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Comparing the performance of species distribution models of *Zostera marina*: Implications for conservation

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A B S T R A C T

Intertidal seagrasses show high variability in their extent and location, with local extinctions and (re-)colonizations being inherent in their population dynamics. Suitable habitats are identified usually using Species Distribution Models (SDM), based upon the overall distribution of the species; thus, accounting solely for spatial variability. To include temporal effects caused by large interannual variability, we constructed SDMs for different combinations and fusions of yearly distribution data. The main objectives were to: (i) assess the spatio-temporal dynamics of an intertidal seagrass bed of *Zostera marina*; (ii) select the most accurate SDM techniques to model different temporal distribution data subsets of the species; (iii) assess the relative importance of the environmental variables for each data subset; and (iv) evaluate the accuracy of the models to predict species conservation areas, addressing implications for management. To address these objectives, a time series of 14-year distribution data of *Zostera marina* in the Ems estuary (The Netherlands) was used to build different data subsets: (1) total presence area; (2) a conservative estimate of the total presence area, defined as the area which had been occupied during at least 4 years; (3) core area, defined as the area which had been occupied during at least 2/3 of the total period; and (4–6) three random selections of monitoring years. On average, colonized and disappeared areas of the species in the Ems estuary showed remarkably similar transition probabilities of 12.7% and 12.9%, respectively. SDMs based upon machine-learning methods (Boosted Regression Trees and Random Forest) outperformed regression-based methods. Current velocity and wave exposure were the most important variables predicting the species presence for widely distributed data. Depth and sea floor slope were relevant to predict conservative presence area and core area. It is concluded that, the fusion of the spatial distribution data from four monitoring years could be enough to establish an accurate habitat suitability model of *Zostera marina* in the Ems estuary. The methodology presented offers a promising tool for selecting realistic conservation areas for those species that show high population dynamics, such as many estuarine and coastal species.

1. Introduction

Seagrasses play an important role in maintaining a diverse and healthy coastal ecosystem (Björk et al., 2008) and providing many environmental functions, which lead seagrass ecosystems to be amongst the most valuable ecosystems in the world (Costanza et al., 1997). However, their habitat is being fragmented and lost worldwide (Duarte, 2002; Hughes et al., 2009), with rates of decline accelerating in recent years (Waycott et al., 2009), and seagrass beds disappearing completely in some areas (Green and Short, 2003; Kirkman, 1997; Short et al., 2006). In contrast to this global crisis of seagrass ecosystems, recent researches have detected a recovery of mixed intertidal beds of *Zostera marina* and *Zostera noltii* in the North Frisian Wadden Sea (Germany) (Dolch et al., 2012), and a steady and linear increase in *Z. noltii* meadow areas within Bourgneuf Bay (France) (Barillé et al., 2010). These encouraging results reveal the potential for seagrass recovery, highlighting the importance of the assignment of suitable areas to permit the conservation of these valuable ecosystems.

Abbreviations: SDM, Species Distribution Models; TPA, total presence area; CPA, conservative presence area.

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Seagrass meadows are highly dynamic ecosystems, maintained through the continuous recruitment of new clones, in combination with the growth and turnover of the shoots (den Hartog, 1971; Duarte et al., 2006). In semi-annual populations, seed production, dispersal, germination and seedling survival additionally determine the bed dynamics. In particular, the intertidal habitat-forming species, such as the semi-annual flexible type of *Z. marina*, but also the perennial *Z. noltii*, have high inter annual variability in extent and location, with local extinction and (re-)colonizations being part of their life strategy (Erftemeijer, 2005; van Katwijk et al., 2006, 2009). Consequently, not all suitable habitats of the species are occupied every year. However, these uninhabited, but suitable, areas are important for seagrasses to survive in the long-term, by providing refuge areas to overcome temporally unsuitable local circumstances elsewhere, for example, to overcome weather conditions such as the presence of ice. Loss of these unoccupied habitats would decrease the possibilities for seagrass survival, enhancing ultimately the risk of extinction. Even if *Zostera* species and their habitats are protected under one or more environmental frameworks at international, European and national scales (Bos et al., 2005; Valle et al., 2011), the protection measures are based often upon the actual distribution of the species in a particular monitored year, rather than the overall available habitat. In this way, human activities (such as: bottom trawling; shellfish and worm collecting; and recreational activities) remain permitted around the seagrass beds. Such activities may lead to damage of the unoccupied habitat of these dynamic populations (Cunha et al., 2012).

Areas that are occupied frequently by seagrass (core areas, hereafter) can be distinguished easily when a time-series of monitoring data is available (Dolch et al., 2012). When seagrass monitoring is infrequent, it is likely to incorporate the core areas, but likely also to exclude large areas that are occupied only occasionally; thereby, underestimating the overall seagrass habitat. If only core areas are protected, a large part of the total distribution could be lost, e.g. in The Netherlands, this amounts to 91% ± 8.59% (Table 1). Therefore, defining the entire potential habitat area needed to maximally protect a species with high temporal dynamics requires frequent monitoring of its distribution. As the seagrass monitoring is laborious and expensive, there is a need for other approaches to be adopted for the delimitation of the conservation areas. One approach could be the use of species distribution models (sensu Guisan and Zimmermann, 2000; SDM, hereafter), to identify suitable seagrass habitats.

In recent years, several techniques to build SDMs have been developed (Elith and Leathwick, 2009; Franklin, 2009; Guisan and Thuiller, 2005). SDMs are based commonly on the overall distribution of a species, without considering if there are ecological differences between frequently and occasionally occupied areas. Likewise, distribution patterns of highly dynamic species (such as seagrasses) may vary considerably between different years of monitoring. In some years, seagrasses may spread to areas which are normally not occupied. Incorporation of such incidental occurrences in a SDM is likely to decreases the robustness of the model. On the other hand, seagrass beds could be damaged or represent only core areas, because of insufficient protection. Models based upon these frequently occupied areas might represent only a part of the total area suitable for the species. Therefore, in the research developed here, different subsets of a time-series of monitoring data were used to build SDMs for a seagrass species. Using a 14-year time-series of distribution data of *Z. marina* in the Ems estuary (The Netherlands), which allows addressing spatio-temporal variability in the modelling, the aims of this research are to: (i) assess the spatio-temporal dynamics of an intertidal seagrass bed of *Zostera marina*; (ii) select the most accurate SDM techniques to model different temporal distribution data subsets of the species; (iii) assess the relative importance of the environmental variables for each data subset; and (iv) evaluate the accuracy of the models to predict species conservation areas, addressing implications for management.

2. Material and methods

2.1. Study area

The Wadden Sea (Fig. 1a) is one of the world's largest international marine wetland reserves (approx. 6000 km^2), bordering the coasts of The Netherlands, Germany and Denmark. Due to its high ecological importance, it is under the protection and conservation frameworks of three main European Directives: the Habitat Directive (92/43/EEC), the Directive on the Conservation of Wild Birds (2009/147/EC); and the Water Framework Directive (2000/60/EC).

The Ems estuary (Fig. 1b), located on the border between The Netherlands and Germany, is one of the most important estuaries intersecting the Dutch Wadden Sea (de Jonge, 2000). The biological and physical processes affecting this estuary have been investigated extensively (Baretta and Ruardij, 1988; de Jonge, 1992a, 1992b, 2000). Dominant physical processes are the tides (range and currents), wind-generated waves, and freshwater inflow from the Ems river and the Westerwoldse Aa river (Fig. 1) (Talke and de Swart, 2006). The availability of a time-series of 14 years on species' distribution and the relatively stable presence of *Z. marina* populations in this area (Bos et al., 2005) during the studied period, together with environmental data availability, were the main reasons to select the intertidal area of this estuary as the study area (Fig. 1c) to undertake this research.

Table 1
Occupied area, core area and potential loss of 14 seagrass beds in The Netherlands. Occupied area is the total area occupied during any of the monitoring years. Core areas are areas with an occupation of equal or greater than 66% of the monitored years. Potential seagrass bed loss is the potential loss if only core areas are protected (data courtesy: Ministry of Transport, Water Management and Public Works (analyses: Annette Wielemaker)).

Water body	Species	Location	Period	Monitoring years	Occupied area (ha)	Core areas (ha)	Potential loss (%)
Wadden Sea	*Z. noltii*	Groningse kwelders	1991–2008	13	115.94	14.05	88
		Tersch-Oosterend	1991–2008	14	50.22	8.25	84
	Z. marina	Ems estuary	1991–2008	14	251.24	15.7	94
		Tersch-haven	1991–2001	7	25.13	1.71	93
Eastern Scheldt	*Z. noltii*	Dortsman	1990–2009	10	58.08	15.09	74
		Kats	1991–2008	10	13.94	2.57	82
		Kattendijke	1990–2009	8	13.89	2.08	85
		Krabbekreek Noord	1990–2009	12	36.42	0.29	99
		Sint Annaland	1990–2009	12	3.35	0	100
		Mastgat	1990–2009	11	4.6	0	100
		Viane	1992–2008	8	19.37	1.22	94
		Zandkreek Noord	1990–2009	18	34.55	0.1	100
		Zandkreek Zuid	1990–2009	18	37.52	7.63	80
		Zuid Beveland	1990–2009	11	34.37	1.18	97