sediment characteristics (mud content). The past distribution scenario revealed significant changes in small-scale spatial distribution patterns of the characteristic modelled species (1970s to 2009) and showed a very good match with historical macrofauna data. Climate change-induced sea-level rise and its local implications for Jade Bay (changes in topography, tidal range and submergence time), and water temperature increase explained the potential macrofauna distribution shifts over the last 4 decades.

KEY WORDS: Ensemble models · Hindcasting · Sea-level rise · Water temperature increase · Wadden Sea World Heritage Site · Seagrass recovery · Marine ecosystems · Benthos

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INTRODUCTION

In recent decades, severe climatic and environmental changes have been observed in coastal waters (e.g. water temperature increases, sea-level rise, changes in coastal morphology), shelf seas (temperature increase, acidification) and the open oceans (acidification), which has resulted in pronounced changes in the

abundance and spatial distribution of characteristic marine species (Fujii & Raffaelli 2008, Wolff et al. 2010, Kröncke et al. 2011, 2013, Fujii 2012, Birchenough et al. 2015, Hiddink et al. 2015). Predictive modelling of potential changes in the distribution patterns of vulnerable ecological communities and endangered or invasive species can be useful in testing hypotheses regarding the role of these changing environmental factors on species distributions, providing valuable guidelines for global or regional nature conservation and management purposes (Franklin 2010, Reiss et al. 2014). Species distribution modelling (SDM) is still a novel discipline for marine ecosystems compared to the broad array of terrestrial applications (Robinson et al. 2011). Ecosystem management in the marine environment is often confronted with fragmentary information on the spatial distribution of marine species and habitats (Reiss et al. 2011, Robinson et al. 2011). SDM techniques provide the tools needed to reduce these gaps in knowledge by calculating full-coverage species distribution maps, correlating sparse biotic data with environmental grid layers (Guisan & Zimmermann 2000, Guisan & Thuiller 2005). Full-coverage and high-resolution environmental data are now more readily available due to recent technological advances, including improved acoustic remote sensing techniques, satellite observations and physical models (Brown et al. 2011, Reiss et al. 2014). Furthermore, innovations in modelling methods (e.g. Elith et al. 2006, Elith & Graham 2009, Franklin 2010) and software packages (e.g. OPENMODELLER, de Souza Muñoz et al. 2011; MODECO, Guo & Liu 2010) enable the user to compare the model performance of multiple modelling algorithms. The ensemble forecasting platform BIOMOD (Thuiller et al. 2009) and its updated version 'biomod2' (Thuiller et al. 2015) allow the user to merge different modelling methods (i.e. classification, regression and machine learning techniques) into a so-called 'ensemble model', reducing the uncertainties arising from using a single algorithm method (Araújo & New 2007, Thuiller et al. 2009). Numerous SDM studies recommend comparing and/or merging multiple modelling techniques (e.g. random forest, generalized linear models, multivariate adaptive regression splines), and calculating different evaluation measures (e.g. Cohen's kappa, area under the receiver operating characteristic curve) (e.g. Elith et al. 2006, Araújo & New 2007, Reiss et al. 2011, 2014, Georges & Thuiller 2013, Hijmans & Elith 2016).

The Jade Bay is a tidal basin in the German part of the UNESCO Wadden Sea World Heritage Site. It is under the protection framework of numerous national (e.g. 3 designated national parks in Ger-

many) and international environmental legislations (e.g. Ramsar Convention, European Habitat- and Birds directive) (Wolff et al. 2010). Because of their relatively sessile habit, benthic species are ideal organisms for small-scale SDM, and are important indicators of environmental changes and disturbances (Herman et al. 1999). Furthermore, the marine benthos is an important food source for secondary consumers (e.g. crustaceans, fish and birds), and plays a key role in nutrient cycling and detritus decomposition (Reiss et al. 2011). Thus, knowledge about potential changes in the spatial distribution of characteristic benthic species is essential for understanding and management of the whole Wadden Sea ecosystem—particularly with regard to potential changes in the food web.

Three macrofauna studies that were carried out in the Jade Bay during the 1970s and in 2009 revealed significant changes in the abundance and spatial distribution of characteristic benthic species (Dörjes et al. 1969, Michaelis 1987, Schückel & Kröncke 2013, Schückel et al. 2015a). These changes were linked to strong climatic and environmental changes that were recorded in the study site over the last 4 decades, such as sea-level rise, water temperature increase, seagrass recovery due to de-eutrophication and species introduction (Schückel & Kröncke 2013, Schückel et al. 2015b). Long-term quantitative benthic studies conducted in the Wadden Sea (Riesen & Reise 1982, Jensen 1992, Kraan et al. 2011) and North Sea (Kröncke et al. 2013) have also indicated strong changes in benthic community structures in response to climatic and environmental changes. However, to our knowledge, few studies have applied SDM to the protected Wadden Sea, focusing on the identification of present suitable habitats for conservation purposes (e.g. macrobenthic species in the western Dutch Wadden Sea: Ysebaert et al. 2002, Kraan et al. 2013; *Zostera marina* in the Ems estuary: Bos et al. 2005, Valle et al. 2013). In the subtidal North Sea, most SDM was carried out on a local scale and modelled the potential present distribution of marine benthic invertebrates (Degraer et al. 2008, Meißner et al. 2008). More recent SDM studies investigated the potential future distribution of native (Jones et al. 2013a, Valle et al. 2014) and invasive species (Jones et al. 2013b, Raybaud et al. 2014) under climate change scenarios, or focused on the entire North Sea (Reiss et al. 2011, Neumann et al. 2013).

The purpose of this study was to apply SDM to predict present and past spatial distributions of characteristic macrofauna species in response to the cli-

matic and environmental changes recorded for the Jade Bay since the 1970s. The availability of high-quality species presences and true species absences (for 2009), multiple high-resolution (5 m) environmental grids (for 2009) and independent historical macrofauna data (for the 1970s) offered a unique opportunity to hindcast and evaluate small-scale macrofaunal distribution patterns for this UNESCO-protected tidal basin. We hypothesized that (1) the present prediction maps accurately represent the potential ecological niches of the 7 characteristic macrofauna species in Jade Bay, (2) characteristic macrofauna distribution shifts between the 1970s and 2009 were attributed to sea-level rise, water temperature increase and seagrass recovery due to de-eutrophication, and (3) the independent historical macrofauna data from the 1970s would accurately evaluate our 1970s past distribution scenario.
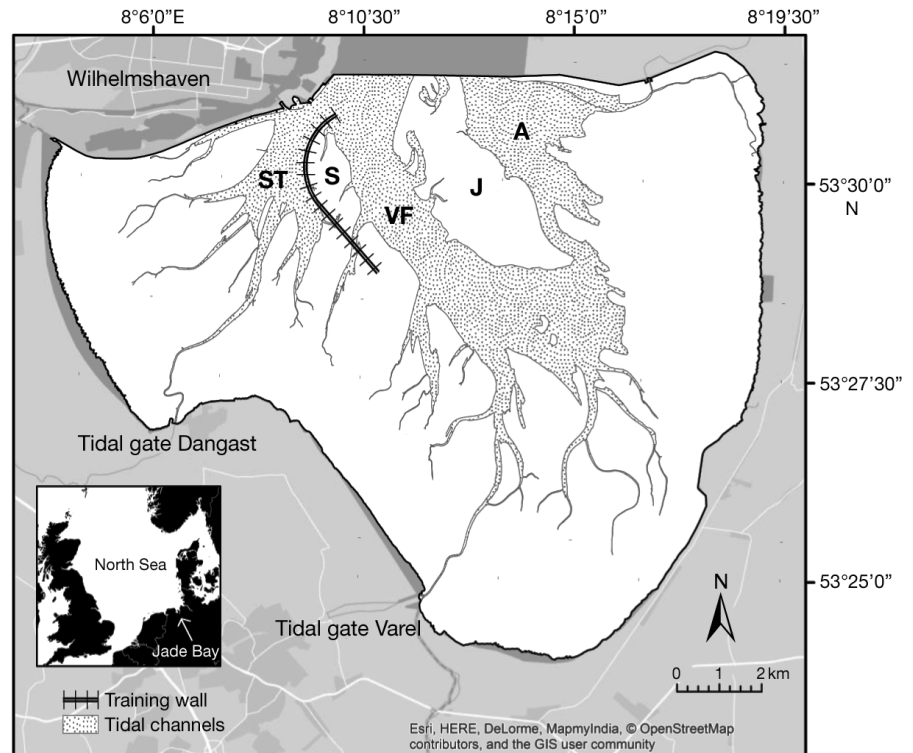

Fig. 1. Study area in the Jade Bay, showing the 3 tidal channels (ST: Stenkentief; VF: Vareler Fairway; A: Ahne), the training wall (built in the 1890s), 2 topographic ridges (S: Schweinsrücken; J: Jappensand) and the 2 tidal gates (near the towns of Dangast and Varel)

MATERIALS AND METHODS

Study area

The Jade Bay (Fig. 1) is a macrotidal basin (tidal range: ca. 3.8 m) with a total area of ca. 158 km^2. It is located in the German National Park of Lower Saxony, and is part of UNESCO's Wadden Sea World Heritage Site. During each tide, strong ebb and flood currents transport ca. 400 000 000 m^3 of North Sea water through a narrow bottleneck east of Wilhelmshaven in and out of Jade Bay (Götschenberg & Kahlfeld 2008). During low tide, ca. 114 km^2 of tidal flats are exposed to atmospheric conditions and only 3 large tidal channels and the tidal inlets remain permanently submersed (Schückel et al. 2013, 2015a). The 5.8 km long training wall, built in the 1890s, ensures the accessibility of the Wilhelmshaven Harbour (Götschenberg & Kahlfeld 2008). The training wall regulates the tidal currents, resulting in muddier sediments in the western and southern parts of the bay (Linke 1939). Three different sediment types can be distinguished: sandflats, mixed sediments and mudflats. Furthermore, mussel beds (*Mytilus edulis*, 2.07 km^2 in 2009) and seagrass beds (*Zostera noltii*,

10.9 km^2 in 2008) form characteristic biogenic structures within the bay (see Schückel & Kröncke 2013). Water column salinity varies between 26 and 30 (Böning & Schnetger 2011).

Macrofauna data

The macrofauna (>0.5 mm) data (i.e. species presences and absences) were collected between April and July 2009. A total of 128 stations covering the entire intertidal area of Jade Bay were established along 8 transects, according to the sampling design of Michaelis (1987) for the 1970s; these transects adequately sampled the 3 different sub-habitats (sandflats: 18 stations; mixed sediments: 29 stations; mudflats: 81 stations). In addition, 29 stations were sampled in the subtidal area of Jade Bay, following the sampling design of Dörjes et al. (1969) for the 1970s. In total, 157 stations were sampled during 2009 (Fig. 2). The intertidal stations were sampled during low tide with a 10 cm diameter cylindrical corer to a depth of 30 cm (total surface: 0.008 m^2, 5 replicates); subtidal stations were sampled via motorboat (0.02 m^2 van Veen Grab, 5 replicates) or onboard the RV

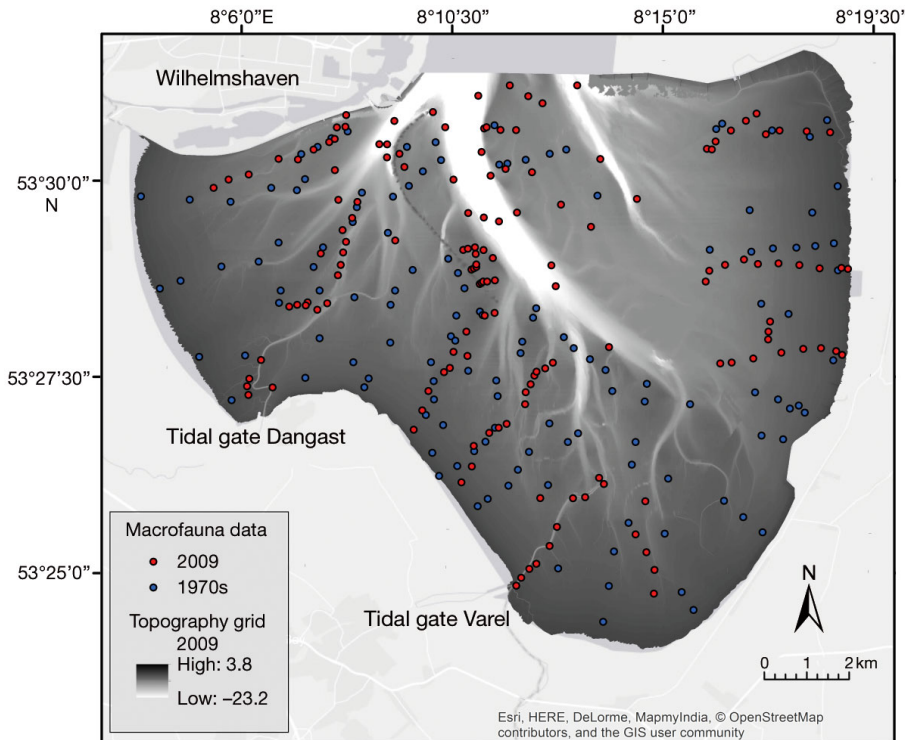Fig. 2. Sampled macrofauna data used for species distribution modelling (sampling campaign: 2009, n = 157) (Schückel et al. 2013) and model evaluation (sampling campaign: 1976/77, n =135) (Michaelis 1987) plotted on the topographic grid for 2009 (Coastal Research Station Norderney)

'Senckenberg' (0.2 m² van Veen Grab, 2 replicates). Methods and sampled surface areas were comparable between inter- and subtidal sampling campaigns (Schückel & Kröncke 2013, Schückel et al. 2015a). Statistical analysis revealed that the replicates and spatial resolution of the samples were sufficient to detect the spatial distribution/presence of the dominant species. For further details on sampling procedures and laboratory work, see Schückel & Kröncke (2013) and Schückel et al. (2015a).

For SDM, the 7 characteristic macrofauna species were chosen according to the criteria that they (1) encompass a wide variety of habitat preferences, (2) model broad and narrow ecological niches, (3) account for diversity (4 different taxa), and (4) model species that showed a significant increase or decrease in abundance over the last 4 decades (Schückel & Kröncke 2013). Based on the analyses of Schückel & Kröncke (2013), we selected the following 7 dominant species: 2 bivalves (*Macoma balthica*, *Cerastoderma edule*), 2 polychaetes (*Scoloplos armiger*, *Arenicola marina*), 1 oligochaete (*Tubificoides benedii*) and 2 gastropods (*Peringia ulvae*, *Retusa obtusa*). For details on the different species' biological traits (feeding modes, mobility, habits) and the number of presences

and true absences used for SDM, see Table 3 and 'Results: Present macrofauna distribution'). The correct nomenclatural authorities of all 7 selected macrofauna species were based on the World Register of Marine Species (WoRMS 2015).

Environmental data

Present environmental grids (representing 2009)

Table 1 provides an overview of the 9 collected and processed environmental variables, the data type, units, reference period and associated data sources. In total, 7 predictor variables were used for SDM; 2 were omitted prior to the modelling procedure because of a high predictor collinearity (r > 0.7, Booth et al. 1994; see 'Materials and methods: Species distribution modelling').

The Institute for Biology and Chemistry of the Marine Environment (ICBM) provided the data for total organic carbon (TOC), mud and chlorophyll *a* (chl *a*) content, along with submergence time, shear stress and summer bottom water temperature (T_{sbw}). Samples were taken from the uppermost surface layer in Jade Bay for analyses of TOC, mud and chl *a* content, on a similar spatial and temporal scale as carried out for the macrofauna samples (Beck et al. 2013, Schückel et al. 2013). Tide-induced submergence time and shear stress were modelled with the Finite Volume Coastal Ocean Model (Fvcom, e.g. Chen et al. 2003) for the German Bight, with a focus on Jade Bay (horizontal resolution: 75 m) (Lettmann et al. 2010). For T_{sbw}, the Regional Ocean Modelling System (Roms, e.g. Haidvogel et al. 2008) with a horizontal resolution of 150 m was applied. Bottom water salinity (S_{bw}) was supplied by the Helmholtz-Centre Geesthacht (HZG), using the General Estuarine Transport Model (Getm) for the German Bight with a horizontal resolution of 1 km (Staneva et al. 2009). The topography grid was provided by the Coastal Research Station Norderney (NLWKN) and derived with Airborne Laserscan and Fan Echosounder (horizontal resolution: 5 m). The ArcGIS (ESRI) shapefile for *Z. noltii* beds was provided by the National Park Administration Wadden Sea Lower Saxony (NLPV), and ob-

Table 1. Environmental variables and associated information (a) the 7 variables employed in our species distribution modelling (SDM) and (b) the 2 variables omitted prior to SDM due to high predictor collinearity (>0.7, Booth et al. 1994). T_{sbw}: summer bottom water temperature; S_{bw}: bottom water salinity; p/a: present/absent; m.a.s.l.: m above sea level. Sources: NLWKN: Coastal Research Station Norderney; ICBM: Institute for Biology and Chemistry of the Marine Environment; SaM: Senckenberg am Meer; HZG: Helmholtz-Centre Geesthacht; NLPV: National Park Administration Lower Saxony Wadden Sea

	Data type	Unit	Reference period	Source
(a) Environmental variables used for SDM				
Submergence time	Modelled data	h d^{-1}	2009 (mean)	ICBM, K. Lettmann
Shear stress	Modelled data	N m^{-2}	2009 (mean)	ICBM, K. Lettmann
Mud content (<63 μm)	Sampled data	%	April–July 2009	ICBM, M. Beck
Chl a	Sampled data	mg m^{-2}	April–July 2009	ICBM, H. Freund, SaM, U. Schückel
T_{sbw}	Modelled data	°C	June/July 2011 (mean)	ICBM, K. Lettmann, A. Vanselow
S_{bw}	Modelled data	psu	2009 (mean)	HZG, C. Geimecke, J. Staneva
Zostera noltii beds	ArcGIS shapefile	p/a	2008	NLPV, G. Millat
(b) Environmental variables omitted prior to SDM				
Total organic carbon	Sampled data	%	April–July 2009	ICBM, M. Beck
Topography	Laserscan and hydroacoustic data	m a.s.l.	1999–2010	NLWKN, H. Westphal

tained by aerial monitoring and ground truthing.

All environmental point data were interpolated with Geostatistical Analyst in ArcGIS 10.2, using the ordinary kriging interpolation method. All processed environmental grids were converted with ArcGIS 10.2 to have the same extent (158 km^2), coordinate system (DHDN Gauss-Krüger zone 3) and resolution (5 m). Topographic data were preferred over bathymetric data because of their higher spatial resolution at the edges of Jade Bay, where important benthic habitats prevail. T_{sbw} during high tide were averaged over the months of June and July 2011 to avoid the effects of the cold winter in 2010/2011. Beck et al. (2013) revealed that most heavy metal contents in Jade Bay were below biologically harmful thresholds. Therefore, little impact of heavy metal pollution on the macrofauna distribution at the study site was assumed and thus neglected in this study.

Past distribution scenario (representing the 1970s)

Based on previous environmental surveys, the 2009 environmental variables submergence time, T_{sbw} and *Zostera* sp. beds were altered for the 1970s past distribution scenario. These variables showed the most significant changes throughout Jade Bay over the last 4 decades. Changes in macrofauna distribution patterns during the last few decades in the European Wadden Sea can be linked to climate change-induced sea-level rise, water temperature increase and de-eutrophication (after agricultural and industrial wastewater discharges) (Reise et al. 2008, Fujii

2012, Kröncke et al. 2013, Schückel & Kröncke 2013, Schumacher et al. 2014).

For the Jade Bay, a mean topographic increase of ca. 28 cm was calculated between the 1970s and 2009 (mean topographical difference between the 2009 and 1969 topography grid). The 1969 grid was provided by the NLWKN and derived from 2 maps: the topographic intertidal map of 1969 (scale 1:25 000) and the intertidal map for 1959 (scale: 1:5000). Götschenberg & Kahlfeld (2008) determined that a rise in the mean tidal range of ca. 10 cm has occurred since the 1970s (due to stronger mean high water vs. almost constant mean low water), which caused the abovementioned topography increase at the study site. Based on this topography increase (i.e. ca. 28 cm since the 1970s), a linear regression between the 2009 topography and the 2009 submergence time (at the 2009 intertidal sampling points) was calculated, and the potential 1970s mean daily submergence time was extracted from the regression line (Fig. 3). According to Fig. 3, the submergence time was increased by 1 h d^{-1} for the 1970s hindcast scenario (i.e. 0.5 h d^{-1} for each incoming tide). Summer sea surface temperatures in the western Wadden Sea have increased by ca. 1.5°C since the 1970s (Van Aken 2008); therefore, the T_{sbw} was decreased by 1.5°C for the 1970s hindcast scenario. Due to the tide-induced permanent mixing of the water column in the Jade Bay tidal basin (Linke 1939), sea surface temperature was assumed to be representative of changes in bottom water temperature. The past spatial distribution of the *Zostera* sp. beds was digitized with ArcGIS 10.2 from a 1970s historical map (Micha-
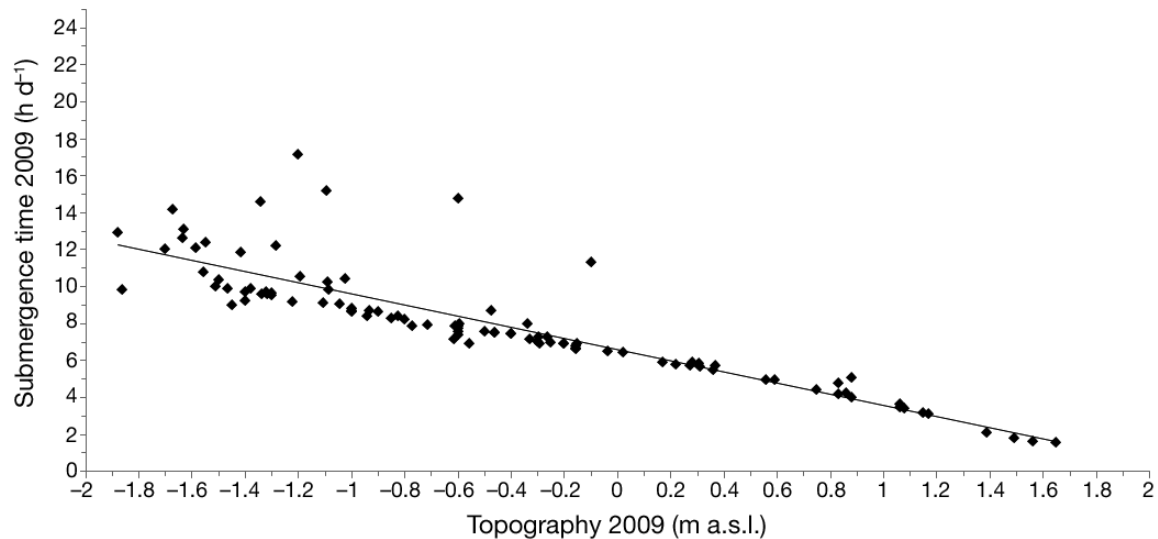
Fig. 3. Topography versus submergence time (for the 2009 intertidal sampling points); extraction of the potential 1970s mean daily submergence time from the regression line was based on a calculated mean increase of ca. 28 cm between the 1970s and the 2009 topographic grids (Coastal Research Station Norderney)

elis 1987). In the 1970s, *Zostera* sp. beds were ca. 8.2 km² smaller compared to the area encompassed in 2009 (see Schückel & Kröncke 2013 and Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m551p013_supp.pdf).

SDM: 'biomod2' ensemble forecasting platform

Model algorithms and settings

SDM correlates species presences or abundances with environmental variables for the same grid cell to calculate the species' ecological niche. Computer algorithms are then used to identify suitable habitats across a user-defined landscape in geographical space (Pearson 2007, Elith & Leathwick 2009). Because of the availability of true species absences, 4 commonly used presence–absence SDM techniques were selected for this study: 2 machine learning methods (random forest, RF: Breiman 2001; and generalized boosting models, GBM: Ridgeway 1999) and 2 regression-based methods (multivariate adaptive regression splines, MARS: Friedman 1991; and generalized linear models, GLM: McCullagh & Nelder 1989). A short description of the 4 applied and merged SDM algorithms and their respective key literature can be found in Table 2.

For the purpose of this study, the ensemble forecasting platform 'biomod2' v.3.1-64 (Thuiller et al. 2015) was applied for species distribution modelling, implemented in R v.3.2.1 (R Development Core Team

2015) (see Supplement 2 at www.int-res.com/articles/suppl/m551p013_supp.pdf). Both 'biomod' and its updated version 'biomod2' have been successfully applied in numerous recent terrestrial and marine SDM studies (e.g. Reiss et al. 2011, Jaeschke et al. 2012, Aguirre-Gutiérrez et al. 2013). Biomod2 enables the user to apply and compare 10 commonly used modelling algorithms (i.e. classification, regression and machine learning techniques). In addition, different evaluation measures can be calculated, such as Cohen's kappa, the true skill statistic (TSS) and the area under the receiver operating characteristic curve (AUC) (Thuiller et al. 2009, 2015). Furthermore, multiple modelling algorithms can be merged in the so-called 'ensemble model', accounting for inter-model variability and reducing the uncertainties arising from using a single algorithm method (Araújo & New 2007, Thuiller et al. 2009).

Biomod2 provides several ensemble building techniques, such as the mean of probabilities or committee averaging. In this study, the mean of probabilities of the selected models was used, which supplies more robust predictions than other ensemble building techniques (Marmion et al. 2009). In addition, the following model settings were altered from default parameters defined by Georges & Thuiller (2013): for GBMs, 3000 trees were used as fitting basis; for RF, 500 trees were built (see Reiss et al. 2011). To estimate the importance of each employed variable for the ensemble model, biomod2 uses a randomization procedure that is independent of the applied modelling algorithm. This procedure uses Pearson's corre-

Table 2. Presence/absence modelling methods merged within the 'biomod2' ensemble forecasting platform (Thuiller et al. 2015) and key references

Modelling technique	Description	Key references
RF: Random Forest	Classification and regression based model, generates multiple classification trees with a randomized subset of predictors, trees are aggregated by averaging	Breiman (2001), Prasad et al. (2006)
GBM: Generalized Boosting Models	The individual models consist of classification or regression trees, in an iterative process a final model is built by progressively adding trees while re-weighting the data poorly predicted by the previous tree	Ridgeway (1999)
MARS: Multivariate Adaptive Regression Splines	Non-parametric regression technique, combines linear regression, spline functions and binary response cursive partitioning, the coefficients differ based on the levels of the explanatory variables	Friedman (1991)
GLM: Generalized Linear Models	Regression models, extensions of linear models, allow for non-linearity (e.g. binomial or Poisson distributions) and non-constant variance structures in the data. A stepwise GLM is run using linear, quadratic or polynomial terms; the stepwise procedure either uses Akaike's or Bayesian information criteria (AIC or BIC) to select the most parsimonious model	McCullagh & Nelder (1989)

lation between the standard predictions (i.e. fitted values) and predictions where the environmental variable has been randomly permuted. Each variable importance score is then displayed as a rank value (i.e. 1 minus the correlation score), with high values indicating high importance of the predictor (Thuiller et al. 2009, 2015). To ensure comparability in the species-specific model, raw variable importance scores were standardized by dividing the score of each predictor by the sum of all predictor scores. Ensemble model response curves were calculated within biomod2 via the algorithm-independent evaluation strip method, recommended by Elith et al. (2005). Therefore, n − 1 variables were set constant to a fixed value (here: mean) and the obtained curve only showed the sensitivity of the model to the specific variable (Thuiller et al. 2015).

Because of high predictor collinearity (Pearson's correlation coefficient, r > 0.7; Booth et al. 1994) 2 environmental variables (TOC and topography) were omitted prior to the modelling procedure. TOC content was highly correlated with mud content (r = 0.82), and topography was highly correlated with shear stress (r = −0.80) and submergence time (r = −0.72). The remaining environmental grids had a maximum collinearity of r = 0.67 (submergence time and shear stress) and therefore fell below the critical threshold of r ≥ |0.7|. A major problem in SDM is that the combination of few species presences and many predictor variables easily leads to model overfitting. Due to this overfitting, model generalizability is reduced, and thus the transferability to new data (Vaughan & Ormerod 2005, Breiner et al. 2015). According to the rule of thumb that species presences should be 10 times larger than the number of environmental variables used for SDM (Harrell et al. 1996), we modelled with a minimum of 40 species presences and 7 environmental predictors that were proven to be essential for the marine benthos at the study site (Schückel et al. 2013, 2015a). We assumed a negligibly small sampling bias in our macrofauna data, as our sampling design captured the entire environmental gradient of the study site, and samples were taken with adequate distance (min. 50 m) for benthic species and full spatial coverage.

Model evaluation: TSS, AUC and independent historical macrofauna data

To assess model accuracy, species presences were randomly split into test data (30%) and training data (70%). In total, 40 runs species^{-1} (10 replicate runs algorithm^{-1}) were performed to account for model variability. Two evaluation measures were calculated within the biomod2 R package: TSS (Allouche et al. 2006) and AUC (Fielding & Bell 1997). In addition, to validate model predictions with an independent data
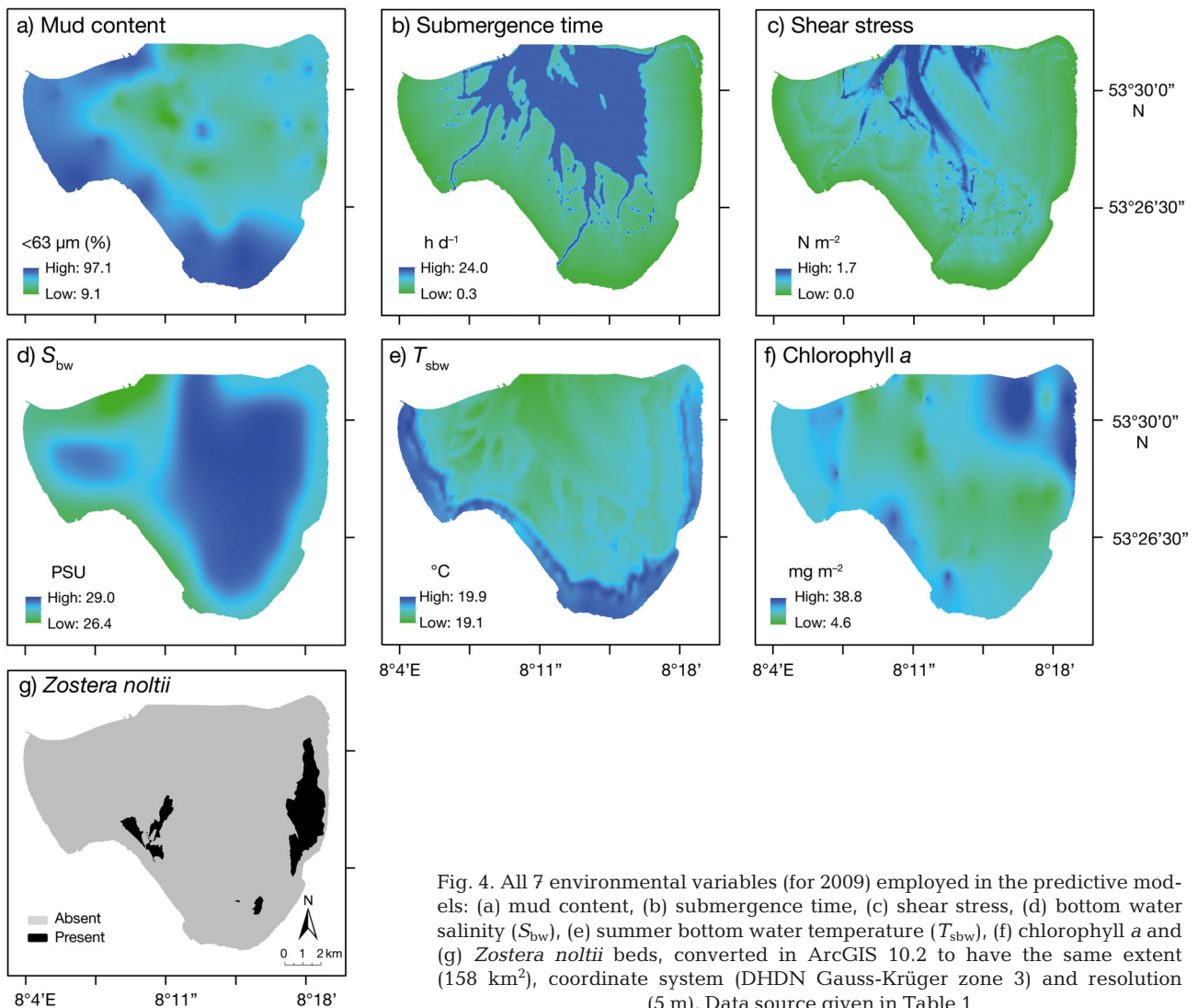
Fig. 4. All 7 environmental variables (for 2009) employed in the predictive models: (a) mud content, (b) submergence time, (c) shear stress, (d) bottom water salinity (S_{bw}), (e) summer bottom water temperature (T_{sbw}), (f) chlorophyll *a* and (g) *Zostera noltii* beds, converted in ArcGIS 10.2 to have the same extent (158 km^2), coordinate system (DHDN Gauss-Krüger zone 3) and resolution (5 m). Data source given in Table 1

set, the 1970s past distribution scenario was compared with historical macrofauna presences, sampled in the 1970s (summer 1976 and 1977) on a comparable spatial and temporal scale as the 2009 data (Fig. 2) (n = 135; details given in Michaelis 1987).

Both evaluation measures were calculated via the proportion of the 2 prediction types 'sensitivity' (correctly predicted presences) and 'specificity' (correctly predicted absences) in the error matrix. Sensitivity and specificity were used because they take into account all 4 elements of the error matrix derived from the test data (true and false presences and absences) (Pearson 2007). The TSS is a prevalence (proportion of presences relative to the number of sampled sites) independent alternative to Cohen's kappa, while retaining all of its advantages (Allouche at al. 2006). Kappa and the TSS require a

specific threshold level, which is essential for the calculation of binary prediction maps. The TSS (formula: 'sensitivity + specificity − 1') ranges from −1 to +1, with values >0.4 indicating a statistically reliable model performance (Landis & Koch 1977, Allouche et al. 2006). The AUC is threshold- and prevalence independent, defined by plotting sensitivity against the corresponding proportion of false positives ('1 − specificity') across the range of possible thresholds (Pearson 2007). The AUC ranges from 0 to 1, with values >0.7 indicating statistically reliable model performance (Hosmer & Lemeshow 2000). To guarantee the most accurate model predictions, only the best fitted model runs above critical TSS values (>0.4) were implemented in the final ensemble model run.

RESULTS

Small-scale present habitat conditions (2009)

An overview of all 7 high-resolution environmental grids employed in the SDM and their respective environmental range at the study site is provided in Fig. 4. The hydrodynamic conditions, expressed as tide-induced submergence time (0.3 to 24.0 h d^{-1}; Fig. 4b) and shear stress (0.0 to 1.7 N m^{-2}; Fig. 4c) gradually decreased with increasing distance to the bottleneck that connects Jade Bay to the open North Sea. Mud content (9.1 to 97.1%; Fig. 4a), S_{bw} (26.4 to 29.0; Fig. 4d) and T_{sbw} (19.1 to 19.9°C; Fig. 4e) followed the above-mentioned hydrodynamic gradient. The highest mud content occurred in the sheltered western and southern upper intertidal areas. Highest T_{sbw} prevailed at the topographically exposed outermost boundaries of Jade Bay. The highest chl a contents (4.6 to 38.8 mg m^{-2}; Fig. 4f) were found in the shallow northeastern and western parts of the study site. The 2 omitted environmental grids (predictor collinearity >0.7), i.e. topography and TOC content, are displayed in Fig. S2 in Supplement 1 at www.int-res.com/articles/suppl/m551p013_supp.pdf). The topography in Jade Bay ranged from a depth of 23.3 m in the navigation channels to 3.8 m a.s.l. on the upper tidal flats. The TOC content ranged from 0.2 to 2.3%, with highest values near the tidal gates in the southwestern parts of the basin and close to the Wilhelmshaven Harbour.

Present macrofauna distribution (2009)

Present ensemble predictions for all 7 modelled species had TSS values >0.70 and AUC values >0.90 (Table 3), indicating good to excellent model performance. The polychaete *Scoloplos armiger* (TSS = 0.91, AUC = 0.98) had the highest model accuracy, whereas the gastropod *Peringia ulvae* (TSS = 0.75, AUC = 0.93) exhibited the lowest model accuracy.

With regard to all 7 studied species, the environmental variables that correlated most significantly with the macrofauna distribution in Jade Bay (≥0.10 standardized variable importance [VI] scores), were submergence time (5 species), mud content (4 species) and shear stress (4 species), followed by chl a content (3 species) and T_{sbw} (2 species). S_{bw} and *Zostera noltii* beds were of minor importance for the macrofauna distribution at the study site (Table 3). Furthermore, 2 species showed a more specialized response to the environmental conditions in Jade Bay

(i.e. their spatial distribution was mainly explained by a single environmental variable; VI ≥ 0.70): *Cerastoderma edule* (submergence time: VI = 0.75) and *P. ulvae* (shear stress: VI = 0.77). The remaining 5 species showed a more generalistic response, i.e. 2 or more environmental variables explained VI ≥ 0.70 of the species' spatial distribution at the study site. The distribution of the more generalistic bivalve *Macoma balthica*, for example, was mainly explained by the 4 predictor variables mud content (VI = 0.51), shear stress (VI = 0.17), submergence time (VI = 0.10) and chl a content (VI = 0.10).

The present ensemble prediction maps (Fig. 5) accurately captured the potential small-scale spatial distribution of the 7 modelled macrofauna species in Jade Bay. Each species was significantly correlated with specific hydrodynamic conditions and related sediment characteristics along the prevailing environmental gradient (exposed, lower sandflats to sheltered, upper mudflats). The polychaete *S. armiger* (Fig. 5c) mainly occurred on the hydrodynamically exposed sandflats in the centre of Jade Bay. In contrast, the bivalve *C. edule* (Fig. 5a) and the polychaete *Arenicola marina* (Fig. 5d) were mainly absent in these exposed, subtidal regions. The 2 bivalves (*C. edule*, *M. balthica*; Fig. 5a,b), 2 annelids (*A. marina*, *Tubificoides benedii*; Fig. 5d,e) and the 2 gastropods (*P. ulvae*, *Retusa obtusa*, Fig. 5f,g) mainly occurred on the sheltered intertidal flats. In addition, some pelophilous species had suitable habitats in the permanently submersed tidal inlets on the upper tidal flats (*T. benedii*, *P. ulvae*) and/or in the 3 large navigation channels (*M. balthica*, *T. benedii*). The 2 gastropods (*P. ulvae, R. obtusa*) and the polychaete *S. armiger* had a high probability of occurrence (PO) on the 'Jappensand' (see Fig. 1), a topographically exposed feature in the centre of the study site, whereas all remaining 4 species had a very low PO. Additionally, *A. marina*, *C. edule* and *R. obtusa* had a low PO on the uppermost tidal flats where the benthic habitat was characterised by the highest mud content and the lowest submergence time and shear stress area-wide.

The species-specific response curves (Fig. 6) revealed significant species–environment relationships in the Jade Bay tidal basin, where a PO above 70% showed most significant positive correlations. The sessile bivalve *C. edule* (suspension feeder) had a significant positive correlation with submergence time (VI = 0.75) between ca. 2.0 and 8.0 h d^{-1} and T_{sbw} (VI = 0.12) below ca. 19.65°C. The sessile bivalve *M. balthica* (interface feeder, IF) showed a significant positive correlation with mud contents (VI = 0.51) above ca. 30.0%. The polychaete *S. armiger* (subsurface deposit

Table 3. Modelled macrofauna species' biological traits (feeding mode, habit, mobility), presences and true absences used for species distribution model (SDM), including the species-specific variable importance (mean of 10 ensemble model runs) and the values of the 2 calculated evaluation measures (true skill statistic [TSS] and area under the receiver operating characteristic curve [AUC]). SUS: suspension feeder; IF: interface feeder; SD: surface deposit feeder; SSD: subsurface deposit feeder; PD: predator (Stamm 1995). Chl a: chlorophyll a, T_{sbw}: summer bottom water temperature; S_{bw}: bottom water salinity. Predictor variables with a standardized biomod 2 variable importance score VI ≥ 0.1 are shown in **bold**

| Species	Taxa	Biological trait		Presences (2009)	True absences (2009)	Variable importance	Evaluation measures (ensemble model)	
		Feeding mode	Habit				TSS	AUC
Cerastoderma edule	Bivalvia	SUS	Sessile	64	87	**1) Submergence time (0.75)** **2) T_{sbw} (0.12)** 3) Mud content (0.03) 4) S_{bw} (0.03) 5) Seagrass beds (0.02) 6) Shear stress (0.02) 7) Chl a (0.00)	0.81	0.96
Macoma balthica	Bivalvia	IF	Sessile	98	53	**1) Mud content (0.51)** **2) Shear stress (0.17)** **3) Submergence time (0.10)** **4) Chl a (0.10)** 5) S_{bw} (0.07) 6) T_{sbw} (0.04) 7) Seagrass beds (0.01)	0.8	0.97
Scoloplos armiger	Polychaeta	SSD	Sessile	43	108	**1) Submergence time (0.46)** **2) Mud content (0.41)** 3) T_{sbw} (0.05) 4) Shear stress (0.04) 5) Chl a (0.03) 6) S_{bw} (0.00) 7) Seagrass beds (0.00)	0.91	0.98
Arenicola marina	Polychaeta	SSD	Burrow dwelling	43	108	**1) Submergence time (0.48)** **2) Mud content (0.25)** **3) Shear stress (0.15)** 4) S_{bw} (0.04) 5) T_{sbw} (0.03) 6) Chl a (0.03) 7) Seagrass beds (0.02)	0.86	0.97
Tubificoides benedii	Oligochaeta	SSD	Sessile	97	54	**1) Mud content (0.47)** **2) $Temp_{sbw}$ (0.28)** 3) Shear stress (0.09) 4) Submergence time (0.09) 5) S_{bw} (0.03) 6) Chl a (0.03) 7) Seagrass beds (0.01)	0.86	0.96
Peringia ulvae	Gastropoda	SD	Free living	94	57	**1) Shear stress (0.77)** **2) Chl a (0.10)** 3) Mud content (0.06) 4) T_{sbw} (0.02) 5) S_{bw} (0.01) 6) Submergence time (0.01) 7) Seagrass beds (0.01)	0.75	0.93
Retusa obtusa	Gastropoda	PD	Free living	94	57	**1) Shear stress (0.41)** **2) Chl a (0.23)** **3) Submergence time (0.18)** 4) Mud content (0.08) 5) $Temp_{sbw}$ (0.06) 6) S_{bw} (0.04) 7) Seagrass beds (0.00)	0.79	0.96
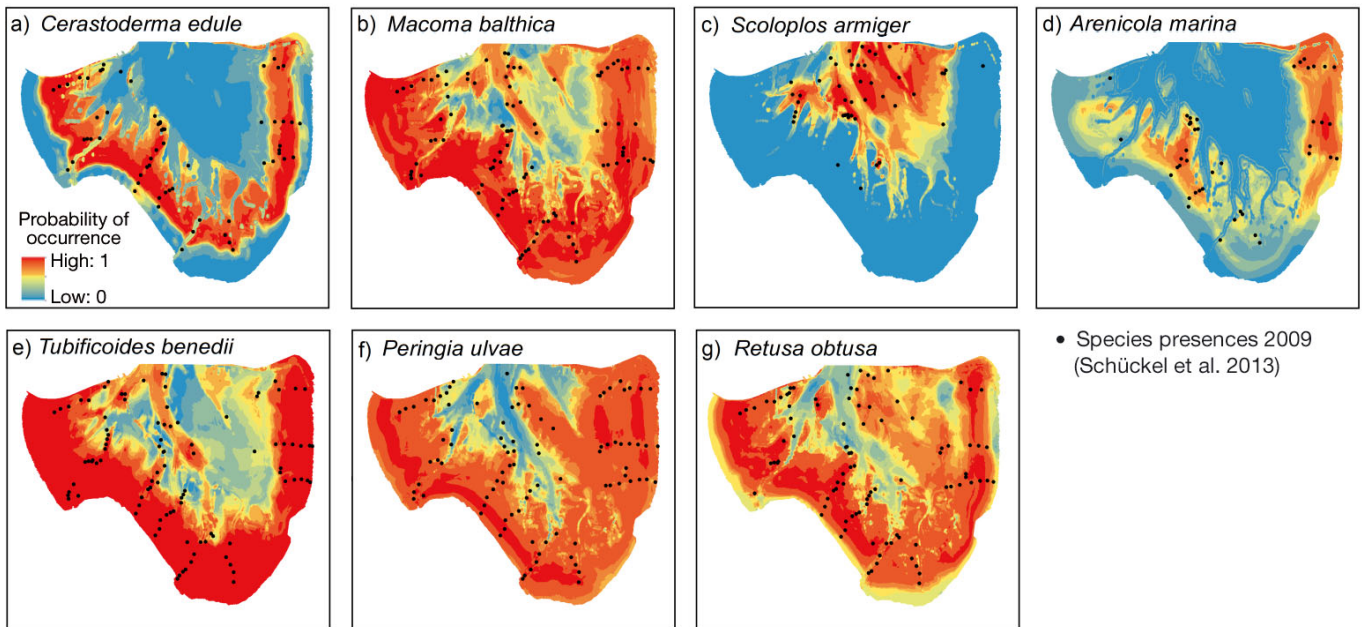
Fig. 5. Present species distribution maps (for 2009) modelled for the Jade Bay: (a) *Cerastoderma edule* (Bivalvia), (b) *Macoma balthica* (Bivalvia), (c) *Scoloplos armiger* (Polychaeta), (d) *Arenicola marina* (Polychaeta), (e) *Tubificoides benedii* (Oligochaeta), (f) *Peringia ulvae* (Gastropoda), (g) *Retusa obtusa* (Gastropoda)

feeder, SSD) showed a significant positive correlation with submergence time (VI = 0.46) above ca. 12.0 h d^{-1} and mud contents (VI = 0.41) below ca. 70.0%. The burrow-dwelling polychaete *A. marina* (SSD) correlated significantly positively with submergence time (VI = 0.48) below ca. 8.0 h d^{-1}, mud contents (VI = 0.25) below ca. 70.0% and shear stress (VI = 0.15) below ca. 0.7 N m^{-2}. The sessile oligochaete *T. benedii* (SSD) showed a significant positive correlation with mud contents (VI = 0.47) above ca. 30.0% and T_{sbw} (VI = 0.28) above ca. 19.2°C. The free living, surface deposit feeder (SD) gastropod *P. ulvae* correlated significantly positively with shear stress (VI = 0.77) below ca. 0.7 N m^{-2}. The free living gastropod *R. obtusa* (predator) correlated significantly positively with shear stress (VI = 0.41) below ca. 0.7 N m^{-2} and chl *a* (VI = 0.23) below ca. 30.0 mg m^{-2}.

Hindcast (1970s) and model evaluation with independent historical macrofauna data

The past distribution scenario showed a very good match with the independent macrofauna presences from the 1970s (Fig. 7). In addition, the 1970s past prediction maps revealed significant changes in the distribution patterns of the characteristic modelled species. The PO of the oligochaete *T. benedii* was significantly lower on the upper mudflats and in the

tidal channels (Fig. 7e). The bivalve *C. edule* was more widespread on the central sandflats and on the uppermost tidal flats, where it was clearly absent in 2009 (Fig. 7a). The polychaete *S. armiger* was more widespread on the lower tidal flats (mixed sediments, Fig. 7c). Potential suitable habitats for the bivalve *M. balthica*, the gastropod *P. ulvae* and the polychaete *A. marina* remained relatively constant between the 2 time periods (Fig. 7b,d,f). In contrast, the PO of *M. balthica* and *P. ulvae* was significantly lower throughout the entire Jade Bay, while the PO of the gastropod *R. obtusa* was significantly lower on the hydrodynamically exposed eastern, lower tidal flats and higher on the uppermost western and southern tidal flats (Fig. 7g).

DISCUSSION

Present macrofauna distribution (2009)

Five of the 7 modelled macrofauna species (*Cerastoderma edule*, *Macoma balthica*, *Scoloplos armiger*, *Arenicola marina*, *Retusa obtusa*) showed a significant correlation with submergence time, highlighting the importance of sea-level rise and its local implications for the study site (i.e. changes in topography, tidal range and submergence time) and the characteristic species under study. Clear effects of
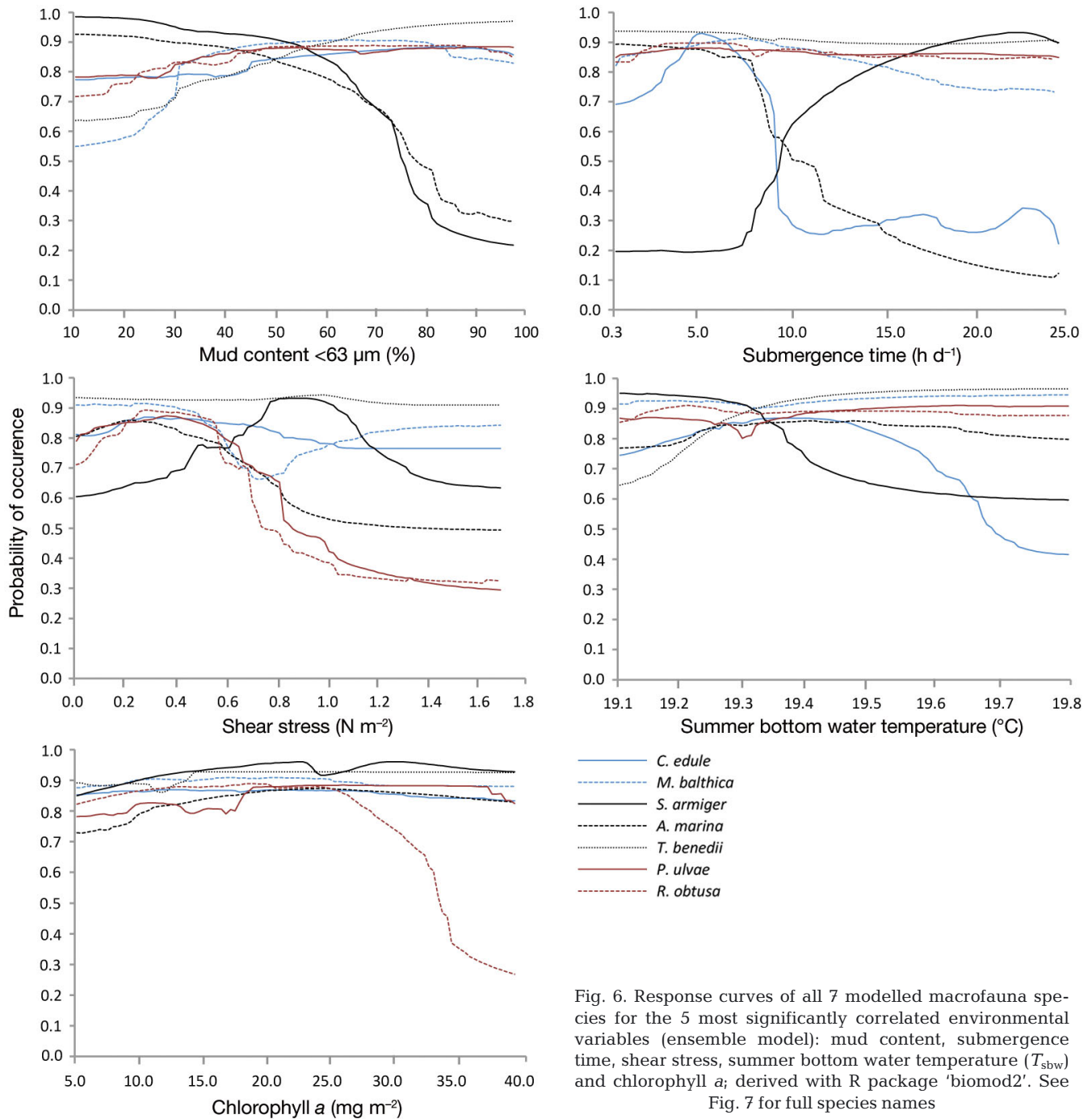
Fig. 6. Response curves of all 7 modelled macrofauna species for the 5 most significantly correlated environmental variables (ensemble model): mud content, submergence time, shear stress, summer bottom water temperature (T_{sbw}) and chlorophyll a; derived with R package 'biomod2'. See Fig. 7 for full species names

sea-level rise-induced changes in topography and submergence time on the spatial distribution of characteristic macrobenthic species have also been found in other Wadden Sea regions (e.g. Fujii & Raffaelli 2008, Fujii 2012, Schumacher et al. 2014).

According to Table 3 (variable importance) and Fig. 6 (response curves), the different biological traits were well reflected in the model results. Suspension

feeders filter organic matter directly in the water column, which explains the significant correlation of *C. edule* (a suspension feeding bivalve) with submergence time (Herman et al. 1999). SD feeders consume organic matter at the sediment surface (Herman et al. 1999, Kröncke 2006), which is represented in the generally higher correlation of the gastropod *Peringia ulvae* (SD) and the bivalve *M. balthica* (IF) with chl a
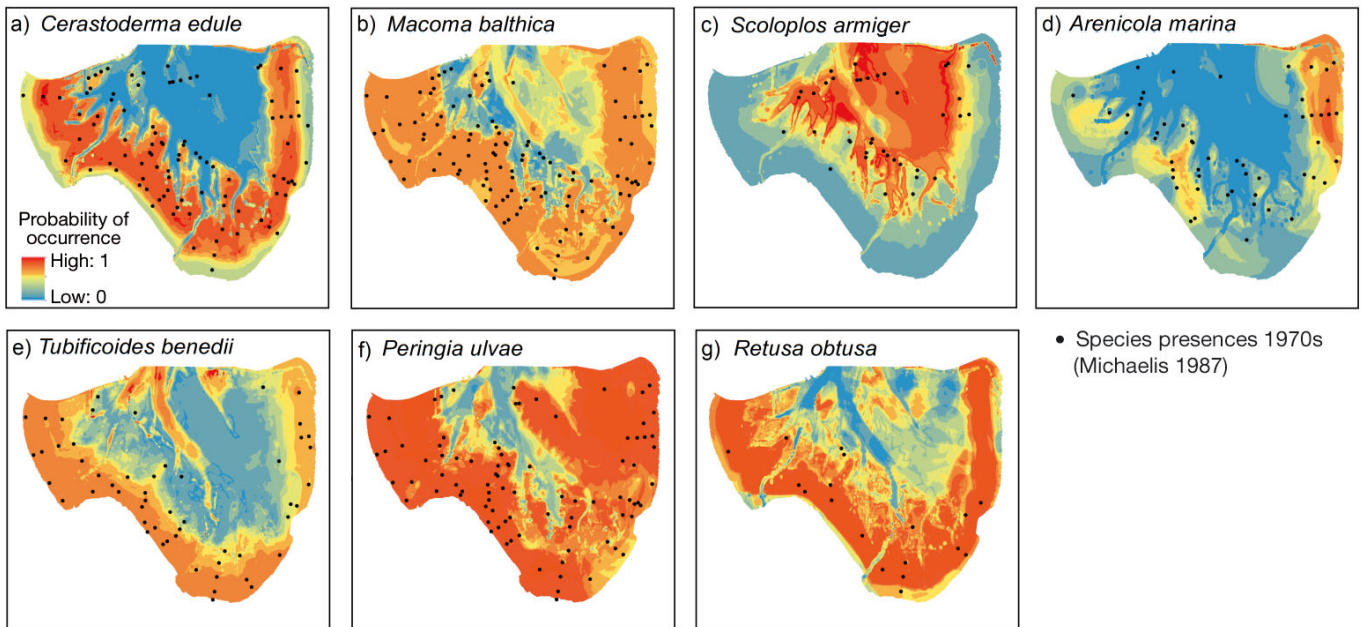
Fig. 7. Past distribution scenario (for the 1970s) for the Jade Bay and model evaluation using independent historical macrofauna data from the 1970s for (a) *Cerastoderma edule* (Bivalvia), (b) *Macoma balthica* (Bivalvia), (c) *Scoloplos armiger* (Polychaeta), (d) *Arenicola marina* (Polychaeta), (e) *Tubificoides benedii* (Oligochaeta), (f) *Peringia ulvae* (Gastropoda), (g) *Retusa obtusa* (Gastropoda)

content, compared to the remaining species under study. IF feeders, such as *M. balthica*, exhibit a certain degree of generalism, i.e. they are able to switch between the ingestion of organic matter from the water column (at the benthic boundary layer) and SD feeding (Kröncke 2006). This generalistic response to environmental conditions is reflected in the variable importance of *M. balthica*, where 4 of the 7 environmental variables (i.e. mud content, shear stress, submergence time and chl *a* content) were significantly correlated with the species spatial distribution at the study site. Both studied gastropods showed a very high correlation with shear stress, which can be related to the drifting behavior of the mud snail *P. ulvae,* which floats at the water surface during high tide using a mucus raft (Anderson 1971). The free living gastropod *R. obtusa* (predator) primarily feeds on Foraminifera and small *P. ulvae* individuals (Stamm 1995). This predator–prey relationship explains the high PO of *R. obtusa* being associated with *P. ulvae*, and thus its high correlation with shear stress and chl *a* content. In the present study, all 3 SSD feeders (i.e. the annelids *S. armiger*, *Tubificoides benedii* and *A. marina*) showed a high correlation with mud content. SSDs consume decomposed organic matter already incorporated in the sediment matrix and are therefore limited by specific grain size characteristics (Fauchald & Jumars 1979, Kröncke 2006).

Because of the shallow and tide-controlled character of tidal flat ecosystems, benthic species are generally eurythermal and thus naturally adapted to strong (daily and seasonal) temperature fluctuations (Linke 1939). Nevertheless, the model output of 2 characteristic species (i.e. *C. edule*, *T. benedii*) revealed a high sensitivity towards specific T_{sbw} in Jade Bay. The PO of the sessile oligochaete *T. benedii* decreased significantly when T_{sbw} fell below ca. 19.3°C. In contrast, the PO of the sessile bivalve *C. edule* decreased significantly when T_{sbw} exceeded ca. 19.6°C. High sensitivity towards specific water temperatures has also been observed for the filter-feeding Pacific oyster *Crassostrea gigas* in the East Frisian Wadden Sea, where 19.0°C was determined as minimum temperature for successful reproduction (Brandt et al. 2008). Extremely cold winters and extremely warm summers, caused by variations in the North Atlantic Oscillation Index since the late 1980s, were determined to be limiting factors for macrobenthic species in the Wadden Sea area, triggering biological regime shifts or changes in recruitment success (Beukema & Dekker 2005, Kröncke et al. 2013). The weaker correlation of all 7 species with the environmental predictor $S_{bw,}$ generally a major factor influencing the macrofauna spatial distribution in estuaries (Ysebaert et al. 1998, Ysebaert & Herman 2002), can be attributed to the tidal bay character of the polyhaline

study site, with little freshwater discharges (Göt-schenberg & Kahlfeld 2008). Although seagrass beds correlated weakly with the predicted present macro-fauna distribution in our study, they function as biostabilizers by enhancing sedimentation processes of finer sediments, reducing turbidity and increasing light penetration, which in turn clearly alters benthic habitats (Bos et al. 2007, Van Katwijk et al. 2010, Schückel et al. 2013).

The present prediction maps of the 7 modelled macrofauna species accurately represent the species-specific ecological niches that have been described for the study site in numerous historical and recent benthic studies (Linke 1939, Dörjes et al. 1969, Michaelis 1987). The model results of the lugworm *A. marina* (Fig. 5d) differ from the results of previous studies, as it is known to have a more widespread oc-currence on intertidal sandflats (Michaelis 1987, Van Bernem 1991, Ysebaert & Herman 2002). We assume that this deviation might have been caused by the sampling design, because the low occurrence of *A. marina* at the study site is difficult to quantify with a 10 cm diameter cylindrical corer. Nevertheless, the species' response curves (Fig. 6) still supply ecologi-cally meaningful information on the relationship be-tween *A. marina* and the environmental conditions at the study site.

Sediment characteristics and hydrodynamic condi-tions (tidal elevation, tidal current velocity) have been identified as major determinants of benthic communities in numerous studies on tidal flat ecosys-tems (e.g. Ysebaert et al. 2003, Van Colen et al. 2009). Schückel et al. (2013) revealed that proxies for hydrodynamic conditions (mud content, submer-gence time) and food availability (chl *a* content) best explained the variability in the present macrofauna community distribution in the Jade Bay intertidal zone. In the subtidal Jade Bay, the present macro-fauna community distribution could be statistically related to tidal current velocity and depth, followed by sediment characteristics (Schückel et al. 2015a). The abovementioned findings agree with our 2009 model results, in which hydrodynamic conditions (submergence time, shear stress) and sediment char-acteristics (mud content) correlated most signifi-cantly with the predicted present (intertidal and sub-tidal) macrofauna distribution in Jade Bay, followed by chl *a* content and T_{sbw}. Two historical studies con-ducted in the Jade Bay intertidal zone during the last 8 decades confirmed the high impact of sedimentol-ogy and hydrodynamics on the spatial distribution and biological traits of the macrofauna (Linke 1939, Michaelis 1987). In the subtidal North Sea, benthic

species are primarily limited by species-specific bot-tom water temperatures and depth (as a surrogate variable for other prevailing environmental factors, e.g. primary production) (e.g. Schückel et al. 2010, Reiss et al. 2011).

Environmental, climatic and biological changes since the 1970s

Our modelled 1970s past distribution scenario sup-ports our hypothesis that macrofauna distribution shifts between the 1970s and 2009 were attributed to climate change-induced sea-level rise (expressed as changes in mean daily submergence time) and water temperature increase. As seagrass beds did not have a major impact on the spatial distribution of macro-fauna at the study site (weak correlation with all 7 species; Table 3), our hypothesis that macrofaunal distribution shifts between the 1970s and 2009 were attributed to seagrass recovery due to de-eutrophica-tion was not supported.

Sea-level rise (as a proxy for morphological and sedimentological changes) and water temperature increase are generally the major environmental vari-ables affecting spatial distribution patterns of marine benthic species with regard to global warming (e.g. Fujii & Raffaelli 2008, Fujii 2012, Birchenough et al. 2015). In particular, sea-level rise has been accelerat-ing significantly in the entire German Bight since the 1990s (Wahl et al. 2011). For the Wadden Sea World Heritage Site, climate change-induced sea-level rise and increases in water temperature have been widely monitored over the past centuries (e.g. Flem-ming & Bartholomä 1997, Van Aken 2008, Wolff et al. 2010, Behre 2011). Tide-induced basins (such as Jade Bay) and estuaries often function as sediment traps (Little 2000). In these systems a sea-level rise-induced topography increase can cause a rise in the tidal range, thus altering overall submergence time (e.g. Götschenberg & Kahlfeld 2008, Flemming 2011). According to Flemming & Bartholomä (1997), Dolch & Hass (2008), Fujii & Raffaelli (2008) and Fujii (2012), sea-level rise will (at least temporarily) in-crease the tidal basin volume and cause an increas-ing demand for external sediment supply as an adap-tation towards new morphodynamic equilibria.

Our hindcast model results revealed that a higher mean daily submergence time (plus 1 h d^{-1}) and a lower T_{sbw} (minus 1.5°C) in the 1970s caused signifi-cant changes in the distribution patterns of the char-acteristic macrofauna species at the study site. In our model we identified a significantly lower PO of the

oligochaete *T. benedii* on the upper mudflats and a significantly lower PO of 3 modelled species (*M. balthica*, *P. ulvae*, *R. obtusa*) area-wide. Clear effects of changes in submergence time and/or water temperatures on the spatial distribution of characteristic macrobenthic species have also been documented for other Wadden Sea regions (e.g. Fujii & Raffaelli 2008, Fujii 2012, Kröncke et al. 2013, Schumacher et al. 2014). The key role of environmental parameters for changes in species' spatial distributions revealed by SDM in the present study (1970s to 2009), was also confirmed by differences in benthic food web models for the Jade Bay (Schückel et al. 2015b).

Evaluation measures and independent historical macrofauna data

Commonly used evaluation measures (e.g. AUC, Cohen's kappa) have been widely criticized in scientific expert circuits (e.g. Allouche et al. 2006, Lobo et al. 2008). The AUC is controversial because of its numerous shortcomings; for example, the extent to which models are carried out highly influences the AUC scores and the rate of well-predicted absences (Lobo et al. 2008). Nevertheless, the AUC has still been recommended as a useful measure to determine model accuracy in numerous SDM studies (e.g. Franklin 2010, Merow et al. 2013). Cohen's kappa has been criticized because it inherently depends on prevalence, which is argued to produce statistical artefacts to estimates of predictive accuracy (Allouche et al. 2006). Therefore, Allouche et al. (2006) introduced the TSS as a prevalence-independent alternative to kappa, while keeping all of its advantages.

SDM is confronted with issues of model uncertainties, which can significantly decrease the accuracy of model prediction. Model uncertainties can be caused by spatially biased input data, the selection of an inappropriate modelling method or the incorporation of false species absences (e.g. Guisan & Thuiller 2005, Araújo & Guisan 2006, Elith & Leathwick 2009, Franklin 2010). Nevertheless, we assume that our model results provide accurate present and past macrofauna distribution scenarios, because of (1) the high-quality and full-coverage macrofauna sampling design (species presences, true species absences) (Fig. 2), (2) the high-quality and high-resolution environmental data basis (Table 1, Fig. 4), (3) the good to excellent evaluation measures in terms of AUC and TSS (Thuiller et al. 2010) (Table 3), and (4) the successful correlation of our past distribution scenario with independent historical macrofauna data

from the 1970s (Fig. 7). Our results show that predictive models are important tools for the identification of conservation areas and for the understanding of potential future changes in marine benthic systems, by testing hypotheses regarding the role of changes in environmental parameters on species' spatial distributions, and thus, ecosystem functioning.

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