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Predicting habitat suitability in temperate seagrass ecosystems

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Abstract

The worldwide observed dramatic decline of seagrasses has typically been attributed to multiple stressors such as eutrophication, disease, sedimentation, and toxicity events. Using principal component analysis and (multivariate) logistic regression, we investigated the importance of 30 commonly measured variables in explaining the presence and absence of the temperate seagrass species *Zostera marina* and *Zostera noltii* at 84 Western European locations. Although many interrelated variables influence seagrass presence in our dataset, presence or absence of both species could be reliably predicted by using only two easy-to-measure variables. A logistic regression model of *Z. marina* correctly predicted 77% of all observations by including water column light attenuation and sediment pore-water reduction oxidation potential (RedOx). The *Z. noltii* model had an 86% accuracy based on only tidal location (intertidal or subtidal zone) and pore-water RedOx. Applying the models to five evaluation sites demonstrated that both models can be usefully applied as tools for seagrass ecosystem restoration and conservation.

Seagrasses are rhizomatous marine angiosperms that form extensive meadows in temperate to tropical regions. These beds are among the most productive ecosystems on Earth and harbor a high biodiversity of animal life. In the last decades, seagrasses have experienced dramatic losses that have been attributed to multiple stressors (Orth et al. 2006). Degradation in temperate regions is attributed mostly to eutrophication, increased water temperature, and disease (Orth et al. 2006). Whereas temperature and disease cause direct damage to seagrasses, eutrophication summarizes a number of indirect and direct problems. In the first place, eutrophication may lead to reduced light as growth of phytoplankton, epiphytes, and macroalgae is enhanced (Burkholder et al. 2007). Moreover, eutrophication can also trigger toxicity events caused by, for instance, increased levels of ammonia (Brun et al. 2002; Van der Heide et al. 2008) or high sulfide concentrations in the sediment pore water (Pedersen et al. 2004).

Because seagrasses are highly important for the ecology and economic value of many coastal zones, numerous efforts have been made to restore seagrass ecosystems (Orth et al. 2006; Van der Heide et al. 2007; Van Katwijk et al. 2009). Even though costs for these projects are high, success is limited and very uncertain (about 30% success; Orth et al. 2006). One explanation for this low success might be that estimations of abiotic habitat suitability of potential restoration sites are unreliable because of the complex interplay of many different stressors. Although a multitude of environmental variables have been found to influence seagrass presence, only a few studies have tried to disentangle the relative importance of multiple abiotic variables for predicting seagrass habitat suitability (Van Katwijk et al. 2000; Short et al. 2002). In this study, we investigate to what extent different abiotic factors correlate with occurrence of the seagrasses *Zostera marina* and *Zostera noltii*, species that dominate seagrass ecosystems in many temperate regions. We sampled 84 different locations scattered all over Western Europe, measuring 30 different environmental variables that are commonly used to evaluate ecosystems. Using logistic regression (LR) analyses, we constructed for both species a simple multivariate model containing the most important environmental variables. To evaluate the usefulness of the models for restoration or conservation, we predicted the probability of occurrence of both species for five sites which had a history of seagrass loss and where recovery or applied restoration measures had different levels of success.

Methods

Data collection—All data were collected in areas where seagrasses were present or were historically present (Fig. 1). The sampling sites in these areas were randomly selected and each site was sampled once in the growth season (May–September) of 2005. Depth of these locations varied between 0.5 m above to 5 m below mean water level. At each site, we recorded presence or absence of both *Z. marina* and *Z. noltii* and noted whether the location was intertidal or subtidal. Next, we sampled and pooled three replicates of the surface water, sediment pore water (top 10 cm), and sediment (top 10 cm). Pore water was sampled using Rhizon pore-water samplers, and sediments were collected with a core sampler. Samples were frozen immediately after collection for transport to the laboratory

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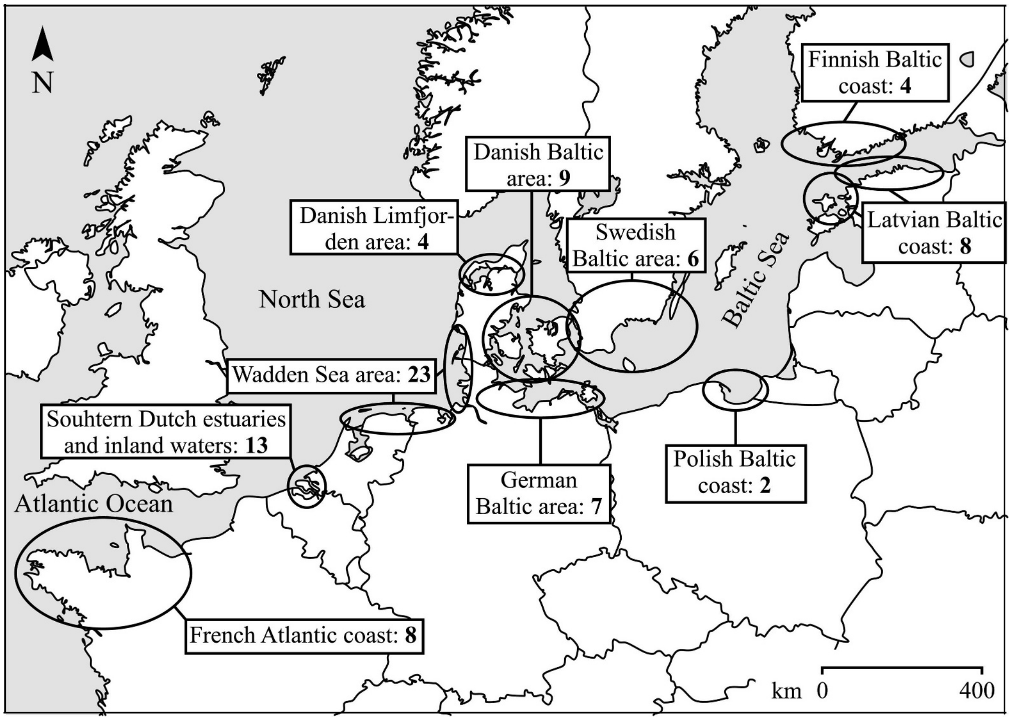

Fig. 1. General overview of the geographical setting of the 84 sampled sites. All sites are located in regions where seagrass is present or has been present in the past.

in Nijmegen (the Netherlands) where they were analyzed. As a measure for hydrodynamic exposure, we calculated the maximum and modified effective fetch length and included the exposure index developed by the Physical Shore-Zone Mapping Task Force of British Columbia, Canada (Howes et al. 1999).

Sample analyses—Apart from the hydrodynamic exposure variables, we included 26 additional commonly measured environmental variables. The light attenuation coefficient of the water column was measured as Photosynthetically Active Radiation (PAR) (400–700 nm) with a quantum light meter (Li-192, Li-Cor). Salinity, pH, and reduction oxidation potential (RedOx) of the sediment pore water were measured immediately after sampling with a multi-probe meter (556 Multi Parameter Sampler, Yellow Springs Instruments). Surface-water salinity and pH were measured on site. Total sulfide (TS) levels in the pore water were determined immediately after sampling by measuring TS with an ion-selective silver-sulfide electrode in a mixed solution containing 50% sulfide anti-oxidation buffer and 50% sample (Lamers et al. 1998). Alkalinity of all water samples was determined by titration with 0.01 mol L^{-1} HCl to pH 4.2 (Lamers et al. 1998). The concentrations of orthophosphate and ammonium in all water samples were measured colorimetrically, using ammonium molybdate and salicylate (Lamers et al. 1998). Nitrate was determined by sulfanilamide after reduction of nitrate to nitrite in a cadmium column (Wood et al. 1967). Total nitrogen and total phosphorus in the surface water were measured as nitrate and orthophosphate after digestion with persulfate (Koroleff 1983). We measured total inorganic carbon (TIC) in pore and surface water as CO_2 on an infrared carbon analyzer (PIR-2000, Horiba Instruments) after conversion of all TIC to CO_2 by phosphoric acid. Organic matter content in freeze-dried sediments was estimated as weight loss on ignition at 550°C. Carbon content and nitrogen content in the sediment were determined on freeze-dried samples by a carbon–nitrogen–sulfur analyzer (type NA1500; Carlo Erba Instruments). Total phosphorus in the sediment was measured on an inductively coupled plasma emission spectrophotometer (Spectroflame, Spectro) after digestion with nitric acid (Smolders et al. 2006*b*). Grain size distribution of the sediment was measured on freeze-dried samples by laser diffraction on a Beckman Coulter particle size analyzer. All devices were calibrated according to standardized procedures provided by the manufacturers. For all analyses, quality assurance measures included blanks, replicate analyses, and matrix spikes. Recoveries from matrix spikes ranged from 95% to 107%. Repeated analyses did not reveal differences greater than 5%.

Data analysis—We used 79 locations of the 84-location dataset for the modeling procedures, thereby excluding five sampling locations. These five sites had a recorded history of seagrass loss and recovery or restoration attempts resulting in different levels of success. After model construction, we used these locations to evaluate usefulness of the models and to exemplify how LR models may be applied for restoration and conservation purposes. The excluded sites were two sites from the Dutch Wadden Sea (Balgzand and Mokbaai), one site from the Baltic Sea (Puck Bay) and two sites from Dutch brackish closed-off water bodies (Lake Grevelingen and De Bol). Balgzand and

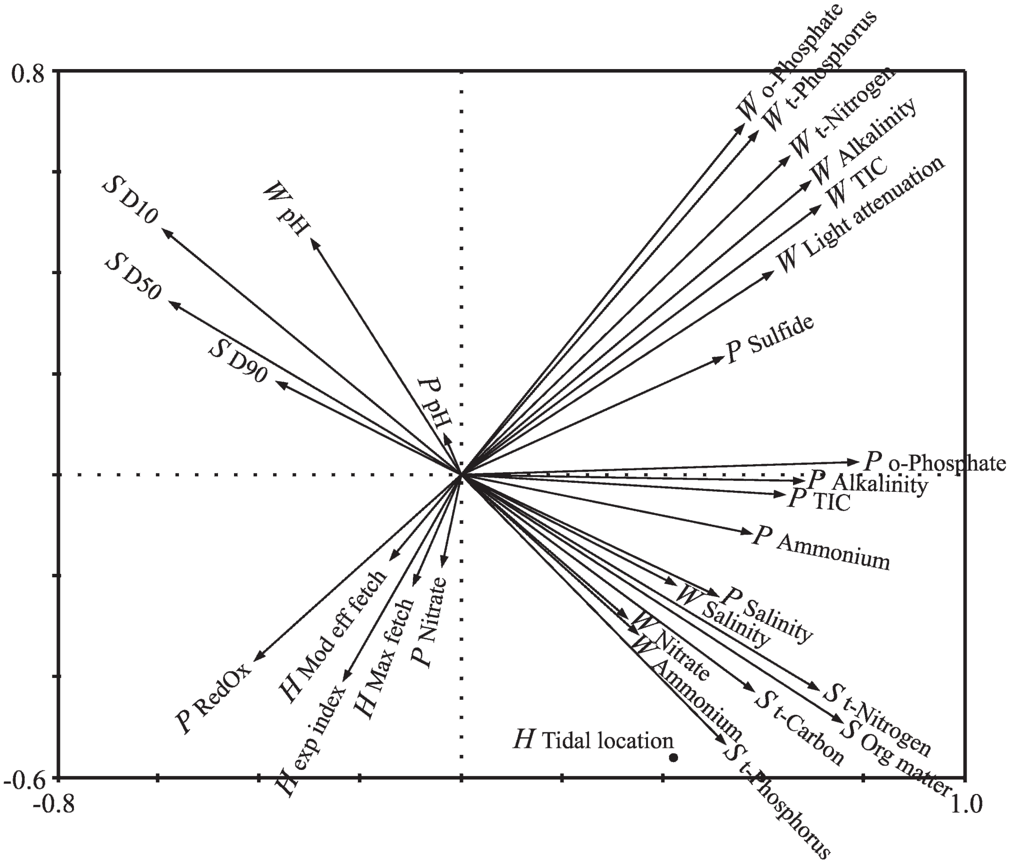

Fig. 2. Results of the PCA showing the relations between all variables included in our analyses. *W* and *P* indicate surface and pore-water variables, respectively. *S* indicates a sediment variable and *H* indicates a variable related to hydrodynamics. Eigenvalues of the *x*- and *y*-axis were 0.272 and 0.156, respectively, indicating that both axes together explained 42.8% of all variance in the dataset.

Mokbaai are both sites where restoration efforts by transplantation have been attempted (Van Katwijk et al. 2009). *Z. marina* transplantations were unsuccessful at both sites, but *Z. noltii* was successfully transplanted at Balgzand in 1993, resulting in a population that is at present still expanding. Puck Bay is a site near the city of Gdansk in Poland, where *Z. marina* is now slowly recovering after the population nearly disappeared in the last century (Boström et al. 2003). *Z. marina* disappeared from De Bol at the end of the 1970s because of eutrophication and changes in the hydrology of the site (Den Hartog 1994). The population at Lake Grevelingen became extinct at the end of the 1990s. Although the cause for this is still not fully understood, it has been suggested that this isolated estuarine population was (over-)adapted to low salinity and could not cope with a dramatic increase in salinity of the lake that took place in the 1980s and 1990s (Kamermans et al. 1999).

To get an overview of the relations between all variables included in this study, we first performed a standardized principal component analysis (PCA). Next, we fitted response curves by binary logistic regression (LR) to the presence–absence data for every variable. The general equation from this analysis describes the probability *P* that a species can occur at a certain value for the fitted environmental variable (Jongman et al. 1995):

$$P(x) = \frac{\exp(\beta_0 + \beta_1 x + \beta_2 x^2)}{1 + \exp(\beta_0 + \beta_1 x + \beta_2 x^2)} \tag{1}$$

The parameters β_0, β_1, and β_2 are regression coefficients, with β_0 as intercept. The equation can yield either a symmetrical bell-shaped (Gaussian) curve if β_2 is significant or a sigmoid curve if β_2 is not significant (and thus excluded). The parameters were analyzed for significance using the likelihood ratio test ($p < 0.05$). We used logarithmically transformed data ($y = \log_{10}(x + 1)$) when these gave a more significant fit. The calculated hydrodynamic exposure index and tidal location (subtidal or intertidal) were analyzed as categorical variables.

Next, we included all significant variables from the LR analysis in a multiple LR (MLR) procedure to construct a multivariate model. The applied equation is similar to function 1, except that a larger number of parameters can now be included (Jongman et al. 1995):

$$P(x) = \frac{\exp(\beta_0 + \beta_{1.1} x_1 + \beta_{1.2} x_1{}^2 + \ldots + \beta_{n.1} x_n + \beta_{n.2} x_n{}^2)}{1 + \exp(\beta_0 + \beta_{1.1} x_1 + \beta_{1.2} x_1{}^2 + \ldots + \beta_{n.1} x_n + \beta_{n.2} x_n{}^2)} \tag{2}$$

Table 1. Results from the logistic regression procedure on single variables for *Z. marina* and *Z. noltii*. *R* indicates the percentage reduction in deviance from a model with only constant β_0. Log indicates whether a variable was logarithmically transformed (y) or not (n). In case of a sigmoid-shaped curve (β_2 is not significant), the effect of a variable of seagrass presence is positive when $\beta_1 > 0$. Variables D10, D50, and D90 indicate the sediment grain size at which 10%, 50%, and 90%, respectively, of the volumetric fraction is smaller.*

		Zostera marina					*Zostera noltii*				
	Unit	Log	β_0	β_1	β_2	*R* (%)	Log	β_0	β_1	β_2	*R* (%)
Surface water											
Light attenuation	m^{-1}	y	3.327	−11.65	—	33.8	n	—	—	—	
Salinity		n	—	—	—		n	−4.458	0.139	—	20.5
pH		n	—	—	—		y	57.98	−61.20	—	11.6
Alkalinity	meq L^{-1}	n	1.626	−0.867	—	5.1	n	—	—	—	
TIC	mmol L^{-1}	n	1.448	−0.786	—	4.5	n	—	—	—	
o-phosphate	μmol L^{-1}	y	0.436	−2.383	—	7.9	n	—	—	—	
t-phosphorus	μmol L^{-1}	y	0.811	−2.310	—	9.1	n	—	—	—	
Ammonium	μmol L^{-1}	y	2.408	−2.755	—	5.6	n	—	—	—	
Nitrate	μmol L^{-1}	n	0.238	−0.143	—	6.4	n	—	—	—	
t-nitrogen	μmol L^{-1}	y	7.198	−4.780	—	17.0	n	—	—	—	
Pore water											
Salinity		n	—	—	—		n	−4.557	0.143	—	20.4
pH		n	—	—	—		n	—	—	—	
Alkalinity	meq L^{-1}	y	3.419	−5.726	—	12.2	n	—	—	—	
TIC	mmol L^{-1}	y	3.414	−5.517	—	11.7	n	—	—	—	
o-phosphate	μmol L^{-1}	y	0.927	—	−0.763	9.1	n	—	—	—	
Ammonium	μmol L^{-1}	y	1.178	—	−0.375	5.9	n	—	—	—	
Nitrate	μmol L^{-1}	n	—	—	—		n	−1.594	0.640	—	11.6
RedOx	mV	n	−0.309	0.004	—	4.8	n	−1.366	0.006	—	9.5
Sulfide	μmol L^{-1}	n	0.047	−0.003	—	7.8	y	−0.480	−0.690	—	6.1
Sediment											
D10	μm	n	−2.623	0.041	-1.2×10^{-4}	14.1	n	−0.232	−0.012	—	5.6
D50	μm	y	−10.56	4.566	—	10.3	y	5.795	−3.145	—	5.5
D90	μm	n	−1.727	0.004	—	5.1	y	10.347	−4.578	—	10.8
Organic matter	% (g : g)	y	1.113	−4.035	—	11.8	n	—	—	—	
t-carbon	% (g : g)	y	0.835	−3.974	—	9.9	n	—	—	—	
t-nitrogen	% (g : g)	y	0.427	−33.39	—	7.6	n	—	—	—	
t-phosphorus	% (g : g)	n	1.071	−0.157	—	8.2	n	—	—	—	
Hydrodynamics											
Maximum fetch	km	n	—	—	—		n	—	—	—	
Effective fetch	km	n	—	—	—		n	—	—	—	
Exposure index†			—	—	—			—	—	—	
Tidal location†			0.241	−1.585		7.9		−2.752	2.959		24.8

* —, not significant.

† Categorical variable.

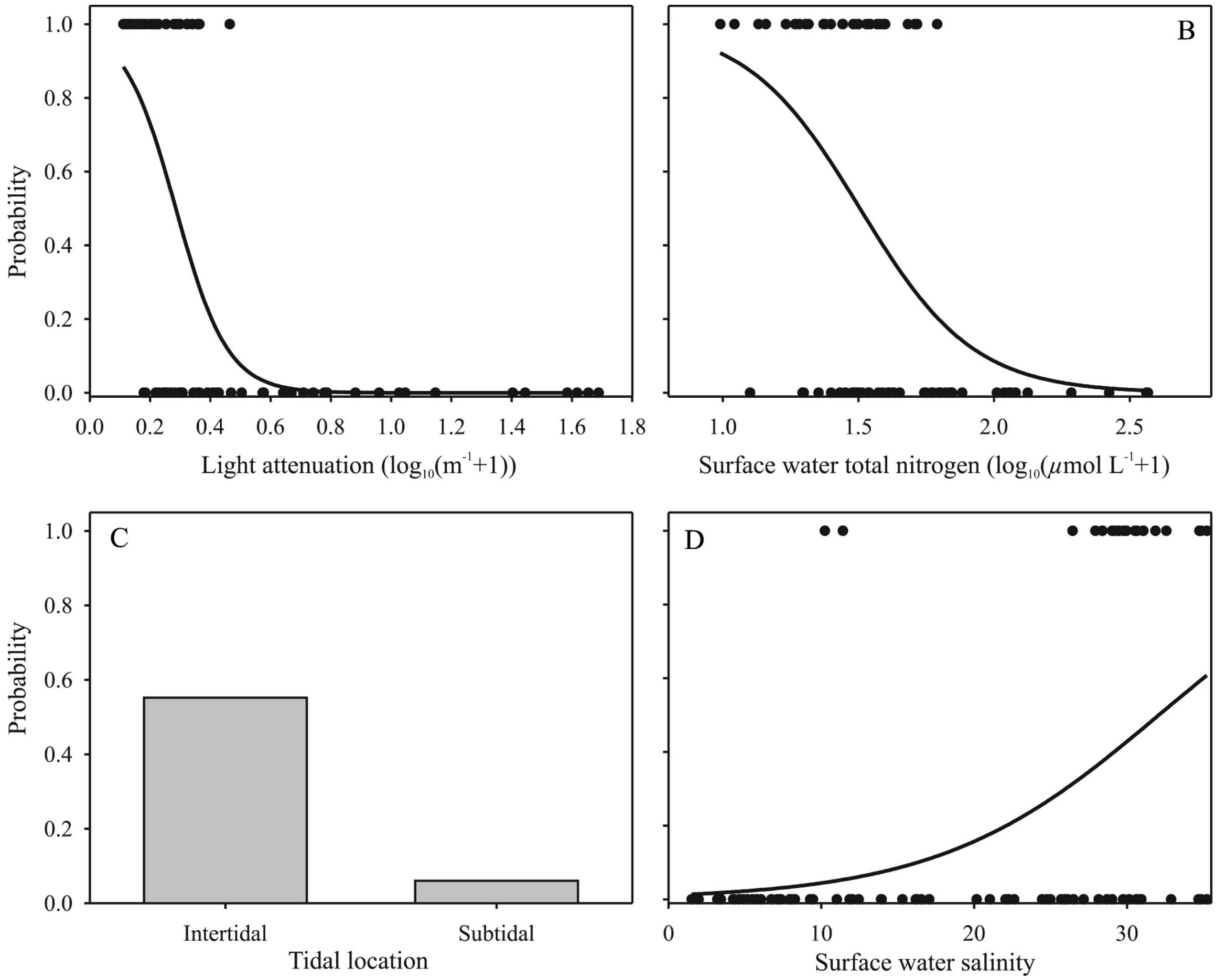

Fig. 3. Probability of presence for (A, B) *Z. marina* and (C, D) *Z. noltii* plotted against the variables that showed the highest significance. Dots are actual observations (1 = present, 0 = absent). The *x*-axes for light attenuation and surface-water total nitrogen are logarithmically transformed.

We used a multiple stepwise regression procedure with forward selection. The likelihood ratio test was applied to determine whether a variable should be included or not ($p < 0.05$). Additionally, we calculated the percentage reduction of deviance compared with the null model that included only a constant term (Peeters and Gardeniers 1998), and applied leave-one-out cross-validation (LOO) to assess the reliability of the resulting model. In this method, the model is built leaving out one single observation from the dataset. Next, the obtained model is used to predict presence or absence for the left-out observation. This procedure is repeated for every observation in the dataset. Based on the results, we calculated prediction success, mean parameter values, and standard deviation for the model parameters. Finally, we applied the obtained models from the multivariate LR procedure to the data from the five sites that were excluded from the analyses to evaluate their potential use as prediction tools for restoration success or failure.

Results

Our 79-site database included 34 observations for *Z. marina* and 19 for *Z. noltii*. PCA revealed that many variables correlated with each other (Fig. 2). For instance, light attenuation showed strong positive correlations with water column variables like total nitrogen, total phosphorus, orthophosphate, TIC, alkalinity, and pore-water sulfide. These variables showed a strong inverse correlation with RedOx. Most surface-water nitrogen and phosphorus variables did not relate strongly with sediment or pore-water nitrogen and phosphorus variables.

Results from the LR analyses (Table 1) show that the parameter for the second-order term (β_2) was not significant in most cases, resulting in sigmoid-shaped curves for the majority of the variables. Light attenuation produced the greatest reduction in deviance for *Z. marina* (33.8%; Fig. 3A), followed by surface-water total nitrogen (17.0%; Fig. 3B). Nearly all nitrogen and phosphorus

Table 2. Results from the multivariate logistic regression analysis, the leave-one-out cross-validation procedure. and evaluation sites.

Zostera marina				*Zostera noltii*			
Multiple logistic regression							
Parameter	Unit	Value		Parameter	Unit	Value	
Constant		3.551		Constant		−3.090	
Light attenuation	m^{-1}	−12.95		RedOx	mV	0.007	
RedOx	mV	0.005		Tidal location*		3.122	
R (%)		37.7		*R* (%)		33.8	
% correct		77.2		% correct		86.1	
Leave-one-out cross-validation							
Parameter	Unit	Mean	SD	Parameter	Unit	Mean	SD
Constant		3.556	0.133	Constant		−3.095	0.094
Light attenuation	m^{-1}	−12.97	0.545	RedOx	mV	0.007	4.12×10^{-4}
RedOx	mV	0.005	3.36×10^{-4}	Tidal location*		3.126	0.099
% correct		75.9		% correct		86.1	
Evaluation sites							
Location	*P*†	Predicted	Observed	Location	*P*†	Predicted	Observed
Balgzand	0.005	0	0	Balgzand	0.697	1	1
De Bol	0.021	0	0	De Bol	0.025	0	0
Grevelingen	0.751	1	0	Grevelingen	0.034	0	0
Mokbaai	0.012	0	0	Mokbaai	0.320	0	0
Puck Bay	0.593	1	1	Puck Bay	0.015	0	0
% correct		80		% correct		100	

* Categorical variable.

† *P* is the probability that either *Z. marina* or *Z noltii* occurs at a site. A prediction is positive (i.e., 1) when probability *P* is over 0.5.

content–describing variables (in water layer as well as sediment) were significant for *Z. marina*, revealing a consistently negative effect of both nitrogen and phosphorus on its probability of occurrence. Nitrogen and phosphorus seem much less important for *Z. noltii*. The greatest reduction in deviance was accomplished by tidal location of the sites (24.8%; Fig. 3C), followed by surface-water salinity (20.5%; Fig. 3D), pore-water salinity (20.4%), pore-water nitrate (11.6%), and surface-water pH (11.6%).

MLR analysis revealed that most of the variance in species presence could be explained by including only two variables in the models of both seagrasses. For *Z. marina*, light attenuation was the most significant parameter in the model. A significant part of the remaining deviance could be explained by including RedOx in the model as a second parameter. The obtained model correctly predicted 77% of all presence–absence data and reduced deviance by nearly 38% (Table 2). Tidal location was the most important variable for predicting *Z. noltii* presence. As for the *Z. marina* model, RedOx was also adopted by the *Z. noltii* model to improve its explanatory potential. The model predicted over 86% of all observations correctly and reduced deviance with nearly 34%. Furthermore, results from the LOO procedure yield a prediction success similar to that of the models constructed from the full dataset (Table 2). The procedure produces low standard deviations for model parameters, with mean parameter values that deviate only slightly from those obtained from the complete dataset.

Finally, we tested the models obtained from the MLR procedure on the five evaluation sites (Table 2). The *Z. marina* model correctly predicted absence or presence in four out of five cases. This model produced a false positive reading for Lake Grevelingen, predicting a probability for presence at this site of over 75%. The *Z. noltii* model correctly predicted all selected test sites.

Discussion

The observed worldwide decline of seagrasses has classically been ascribed to a multitude of environmental factors (Orth et al. 2006). Here, we show through the use of LR that presence or absence of the temperate species *Z. marina* and *Z. noltii* in the European coastal zone can be predicted to a large degree of confidence by only two easy-to-measure variables: light attenuation and RedOx for *Z. marina* and tidal location and RedOx for *Z. noltii*. This is remarkable because all sites from our dataset were sampled only once, thereby probably increasing noise because of infrequent events (e.g., algal blooms, toxicity events). Moreover, our analyses of five evaluation sites illustrate that the models can be useful tools to monitor (change in) habitat suitability for conservation purposes or for selecting suitable sites for restoration projects. For example, based upon our results, *Z. marina* transplantations at Balgzand or Mokbaai might not have been attempted. Instead, Lake Grevelingen could have been selected, because our model indicates that this site is more suitable. Because Lake Grevelingen is a closed-off water body, it is also likely that natural reestablishment from more salt-tolerant *Z. marina* populations is difficult at best. This might help explain why the species has not returned to the site, and illustrates why restoration by transplantation may be particularly necessary at this site.

Although both multivariate logistic models include just two variables, our results do not imply that seagrass presence is dependent on only these variables. The analyses merely show that the included variables are good indicators for general seagrass habitat suitability. Notably, single LR analyses demonstrated that seagrass occurrence correlated with many variables, and PCA showed that these variables were strongly interrelated. For instance, light availability is often indirectly dependent on nutrient content of the water layer (Burkholder et al. 2007), whereas pore-water RedOx conditions are typically related to organic matter degradation rates and resulting toxic sulfide levels (Smolders et al. 2006a). Increased nutrient levels in the water layer are well known to result in an increased growth of algae in the water layer. Apart from decreasing light availability, enhanced algal production also increases input of easily degradable organic matter into the sediment (Dahllof and Karle 2005). Such an increase will result in increased decomposition rates (involving sulfate reduction) along with a concomitant decrease of the RedOx potential and an increase of sulfide concentrations. Faster organic matter decomposition will raise inorganic carbon levels of the system and increase oxygen consumption rates of the sediment. The latter may, together with the increased sulfide concentrations, strongly affect the vitality of seagrass root systems (Pedersen et al. 2004). Thus, our results indicate that seagrass presence is probably often dependent on multiple interrelated factors, but because of strong correlations among variables, inclusion of only a few variables in prediction models can be sufficient to predict seagrass habitat suitability.

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