Mapping and modeling of eelgrass (*Zostera marina* L.) distribution in the western Baltic Sea

Philipp R Schubert[1]*, Wolfgang Hukriede[1], Rolf Karez[2], and Thorsten BH Reusch[1]

[1] GEOMAR Helmholtz Center for Ocean Research Kiel, Evolutionary Ecology of Marine Fishes, Düsternbrooker Weg 20, D-24105 Kiel, Germany

[2] State Agency for Agriculture, Environment, and Rural Areas Schleswig-Holstein (LLUR), Hamburger Chaussee 25, D-24220 Flintbek, Germany

* Corresponding author: Philipp R Schubert, pschubert@geomar.de, Düsternbrooker Weg 20, D-24105 Kiel, Germany, Tel.:+49-(0)431-600-4538

Abstract

In the northern hemisphere, *Zostera marina* is the most important and widespread seagrass species. Despite its ecological importance, baseline data on eelgrass distribution and abundance are mostly absent, particularly in subtidal areas with relatively turbid waters. Here we report a combined approach on vegetation mapping in the Baltic Sea coupled to a species distribution model (SDM). Eelgrass cover was mapped continuously in 2010/11 with an underwater tow-camera along ~400 km of seafloor. Eelgrass populated 80 % of the study region and occurred at water depths between 0.6 and 7.6 m at sheltered to moderately exposed coasts. Mean patch length was 128.6 m, but was higher at sheltered locations, with a maximum of > 2,000 m. The video observations (n = 7,824) were used as empiric input to the SDM. Using generalized additive models (GAM), three predictor variables (depth, wave exposure, and slope), which were selected based on Akaike's information criterion (AIC), were sufficient to predict eelgrass presence/absence. Along with a very good overall discriminative ability (ROC/AUC = 0.82), depth (as a proxy for light), wave exposure, and slope contributed 66 %, 29 %, and 5 %, respectively, to the final model. The estimated total areal extent of eelgrass in the study region amounts to 140.5 km² and comprises about 11.5 % of all known Baltic seagrass beds. The present work is, to the best of our knowledge, the largest study undertaken to date on vegetation mapping and the first to assess distribution of eelgrass quantitatively in the western Baltic Sea.

Keywords

species distribution, GAM, habitat mapping, habitat modeling, depth limit, patchiness

Introduction

Seagrass meadows are among the most productive and valuable ecosystems on Earth (Costanza et al. 1997). They act as ecological engineers (sensu Wright & Jones 2006) and provide a multitude of important ecological services (Hemminga & Duarte 2000, Larkum et al. 2006). At the same time, seagrass meadows are threatened worldwide by eutrophication, overfishing, coastal development, diseases, invasive species, and climate change (Reusch et al. 2005, Orth et al. 2006, Williams 2007, Moksnes et al. 2008, Waycott et al. 2009, Bockelmann et al. 2013). The areal extent of seagrass populations around the globe was recently estimated to decline at a rate of about 1.5 % yr^{-1}, summing up to a total loss of seagrass area of at least 3,370 km^2 between 1879 and 2006, representing 29 % of the maximum area measured ever (Waycott et al. 2009). This loss rate is higher than for most other threatened ecosystems. Additionally, the rate of decline in seagrass meadows has accelerated over the past 8 decades from < 1 % yr^{-1} before 1940 to 5 % yr^{-1} after 1980 (Waycott et al. 2009). Locally, the observed global loss of seagrass could be masked by the great variability of seagrass distribution (Frederiksen et al. 2004, van Tussenbroek et al. 2014) or even recovery of seagrass populations in some areas following release from stressors (e.g. Vaudrey et al. 2010).

In the Baltic Sea, the largest brackish water body of the world's oceans, sublittoral eelgrass (*Zostera marina* L.) meadows are one of the most important and extensive coastal ecosystems, covering at least 1,227 km^2 from the Kattegat through to the North Eastern Baltic Sea (Boström et al. 2014). Eelgrass beds play an important role in coastal protection, help to remove excess nutrients and provide food and nursery ground for economically important fish species like cod, herring, eel, and plaice (e.g. Touchette & Burkholder 2000, Beck et al. 2001, Christianen et al. 2013). Local studies indicate that eelgrass may cover large areas in shallow waters (< 10 m) along the German coast (HELCOM 1998, Schubert et al. 2013, Boström et al. 2014). Yet, despite its presumed ecological importance for the coastal ecosystem in German waters, baseline data on eelgrass distribution, abundance, and spatial structure are virtually absent.

To assess the importance and function of eelgrass beds in the western Baltic Sea, baseline data on abundance, distribution, and spatial structure are urgently needed (Boström et al. 2002). Abundance and areal extent data of eelgrass are the foundation for any sensible calculations on production, nutrient cycling, carbon sequestration, importance for fish stocks, sediment transports and other ecosystem services. Structure or spatial patterns of seagrass meadows can affect benthic community composition and ecosystem responses on varying scales from meters to hundreds of kilometers (Robbins & Bell 1994, Turner et al. 1999). And while concepts of landscape ecology become more widely used in seagrass research (Boström et al. 2006 and references therein), baseline data of seagrass landscapes like patchiness or fragmentation are still missing.

Distribution maps on the basis of georeferenced presence/absence data are needed for managing as well as for monitoring purposes, as eelgrass areal extent, health status, and depth limits are employed as important indicators to assess the environmental status for several international directives or conventions, viz. HELCOM, EU Water Framework Directive (WFD) and EU Marine Strategy Framework Directive (MSFD 2008, HELCOM 2009, Backer et al. 2010). Distributional data of eelgrass are also needed to assess the monetary value of ecosystem services provided by eelgrass habitats (Baden et al. 2003, Rönnback et al. 2007, Mangi et al. 2009). Lastly, these data are prerequisites for managers and local communities to preserve and protect local ecosystem functioning in the course of planning and maintaining coastal infrastructure (harbors, piers, coastal protection, dredging of waterways etc.).

One possible reason for the lack of studies concerning distribution and abundance of eelgrass in the Baltic Sea could be that large-scale mapping of sublittoral vegetation in visually deep waters (deeper than vertical visibility, prohibiting remote sensing from aerial photography or satellite imagery) is costly, time-consuming and, in contrast to remote sensing, does not yield the areal extent of submerged vegetation directly. Thus, depending on mapping design and method (e.g. SCUBA, drop-camera, tow-camera), in turbid waters only transect or point data are generated, which leave out large non-surveyed areas. To minimize costs of laborious mapping methodologies and to extrapolate statistical relationships from sampled to non-surveyed areas, species distribution modeling (SDM) of seagrass occurrence in relation to geophysical factors has recently been applied as a complementary approach (Bekkby et al. 2008, Grech & Coles 2010, Downie et al. 2013, March et al. 2013a). Particularly at larger scales (> 50 km), distribution modeling has contributed to a better understanding of the geophysical factors and processes structuring the distribution of seagrasses. Additionally, SDM allows scientists (1) to identify the potential distribution range of eelgrass under possibly changing conditions (e.g. light limitation due to eutrophication) and (2) to estimate past changes in eelgrass distribution via falsely predicted absences or presences. SDM is particularly useful in species that are common and widely distributed, have a relatively stable distribution, and are not extending their range (Guisan & Thuiller 2005). These criteria apply for eelgrass in the western Baltic Sea.

The present work combines the largest and most thorough study undertaken to date on vegetation mapping in the Baltic Sea – accomplished by towing an underwater camera system along transects of about 400 km length – with a subsequent SDM and GIS analysis, which identifies geophysical factors that influence eelgrass occurrence, and allows extrapolation into non-surveyed areas. More specifically, the main objectives of our study were to explore eelgrass distribution along the northern German Baltic Sea coast and to locate current depth limits (shallow and deep) of the meadows. Additionally, the mapping should help to reveal the population's spatial structure with regard to cover and patchiness. With the model, we tried to estimate the areal extent of eelgrass populations in the study region and the influence of a range of geophysical factors on eelgrass distribution. Finally, for possible restoration projects we tried to locate sites where eelgrass is missing despite suitable conditions for growth.

Methods

Study region

The study region is situated in the Baltic Sea, the largest brackish water basin in the world, which is characterized by steep physical and chemical gradients, limited water exchange, low biodiversity and strong anthropogenic impacts (Elmgren 2001). Eelgrass was mapped and modeled along the coastline of Schleswig-Holstein (SH), between Denmark in the North and the German federal state of Mecklenburg-Western Pomerania in the Southeast (total sea area ca. 3,680 km², Fig. 1). The outer coastline of SH has a length of 397 km (including the island of Fehmarn, not including the Schlei Fjord). Water depths in the shallow western Baltic Sea range from 0 to 40 m, but we restricted our field study to the extent of the potentially habitable depth zone for eelgrass today (0–10 m depth). The total area of this depth zone in the study area is ca. 588 km² (not including the Schlei Fjord), according to bathymetry data (see section '*Geophysical predictor variables*'). The reason for not including the river-like Schlei Fjord (Fig. 1) was its strongly reduced visibility along with high agricultural nutrient input, which prevent growth of eelgrass in most of the fjord (Fürhaupter et al. 2003). However, model predictions were calculated for the Schlei area to find out whether additional factors might affect eelgrass distribution in the fjord.

Surface salinity in the region may vary between ~8 and ~26 psu (continuous logging of the German Federal Maritime and Hydrographic Agency [BSH] between 2004 and 2012), depending on the inflow of fully saline North Sea water, location, and depth. Tides are negligible, but wind driven water level changes are common. Currents and wave exposure are generally weak in the study region, as it is well protected from prevailing westerly winds and relatively enclosed. Maximum significant wave height rarely exceeds 3 m (Petterson et al. 2012). The climate regime is cold temperate with water temperatures in the study region ranging from 1 °C in February to 20 °C in August (Siegel & Gerth 2011). Occasionally, severe winters can lead to the formation of sea ice in the region. Geologically, the study region is a “Fjord Coast”, with fjords (Eckernförder Bay and Kiel, Schlei, and Flensburg Fjord), bays, sandy coasts, some cliffs and only one large island (Fehmarn). The study area is dominated by sandy and muddy sediments, with infrequent small to large boulders in some locations. No bedrock exists along the Baltic coast of SH. Eelgrass is common on sandy bottoms along the entire German Baltic coast (Boström et al. 2014), but precise data about its distribution, abundance, depth limits, areal extent, or meadow structure has not been published so far.

Mapping

Mapping was conducted in the summer season (between June and August) in the years 2010 and 2011. Eelgrass was recorded continuously along transects with an underwater tow-camera (1/3” Color CCD-sensor in a water proof housing, resolution: 512 x 582 pixel, sensitivity: 0.5 Lux, image angle: 92°, lens: 3.6 mm), deployed from a small boat (< 6 m) travelling at idle speed (ca. 2–4 km h^{-1}). The field of view depended on height of the camera above the seafloor (0.8–1.5 m) and varied between 2 and 7 m^2. The video signal was digitally overlayed in an onboard-unit with additional data (depth, position, date, time, and transect identifier) and recorded on hard disk for further analyses. Depth, position, and time were provided by an echo sounder and a GPS receiver included in the onboard unit and recorded in a standard format (NMEA 0183-file, National Marine Electronics Association).

Video transects ran parallel and perpendicular to the shore. Parallel transects (PTs) were conducted to detect eelgrass presence or absence at a certain coastal stretch in a depth of 3–4.5 m (depth of densest eelgrass cover along German Baltic Coast, pers. obs.) and included virtually the entire study area. Perpendicular transects (VTs) provided information about shallow and deep depth limits (an important indicator for the WFD) and depth dependent changes of eelgrass distribution. VTs were distributed over the length of the entire coast and ranged from about 0.5 to 10 m depth with lengths between 70 and 3,270 m (n = 110), depending on slope of the coast. The distance between single

VTs was approx. 2 km. The videos of both transect types covered approx. 400 km of seafloor (PTs: 315 km, VTs: 84 km).

Eelgrass coverage and additional observations (sediment type, algae and blue mussel occurrence) were assessed continuously by examination of the video on a computer screen. These observations were then automatically combined with the NMEA data using a specifically designed computer program (unpublished program: *GAZER*, by W. Hukriede & P.R. Schubert), which produced a protocol file for further analyses. Spatiotemporal resolution for single observations was thus dependent on velocity of the boat and frequency of GPS measurements, which was between 0.25 and 1 Hz, resulting in variable distances between single observations along transects of 1–5 m. Eelgrass cover along the transects was estimated semi-quantitatively by applying an extended Braun-Blanquet (1964) six classes scale of 0, < 10, 10–25, 25–50, 50–75, and 75–100 %. Due to the large amount of video data, four different observers were assigned to this task. Intercalibration showed that results for individual observers did not differ significantly when cover classes were used (data not shown). Presence/absence observations used for modeling were indiscernible between observers.

Eelgrass patchiness on a meter-scale was calculated using Montefalcone's patchiness index PI (Montefalcone et al. 2010), referred to as "grain" by Pielou (1977). In order to calculate the index, presence/absence data from along the coast-parallel transects were used. We defined the PI to be the number of 0-1- or 1-0-transitions per 500 m of straight-line transect length. Additionally, the mean length of patches and median cover class of eelgrass were computed for every 500 m section along the coast. Differences between mean patch lengths of exposed versus sheltered sections were assessed with a two-sample t-test.

Modeling

The species distribution model (SDM) for eelgrass was fitted using the method of generalized additive models (GAM, Hastie & Tibshirani 1990) and a set of three predictor variables (depth, slope, and wave exposure, see section: '*Geophysical predictor variables*'). GAMs are a semi-parametric extension of generalized linear models (Hastie & Tibshirani 1990) and their ability to fit complex non-linear responses has made GAMs one of the most used SDM methods in the recent past (Downie et al. 2013). The model's parameters were calculated applying the GRASP software package ("Generalized regression analysis and spatial prediction", Lehmann et al. 2002) within "R" (R Development Core Team 2008). To avoid a bias due to the variable distance between observations during the two year survey (see section '*Mapping*'), distances were standardized to 5 m for the model input. Where needed, GPS position and predictor variables were interpolated between two neighboring readings (max. interpolated distance = 5 m). Data about eelgrass occurrence (presence/absence) were taken directly from the protocol file and were not interpolated.

To obtain a sound data base for the modeling process, observations with erroneous or missing depth data were removed. We then applied two filters on the database (all observations: n = 70,704). First, to achieve a balanced depth distribution, we reduced the skew of depth data originating from the predominance of PTs in depth range of 3–4.5 m (Table 1). To this end, the amount of all surplus observations in the nine depth meter classes from 0 to 9 was randomly reduced to match the amount of observations in the 1–2 m depth class (n = 1,924). For the two edge depth classes of 0–1 m and 8–9 m that had fewer observations (n = 267 and n = 593, respectively) all observations were used for our model, resulting in a total of n = 14,328 observations after applying the first filter.

As a second filter, we randomly excluded 6,504 absences from the observation data to avoid the adverse consequences of a large number of absences (Lehmann et al. 2002) and to obtain the recommended balanced prevalence with similar numbers of absences and presences (Liu et al. 2005). The ensuing prevalence equality enabled us to translate eelgrass prediction values directly into probabilities of encounter without further modification (Liu et al. 2005). After applying the second filter, 7,824 observations were left for the modeling process.

Finally, correlations between the three chosen predictors (see section '*Geophysical predictor variables*') were calculated to ascertain the avoidance of functional dependencies between predictors, which would be misleading when estimating the model (Lehmann et al. 2002). However, correlations between any pairs of predictor variables were weak and non-significant (all $R^2 < 0.08$); thus no predictor had to be removed from the modeling process.

To estimate the total area of eelgrass in the study region, the modeled probability to find eelgrass at a certain location (0–0.95) was multiplied with the area for the prediction. Resolution of the model was 100 m, resulting in an area of prediction of 10,000 m² for each point within the prediction grid.

Geophysical predictor variables

In our SDM, the variables depth, slope, and wave exposure determined the response variable (probability of eelgrass occurrence). Additional predictors (salinity, temperature, and sediment class) did not have significant influence on the response variable and were not incorporated in the model (data not shown).

Water depths along the surveyed transects were measured in the field with an echosounder (EchoPilot Bronze Depth+, frequency: 150 kHz, accuracy: 0.1 m). Depths for non-surveyed locations were derived from a digital elevation model (DEM) of the south-west Baltic Sea with a horizontal resolution of 50 m. The DEM was provided by the State Agency for Agriculture, Environment, and Rural Areas Schleswig-Holstein (LLUR, 2004) and is based on a depth survey of the German Federal Maritime and Hydrographic Agency (BSH, 2002) and a digital topography of Leibniz Institute for Baltic Sea Research Warnemünde (IOW). The coast’s slope was calculated from the DEM using the ArcGIS Spatial Analyst tool ‘slope’ with a horizontal resolution of 50 m. Wave exposure (WE) was modeled following the procedure described by Ekebom (2003), which quantifies wave exposure as apparent wave power in watts. For these calculations we used fetch (capped at 30 km) and wind speed, both for 36 directions of the compass rose, in the period from 1998 to 2011 (14 years). Wind data for every grid point (resolution: 100 m) were obtained from the nearest of 7 weather stations from the German Weather Service (DWD) and the GEOMAR (only data from Kiel Lighthouse). Wind speed was time-averaged from one hour (DWD) or 8 minutes (GEOMAR) values and measured in m s^{-1}. In addition to the average wind speed, WE was calculated for different wind speeds below and above iterated thresholds with steps of 1 m s^{-1}. To find the best model, all wind speeds were tested and validated. WE values calculated with wind speeds above 6 m s^{-1} scored highest in AIC values (Table 2) and were incorporated into the final model.

Model fitting and validation

As a tool for model selection, we used Akaike's information criterion (AIC, see Burnham & Anderson 2001) within the GRASP-package. The AIC procedure allows ranking candidate models relative to each other according to parsimony and goodness of fit. Of all candidate models, the resulting final model (Model 1, Table 2) was used to predict spatial distribution of eelgrass.

To protect against over-parametrization, the final SDM was verified applying a cross-validation method, with the threshold-independent receiver-operating characteristic ROC (Fielding & Bell 1997) and its associated AUC ("area under the curve") as the statistic of interest. The cross-validation was made with five subsets (folds) of the entire dataset (five-fold cross-validated ROC). To estimate the precision of the AUC and to obtain confidence intervals, bootstrap resampling of the entire dataset (4000 iterations) was applied (Efron 1979). The AUC value of ROC-plots can take values between 0.5 and 1.0. Following the classification of Hosmer & Lemeshow (2000) values below 0.7 are regarded as having a poor, 0.7–0.8 a satisfactory, 0.8–0.9 a very good, and above 0.9 an excellent discriminative ability.

Besides correctly predicted presences and absences, even the best SDM will make false predictions for both types of observations. These false predictions are normally summarized in a confusion matrix (Table 3) and can hold interesting information. In the case of abundant eelgrass, falsely predicted presences merit attention, as they could indicate locations well suited for potential restoration of eelgrass meadows. Following the precautionary principle, a threshold of 5 % probability of error in predicting the presence of eelgrass was employed to define falsely predicted presences and locate potential restoration sites. For the confusion matrix, a threshold of 0.48 (= highest Kappa *K)* was chosen, assuming that both error types (falsely predicted absences and falsely predicted presences) are equivalent (Fielding & Bell 1997).

Results

Mapping results

We found that eelgrass grew along most (80 %) of the coastline in the study area with just a few areas as exceptions (Fig. 2). 63 km of the 315 km surveyed transect length along the shore exhibited no eelgrass (20 %). Dense eelgrass meadows (≥ 50 % cover) populated about 70 km (22 %) of mostly sheltered coastline. Eelgrass depth limits of meadows (meadow definition: eelgrass cover ≥ 10 %), were assessed along 110 perpendicular transects (VT), 97 of which featured eelgrass meadows. The deep depth limit ranged between 2.2 and 7.6 m (mean = 5.3 m, SD = 1.27, n = 97), while the shallow depth limit lay between 0.6 and 5.7 m (mean = 2.3 m, SD = 1.27, Fig. 3). With only a few exceptions, both depth limits were shallower in fjords, bays, and other sheltered locations than in moderately or highly exposed locations on open coastlines and headlands.

The patchiness index (PI) for eelgrass, measured as transitions between eelgrass and no eelgrass per 500 m of transect length (‘section’), ranged between 0 and 68 (mean = 16.1, SD = 12.7, n = 482). PI = 0, meaning that one patch covered the entire section, was found at 30 of 482 sections, all situated inside fjords and bays. Mean calculated wave exposure for these 30 sections was 273.4 watts (SD = 200.9 watts, n = 30), compared to an overall mean wave exposure for all sections of 430.4 watts (SD = 253.0 watts, n = 482). Mean patch length for all sections was 128.6 m

(SD = 286.5 m, n = 482) with maximum patch lengths of > 2,000 m found off Gelting, Sierksdorf, Burg (Fehmarn), and Grossenbrode (Fig. 2). Minimum patch lengths of 1–5 m were found mainly at exposed coasts. Mean patch length of sections from the upper half of the wave exposure range was significantly smaller than mean patch length from the lower half (74 versus 294 m, t-test: $n = 482$, $T = 5.85$, $p < 0.0001$). The median of all 482 500-meter-sections was in class 2, equivalent with a cover of 10-25 %.

Modeling results

Mapping results were complemented by our modeling results, which enabled us to appoint driving factors of eelgrass distribution and estimate the total eelgrass area. AIC calculations within the GRASP software confirmed the presumption that incorporating all three geophysical predictor variables (depth, slope, and wave exposure) led to best modeling results (Table 2). Models integrating the predictor 'wave exposure' (WE) with exceeding wind speeds (Models 1–5) scored consistently higher than either those with averaged wind speeds (Model 7) or wind speeds below certain thresholds (Model 6). Besides producing different AIC values, the models' visual appearances as maps revealed substantial and meaningful differences in eelgrass distribution for models with exceeding wind speeds compared to those with winds below certain thresholds (data not shown). These differences are in good accordance with our mapping results and confirm that eelgrass distribution is mainly shaped by stronger winds.

Contributions of the respective predictors to the final model (Model 1, Table 2), calculated as amount of explained variation that each predictor variable contributed to the model, were 66.3 % for 'depth', 29.2 % for 'wave exposure', and 4.6 % for 'slope' (Table 4). This predictor hierarchy was mirrored in the AIC values for different models (Table 2): dropping only 'slope' from the model (Model 8 and 9) lead to a higher ranking than dropping either 'WE' (Model 10) or 'depth' (Model 12 and 14). The same ranking ensued when the model was built with just one predictor: integrating ‘depth’ alone (Model 11) lead to a better model than ‘WE’ alone (Model 13 and 15); ‘slope’ alone (Model 16) scored lowest.

Results of the five-fold cross-validated ROC of our final model showed an AUC of 0.81908 (95 % confidence interval: 0.81894–0.81923), indicating a ‘very good’ discriminative ability (after Hosmer & Lemeshow 2000). GAM response curves of each of three predictor variables (Fig. 4) showed how environmental gradients shape eelgrass distribution in the western Baltic. Response of eelgrass to depth was bell-shaped with an optimal depth for eelgrass in the study region between 2 and 4 m. Response to slope showed a clear minimum at ca. 1.1° with more positive responses for both flatter and steeper inclinations. WE was clearly negatively correlated with eelgrass occurrence; only within a small range at medium exposures (500–1000 watts) no change in the response variable was apparent (Fig. 4).

The resulting prediction map for our final model in the study region had a horizontal resolution of 100 m and encompassed areas with a depth of up to 10 m (Fig. 5). The calculated total area populated with eelgrass summed up to 140.49 km² or 23.91 % of the entire potentially habitable depth zone for eelgrass (depth 0–10 m, area: 587.58 km²).

Predicted and observed presences/absences at a threshold of 0.48 are summarized in the confusion matrix (Table 3). The ensuing correct classification rate for this threshold is 73.9 %. Putting more importance to falsely predicted presences and applying a more conservative threshold of 5 % probability of error, at 194 surveyed locations eelgrass was falsely predicted as being present. These falsely predicted presences spread over the entire surveyed coast (Fig. 6). With just a few exceptions in the Lübeck Bay, most of these locations lay in sheltered areas with large eelgrass meadows, owing to small scale variation below the model’s (and its predictors’) resolution. Thus, only relatively few falsely predicted presences to suggest possible restoration sites were encountered. Promising areas are situated at the inner Eckernförde Bay, the east coast of Fehmarn, and off Brodten Cliff (Fig. 6).

Discussion

To the best of our knowledge, our study is the most data rich underwater survey of submersed vegetation undertaken to date. We found that the area covered by sublittoral seagrass beds along the northern German Baltic coast is comparable to the areal extent of (mostly intertidal) seagrass beds in the Wadden Sea (Dolch et al. 2013), but due to differences in growth form and seagrass species, total biomass of western Baltic Sea populations is expected to surpass North Sea populations by far. The areal extent comprises about 140/1,222 km² = 11.5 % of all known Baltic seagrass beds and 140/1,482 km² = 9.4 % of northern European seagrass populations (Boström et al. 2014). The species distribution model (SDM) derived from our extensive data basis has very good predictive power and provides additional information about eelgrass distribution and possible restoration sites.

The acquisition of accurate distributional data of eelgrass in turbid waters is costly and time-consuming, yet indispensable for managing and monitoring purposes. Our results show that a combined approach of geo-referenced video transects and subsequent species distribution modeling (SDM) can overcome the weaknesses of both methods and lead to distribution maps of satisfying quality covering the entire target area. Although video-mapping covers only narrow line-transects of about 1–3 m width, this method provides additional information on eelgrass patchiness, exact depth limits, and health status. Moreover, additional environmental data such as sediment characteristics or macroalgae cover can be obtained. Compared to sonar techniques, which recently became more widely used to survey seagrasses (e.g. Lathrop et al. 2006, Lefebvre et al. 2009), video-mapping has the advantage of a direct observation without the risk of misinterpreting results and needs no minimum cover value below which eelgrass is not detected. Despite its drawbacks, for turbid waters video-mapping remains the preferred method to map abundant and easily identifiable species like eelgrass down to their maximum colonization depth.

Species distribution modeling should ideally accompany any data acquisition in order to fill in unsurveyed areas and develop maps of areal coverage. As an extra value, potential restoration sites can be identified. Additionally, future distribution of eelgrass in the face of predicted environmental change can be modeled and integrated in coastal managing plans and directives. For example, for the Baltic Sea region increases in wave exposure due to changing wind speeds and directions are predicted (BACC Author Team 2008) and will likely have substantial effects on eelgrass distribution. With the model, these effects can be quantified. Concerning the model input, accurate and abundant distributional data along with concomitant physical factors (e.g. depth or wave exposure) of similar resolution in the modeled area are important prerequisites to develop useful and reliable SDMs. Our model input encompassed the entire modeled area and included all obvious environmental gradients that are present in the study region. The coastline in northern Germany has a simple geomorphology with just one big island and few peninsulas or inlets, facilitating a proper prediction of vegetation distribution with relatively few abiotic factors. Moreover, the basis of our SDM was exceptionally data rich with about 8000 presence/absence data-points on eelgrass for a prediction area of 588 km^2. Table 5 shows a comparison between the present and past studies concerning submarine vegetation. Of those studies, our observational input had the highest resolution. Consequently, our model's resulting response curves (Fig. 4) exhibit a high statistical confidence level and the model's high AUC values (and narrow confidence intervals of the AUC values) indicate that it has higher predictive power than comparable models. Still, modeling results are always dependent on the quality and resolution of the predictors used. In our model, small-scale variations (< 100 m) of eelgrass distribution are below the predictors' resolution, explaining most of the falsely predicted presences in areas with high eelgrass cover. However, the cross-validation of the model showed that the predictions for the entire study area forecast the presence (and absence) of eelgrass with very high certainty.

Three geophysical factors were sufficient to achieve a very good predictive ability of the final model (fivefold cvROC = 0.82). Of the three factors, ‘depth’ had the greatest influence on model output, followed by ‘wave exposure’ and ‘slope’. The response curve shows the expected bell-shape, which can be explained by an irradiance gradient (Krause-Jensen et al. 2003), depth being a proxy for light attenuation with increasing depth. Seagrasses and eelgrass in particular have relatively high light requirements (Larkum et al. 2006) and can only grow down to a compensation depth where at least 11 % of surface irradiance remains (Duarte 1991). Based on our findings, this compensation depth ranges between 4 and 7 m in the study area and is positively correlated with the factor ‘wave exposure’. This correlation is plausible, if one considers wave exposure as a proxy for water transparency (besides its other effects). With increasing exposure, high nutrient levels from human settlements or freshwater run-offs become more diluted and hence productivity of plankton and macroalgae decreases, leading to clearer water and less epiphyte growth on eelgrass at more exposed locations. At neighboring Danish coasts, Greve & Jensen (2005b) showed that depth limits of eelgrass largely depend on location along an exposure gradient from inner to outer bays to open coastal waters, reflecting a corresponding gradient in water transparency. Thus, though not incorporated into the model directly, light conditions are indirectly accounted for by the factors ‘depth’ and ‘wave exposure’. Nevertheless, we think that the model could have been improved by adding a fourth factor, describing light conditions, if sufficient data (e.g. from satellites) had been available. Data on light conditions would specifically help to explain the lack of eelgrass in locations that appear ideal for eelgrass according to the model prediction.

Wave exposure was found to be the second most important factor. Wave action and strong currents can lead to sediment movement, which may bury plants, expose roots and rhizomes, and even uproot entire plants (Preen et al. 1995). Hence, physical disturbance through wave action is considered to be one of the main extrinsic factors controlling the spatial structure of seagrass meadows (Clarke & Kirkman 1989, Duarte et al. 1997). Wave exposure in our model is negatively correlated with the probability to find eelgrass, which corroborates other studies (Krause-Jensen et al. 2003, Downie et al. 2013, March et al. 2013a). The most exposed coastlines in the study area, such as the north-west coast of Fehmarn or south of the Schlei Fjord, are lacking eelgrass altogether, while the most sheltered locations often feature dense and extensive meadows (Fig. 3 and 6). Results from our patchiness analysis on a meter-scale show a similar pattern, exhibiting significantly smaller patch lengths at exposed versus sheltered locations. Contrasting to other regions in the world, even the most exposed stretches of our coast should facilitate eelgrass growth, if only wave exposure was considered. Other surveys have demonstrated that at exposed coasts, seagrass populations tend to shift their distribution towards greater water depth, for example in the Mediterranean (Infantes et al. 2009). In our turbid waters, this exposure evasion is not possible and highly exposed coasts throughout the Baltic are thus devoid of eelgrass (Boström et al. 2014).

The question remains whether these exposed areas were populated historically, before eutrophication set in in the mid-20th century and water clarity was much higher. Although quantitative distribution data are absent, it is likely that eelgrass was historically more abundant and occurred at greater depth in the German part of the Baltic Sea. The most detailed and comparable evidence comes from the adjacent Danish waters, where time series since 1900 show a decline in depth limits of eelgrass from an average of 4.3–8.5 m to an average of 1–5.4 m (Krause-Jensen et al. 2005), resulting in an area loss of 75 % (Boström et al. 2003). Secchi depth data, which are closely linked to macrophyte depth limits (Nielsen et al. 2002, Greve & Krause-Jensen 2005a, Krause-Jensen et al. 2008, Krause-Jensen et al. 2011), show a related decrease from 9.5 to 6.0 m in the shallow Baltic Sea between an early (1903–40) and a late (1957–99) period (Dupont & Aksnes 2013) and further strengthen the hypothesis that loss of deeper meadows since the 1960s is mainly caused by light limitation along with eutrophication (Reinke 1889, Schramm 1996, Munkes 2005, Meyer & Nehring 2006, Schories et al. 2009). Today, maximum depth limits in our study area are less than 8 m, with eelgrass covering about 36 % of the depth zone between 0 and 8 m. If we conservatively assume that about the same percentage of the potentially habitable area was populated historically down to a depth of 12 m, the total area of historical eelgrass populations amounts to 288 km^2, corresponding to an estimated area loss of about 148 km^2 or 51 % since before the 1960s. Fortunately, Secchi depths and macroalgae depth limits have shown a slow increase over the last two decades in the south-west Baltic Sea /

North Sea region (Pehlke & Bartsch 2008, Wiltshire et al. 2008, Fleming-Lehtinen & Laamanen 2012), indicative of a reversal of the eutrophication process. Our observations confirmed these findings, showing also an increase of 1–1.5 m of the eelgrass depth limit compared to preceding studies or reports (Schories et al. 2005, Meyer & Nehring 2006).

The river-like Schlei Fjord has a length of 42 km and is surrounded by farmland and pasture. Strongly reduced visibility along with high agricultural nutrient input prevent growth of eelgrass in most of the fjord except for a small area (ca. 2.6 km²) around the outlet to the open sea (Fürhaupter et al. 2003). The low visibility is caused by extensive plankton production and slow exchange with the open Baltic Sea (Rieper 1976). However, historically at least two-thirds of the Schlei were populated with eelgrass (Meyer et al. 2005), and our model likewise predicts a high probability throughout the Schlei to find eelgrass (Fig. 5). The fjord comprises a total area of about 50 km², most of which is less than 5 m deep, so the total eelgrass area lost in the fjord amounts to at least 30 km².

The factor ‘slope’ only had a small effect on the model output (4.6 %), but the AIC analysis suggests that this effect is sufficient to justify an inclusion in the final model (Table 2). Some studies found similar effects of slope on macrophyte distribution (Duarte & Kalff 1990, Bekkby et al. 2008), but others did not, particularly in gently sloping terrains like in our study area (Krause-Jensen et al. 2003, Downie et al. 2013). The observability of the effects of slope in our model may be a consequence of the size of the extensive data set, which allows even minor predictors to yield a significant impact.

Given the estimated total extent of eelgrass meadows in the study area (ca. 140 km²), their frequent occurrence along most of the coast, and high productivity of eelgrass meadows in general (Duarte et al. 2005), eelgrass habitats form the largest and most productive coastal ecosystem in the German part of the Baltic Sea. Assumptions on productivity of eelgrass vary depending on study region, but are generally estimated to be between 300 and 900 g C m^{-2} a^{-1} (McRoy 1974, Penhale 1977, Wium-Andersen & Borum 1984, Pedersen & Borum 1995), leading to a rough primary production estimate between 42 and 126 kt C a^{-1} in our study area. Eelgrass meadows in the Kattegat and western Baltic region are known to have a relatively high production compared to eelgrass meadows in other regions

(Boström et al. 2014). Thus the actual primary production of eelgrass in our study area will likely be closer to the upper end of this range.

In their function as ecological engineers (*sensu* Wright & Jones 2006) eelgrass meadows not only provide food and nursery ground for locally important fish species, but also help to remove excess nutrients. Annual uptake of nitrogen (N) and phosphorus (P) by eelgrass in a comparable Danish meadow was estimated to be 34.5 g N m^{-2} a^{-1} and 3.2 g P m^{-2} a^{-1} (Pedersen & Borum 1993, 1995). For the eelgrass area of our study region, this would result in an annual incorporation of about 4.83 kt N a^{-1} and 0.45 kt P a^{-1}. Regardless of whether this amount is recycled internally, buried in the sediment, or exported to terrestrial habitats, it will not be available for the production of algae or plankton and thus eelgrass nutrient uptake helps to prevent negative effects of eutrophication like algae blooms (Hemminga et al. 1991, Dudley et al. 2001). To prevent the same amount of nitrogen or phosphorus from entering the Baltic Sea, an additional wastewater treatment plant capacity would be needed that equals 3.6 (for N) or 2.3 (for P) times the largest wastewater treatment plant in Schleswig-Holstein ("Klärwerk Kiel"; 425,000 inhabitant equivalents; Location: 54.453° N / 10.185° E; annual filter capacity: 1.34 kt N a^{-1}, 0.20 kt P a^{-1}; pers. comm. M. Wuttke).

Patchiness of seagrass habitats is ecologically relevant and can have positive and negative effects on the associated fauna depending on local ecological relationships and spatial scale (Boström et al. 2006). It is positively correlated with diversity and abundance of a wide range of organisms from crustaceans to fish (McNeill & Fairweather 1993, Eggleston et al. 1998, Salita et al. 2003, Hovel & Fonseca 2005) and strongly reduces predation success of foraging fishes (Hovel & Lipcius 2001). On the other hand, patchier meadows are reported to exhibit lower seagrass biomass and shoot density and higher predation rate and subsequent mortality of associated clams (Irlandi 1994). Patchiness of seagrass habitat is essentially caused by external factors, mainly wave exposure and sediment characteristics (Fonseca & Bell 1998). Seagrass landscapes have been found to be more homogenous at non-exposed and more heterogeneous and patchier at exposed, disturbed sites (Fonseca & Bell 1998, Bell et al. 1999, Frederiksen et al. 2004). Our results support these observations, showing significantly longer patch length and a lower patchiness index at more sheltered versus exposed sites. As well as for the surveyed region as for an area of such size (588 km²), the present study provides the first estimate of eelgrass habitat patchiness, which enables further quantitative valuations of this important ecological factor.

The Water Framework Directive of the EU (WFD) aims to achieve a ‘good environmental status’ in all surface and ground waters including coastal waters up to 1 nautical mile (= 1,852 m) off the coastline (WFD 2000). To this end, actual status and changes of important indicator species such as eelgrass have to be monitored regularly, including the south-western Baltic (Fürhaupter & Meyer 2009). With the present work we added knowledge on eelgrass cover and depth limit from 110 perpendicular transects and 315 km of parallel transects along the coast; and for the first time the areal extent of eelgrass could be calculated for the whole outer Baltic coastline of Schleswig-Holstein. We were able to derive a highly validated model and are now able to predict the potential of seagrass occurrence also for the areas outside our surveyed transects. For coastal management, the model allows more informed decisions and could be used instead of costly monitoring of actual occurrence.

Using the model, we currently identified three potential sites for eelgrass restoration in the study region. So far, there have not been any environmentally-based eelgrass restoration projects in German waters (Meyer & Nehring 2006) and only one scientific project, which tested the practical issues of colonization success like substrate nutrient content, density, and competition within planted patches (Worm & Reusch 2000). In the future, the EU could force member states on the basis of the WFD to actively promote water quality e.g. by restoration of lost eelgrass habitats, a measure not uncommon in the USA (Orth et al. 2010). Our model proposes potential sites for restoration on the basis of falsely predicted presences. The influence of factors other than the three chosen model predictors may be responsible for the observed errors and therefore prevent a successful colonization. However, we think that our model’s predictions provide a starting point for a discussion about possible locations for eelgrass restoration projects in the western Baltic Sea.

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Figures and Tables

Figure 1: Regional map of study area showing the potentially habitable depth zone for eelgrass in green (0–10 m). Wind stations: 1. Flensburg, 2. Schleswig, 3. Schönhagen, 4. Kiel Lighthouse, 5. Putlos, 6. Fehmarn, 7. Travemünde.

Figure 2: Map of observed eelgrass cover along surveyed camera transects. Eelgrass cover is shown in 6 classes (class 0: 0 %, class 1: < 10 %, class 2: 10-25 %, class 3: 25-50 %, class 4: 50-75 %, class 5: 75-100 %). Place names given for selected locations. Transect width is not to scale.

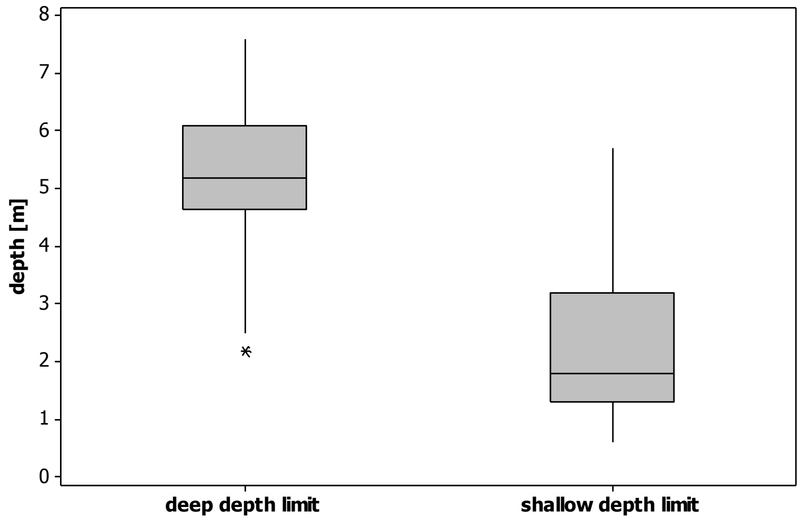

Figure 3: Box plot of depth limit range for deep and shallow depth limits along perpendicular mapping transects with eelgrass (n = 97), showing quartiles, median, and outliers (*).

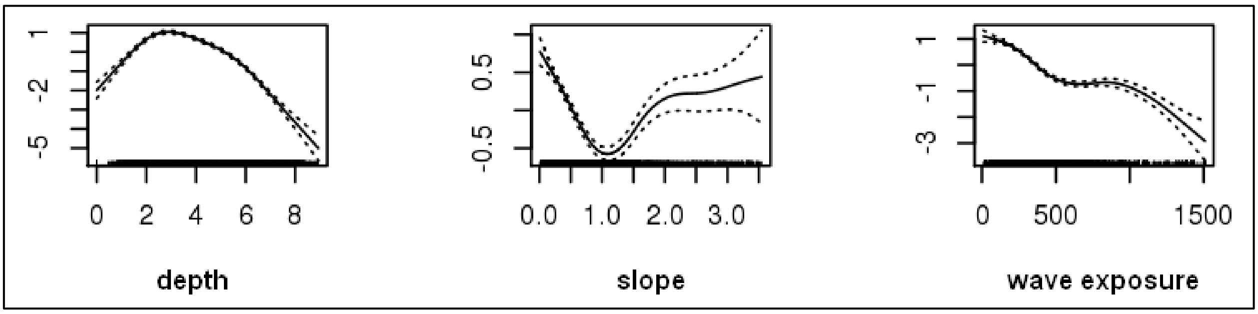

Figure 4: Response curves of eelgrass presence/absence to the predictor variables *depth*, *slope* and *wave exposure* in the GAM analysis for the final model (Model 1). The depth x-axis is presented in meters, the slope x-axis in degrees, and the wave exposure x-axis in watts. The y-axis represents the additive contribution of each variable (range differs between panels). Black lines above x-axis represent observation range. Dashed lines represent 95 % confidence interval limits.

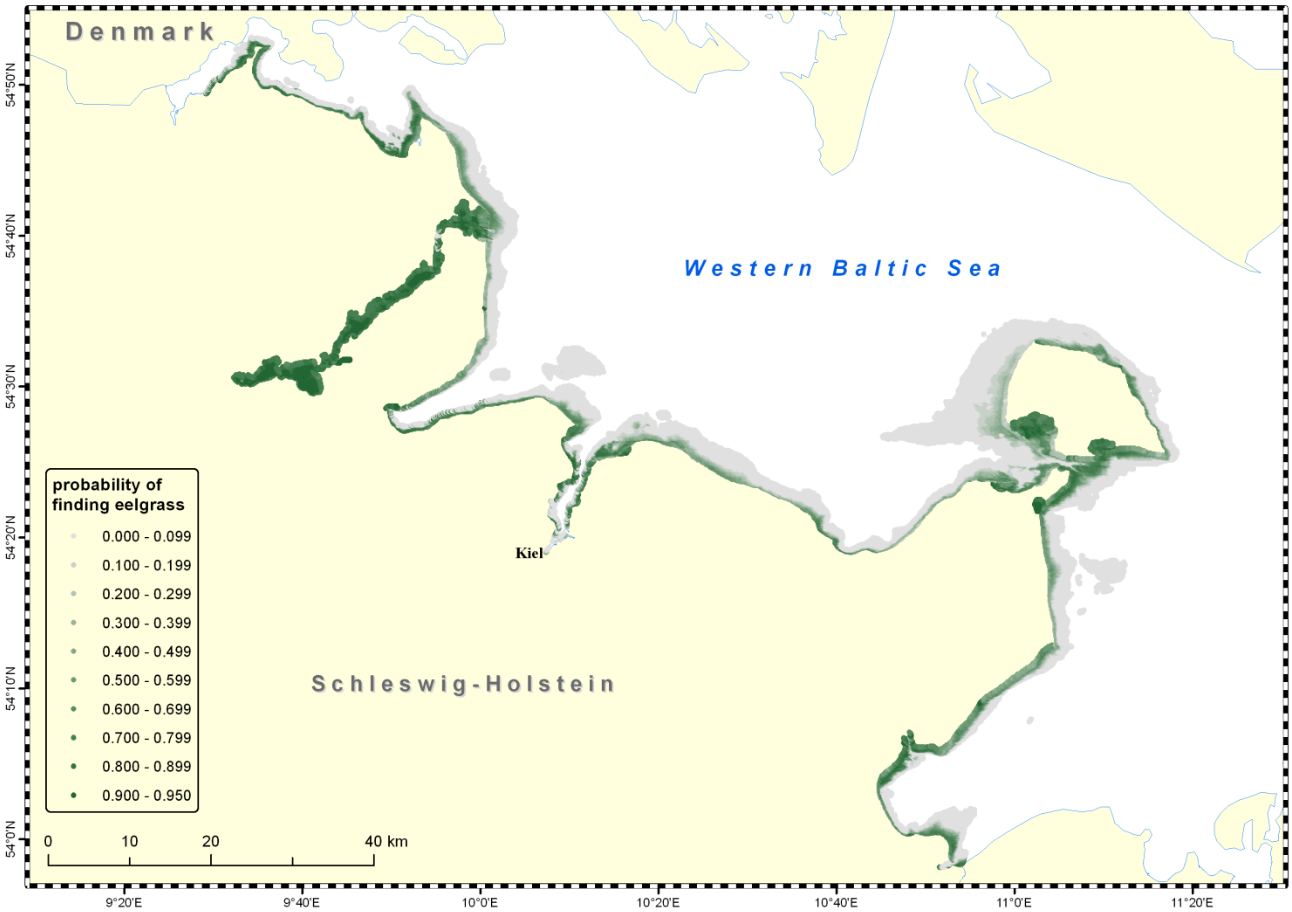

Figure 5: Map of predicted probability of eelgrass occurrence along the coast of Schleswig-Holstein for the final Model (Model 1). The darker green the area, the larger the probability to find eelgrass. Horizontal resolution of the model is 100 m, maximum depth is 10 m (indicated in grey).

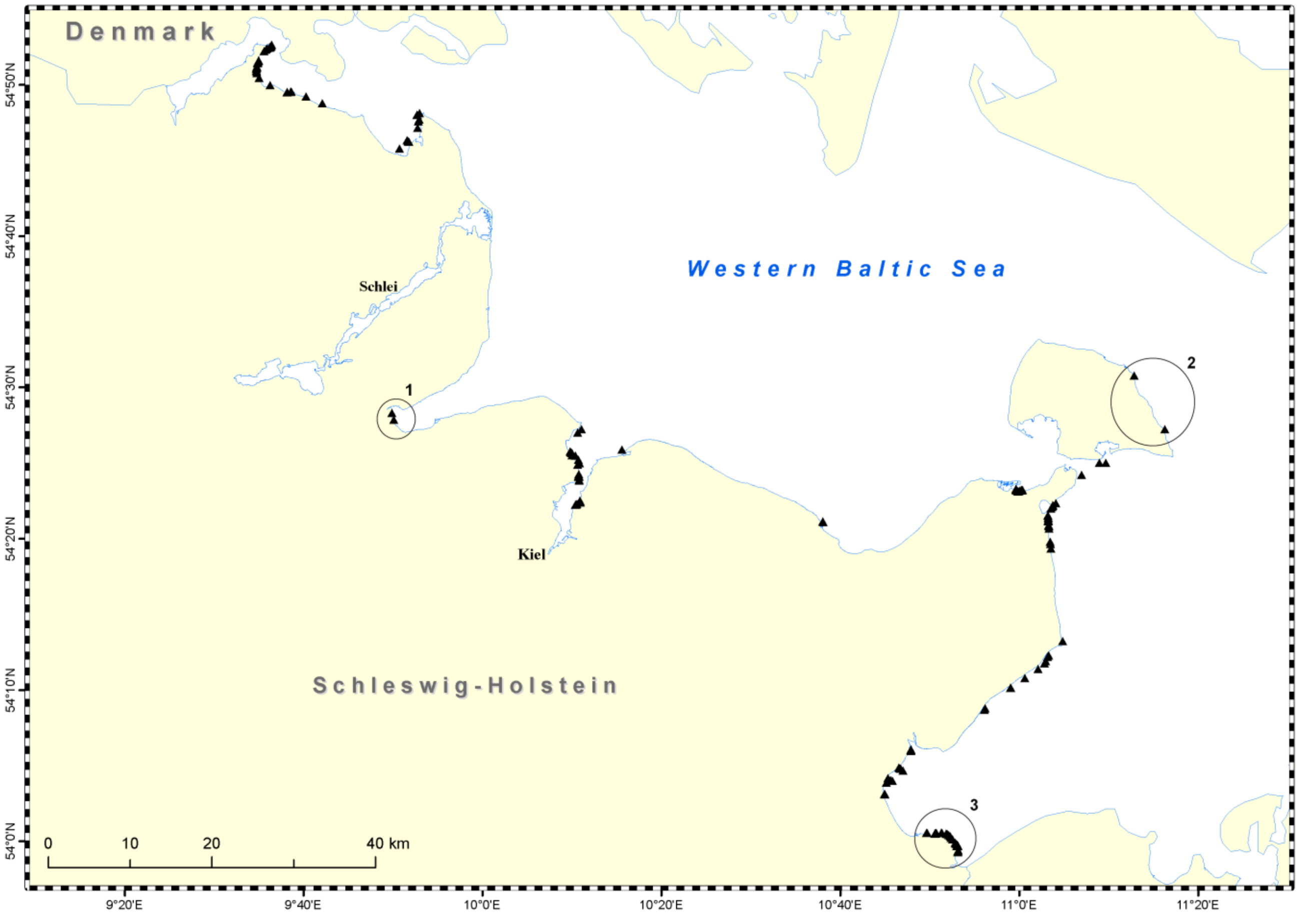

Figure 6: Map of falsely predicted presences (with 5 % probability of error in predicting the presence of eelgrass) for the final model (Model 1). Small triangles show locations where eelgrass is absent although the modeled probabilities to find eelgrass are high (> 0.77). Open circles show potential restoration sites (1: Eckernförde Bay, 2: Fehmarn-East, 3: Brodten Cliff). The Schlei Fjord was excluded from the analysis.

Table 1: Number of all observations of eelgrass presence/absence per depth class.

depth class	n
0 - 1 m	267
1 - 2 m	1,924
2 - 3 m	9,759
3 - 4 m	25,653
4 - 5 m	20,594
5 - 6 m	5,667
6 - 7 m	3,623
7 - 8 m	2,565
8 - 9 m	593

Table 2: Model selection based on Akaike's information criterion (AIC). Results sorted with ascending AIC values (i.e. descending model performance). The response variable is *Zostera marina* occurrence (presence/absence), predictor variables are *depth, slope* and *wave exposure (WE)* comparing average and threshold wind speeds with selected threshold velocities. Δ is the difference from the best model. ROC/AUC denotes the results of the area under the ROC curve for each model (AUC < 0.7: poor, 0.7–0.8: satisfactory, 0.8–0.9: very good, > 0.9: excellent discriminative ability).

Rank	Predictor variables	AIC	Δ	ROC/AUC
1	Depth + Slope + WE (≥ 6 ms^{-1})	8074.7	0.0	0.8207
2	Depth + Slope + WE (≥ 7 ms^{-1})	8089.9	15.2	0.8199
3	Depth + Slope + WE (≥ 5 ms^{-1})	8095.9	21.2	0.8192
4	Depth + Slope + WE (≥ 8 ms^{-1})	8125.1	50.4	0.8177
5	Depth + Slope + WE (≥ 4 ms^{-1})	8129.8	55.1	0.8166
6	Depth + Slope + WE (< 10 ms^{-1})	8147.0	72.3	0.8159
7	Depth + Slope + WE (avg)	8215.8	141.1	0.8115
8	Depth + WE (≥ 6 ms^{-1})	8305.9	231.2	0.8052
9	Depth + WE (avg)	8454.5	379.8	0.7961
10	Depth + Slope	8779.8	705.1	0.7728
11	Depth	8982.8	908.1	0.7559
12	Slope + WE (≥ 6 ms^{-1})	9957.4	1882.7	0.6884
13	WE (≥ 6 ms^{-1})	10032.0	1957.3	0.6733
14	Slope + WE (avg)	10116.0	2041.3	0.6637
15	WE (avg)	10189.0	2114.3	0.6574
16	Slope	10727.0	2652.3	0.5725

Table 3: Confusion matrix table of the final model showing the observed and predicted presences/absences and respective percentages at a threshold of 0.48 (Kappa *K).* Correct classification rate at this threshold is 73.9 %.

	observed presence	observed absence
predicted presence	3,137 (40.1%)	1,267 (16.2%)
predicted absence	775 (9.9%)	2,645 (33.8%)

Table 4: Descriptive statistics of predictor variables *depth, wave exposure* and *slope* separated for eelgrass presences and absences and their contributions to the final model (Model 1).

	Eelgrass presences						Eelgrass absences						Model
Predictor	**N**	**Mean**	**SD**	**Min.**	**Median**	**Max.**	**N**	**Mean**	**SD**	**Min.**	**Median**	**Max.**	**contribut. [%]**
Depth [m]	3912	3.462	1.476	0.000	3.200	8.116	3912	4.989	2.180	0.000	5.191	8.931	**66.3**
Wave exposure [W]	3912	339.2	244.2	9.3	279.0	1379.7	3912	515.4	330.5	18.0	441.1	1509.0	**29.2**
Slope [°]	3912	0.792	0.687	0.020	0.571	3.545	3912	0.744	0.660	0.011	0.564	3.509	**4.6**

Table 5: Overview of studies combining vegetation mapping with subsequent species distribution models. Prediction area was either obtained from the text or approximated from provided maps. GAM: generalized additive model, MAXENT: maximum entropy, WE: wave exposure.

Paper	**Location**	**Species (Group)**	**Prediction area [km²]**	**Number of observation points**	**Observation points per km² of prediction area**	**Mathematical model**	**Predictors tested**	**Predictors in the final model**
Bekkby et al. (2008)	Norway, North Atlantic	*Zostera marina* (Seagrass)	625 (total area)	695	1.1	GAM	depth, different WEs, slope, enclosedness, different current speeds	depth, WE (5 years avg), slope
Bekkby & Moy (2011)	Norway, Skagerrak	*Saccharina latissima* (Phaeophyceae)	~1,665 (total area)	333	0.2	GAM	depth, WE, slope, light exposure, terrain curvature, probability of rocky seabed	depth, WE, slope
Downie et al. (2013)	Finland, Baltic Sea	*Zostera marina* (Seagrass)	206 (photic zone)	350	1.7	GAM / MAXENT	depth, slope, turbidity, distance to sandy shores, WE	depth, WE, distance to sandy shores
Grech & Coles (2010)	Australia, West Pacific	seagrass habitat	~22,600 (< 15 m)	11,562	0.5	Bayesian Belief Network	season, section, bathymetry, substrate, sea surface temperature, tidal range, spatial extent of flood plumes, WE	season, section, bathymetry, substrate, sea surface temperature, tidal range, spatial extent of flood plumes, WE
March et al. (2013a)	Spain, Mediterranean	*Posidonia oceanica* (Seagrass)	~100 (< 43 m)	857	8.6	Bayesian hierarchical model	depth, slope, WE, water residence time, multispectral data	depth, slope, near bottom orbital velocity, water residence time, multispectral data
March et al. (2013b)	Baleares, Mediterranean	*Posidonia oceanica* (Seagrass)	~50 (< 38 m)	336	6.7	Bayesian hierarchical model	depth, slope, WE	depth, slope, WE
This study	**Germany, Baltic Sea**	***Zostera marina* (Seagrass)**	**588 (< 10 m)**	**7,824**	**13.3**	**GAM**	**depth, different WEs, slope (temperature, salinity, sediment class)**	**depth, WE (> 6 m/s), slope**

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