

Predicting the effects of sea level rise on salt marsh plant communities: does vegetation age matter more than sea level?

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Background and aims – Salt marsh plant communities will be among the first to be exposed to the predicted increase in sea level and to the associated environmental changes. The objectives of this study were to evaluate the influence of three major environmental variables (elevation above sea level, distance from the sea, vegetation age) on vegetation diversity in salt marshes and to predict vegetation changes in the year 2100 according to different scenarios of sea level rise.

Methods – Plant communities were sampled in 1257 plots of 1 m² distributed along transects randomly positioned perpendicular to the shoreline in the Bay of Somme (Picardy, France). Digital elevation model data were used to determine the plot elevation and the distance between the plots and the shoreline. Three centuries of changes in the vegetation cover were reconstructed using historical maps and aerial photographs to estimate the vegetation age. We investigated the relationships between elevation above sea level, distance from the sea, vegetation age and vegetation richness and composition using mixed models. Predictive models of species richness and cover of dominant halophytes were built using the parameter estimates of the previous mixed models and the projections of the explanatory variables in 2100 according to the different sea level scenarios from +0.5 m to +2.5 m.

Key results – Mixed models showed that species richness mainly increased with vegetation age. The halophytes exhibited contrasting patterns along elevation and age gradients. Sedimentation rates may counteract the sea level rise until the latter reaches a critical rate that drowns the marsh vegetation.

Conclusions – Because the proportions of ancient vegetation will be higher in the bay, mean plant species richness may be higher in predicted communities in 2100 than in recently sampled communities.

Key words – Salt marsh, plant community, species richness, halophytes, historical factors, sea level rise, *Salicornia*, *Aster tripolium*, Baie de Somme.

INTRODUCTION

Salt marsh plant communities are associated with a narrow range of soil topographic elevation and will be one of the first to feel the effects of predicted increase in sea level. The modern rates of sea level rise started at the beginning of the 20th century (Gehrels & Woodworth 2013) and their first impacts on coastal areas and vegetation have already been recorded (Donnelly & Bertness 2001). In many cases under existing inundation conditions, below-ground production and induction of sedimentation through baffling by above-ground macrophyte biomass are declining as sea level is rising (Voss et al. 2013). Thus, the reduced macrophyte productivity and

capacity even to retain existing marsh surface elevations reflect failure in accretion feed-back processes, threatening the persistence of salt marshes (Voss et al. 2013). Most of the predictions of the response to sea level rise focus on the habitat and landscape scales (Vestergaard 1997, Stralberg et al. 2011, DeLaune & White 2012, Rogers et al. 2012), while responses at the community scale are less explored (Tolley & Christian 1999, Sharpe & Baldwin 2012), and require much more assessment and consideration for the planning of the future coastal areas.

The extent to which the sea level rise may affect coastal plant communities depends on the magnitude of sea level rise. According to estimates from the Intergovernmental

Panel on Climate Change (IPCC), global warming until 2100 may cause a global mean sea level rise of 0.18–0.59 m (Meehl et al. 2007). Nevertheless, the accuracy of the climate models is limited by the complex and multifactorial nature of the causes of sea-level rise (Cazenave et al. 2008, 2009, Nicholls & Cazenave 2010) and discrepancies (up to 80% of error) may appear between the observed data and the projections (Cazenave & Llovel 2010, Zecca & Chiari 2012). Since then, these predictions have been reworked (IPCC 2013) and improved to better capture the contributions due to fast ice dynamics (Pfeffer et al. 2008) or integrate observed sea-level trends in semi-empirical models (Vermeer & Rahmstorf 2009). Larger changes (Rahmstorf 2007, Vermeer & Rahmstorf 2009, Katsman et al. 2011, Pelling et al. 2013) and accelerations of sea level rise may be expected throughout the 21st century (Nicholls & Cazenave 2010, Church & White 2011, Woodworth et al. 2011), with projections ranging up to c. +2 m because of acceleration of global warming and possible role of the Greenland and West Antarctic ice sheets and regional factors. Furthermore, seasonally and spatially non-uniform variations in sea level rise are likely to occur, increasing the level of the sea locally over the globally predicted mean values (Milne et al. 2009, Pickering et al. 2012). In the southern North Sea, the sea level rise projections for 2200 range up to c. +3.5 m (Katsman et al. 2011). Regarding the underestimation of the sea level rise in the past models and projections and the plausible appearance of new sources of climate warming (Gorham 1991, DeConto et al. 2012, Fan et al. 2013, Gong et al. 2013), extreme scenarios cannot be excluded. These extreme scenarios are also valuable when the sea level rise combines with extreme climatic events, such as hurricane surge and waves (Smith et al. 2010). Many recent studies propose adaptation strategies in the planning for the future coastal communities based on the revised values of the sea level rise of 1 m, 2 m or even 5 m by the end of the century (Parker et al. 2013). Other site specific conditions such as enhanced sediment accretion (Wolanski et al. 2004) or accelerated erosion caused by human activities (Castillo et al. 2000) or related to climate change, i.e. sea-level rise and increased wind and wave activity (Kim et al. 2011), may be also implied in the response of estuarine systems to sea level rise (Pont et al. 2002) and thus, local topographic variables are needed to ameliorate predictions in a given site.

Marsh elevation above the sea level and distance from the shoreline are the two vertical and horizontal topographic variables that will be directly modified by sea level rise. These two variables are also related to numerous environmental determinants of vegetation composition: frequency and duration of inundation, soil drainage, salinity and nutrients, mechanical erosion by sea waves (Vestergaard 1997, Khedr 1998, Silvestri et al. 2005). Elevation and distance from the shoreline are not necessarily correlated (Silvestri et al. 2005): both micro- and macro-cliffs are commonly found very close to the shoreline along the European coast (see the Normandy and Picardy coasts), while continental marshes can develop under the sea level because protected by natural or engineered coastal barriers (see the Netherland coasts). In the next decades, most of salt marsh areas will be exposed to increasing frequency of inundation, salt water intrusion, soil waterlogging, hypoxia and mechanical erosion

by waves. These new conditions may modify the survival, growth, reproduction and competitive ability of halophytes (Tolley & Christian 1999, Egan & Ungar 2000, Huckle et al. 2000, Woo & Takekawa 2012, Alhdad et al. 2013), may cause a displacement of vegetation zones up-estuary and up the intertidal platform (Vestergaard 1997) or may produce a complex mix of changes in the plant distribution (Watson & Byrne 2009) and, finally, may alter biochemical cycles and ecosystem processes and services in the estuarine floodplain (Miller et al. 2001, Chmura 2013, DeLaune & White 2012).

Historical dimension is usually forgotten in the models predicting the effects of sea level rise on the coastal vegetation, although the age of the vegetation has been recently evoked as a major factor influencing the spatio-temporal dynamics of the salt marsh plants (Veeneklaas et al. 2013). A new vegetation patch installed in 2010 will be 90 years older in 2100. This age effect on vegetation diversity is almost never considered in models and rarely disentangled from other environmental factors such as distance from the sea or elevation. Historical maps and the written history of disturbance events represent effective tools to trace estuarine vegetation changes (Civco et al. 1986, Dijkema 1987, Bromberg & Bertness 2005, Godet & Thomas 2013) and to explain current species diversity (Coverdale et al. 2013). The species–time relationship (Rosenzweig 1995) may be applied to estuarine floodplains in which recent and ancient vegetation patches coexist in a dendritic landscape mosaic constantly remodelled by the influence of the sea and human activities. In this system, the older vegetation patches had more time to accumulate species than the recent ones. The number of species may also increase over time because habitat quality is likely to change as the salt marsh ages; soil drainage and nutrients increase, while salinity decreases with age (Bertness & Ellison 1987, Olff et al. 1997, Houwing et al. 1999, Veeneklaas et al. 2013). In such environmental conditions, late successional communities will develop and host a higher number of generalist and salt-intolerant species from terrestrial environments and continental wetlands (Chabrierie et al. 2001, Géhu & Wattez 2007) and are expected to be richer than recent communities harbouring a small set of pioneer halophytes.

Our aim is (1) to test the effect of three important environmental variables (elevation above sea level, distance from sea and vegetation age) on salt marsh vegetation richness, composition and biomass and (2) to predict vegetation changes in 2100 according to the different scenarios of sea level rise.

For this, we used a recent large data set collected in the Bay of Somme (France), a medium-sized estuary preserved from the development of industrial areas and harbour facilities, and used mixed models to test the effects of environmental and historical variables on plant communities. Then, we extracted the parameter estimates of these mixed models and used the projections of sea level rise and vegetation age values in 2100 to build new predictive models. We hypothesize that sea level rise will reduce the total salt marsh area but will increase the proportion of ancient vegetation in the bay and, consequently, the local number of species.

MATERIAL AND METHODS

Study site

Located in the Eastern Channel between Marquenterre/Le Crotoy in the North and Saint-Valery-sur-Somme/La Pointe du Hourdel in the South, the Bay of Somme (50.20°N 1.62°E) is the second largest estuarine system in Northern France. This macrotidal estuary has a tidal range of 9.79 m and receives low fresh water input mainly from the Somme River ($30 \text{ m}^3 \cdot \text{s}^{-1}$). The other river (Maye) and smaller channels have low runoffs and thus the marine influence dominates the site (Rybarczyk & Elkaïm 2003). The salt marsh vegetation of the Bay of Somme covers 1909 ha. Due to low inputs from the river and strong hydrodynamic conditions at the mouth of the bay, the salt marshes have been largely patterned by natural flooding, tidal wave events and by sheep grazing and plant successions. Further, the human activities such as embankments, building of seawalls, levees and dykes, have also influenced the spatial dynamics of the bay (Lefèvre & Regrain 1977) at least over the last four centuries. Navigation ways are sometimes locally dredged to reduce silting in the bay but this management method systematically leads to very short-term and temporary results. The landscape of the bay currently forms a mosaic of vegetation patches varying in age which are included in a dendritic network of chan-

nels (fig. 1). The zonation of the vegetation is typical of a salt marsh ecosystem but is locally altered by the presence of ponds established by hunters. The most frequent species are *Elymus athericus* (35.9% of the plots), *Halimione portulacoides* (31.7%), *Puccinellia maritima* (31.6%) and *Aster tripolium* (30.4%). The bay is used for traditional purposes: harvesting of edible plants, extensive sheep grazing, hunting, cockle and inshore fishing and touristic activities (Meirland et al. 2013). Four main plants are collected in the bay, *Salicornia fragilis*, *Aster tripolium*, *Halimione portulacoides* and *Suaeda maritima*, and are marketed fresh for cooking in the Picardy and Normandy regions or transformed and exported.

Sampling

The vegetation was sampled in 1257 plots of 1 m^2 distributed in a total of 19 transects positioned perpendicular to the shoreline to take into account the vegetation zonation typical of salt marshes (Emery et al. 2001, Costa et al. 2003). Transects were spaced at a mean distance of 605 m and plots by a distance of 30 m along transects. In each plot, the cover of all vascular plant species and species richness were measured in July and August from 2009 to 2012. Plots with late flowering plants (*Salicornia* and *Atriplex* genus) were visited a second time in September to identify the species.

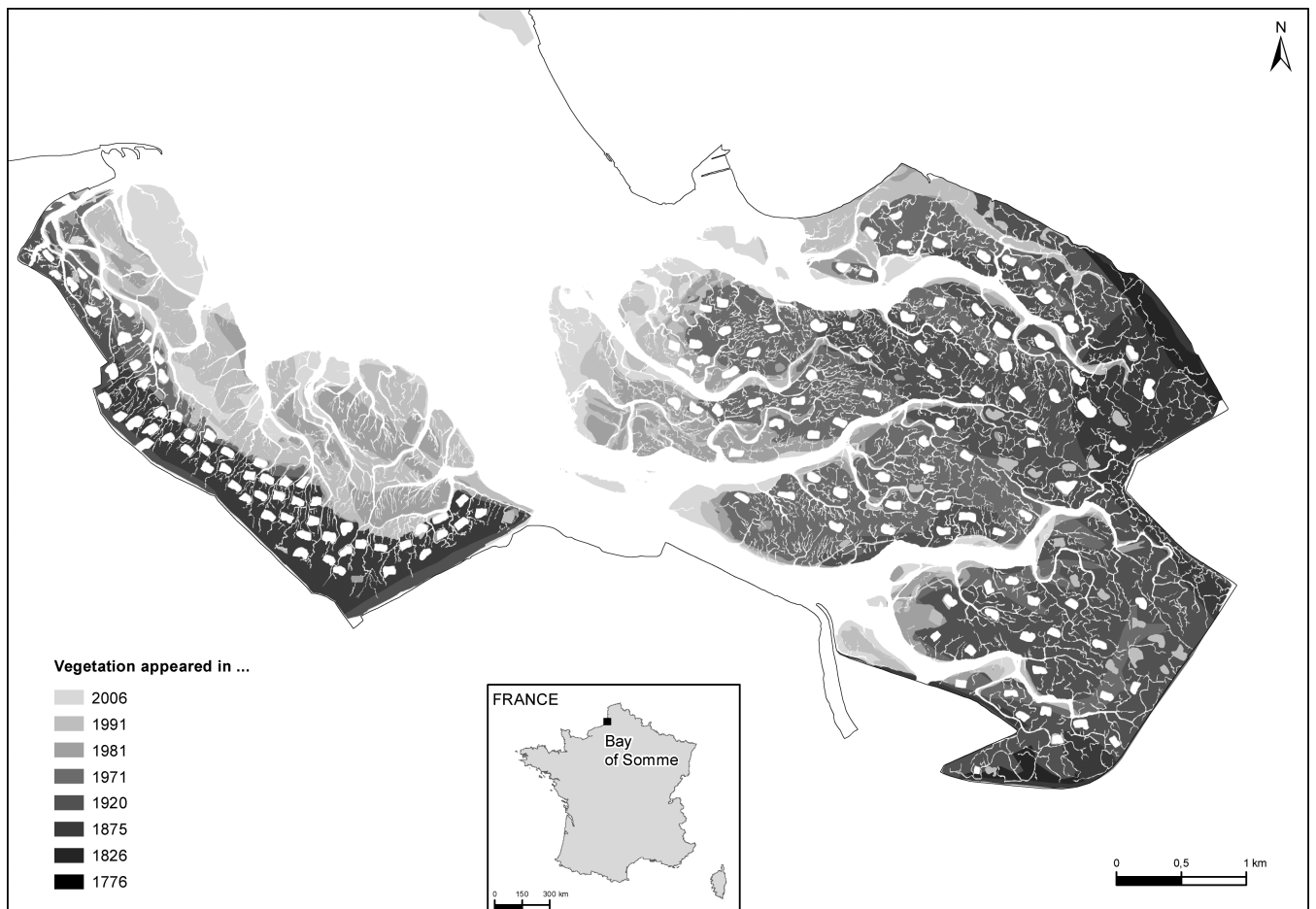


Figure 1 – Vegetation map of the bay of Somme showing the dates of vegetation formation extracted from historical documents and aerial images.

To evaluate the effects of local conditions on plant communities, three main environmental variables (elevation above sea level, distance from the sea and vegetation age) were selected because they are major determinants of plant diversity in salt marsh systems and/or because they will be influenced by sea level rise. The elevation of each plot above the sea (variable noted 'ALTISEA') was extracted

from the official Digital Elevation Model (DEM) 'RGE® ALTI' of the French National Geography Institute (IGN 2012; LIDAR data, available at <http://professionnels.ign.fr/rgealti>). The DEM was integrated in a Geographic Information System (GIS; ArcGis® v.10.1, ESRI). The elevation of the shoreline was defined by the lowest elevation of the sea-vegetation contact point recorded in our data set. This lowest

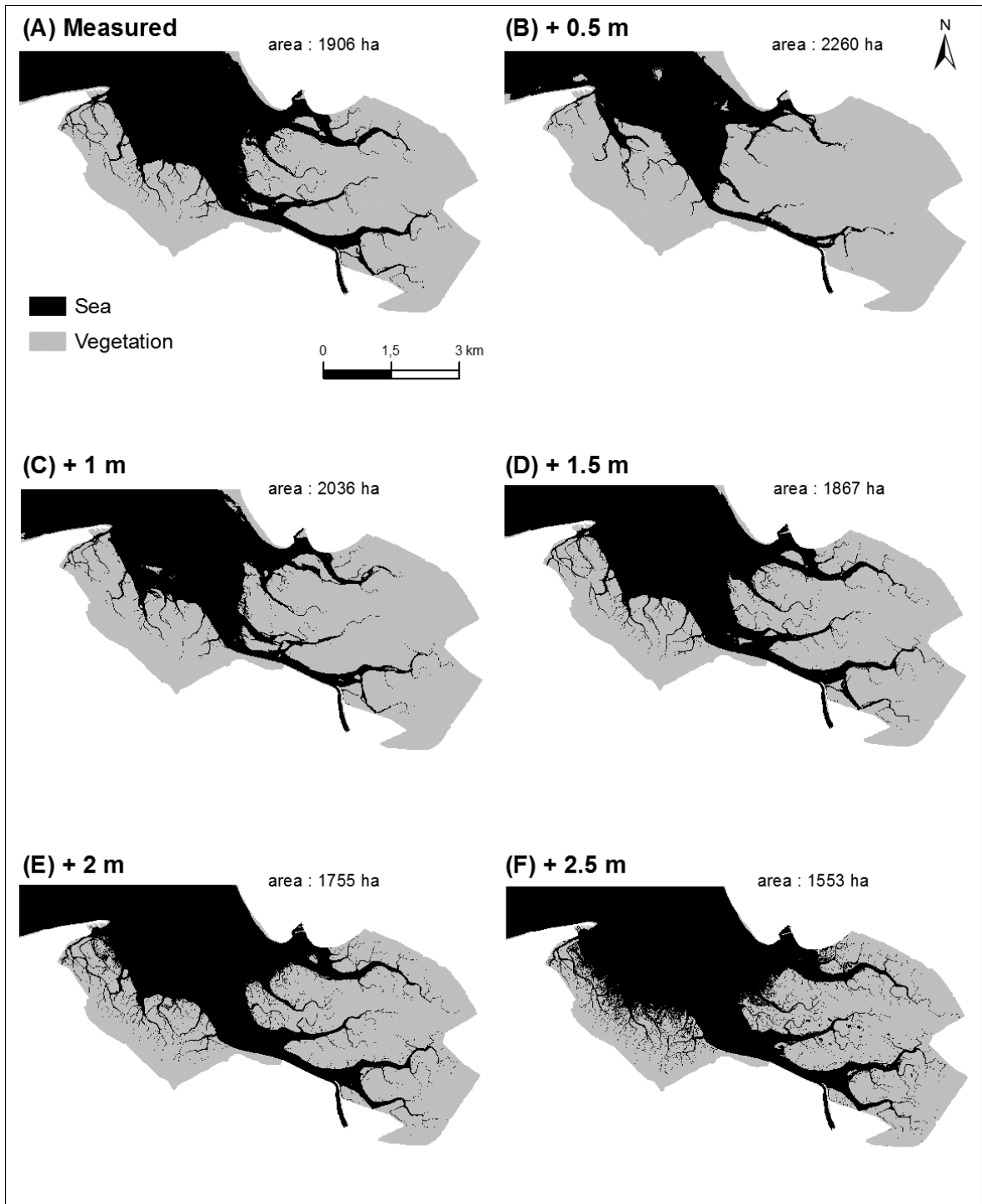


Figure 2 – Vegetation maps of the bay of Somme with scenarios of sea level rise from +0.5 m to +2.5 m in 2100. The areas of vegetation are noted above each map.

sea-vegetation contact point was at 3.25 m above the fundamental landmark in the legal altimetry system, and at 7.64 m above the local hydrographic zero measured at Cayeux-sur-Mer in the Bay of Somme (SHOM 2012). The distance between each plot and the nearest shoreline (variable noted 'DISTSEA') was calculated using the 'NEAR' tool in the GIS.

To evaluate the age of vegetation formations in the Somme Bay, changes in vegetation cover were reconstructed in the GIS using historical maps: La Bretonnière, Méchain and Oeuillio des Bruyères's maps (drawn c. 1776), French military 'Etat Major' maps (c. 1826) and administrative 'Ponts et Chaussées' maps (c. 1875), and aerial photographs (1920, 1971, 1981, 1991) and field surveys (2006; fig. 1). The vegetation cover was available on these documents. At each plot, vegetation age ('AGE') was estimated by calculating the time difference between the plot sampling date and the map on which the vegetation was first represented.

At a larger scale, to estimate vegetation biomass around each plot, we calculated a normalized difference vegetation index (NDVI) generated from satellite data of a Landsat GLS scene of June 2009 (USGS-NASA; pixel size: 30 x 30 m; available at <http://earthexplorer.usgs.gov/>). NDVI is commonly used as an estimator of vegetation production especially on coastal marsh landscapes (see Chabrierie et al. 2001 for the Seine estuary) characterized by low topographic contrasts. This biomass could be influenced by sea level rise through the modification of the shoreline and dominant plants in communities.

Maps of the vegetation cover in the Bay of Somme in 2100 were produced in GIS for five sea level rise scenarios by increasing the sea level by +0.5 m, +1.0 m, +1.5m, +2.0 m and +2.5 m (fig. 2). In these scenarios, the accretion of the marsh platform was included by calculating the height of sediment input that occurred in the bay during the last decades, as following: $ACCRETION = (\text{meanALTI}_{2006} - \text{meanALTI}_{1920}) / (2006 - 1920)$, where meanALTI_{2006} and meanALTI_{1920} are the mean elevations of the marsh areas which were first represented on the maps of 2006 ($n = 2\,919\,665$ pixels of 1 m^2) and 1920 ($n = 3\,997\,617$ pixels of 1 m^2), and 2006 and 1920 are the dates of the respective maps. We found an average accretion of $1.36\text{ cm}\cdot\text{year}^{-1}$ over this period, which is similar to the range of measures recorded by other studies (between 1 and $1.8\text{ cm}\cdot\text{year}^{-1}$) in the Bay of Somme and in its vicinity (Badaire et al. 1994, Marion 2007). The predictive maps were used to calculate the elevation of each plot above the sea level ('ALTISEA₂₁₀₀') and the distance between each plot and the nearest shoreline ('DISTSEA₂₁₀₀') in 2100 according to the different scenarios. The age of the vegetation formations in 2100 was calculated for each plot as following: $AGE_{2100} = AGE_{\text{sampling year}} + (2100 - \text{sampling year})$. The other natural or anthropogenic events, such as storms or constructions of ditches and dikes in the bay, may modify the intertidal platform in the next century. These scenarios were not considered here because hardly predictable, related to random processes or site-specific policies.

Nomenclature

The nomenclature of the taxa follows Lambinon et al. (2004), and Lahondère (2004) for the genus *Salicornia*.

Data analyses

First, the effects of elevation above sea level (ALTISEA), distance from the sea (DISTSEA) and vegetation formation age (AGE) on community species richness (SR) and biomass (NDVI) and on the cover of dominant halophytes (*Aster tripolium*, *Elymus athericus*, *Festuca rubra* subsp. *litoralis*, *Halimione portulacoides*, *Puccinellia maritima* and *Salicornia fragilis*) were tested using mixed models. These species were chosen because they dominate the species-poor communities of the bay and explain the major compositional changes. They may also exhibit contrasting patterns along environmental gradients. In the models, the transect was introduced as a random effect term to account for the autocorrelation between the plots of a transect. All models were built using SPSS (version 17.0, IBM Corp., Somers, NY, US).

Second, using the approach of Duckworth et al. (2000), prediction models of species richness, biomass and cover of dominant halophytes were built using the parameter estimates of the previous mixed models and the values of the explanatory variables in 2100 (ALTISEA₂₁₀₀, DISTSEA₂₁₀₀ and AGE₂₁₀₀). For example, the species richness in a sampling plot predicted with a sea level rise of +1.5 m in 2100 is calculated as following: $SR_{2100,+1.5m} = A_{\text{model}} \times \text{ALTISEA}_{2100,+1.5m} + B_{\text{model}} \times \text{DISTSEA}_{2100,+1.5m} + C_{\text{model}} \times \text{AGE}_{2100} + Z_{\text{model}}$ where A_{model} , B_{model} , C_{model} are the parameter estimates of the explanatory variables ALTISEA, DISTSEA and AGE and Z_{model} is the intercept in the mixed models. For each of the sea level scenarios, mean predicted values of SR, NDVI and species covers were calculated in the plots remaining above the sea level.

RESULTS

The study area (fig. 1) showed a complex network of channels in which vegetation patches varying in age and shape are embedded. The history of vegetation colonization was also complex because patterned by centuries of sedimentation and erosion processes. Although very recent vegetation patches (appeared in 2006) were close to the shoreline, old ones were found both very far and very close to the shoreline (see the dark grey patches in the map of fig. 1). The high proportion of vegetation installed during the last century could be a response to increasing human activities (embankment, sediment deposit from continental agricultural landscapes and carried by the river, ...) and to the natural erosion of old patches by the sea for several centuries. Finally, the bay of Somme was a typically changing landscape providing a diversity of habitats for plants and animals.

A total of 47 taxa of vascular plants were present in the 1257 plots; 66% of which were halophytes (*Artemisia maritima*, *Aster tripolium*, *Bolboschoenus maritimus*, *Elymus athericus*, *Glaux maritima*, *Halimione portulacoides*, *Limonium vulgare*, *Puccinellia maritima*, *Salicornia* spp., *Spartina anglica*, *Spergularia marina*, *Suaeda maritima*,

Table 1 – Effects of elevation, distance from the sea, and vegetation age on species richness, NDVI and species covers.

Transect was used as a random factor in mixed models (n = 1257 sampling plots). ¹: parameter estimate; ²: standard error; ³: degrees of freedom. Dependent variables: SR: species richness in plots; NDVI: Normalized Difference Vegetation Index measured in 2009; species covers (%) measured in plots for *Aster tripolium*, *Elymus athericus*, *Festuca rubra* subsp. *litoralis*, *Halimione portulacoides*, *Puccinellia maritima* and *Salicornia fragilis*. Explanatory variables: ALTISEA: elevation above the sea level (m), DISTSEA: distance from the shore line; AGE: vegetation age extracted from historical maps and aerial images.

Dependent variables	Explanatory variables	Par. est. ¹	S.E. ²	D.F. ³	t-value	P-value ⁴
SR	Model constant	2.7687	0.1896	146.91	14.60	< 0.0001
	ALTISEA	-0.1397	0.1189	964.83	-1.17	0.2403
	DISTSEA	0.0006	0.0003	1225.58	2.26	0.0239
	AGE	0.0064	0.0014	1252.17	4.65	< 0.0001
NDVI	Model constant	0.2679	0.0211	33.67	12.72	< 0.0001
	ALTISEA	0.0735	0.0080	1247.14	9.17	< 0.0001
	DISTSEA	-0.0001	0.00002	1242.65	-4.80	< 0.0001
	AGE	0.0006	0.0001	1242.08	7.02	< 0.0001
<i>Aster tripolium</i>	Model constant	16.1450	1.5198	57.11	10.62	< 0.0001
	ALTISEA	-6.5909	0.7826	1251.19	-8.42	< 0.0001
	DISTSEA	-0.0023	0.0017	1250.75	-1.36	0.1737
	AGE	-0.0153	0.0089	1247.82	-1.72	0.0857
<i>Elymus athericus</i>	Model constant	-31.2530	3.5895	144.50	-8.71	< 0.0001
	ALTISEA	26.0794	2.1481	1172.23	12.14	< 0.0001
	DISTSEA	0.0197	0.0047	1248.99	4.22	< 0.0001
	AGE	0.0142	0.0246	1252.86	0.58	0.5645
<i>Festuca rubra</i> subsp. <i>litoralis</i>	Model constant	-8.5604	3.3007	181.16	-2.59	0.0103
	ALTISEA	13.5278	1.9691	1195.23	6.87	< 0.0001
	DISTSEA	-0.0191	0.0043	1250.33	-4.49	< 0.0001
	AGE	0.0330	0.0226	1252.86	1.46	0.1446
<i>Halimione portulacoides</i>	Model constant	19.6154	5.2838	57.86	3.71	0.0005
	ALTISEA	9.9763	2.5564	1252.99	3.90	0.0001
	DISTSEA	-0.0236	0.0055	1249.14	-4.28	< 0.0001
	AGE	-0.1794	0.0291	1247.23	-6.17	< 0.0001
<i>Puccinellia maritima</i>	Model constant	20.7962	3.9242	130.72	5.30	< 0.0001
	ALTISEA	-4.6215	2.2956	1205.92	-2.01	0.0443
	DISTSEA	-0.0099	0.0050	1251.65	-2.00	0.0457
	AGE	0.0823	0.0263	1252.44	3.13	0.0018
<i>Salicornia fragilis</i>	Model constant	13.2773	1.3324	63.35	9.96	< 0.0001
	ALTISEA	-6.4527	0.6461	1253.00	-9.99	< 0.0001
	DISTSEA	0.0034	0.0014	1249.54	2.44	0.0149
	AGE	-0.0091	0.0073	1247.77	-1.24	0.2139

Triglochin maritima). The mean (\pm SE) species richness was 3.03 (\pm 0.05) per plot.

Mixed models (table 1) showed that species richness increased primarily with vegetation age and, to a lesser degree, with distance from the sea. Biomass estimated by NDVI increased with elevation and age and decreased with distance from the sea. Halophytes exhibited highly contrast-

ing patterns along elevation, distance from the sea and age gradients. Elevation above sea level was a significant explanatory variable in all the species models, influencing *Aster tripolium*, *Puccinellia maritima* and *Salicornia fragilis* negatively and, *Elymus athericus*, *Festuca rubra* subsp. *litoralis* and *Halimione portulacoides* positively. Distance from the sea influenced *Festuca rubra* subsp. *litoralis*, *Halimione*

portulacoides and *Puccinellia maritima* negatively and, *Elymus athericus* and *Salicornia fragilis* positively. Vegetation age (AGE) was the most significant explanatory variable in two species models and influenced *Halimione portulacoides* negatively and *Puccinellia maritima* positively.

The area of vegetation in the bay increased in the +0.5 m and +1.0 m sea-level rise scenarios (fig. 2B & C), indicating that the rate of accretion would be higher than the rate of sea-level rise. Beyond this range of sea-level rise (> +1.5 m), the sea-level rise is no longer countered by accretion and vegetation area strongly decreased as the extent of sea-level rise increased (fig. 2). As the sea level rises by +2.0 m and +2.5 m, 7.9% and 18.3% of the vegetation area would be lost, respectively. Above a threshold +1.5 m of sea level rise, there would be a sharp decline in the number of sampling plots remaining above the sea level (fig. 3A). Among the 1257 sampling plots, only 1076 and 859 of them would remain above the sea level after a rise of +2.5 m and +3.0 m, respectively. Beyond the threshold of +1.5 m, the mean elevation of the plots above the sea-level (fig. 3B) and the mean distance between the plots and the shoreline (fig. 3C) would decline with increasing sea-level. With rising sea-level, the proportions of ancient vegetation would increase in the bay (fig. 3D), as the most recent areas and pioneer habitats are mostly close to the shoreline (fig. 1) and, thus, would be the first to be covered by the sea.

In the prediction models, mean plant species richness would increase (fig. 4A) and mean primary production estimated by NDVI would first increase and then decline (fig. 4B) with increasing sea-level rise scenarios. The covers of species abundant in the lower marsh areas (*Aster tripolium*, *Salicornia fragilis*; fig. 4C & H) would decrease in the lowest scenarios (+0.5 m and +1.0 m) and would increase in the highest ones (> +1.5 m). Species from higher marsh areas (*Elymus athericus*, *Festuca rubra* subsp. *litoralis*) would show opposing variation patterns (fig. 4D & H). Species associated with ancient habitats (*Puccinellia maritima*; fig. 4G) would increase in cover, while species disadvantaged in the oldest marshes (*Halimione portulacoides*; fig. 4F) would decrease.

DISCUSSION

Historical factors matter in community prediction models

The time elapsed since the salt marsh formation is the most important factor in explaining species richness. We found a positive influence of vegetation age on species richness indicating that more species will be able to survive the environmental conditions that progressively develop as the vegetation ages. This is consistent with the species accumulation predicted by the species-time relationship (Rosenzweig

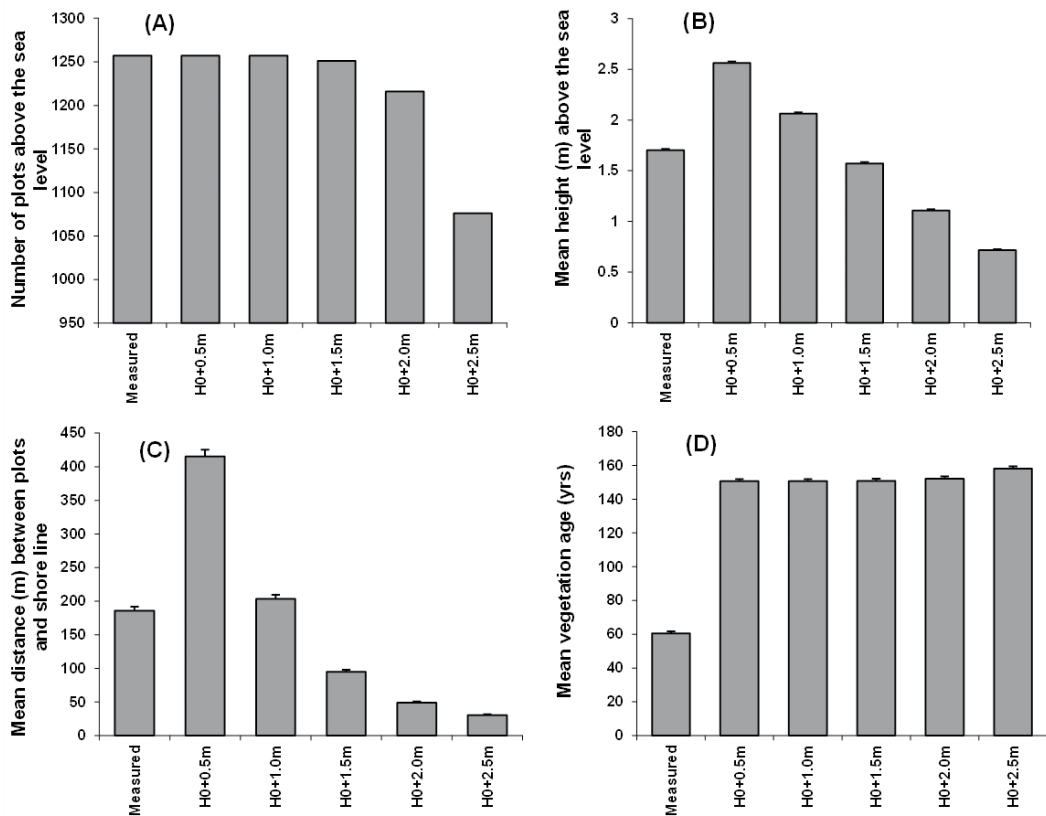


Figure 3 – Mean values (± S.E.) of independent variables with different sea level rise scenarios in 2100: A, number of plots remaining above the sea level with different sea level rise scenarios; B, mean height of plots above the sea level (m); C, mean distance between plots and shoreline; D, mean vegetation age (years) among plots remaining above the sea level in 2100 with different sea level rise scenarios. Measured: mean variable value from collected data; +0.5 m to +2.5 m: mean variable value in scenarios of sea level rise from +0.5 m to +2.5 m.

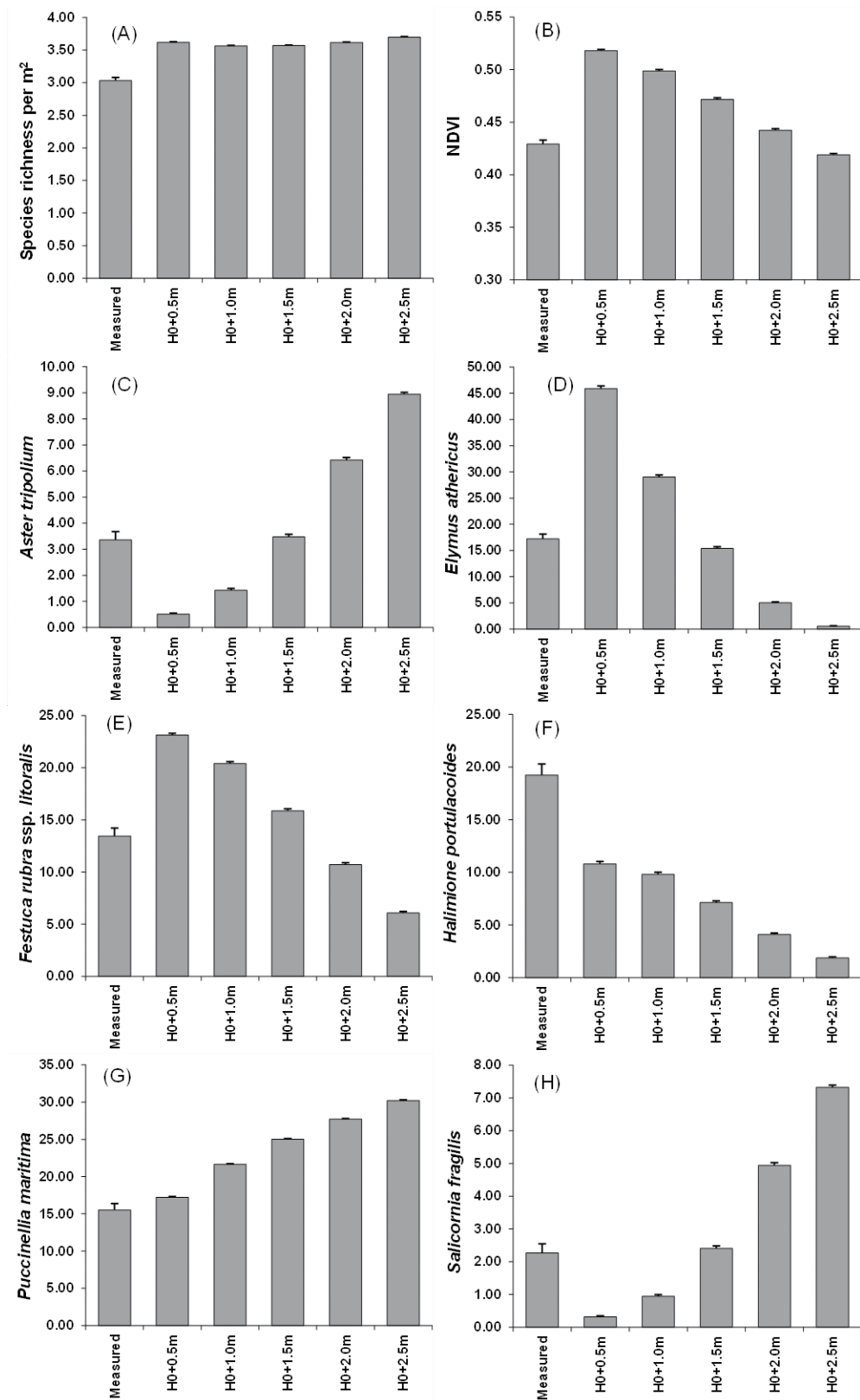


Figure 4 – Predictions of mean values (\pm S.E.) of dependant variables with different sea level rise scenarios in 2100: A, mean values (\pm S.E.) of species richness; B, mean values (\pm S.E.) of NDVI: Normalized Difference Vegetation Index; C–H, mean cover values (\pm S.E.) of *Aster tripolium*, *Elymus athericus*, *Festuca rubra* subsp. *litoralis*, *Halimione portulacoides*, *Puccinellia maritima* and *Salicornia fragilis* in plots. Measured: mean variable value from collected data; +0.5m to +2.5m: mean variable value in scenarios of sea level rise from +0.5 m to +2.5 m.

1995) and with the observations made in other estuaries along the English Channel; where during plant successions, species-poor pioneer communities composed of a few halophyte specialists are progressively replaced by mixed communities in which both sub-halophytes and generalists from terrestrial habitats and continental wetlands coexist (Le Neuveu 1984, Chabrierie et al. 2001, Géhu & Watzet 2007). The species pool concept (Pärtel et al. 1996, Zobel et al. 1998) has been successfully applied to the salt marsh environments (Wolters et al. 2008), where the local diversity of a given site is limited by the dispersal ability of a regional set of species and by their ability to grow at a site. The sets of species that are able to develop in recent and ancient areas are not equivalent. The large species pool (combining salt-tolerant species and continental species) which are able to populate the late successional stages may explain why the gain of species through accumulation with time in ancient vegetation patches is superior to the loss of species with time by competitive exclusion of the few pioneer halophytes.

In the mixed model of species richness, the effect of the age of the saltmarsh is significant ($p < 0.0001$), while the effects of elevation is insignificant ($p = 0.2403$) and the influence of distance from shoreline is low ($p = 0.0239$). This suggests that, even while considering sea level rise, the age of the vegetation patches remaining above the sea level is of the greatest importance for predictions of species richness. In extreme scenarios ($> +1.5$ m) proposed here for 2100, the proportions of plots with ancient vegetation increases as the sea level rises (fig. 3B) because the very recent and flat areas of pioneer vegetation close to the coastline are among the first to be covered by the sea in the bay landscape. As age matters more than distance from the sea in local diversity predictions, pioneer species characteristic of early successional stages would not necessarily be able to replace, or at least to integrate the communities of the very latest successional stages of the oldest patches, even if the sea level rises. This is consistent with many studies which showed an asymmetric competition between species of different successional stages, where the late successional stage species limit the development of the species of the earlier stage even if the latter are able to grow along the whole salinity gradient of a given marsh (Huckle et al. 2000, Egan & Ungar 2001, Crain et al. 2004, Pennings et al. 2005).

NDVI exhibited an initial increase of the plant production at +0.5 m compared to the measured present-day values and then demonstrated subsequent sharp declines of this primary production with increasing sea levels (fig. 4B). The same variation pattern was found by Voss et al. (2013) and interpreted as an anticipated response of marsh macrophytes to inundation caused by sea level rise. Previous studies have shown that sea level rise may promote plant production in some conditions (Morris et al. 2002). The low biomass estimated by NDVI in the most remote areas of the coast (table 1) may be also due to several factors, among which the increase in grazing pressure or in harvesting frequency of edible plants, soil drainage or dominance of prostrate or short species (*Puccinellia maritima*; table 1 and fig. 4). The initial increase of primary production at +0.5 m may also be the result of an age effect, i.e. the effect of age difference between the year of sampling and the year 2100. Salt marsh soils be-

come enriched with carbon (Choi et al. 2001) and nutrients (Oloff et al. 1997) with age; and this may stimulate ecosystem productivity until sea-level rise reaches a critical rate that submerges the marsh vegetation (Mudd et al. 2009). In this context, physical effects of waves should also increase and affect plant biomass by uprooting of plants. The interactions between sedimentation rates and sea-level rise could also influence future primary production patterns, but the magnitude of the effect of these potentially interacting factors is difficult to evaluate in such estuarine systems characterized by a high variability of environmental conditions. In contrast to species richness, primary production steeply declines from +0.5 m to +2.5 m as the NDVI is mainly negatively influenced by elevation above the sea level (table 1). This result is consistent with many studies which showed a decline in the biomass of halophytes with increase in the sea level (Pont et al. 2002, Woo & Takekawa 2012, Alhdad et al. 2013). In the next decades, these sharp variations in primary production may alter or stimulate many ecosystem services in the bay, such as primary biomass inputs in the trophic network (Adam 1990) and carbon sequestration (Mudd et al. 2009). Above a threshold of +1.5 m, the rise of the sea-level is no longer countered by accretion and some edible plant species may increase their production (*Aster tripolium*, *Salicornia fragilis*; fig. 4C & H) while other species, marketed or used for sheep diet (see *Halimione portulacoides*, fig. 4F; *Festuca rubra* subsp. *litoralis*, fig. 4E) may decrease.

Contrasting responses of species to sea level rise

In the lowest prediction models (< 1.5 m), the effects of sedimentation accumulation is stronger than the effects of sea-level rise. Consequently, species of upper marshes (*Festuca rubra* subsp. *litoralis* and *Elymus athericus*) may increase and probably over-compete and replace pioneer halophytes (*Aster tripolium* and *Salicornia fragilis*, fig. 4).

Beyond a threshold of +1.5 m, a part of the marsh vegetation is submerged by the sea, the mean height of the plots above the sea-level and the distance between the plots and the shoreline decreased from optimistic to pessimistic scenarios (fig. 3). Consequently, a longer shoreline and a more complex sea-vegetation interface develops in the bay with rising sea-level (fig. 2D–F) favouring the development of pioneer halophytes in low elevation areas close to the coast (*Aster tripolium*, *Puccinellia maritima* and *Salicornia fragilis*, fig. 4). On the contrary, species of medium and upper marshes (*Halimione portulacoides*, *Festuca rubra* subsp. *litoralis*) and remote salt marsh-continental ecotones (*Elymus athericus*) may decline. As the mean vegetation age increases in the bay with increasing sea-level (fig. 3D), *Halimione portulacoides* will be disadvantaged while *Puccinellia maritima* will be promoted by future changes. The six studied species showed contrasting responses to elevation, distance from shoreline and age gradients (table 1) indicating that a species-level analysis is necessary to understand the effects of sea level rise on vegetation.

The positive effect of increasing sea level rise on the *Salicornia fragilis* population (fig. 4H) is consistent with the results of previous studies and may be due to the increase in flooding events and salinity at the bay. A higher inundation is

known to increase the survival of the *Sarcocornia* seedlings during the growing season and intermediate levels of inundation (50% to 75%) increase the height of the adults at the end of the growing season (Woo & Takekawa 2012). Consequently, individuals from the lower marsh areas close to the shoreline exhibit continuous growth throughout the summer (Jefferies et al. 1981) in contrast to those in the higher marshes. Moreover, flooding increases the recruitment of *Salicornia* individuals from the seed bank and thus facilitates the emergence of new cohorts of seedlings throughout the year (Egan & Ungar 1999). Higher submersion frequency and duration could create microsites of bare soil and gaps within the vegetation belt close to the new shoreline. These small scales openings could be used as regeneration niches (Grubb 1977) by pioneer halophytes that could enter and persist in the community. Sea level rise will also increase the exposure of the marsh platform to high concentrations of NaCl that may have a positive effect on the total germination percentage of *Salicornia* during the entire season (Khan et al. 2000). As *Salicornia* species are more competitive at higher salinities (Mahall & Park 1976, Callaway & Zedler 1997, Egan & Ungar 2001), a rising sea level may result in an increase in their cover (fig. 4H).

As elevation above the sea level is the main factor that strongly affects *Aster tripolium* (table 1), its population is expected to increase in the bay with increasing sea level rise (fig. 4C). Many studies corroborate this result and show that this species is characteristic of the lower marshes (Bakker & de Vries 1992) and that its growth is enhanced under flooded and saline conditions (Lenssen et al. 1995). Similar developmental requirements have also been observed for *Puccinellia maritima* in earlier studies (Lenssen et al. 1995), and explain the negative effect of the elevation and distance from the sea on this species (table 1) which is typical of the lower marshes (Langlois et al. 2003). This species is also highly positively influenced by vegetation age (table 1) which reinforces its potential for progression in the next decades (fig. 4G). This result is consistent with the works of Erfanzadeh et al. (2010) who found that *Puccinellia maritima* is one of the three dominant plants in ancient marsh.

Mixed models show that both the species, *Festuca rubra* subsp. *litoralis* and *Halimione portulacoides*, were influenced positively by elevation and negatively by the distance from the sea. This common negative response to the influence of the sea would lead to their decrease with the sea level rise (fig. 4E & G), even if *Festuca rubra* subsp. *litoralis* may benefit from sedimentation in the low scenarios (between +0.5 m and +1.5 m). These two species typical of the well-drained and upper marshes (Chapman 1950, Gray & Scott 1977) would lose out in a high sea level rise scenario. It has been seen that under waterlogged conditions, the growth of salt marsh populations of *Festuca rubra* is depressed (Davies & Singh 1983). *Halimione portulacoides* also shows superficial rooting on waterlogged soil and thus is sensitive to inundation (Van Diggelen 1991). Moreover, increased salinity is known to reduce the rates of CO₂ assimilation for *Halimione portulacoides* (Redondo-Gómez et al. 2007) and to reduce the growth of *Festuca rubra* subsp. *litoralis* (Rozema et al. 1978).

Elymus athericus (also known as *Agropyron pungens*, *Agropyron pycnanthum*, *Elymus pycnanthus*, *Elytrigia atherica* and *Elytrigia pugens*) was absent or occurred at very low densities in the historical and botanical records of the Bay of Somme (Géhu et al. 1975). But in the past decades, the species has been increasing in cover on the upper salt marsh areas and close to the dikes (Meirland 2011). This rapid expansion has been noted in many other salt marshes of the English Channel and of the North sea (Bockelmann & Neuhaus 1999, Valéry et al. 2004, Laffaille et al. 2005, Thyen & Exo 2005, Veeneklaas et al. 2013), and was interpreted to be an outcome of the natural succession with relation to the modifications of the patterns in the vertical accretion of the soil with marsh age (Veeneklaas et al. 2013). This may explain why *Elymus athericus* cover increases when accretion is superior to sea level rise (+0.5 m scenario) (fig. 4D). Nevertheless, the spread of the species remains limited in the lower marshes due to competition by halophytes (Bockelmann & Neuhaus 1999), and can be countered by grazing and mowing in the upper marshes (Andresen et al. 1990, Van Wijnen et al. 1997, Veeneklaas et al. 2011). The species is also known to be restricted to high elevation characterized by sediments with high redox potential (Davy et al. 2011); this confirms the strong effect of the variable ALTISEA in the mixed model (table 1) and the decrease of the species in the higher sea level rise scenarios (fig. 4D). In the Bay of Somme, *Elymus athericus* also dominates on soil with higher nitrogen and organic matter and lower salt content (Géhu & Watez 2007). In comparison to the observation of the spread of this grass along the European coasts, our model predicts a reverse trend in the future dynamics of *Elymus athericus*. With sea level rise, the halophytes may migrate towards the upper marsh areas and over-compete with *Elymus athericus* (Bockelmann & Neuhaus 1999), which explains its steep decrease in the next decades (fig. 4D). This predicted decline may be an opportunity to restore ecosystem processes and services altered by the spread of *Elymus athericus* (Valéry et al. 2004, Laffaille et al. 2005, Pétilion et al. 2005a), but the decline of *Elymus* may also have negative effects on the biodiversity and the conservation value of the salt marshes (Pétilion et al. 2005b, Pétilion et al. 2009).

At the regional scale, similar consequences of sea-level rise on halophyte species could be expected, especially in the bays of Canche, Authie or in the Seine estuary hosting common species with the bay of Somme. Our method could be applied in other estuarine systems of temperate regions where historical data are available. In the extreme sea-level rise scenarios, the increase of edible halophytes (*Aster tripolium* and *Salicornia* species) could benefit to local markets but the consequences on the other ecosystem services are poorly understood. For example, the traditional grazing activities in the bay of Somme (Meirland et al. 2013) could be influenced by the predicted sea-level rise but the magnitude of this influence is tricky to estimate. Indeed, the main plants of sheep diet (*Puccinellia maritima*, *Festuca rubra*, *Elymus athericus* and *Aster tripolium*) showed contrasted variation patterns with sea-level rise (fig. 4). The trend could be an increase of the most salt-tolerant species in their diet.

CONCLUSION

In a near future, the rise of the sea level would influence the plant communities living in the salt marsh landscapes according to two main mechanisms. First, a heterogeneous vegetation would develop along the new shoreline and would promote the penetration of pioneer halophytes into areas very close to the coast. These pioneer halophytes are more sensitive to the distance from the sea than to the vegetation history. Second, the ancient vegetation patches in the upper marshes will be older in the year 2100 and thus will have time to accumulate more species. These old patches would dominate in proportion in the landscape and would host species-rich and late successional communities. Although the mean local species richness would increase with time in the marsh, the total area of marsh remaining above the sea level would sharply decrease in the landscape if sea level rise is not countered by accretion processes. Like in most of the coastal areas of the world, embankments, seawalls and other dykes protect the coastal cities of the Bay of Somme from the sea intrusions. In a sea level rise perspective, these man-made physical barriers could limit extensive transgression and long-distance migration of successional vegetation stages toward the interior of the continent and, *in fine*, would preclude the formation of new salt marsh habitats. In this perspective, a next step would be to build models including disturbances of sediment deposits, storm events, engineered buildings such as breakwaters, ditches and depolderisation projects.

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