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A global analysis of the seaward salt marsh extent: the importance of tidal range

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Abstract:

Despite the growing interest in ecosystem services provided by intertidal wetlands, we lack sufficient understanding of the processes that determine the seaward extent of salt marsh vegetation on tidal flats. With the present study, we aim to establish a globally valid demarcation between tidal flats and salt marsh vegetation in relation to tidal range.

By comparing results from a regional GIS study with a global literature search on the salt marsh-tidal flat border, we are able to define the global critical elevation, above which salt marsh plants can grow in the intertidal zone. Moreover, we calculate inundation characteristics from global tide gauge records to determine inundation duration and frequency at this predicted salt marsh - tidal flat border depending on tidal range.

Our study shows that the height difference between the lowest elevation of salt marsh pioneer vegetation and mean high water increases logarithmically with tidal range when including macrotidal salt marshes. Hence, the potentially vegetated section of the tidal frame below mean high water does not proportionally increase with tidal range.

The data analysis suggests that inundation frequency rather than duration defines the global lower elevational limit of vascular salt marsh plants on tidal flats. This is critical information to better estimate sea level rise and coastal change effects on lateral marsh development.

Introduction

Coastal salt marshes worldwide provide important ecosystem services to society as the final terrestrial frontier facing the open tidal flats. Upon submersion, the vegetation buffers waves and currents to stabilise the coast and trap sediment to increase surface elevation [*Cahoon et al.*, 1996; *Temmerman et al.*, 2013; *Möller et al.*, 2014]. Salt marshes often front coastal infrastructure such as dikes making them an important part of coastal protection measures [*Temmerman et al.*, 2013; *Möller et al.*, 2014] while storing large amounts of carbon in their soil [*Duarte et al.*, 2013]. The biogeomorphic feedbacks, arising from interactions between sediment transport and vegetation growth, lead to complex self-organized landscapes and a non-linear response to environmental forcing [*van de Koppel et al.*, 2005; *Marani et al.*, 2010; *Balke et al.*, 2014]. The border between salt marsh vegetation and the tidal flat is of general ecological importance as it determines the ratio of vegetated and bare intertidal area within the intertidal zone and hence e.g. the length over which salt marsh vegetation can attenuate waves or the available area for foraging birds on tidal flats. Although regional definitions of the critical elevation above which salt marsh pioneer plants are able to survive, can be found in the scientific literature (see e.g. *Hinde*, 1954; *Mckee and Patrick*, 1988; *Castillo et al.*, 2000; *Morris et al.*, 2002; *Suchrow and Jensen*, 2010), a global data driven comparison is lacking. This is surprising, as scientists have been very successful in testing and developing general ecological principles in the intertidal zone especially regarding species zonation [*Adams*, 1963; *Bertness et al.*, 2002; *Costa et al.*, 2003]. Accelerated sea level rise, changes in tidal range, changing weather pattern and increasing anthropogenic pressure on the coastal zone worldwide however call for a global definition of this marine-terrestrial border and influences thereon.

Despite their adaptive nature, salt marsh and also mangrove ecosystems have increasingly gained attention in recent years as rising sea levels may pose a threat through drowning (i.e. sediment accretion rates < rates of SLR, [*Reed*, 1995; *McKee et al.*, 2007; *Mariotti and Fagherazzi*, 2010; *Kirwan and Megonigal*, 2013]) and wetlands are ‘squeezed’ between rising sea levels and coastal infrastructure [*Doody*, 2004]. *Kirwan et al.*, [2016], however, recently highlighted that focusing on vertical salt marsh development is not sufficient to predict future development and identified lateral marsh development as one of the main knowledge gaps. The influence of changing tidal range on salt marsh functioning has gained much less attention than effects of changes in mean sea-level (but see modelling study by *Kirwan and Guntenspergen* [2010]). Sea-level rise is however known to positively and negatively affect tidal range locally with unknown consequences for salt marsh development [*Woodworth et al.*, 1991; *Pickering et al.*, 2012]. These changes are reinforced by deepening of shipping channels, the construction of dikes and closures that increase tidal range, or on the contrary, by storm surge barriers reducing tidal range behind them, even while they remain open [*Woodworth et al.*, 1991; *Pickering et al.*, 2012]. The Dutch coast is a prime example of a highly modified coastline. After the construction of the storm surge barrier in 1987 at the Oosterschelde (SW Netherlands), tidal range has decreased by 12% within the former estuary [*Louters et al.*, 1998] (see Fig. 1 A station Stavenisse). Closing-off of the Zuiderzee in the Netherlands in 1932 has led to a sudden increase in tidal range in front of the new dike by up to 50 cm [*Jonge et al.*, 1993] (see Fig. 1A station Harlingen). Deepening of estuaries to allow the passing of increasingly big vessels to the major harbors have led to an increase in tidal range of several decimeters for example in the Westerschelde (SW Netherlands) and the Elbe estuary (Germany) [*Meire et al.*, 2005; *Kerner*, 2007] (see Fig. 1A, station Terneuzen). Natural variability of tidal range due to the 18.6 year nodal tidal cycle (see e.g. Fig. 1A station Terneuzen) will affect the salt marsh inundation regime on top of such anthropogenic changes and is often not accounted for due to its long return time [*Beeftink*, 1985]. With increasing development of coastal infrastructure (e.g. tidal power stations, storm surge barriers, dikes) and an increasing need for flood defence due to climate change (e.g. with new embankments in subsiding deltas [*Syvitski et al.*, 2009]) anthropogenic impact on low lying coastal areas will further increase. China for example is currently establishing new large scale embankments for their economic growth in coastal areas [*Ma et al.*, 2014].

Scientific reports in coastal ecology and coastal engineering often quote the general lowest elevation of salt marsh pioneer vegetation from regional studies [*Hinde*, 1954; *Adams*, 1963; *Redfield*, 1972; *Gordon et al.*, 1985; *Castillo et al.*, 2000; *Costa et al.*, 2003; *Silvestri et al.*, 2005]. Most of those studies define the marsh - tidal flat border with tidal benchmarks. This border was for example defined to be at Mean Low Water (MLW) (e.g. in Spring Harbour [*Hinde*, 1954] or at microtidal sites along the U.S. Atlantic coast [*Mckee and Patrick*, 1988]), at Mean Sea Level (MSL) (e.g. used in a model by *D'Alpaos et al.*, 2007) or at a certain elevation below Mean High Water (MHW) (e.g. 20 - 40 cm below MHW in the Dutch Waddensea [*Bakker et al.*, 2002]). Few studies attempt to make general statements across tidal ranges about the salt marsh – tidal flat border, often not supported by data. *Odum* [1988] for example limits salt marsh occurrence to the upper 2/3rd of the tidal frame whereas others use Mean High Water of Neap tides (MHWN) as the lower limit for salt marsh occurrence [*Adam*, 2002; *Doody*, 2008; *Plater and Kirby*, 2011]. *Mckee and Patrick* [1988] provide to our knowledge the only data driven study comparing a number of sites from a literature review along the Atlantic U.S. coast. They showed that the lowest elevation of *Spartina alterniflora* occurence relative to MLW increases with greater tidal range, whereas they found no differences along the climatic/latitudinal gradient. This study however is lacking a global comparison and sites with tidal ranges above 3 m.

The mechanisms limiting survival of salt marsh vegetation in the intertidal zone differ between small seedlings and mature vegetation. Initial establishment of salt marsh pioneer plants from seed may be limited by tidal currents and waves as seedlings require 2-3 days free from inundation to anchor against subsequent flooding (i.e. Window of Opportunity) [*Wiehe*, 1935; *Balke et al.*, 2014]. After seedlings surpass the critical seedling stage [*Corenblit et al.*, 2015] increased rooting depth and attenuation of hydrodynamic energy within a dense vegetation cover lead to higher tolerance to physical disturbance by tides, even during storm events [*Spencer et al.*, 2015]. Establishment from seed can lead to sudden colonization of large areas even several tens of meters away from the marsh edge in only one growing season when the conditions are favourable and dispersal is not limited [*Balke et al.*, 2014]. Other expansion mechanisms such as clonal growth and establishment from displaced marsh fragments but also lateral erosion of salt marshes generally act on longer time scales and only affect the current marsh edge [*van der Wal and Pye*, 2004; *van de Koppel et al.*, 2005; *Mariotti and Fagherazzi*, 2010]. Morphological adjustments such as cliff retreat occur at maximum rates of a few meters per year [*van der Wal and Pye*, 2004]. Direct dieback of mature salt marsh vegetation may largely be caused by exceeded physiological tolerance to flooding [*Hinde*, 1954; *Morris et al.*, 2002; *Langley et al.*, 2013], although drought and potential hypersalinity may also be lethal to plants [*Hughes et al.*, 2012]. Generally, it is important to note that the lowest elevation suitable for seedling establishment may not be the same as the lowest elevation at which established salt marsh plants can survive flooding or clonally expand. Especially in meso- to macrotidal marshes, tidal flats may remain bare although the inundation-duration at the tidal flat is far below the physiological limits to flooding (e.g. < 80% of time flooded for *Spartina* spp. [*Hinde*, 1954; *Langley et al.*, 2013]. We hypothesize that the lowest possible elevation for salt marsh establishment is generally limited by inundation frequency as salt marsh vegetation will immediately colonize large areas if disturbance is below a critical threshold [in the sense of *Balke et al.*, 2014]. The contrasting drivers and rates of change of marsh progradation and marsh retreat may have important implications on how we predict salt marsh resilience and lateral development in times of changing tides and accelerated sea-level rise.

In this synthesis, we compare data from remote sensing and monitoring studies along the Dutch and German North-Sea coast with a global literature search to correlate tidal range with the lower limit of salt marsh vegetation relative to tidal datums. A global tide gauge dataset is analyzed to calculate inundation characteristics in relation to the theoretical elevation of the transition zone from the tidal flat to the pioneer vegetation. Finally, we discuss how changes in tidal range due to sea level rise and coastal engineering may affect lateral salt marsh development worldwide.

Materials and Methods

Elevation of the Salt Marsh – Tidal Flat Border:

The elevation of the salt marsh-tidal flat border is defined here as the lowest elevation of the pioneer vegetation of the genera *Salicornia* spp. and *Spartina* spp.. This border was determined from i) a global literature search and from ii) a GIS analysis of monitoring and remote sensing data from a) the German Waddensea area within the federal state of Schleswig-Holstein (mesotidal, average salinity: 22-30), b) the Dutch Oosterschelde (mesotidal, average salinity: 28-33) and c) the Dutch Westerschelde estuary (meso- to macrotidal, average salinity: 13-28) up to the Belgian border. These three study sites (see Fig. 2) were chosen because LiDAR (Light detection and ranging) data are available from the same year as vegetation survey data based on aerial photographs. Moreover, the sites span over meso- to macrotidal environments whereas the pioneer species are the same at all sites. Data from contrasting locations are necessary because the tidal range gradient is also always a spatial gradient (e.g. from North to South in the Schleswig-Holstein dataset and from West to East in the Westerschelde dataset) along which many other important parameters such as wave fetch and salinity may change. Hence, we pooled the GIS study data with the global literature data for further analysis (see supporting information).

German Data Set

Vegetation: Vegetation survey data following the classification of the *Trilateral Monitoring and Assessment Programme* (TMAP) [*Petersen, et al.*, 2014] were available for the entire coast of the federal state of Schleswig-Holstein. This vegetation data are based on classified near infrared aerial photographs (< 40cm resolution) and ground truthing from 2006 and was provided by the LKN-SH (Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein). Polygons with pioneer vegetation were selected based on TMAP vegetation classification: S1.1 *Spartina anglica* type pioneer vegetation (Natura 2000 type 1320), S1.2 *Salicornia* spp./Suaeda *maritima* type pioneer vegetation (Natura 2000 type: 1310) and S1.0 unspecific salt marsh pioneer vegetation. The minimum vegetation cover for an area to be declared pioneer vegetation was 10%.

Elevation: LiDAR data from 2005 to 2006 with a resolution of 1m and absolute vertical accuracy of better than 20 cm was available for the entire North-Sea coast of Schleswig-Holstein and provided by LKN-SH (Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz).

Tidal data: Data on averaged recent tidal conditions (hydrological years 2001-2010) were provided by the LKN-SH for 18 stations along the North-Sea coast of Schleswig-Holstein. Mean High Water of Neap tides (MHWN) along the Schleswig-Holstein coast for 2007 were provided by the BSH (Bundesamt für Seeschifffahrt und Hydrographie). For the analysis of yearly Mean Tidal Range (MTR), long-term time series of High Water (HW) and Low Water (LW) from Schleswig-Holstein were analyzed for Wittdün (1934-2012), provided by LKN-SH. MTR was also analysed for two tide gauges in Lower Saxony with data from Norderney (1935-2012) and Cuxhaven (1900-2012) provided by the BfG (Bundesanstalt für Gewässerkunde) and WSV (Wasser- und Schifffahrtsverwaltung des Bundes).

Dutch Data Set

Vegetation: Vegetation surveys of the salt marshes are regularly conducted in the Netherlands based on 1:5000 false colour aerial photographs and were provided by RWS (Rijkswaterstaat) for the Oosterschelde (2007) and the Westerschelde (2010). Salt marsh pioneer vegetation was defined based on percentage cover as >5% cover of *Spartina* spp. and/or *Salicornia* spp. when no other vegetation was present and >50% cover of *Spartina* spp. and/or *Salicornia* spp. when other vegetation was present in the same polygon.

Elevation: LiDAR data from the same year as the vegetation survey were provided by RWS for the Westerschelde (2010) and the Oosterschelde (2007) with a 2m resolution raster and absolute vertical accuracy better than 20 cm.

Tidal data: Data on averaged recent tidal conditions (‘Slotgemiddelden 2011’) were provided by RWS for 7 tide gauges in the Schelde Estuary. For the analysis of yearly MTR, long-term time series of HW and LW in the Netherlands were analyzed for Terneuzen (1900-2012), Stavenisse (1957-2012), Harlingen (1900-2012) and Delfzijl (1900-2012).

GIS Analysis of Regional Data Sets:

ArcGIS was used to determine the elevation of the tidal flat just in front of the mapped pioneer vegetation (Fig. 3). A 10 m buffer was created around all polygons with pioneer vegetation defined as described above. These buffer polygons were then erased by the polygons of all other vegetation types (erase function) leaving only the seaward areas outside the vegetation cover. This was necessary since the LiDAR scans do not always penetrate the vegetation, hence surface elevation readings should be taken on the tidal flat just outside the pioneer vegetation. All LiDAR datasets were reduced to 5 m resolution using the nearest neighbour reclassification method prior to the extraction of height information. Two readings of the original LiDAR raster dataset were taken from the tidal flat 0-10 m in front of the pioneer vegetation for every 5 m width of salt marsh edge. Problems however remain where pioneer vegetation borders tidal creeks, dikes and groins. These areas were manually removed from the analysis based on the topography of the LiDAR raster (see Fig. 3B).

Twenty-five Thiessen polygons (i.e. polygons in which each point is closer to its associated point than to any other point) were created for the tidal stations close to the vegetation surveys (see dots in Fig. 2B,C for distribution of tide gauges). Between 860 and 32000 data points (see supporting information Table 1) at the seaward salt marsh - tidal flat border were extracted from the LiDAR raster for each Thiessen polygon depending on the covered area and the shape of the coast. The elevation data were spatially joined to the tidal information for each polygon. Linear mixed models were applied separately to the Dutch and the German dataset (R Package: nlme), with the Thiessen polygon as random effect. The model describes the best statistical fit and determines the correlation between tidal range and elevation of the tidal flat - salt marsh transition relative to MHW. Median, upper and lower quantile of elevation data were calculated for each polygon. The lower quantile was defined as the 'lowest possible elevation' of salt marsh pioneer vegetation for comparison with the literature review data.

Literature Review on Elevation of the Pioneer Vegetation:

A literature search was performed with scopus and google scholar for studies that report mean tidal range, elevation of mean high water (i.e. as a reference tide level) and the lowest elevation of salt marsh pioneer vegetation in the intertidal zone (Fig. 2A). We limited the search for the genera *Spartina* spp. and *Salicornia* spp., both globally distributed salt marsh pioneers in the temperate zone. Whereas *Salicornia* is absent from South America and Australasia [*Kadereit et al.*, 2007], *Spartina anglica* and *Spartina alterniflora* are invasive in many parts of the world [*Nehring and Hesse*, 2008]. Surprisingly few studies report site specific information on elevation of the seaward salt marsh border relative to a tidal datum and tidal range. A total of 37 locations from 15 scientific articles were derived from literature after the search had been narrowed down to 70 peer reviewed articles on salt marsh pioneer vegetation. Data points from the study by *Mckee and Patrick* [1988] were included when the lower limit of *S. alterniflora* was reported relative to MHW. The results and coordinates of the sites are available in the supporting information.

Global Tide Gauge Data:

Global hourly tide gauge records were downloaded from the GLOSS database (University of Hawaii Sea Level Center: http://ilikai.soest.hawaii.edu/uhslc/woce.html) and filtered for stations that are located in areas that support salt marsh vegetation (see supporting information S2). Salt marsh abundance GIS layers were based on *Hoekstra and Molnar* [2010] (supporting information S3). The time series were reduced to a period from January 1990 to December 2010, 155 stations from the database provided data for this period in areas supporting salt marsh vegetation. To calculate MHW and MLW, the data were reduced to daily minimum and daily maximum values. The difference of the averaged daily maximum and minimum values is defined here as mean tidal range. This simplification was applied in order to include data from stations with very low tidal range, where high and low water values are not easily distinguishable from the time series. The inundation duration gradient was calculated for each station in R by counting the hours of inundation for each centimeter increment along the inundation gradient. Frequency of inundation events was analyzed by counting the events at which sea level surpassed a certain elevation along the inundation gradient. Data presentation was done using the rgl package in R.

Inundation Model

Two 30 day simulated tidal signals were generated to calculate the same inundation characteristics (i.e. inundation duration and inundation frequency) as performed for the GLOSS dataset. This analysis aims to illustrate how inundation characteristics differ, especially at the upper intertidal zone (i.e. corresponding to the area above MHWN) when more than one partial tide is considered in an inundation model.

A simple sine curve (equation 1), which is often used in salt marsh modelling studies (see e.g. [*Mariotti and Fagherazzi*, 2010]) and two superimposed sine curves (equation 2) with a 12.42 and a 12 day period representing the M2 and S2 partial tides (i.e. a spring neap tidal cycle) were simulated.

$$h_1(t) = 100 * \cos\left(t * \frac{2\pi}{12.42}\right) \ (1)$$

$$h_2(t) = 100 * \cos\left(t * \frac{2\pi}{12.42}\right) + 20 * \cos\left(t * \frac{2\pi}{12}\right) \ (2)$$

Results

GIS Study

A linear mixed model for the Schleswig-Holstein dataset provided the best statistical fit and shows that the elevation of the tidal flat- salt marsh border relative to MHW (Pio_h [cm]) is declining with increasing tidal range (MTR [cm] = MHW - MLW) with Pio_h = -0.11*MTR-13.62 (P=0.017). The same analysis for the data from the Dutch Westerschelde and Oosterschelde showed a similar relationship with Pio_h = -0.26*MTR+ 11.13 (P=0.066). With each cm increase in MTR, i.e. for each 0.5 cm increase in MHW, the elevation of the tidal flat fronting the marsh decreases by 0.11 cm relative to MHW in Schleswig Holstein and by 0.26 cm relative to MHW in the Dutch Delta. The majority of the elevation derived from the tidal flat fronting the marsh edge for all sites was found to lie below the provided astronomic Mean High Water of Neap tides (MHWN) for each polygon (Fig. 4).

Global Literature Data

The lower quartiles of the elevation data for each polygon from the regional GIS study (Fig. 4) were defined as the lowest possible elevation for marsh vegetation to be compared with the reported lowest elevation of salt marsh vegetation from global literature (Fig. 5). This combined global marsh edge elevation relative to MHW is negatively correlated to tidal range with a logarithmic curve as the best fit (R^2=0.39, P<0.001) (Fig. 5). Hence, the potential salt marsh area between the pioneer vegetation elevation and MHW does not proportionally increase with tidal range. The dataset does not contain any macrotidal marshes below 45° latitude as none were found in the literature (see supporting information S1). Excluding macrotidal marshes from the regression analysis would result in a linear relationship as the best fit.

Global Tide Gauge Data

Inundation duration calculated from the GLOSS global tide gauge data, increased linearly from 0% at and above MHW to 100% just below MLW (Fig. 6A). The distribution of inundation events, expressed as average number of inundations per day, shows a bell shape with an increasingly wide flat plateau at the maximum value of 2 inundation events per day at larger tidal ranges. Whereas inundation events (i.e. frequency of change from exposed to inundated conditions) at higher elevations were limited due to lack of flooding events, inundation events at lower elevations were limited due to very long inundation duration and hence lack of exposure events. Projecting the results of the global and regional logarithmic regression between tidal range and the salt marsh - tidal flat border (see equation in Fig. 5) onto the inundation characteristics showed that inundation duration at the theoretical border between salt marsh and tidal flat decreased with tidal range (see black dots in Fig. 6a). Inundation frequency at this elevation remained on average just below 2 inundation events per day across the tidal range gradient (Fig. 6b). This is where inundation frequency dropped from its maximum (i.e. at the right side of the curve plateau) which corresponded with mean high water of neap tides.

Inundation Model

The simple model comparing a single sine curve as a simulated tidal inundation with a tidal time-series consisting of two superimposed sine curves (i.e. spring-neap) illustrate the mechanism behind the inundation frequency curve in Fig. 6b. Whereas inundation duration was similar between the two tidal models (Fig. 7b), inundation frequency was reduced at both ends of the elevational gradient when adding a second tidal constituent (i.e. the spring-neap tidal cycle) to the single sine curve (Fig. 7c, right).

Discussion

The lowest elevation at which vascular salt marsh plants can still colonize tidal flats has been described by many authors, although mainly without sufficient data to support a global definition and often with regionally varying results. In times of global climate change, however, we need to be able to predict salt marsh development relative to changes in tidal range and sea level at a global scale. We show that globally, the potentially vegetated zone between Mean High Water and the lowest possible elevation for pioneer vegetation does not proportionally increase with tidal range for meso- to macrotidal marshes. Thus, with increasing tidal range the lowest elevation suitable for pioneer vegetation may increase faster than Mean High Water levels. Projecting our GIS and literature search data on a global tide gauge analysis suggests, that the global salt marsh tidal-flat border is generally located at an elevation above which inundation frequency starts to drop below its maximum (Fig. 6b). This critical elevation is defined by the tidal constituents and potentially weather induced sea level variability (see Fig. 7) and elevation roughly corresponds to the mean high water of neap tides. This has important implications for predicting effects of sea-level rise and changing tidal range on lateral marsh development.

Apart from tidal range other factors can influence the elevation at which pioneer vegetation is able to settle. This is also apparent from our dataset, as elevation of the tidal flat fronting the salt marsh pioneer vegetation can vary up to 1 m near the same tide gauge at the regional scale (Fig. 4) and up to 1.5 m for sites with the same tidal range at the global scale (Fig. 5). This variability may be attributed to factors influencing suitable elevation for marsh establishment such as wave exposure [*Callaghan et al.*, 2010; *Balke et al.*, 2015] and salinity [*Odum*, 1988] or other environmental factors such as bioturbation, herbivory or soil anoxia [*van Wesenbeeck et al.*, 2007; *He et al.*, 2014]. However, since we did not directly determine the height within the marsh but the tidal flat in front we cannot draw conclusions from the variability of the GIS study results within each Thiessen polygon. Many environmental factors vary spatially with tidal range such as salinity along estuarine gradients and are therefore difficult to detect in a correlative study. It also has to be highlighted that only eight studies on the pioneer zone elevation at sites with a tidal range > 4 m were found in the literature. We therefore suggest further research to disentangle physical and biological reasons for this global demarcation with a global multivariate approach based on locally measured data.

At the marine-terrestrial border, organisms that require to be submerged for the majority of the time (e.g. algae) are replaced by organisms that require to be emergent in order to grow and reproduce (e.g. vascular salt marsh plants). It is clear from our study however, that the 50% inundation-duration border or mean sea level is not a good estimation for the division between marine and terrestrial life. Salt marsh vegetation may only grow down to around the half tide line (1/2 tidal range) where tidal range is negligible (Fig. 5). In meso- to macrotidal sites the globally averaged salt marsh – tidal flat border is situated several tens of centimetres to a few meters above the half tide line and is thus inundated much less than 50% of the time (Fig. 5 and 6). However, our results show that for meso- to macrotidal sites, inundation still occurs twice daily above the half tide line (Fig. 6B). The globally predicted salt marsh border is located at elevations above the half tide line where inundation frequency starts to drop from its maximum of two inundations per day (i.e. for semidiurnal tides), leaving the tidal flat occasionally free from inundation (Fig. 6B). This is also shown by the regional GIS study (Fig. 4) where the pioneer vegetation is situated just below the calculated astronomic MHWN, hence at an elevation where inundation free days start to occur. This critical elevation is created by superimposition of tidal constituents (Fig. 7) and weather induced sea level variability. Such inundation free days are crucial for salt marsh vegetation to establish on tidal flats [*Wiehe*, 1935; *Balke et al.*, 2014]. Our study therefore suggests that inundation frequency and not inundation duration should be used to globally predict the potential seaward salt marsh border, especially for marshes with larger tidal ranges. The deterministic approach used in this study to calculate inundation frequency from real data may serve as a useful tool to estimate elevations of vegetation establishment (e.g. when planning salt marsh restoration). Also mangrove seedling establishment was shown to be limited by inundation frequency [*Balke et al.*, 2011] and further global studies need to show how tidal range affects the lower elevational limits of mangrove establishment and survival.

Coastal engineering for safety and for accessibility of the major ports are most likely the main local drivers to changes in tidal range (Fig. 1). However, it is not always clear what has caused a positive or negative trend in tidal range development [*Flick et al.*, 2003]. A modelling study showed that tidal range is directly influenced by sea level rise, whereas some areas may experience an increasing tidal range and other areas may experience a decreasing tidal range [*Pickering et al.*, 2012]. In the Waddensea area tidal range has been altered directly by human activity due to the embankment of many intertidal areas since the 17th century [*Jonge et al.*, 1993]. The closure of the Zuiderzee with the construction of the Afsluitdijk in 1932 had a particularly large impact and has led to a sudden increase in tidal range by 50 cm with long lasting effects on the coastal geomorphology and ecology [*Jonge et al.*, 1993; *Dastgheib et al.*, 2008]. Our data show that if tidal range would increase (e.g. due to embankment or dredging, see Fig. 1) this would lead to a greater increase in the lowest possible elevation of pioneer vegetation compared to the increase in MHW. This is under the assumption that tidal range increases symmetrically and that increase in MHW is half of the increase in tidal range (Fig. 4 and 5). At the Oosterschelde, where tidal range at Yerseke has suddenly dropped from 3.7 to 3.24 m after construction of the storm surge barrier [*Louters et al.*, 1998] the predicted potential elevation for establishment of pioneer vegetation may have decreased relative to the local geodetic datum (Fig. 4). Such changes are difficult to detect in the field as the tidal flat morphology is also changing with tidal range. Further studies are needed to disentangle long-term morphological response (i.e. decadal time scales [*Dastgheib et al.*, 2008]) and short term vegetation response (i.e. colonization of new areas, see e.g. [*Balke et al.*, 2014]) to changes in tidal range. The absence of new seedling establishment along salt marsh coasts (especially absence of the annual pioneer *Salicornia* spp.) can serve as an early warning signal for changing inundation regimes where the existing marsh may not yet show any signs of drowning or retreat. Our study can be useful to coastal managers as it can help to a) establish a baseline for the possible salt marsh extent, for example within habitat protection legislation and b) detect areas with insufficient surface elevation for marsh rejuvenation and hence reduced resilience.

Conclusions

Ongoing and projected sea-level rise have created awareness of managers and scientists for future threats to coastal ecosystem health. The majority of studies however focus on whether vertical sediment accretion can keep pace with sea-level rise [*Reed*, 1995; *Kirwan and Megonigal*, 2013]. Although there is evidence for changing tidal ranges both due to sea-level rise and coastal engineering worldwide [*Flick et al.*, 2003; *Pickering et al.*, 2012] studies about their effects on lateral intertidal wetland development are scarce [*Kirwan et al.*, 2016]. Our study highlights the importance of inundation frequency for salt marsh development at the upper part of the tidal frame where inundation is driven by the spring neap tidal cycle and weather induced sea level changes. Lateral marsh development may react very rapidly to decreasing flooding frequencies but more slowly to increasing flooding frequencies. Especially to determine coastal ecosystem resilience future studies should aim to consider both, the threats to vertical and to lateral marsh development and thus the effects of rising mean sea levels versus changes in tidal range and inundation frequency pattern. Local effects on tides due to construction of storm surge barriers or dikes, deepening of shipping channels and land reclamation are still increasing worldwide and their importance to salt marsh dynamics need to be assessed independently from global sea level rise.

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Figure legends:

Fig. 1 A) Examples of tidal range development along the Dutch and German North-Sea coast. Whereas the closure of the Zuiderzee has lead to a sudden increase in tidal range at Harlingen, the construction of the Oosterschlde storm surge barrier has had the opposite effect at Stavenisse. **B)** Location of the tide gauges, salt marsh area is indicated in black. Colours correspond to the water level time series of each location.

Fig. 2 A) Location of studies from the literature search on the reported salt marsh – tidal flat border. **B)** Location of the Thiessen polygons and their respective tide gauges (points) of the regional GIS study. Salt marsh pioneer vegetation is marked in black.

Fig. 3 A) Example of the seaward pioneer vegetation border from the Westerschelde dataset. **B)** Example of the seaward pioneer vegetation border from the Schleswig-Holstein dataset. The yellow to red (low to high elevations) color-coded dots represent the extracted elevation at the seaward edge of the marsh pioneer vegetation.

Fig. 4 Summary of regional GIS study results. Median elevation of pioneer vegetation relative to mean high water per polygon ($Piomed_h$ [cm]) is linearly correlated to Mean Tidal Range (MTR [cm]): $Piomed_h = -0.23*MTR+13.17$ ($R^2= 0.58$; $P<0.001$). Error bars show upper and lower quartile of pioneer vegetation elevation relative to mean high water for each polygon.

Fig. 5 Global salt marsh - tidal flat border relative to mean high water with data from the global literature search (black) and from the regional GIS study (grey) (data in supporting information S1). Mean Tidal Range (MTR [cm]) is logarithmically correlated to elevation of the pioneer vegetation relative to mean high water (Pio_h [cm]): $Pio_h = -108.23*\log_{10}(MTR)+163.21$ ($R^2=0.39$, $P<0.001$). Dashed lines represent 95% confidence interval.

Fig. 6 A) 3D plot of the inundation duration gradient for selected tide gauges from the GLOSS (Global Sea Level Observing System) database (data between 1990 and 2010). Black dots represent the theoretical salt marsh – tidal flat border (equation of Fig. 5). **B)** 3D plot of inundation events (expressed as average number of inundation events per day). Black dots represent the theoretical salt marsh – tidal flat border (equation of Fig. 5).

Fig. 7 A) Simulated tidal sine curve and two superimposed sine curves representing a simplified spring-neap tidal cycle. B) Calculated inundation duration percentage along the elevational gradient. C) Calculated inundation frequency of the simulated tide data. The same analysis was applied to real tide data in Fig. 6.

Fig. 1

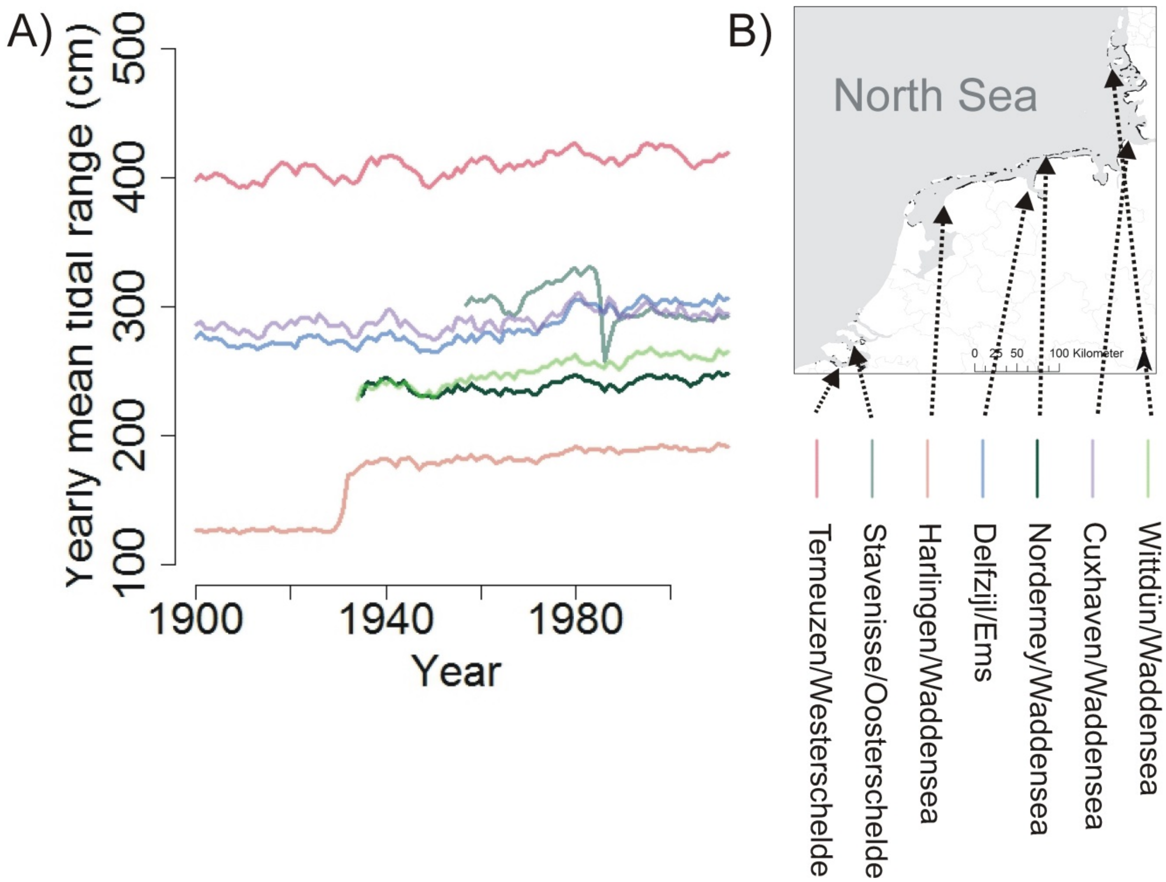

A)
Yearly mean tidal range (cm)
100
200
300
400
500
1900
1940
1980
Year
B)
North Sea
0 25 50 100 Kilometer
Terneuzen/Westerschelde
Stavenisse/Oosterschelde
Harlingen/Waddensea
Delfzijl/Ems
Norderney/Waddensea
Cuxhaven/Waddensea
Wittdün/Waddensea

Fig. 2

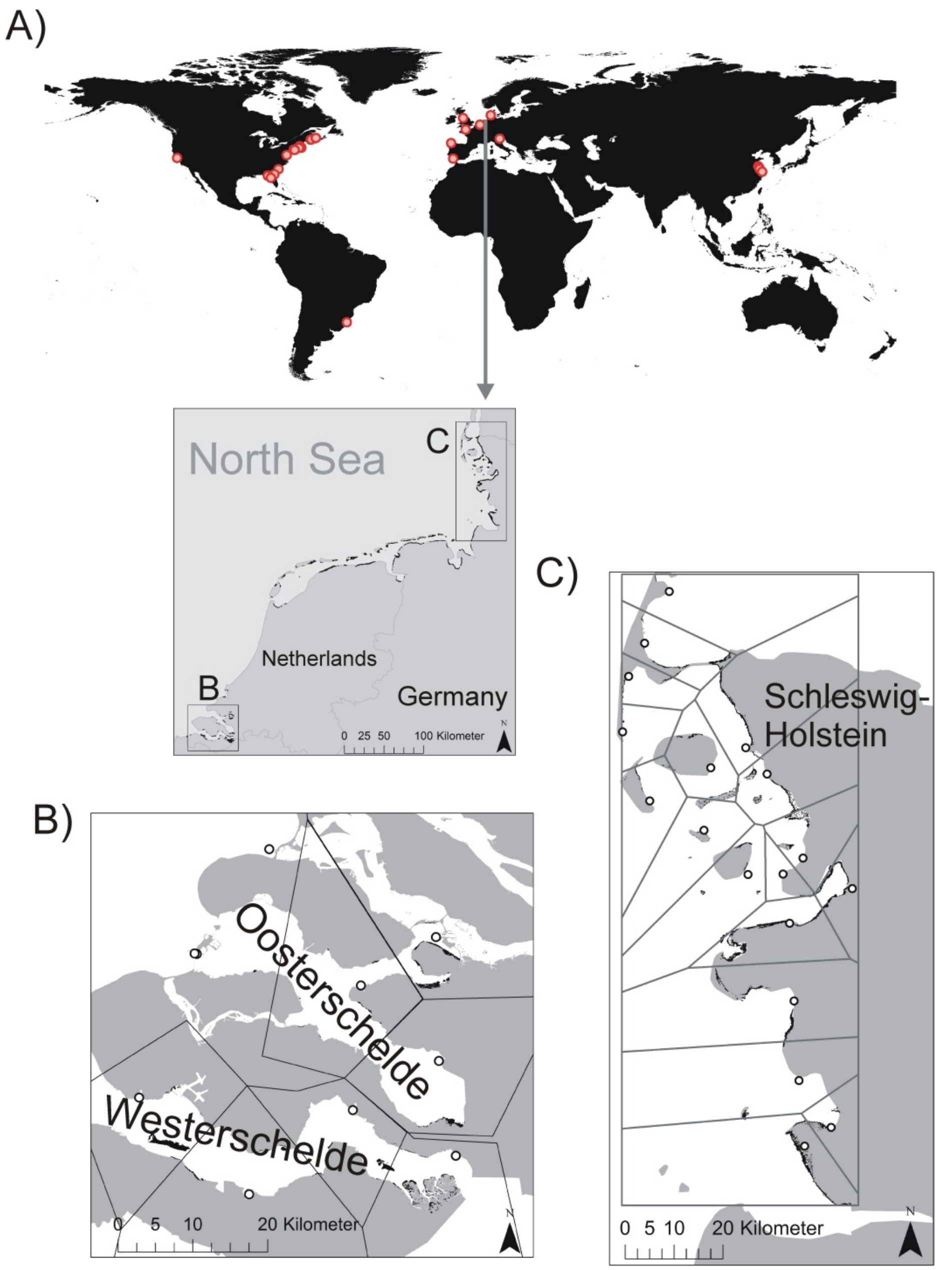
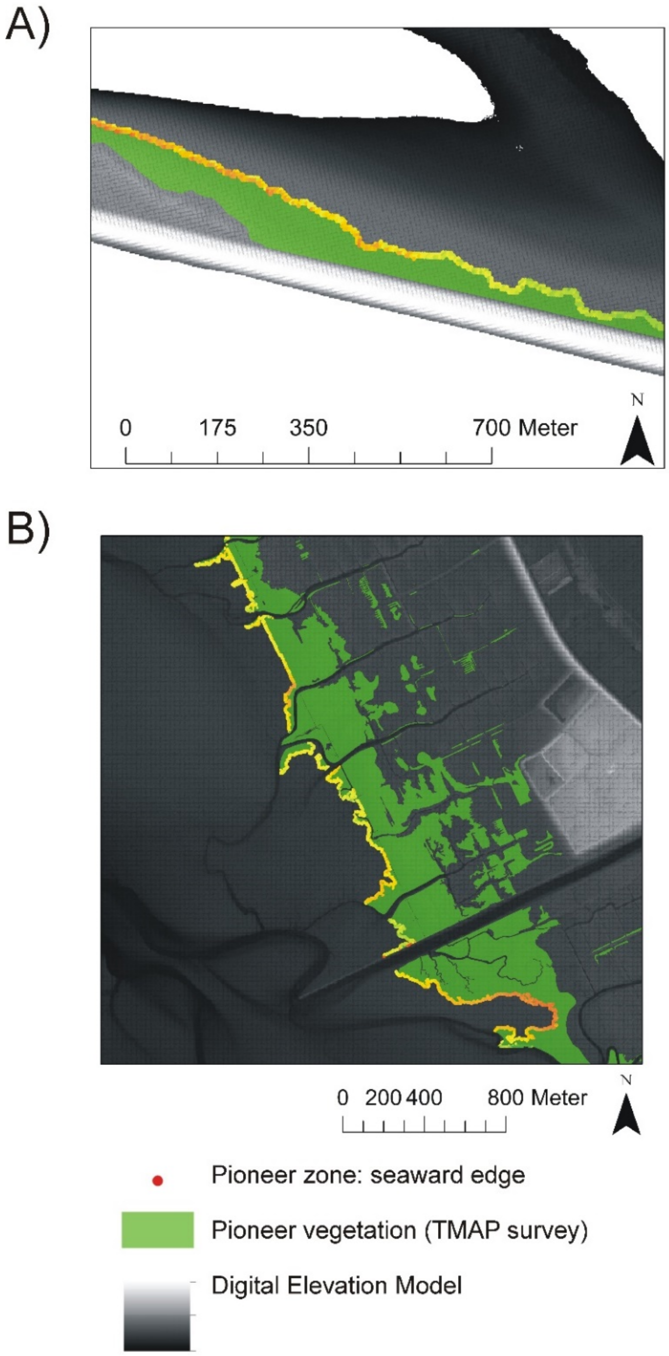
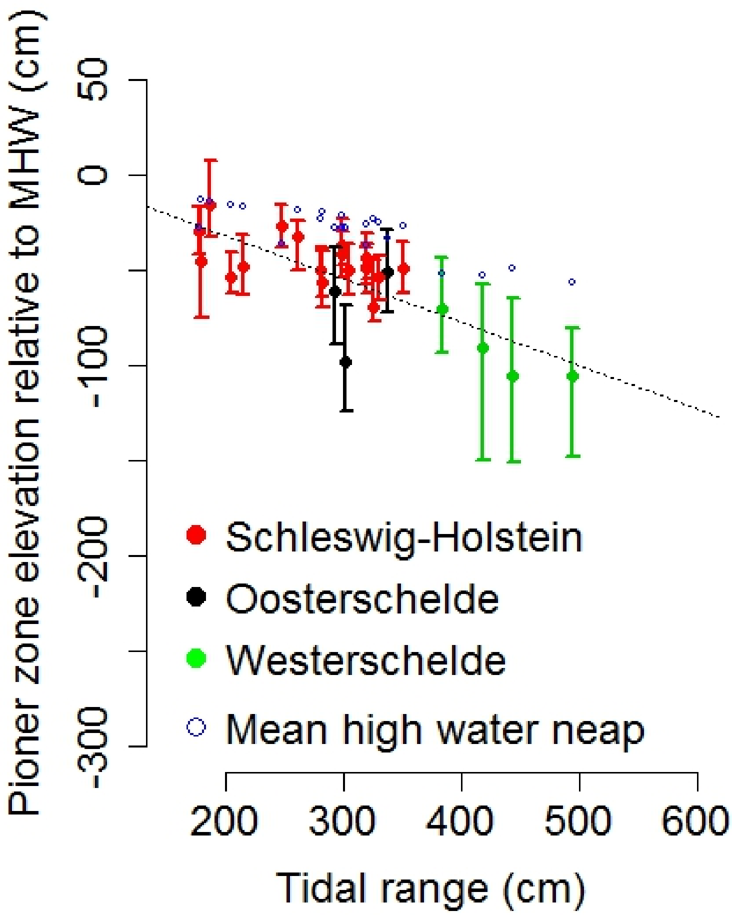

A)
North Sea
C
Netherlands
B
Germany
0 25 50 100 Kilometer
C)
Schleswig-Holstein
0 5 10 20 Kilometer
B)
Oosterschelde
Westerschelde
0 5 10 20 Kilometer

Fig. 3


A)
0
175
350
700 Meter
N
B)
0 200 400
800 Meter
N
Pioneer zone: seaward edge
Pioneer vegetation (TMAP survey)
Digital Elevation Model

616 **Fig.4**



617

618

Fig. 5

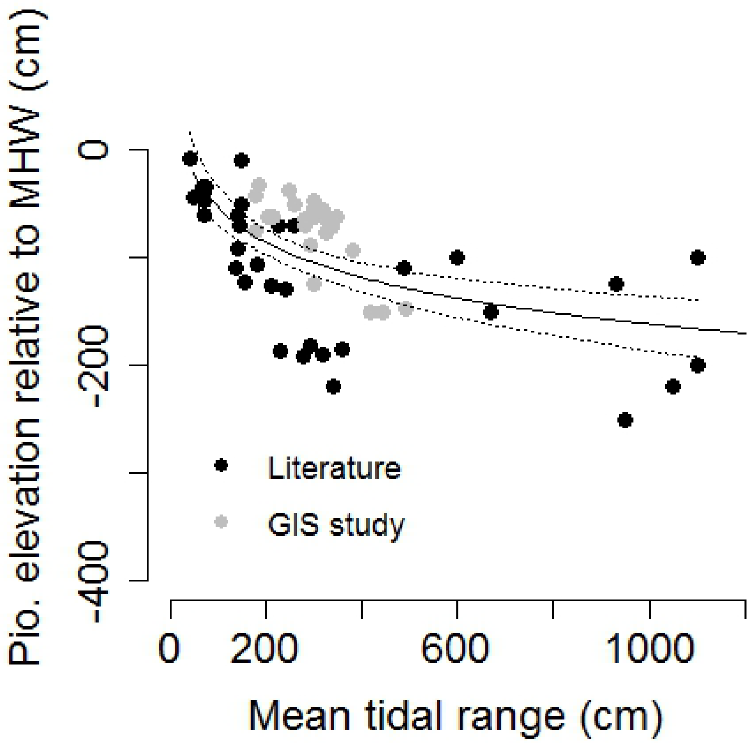

Pio. elevation relative to MHW (cm)
0
-200
-400
Literature
GIS study
0
200
600
1000
Mean tidal range (cm)

Fig. 6

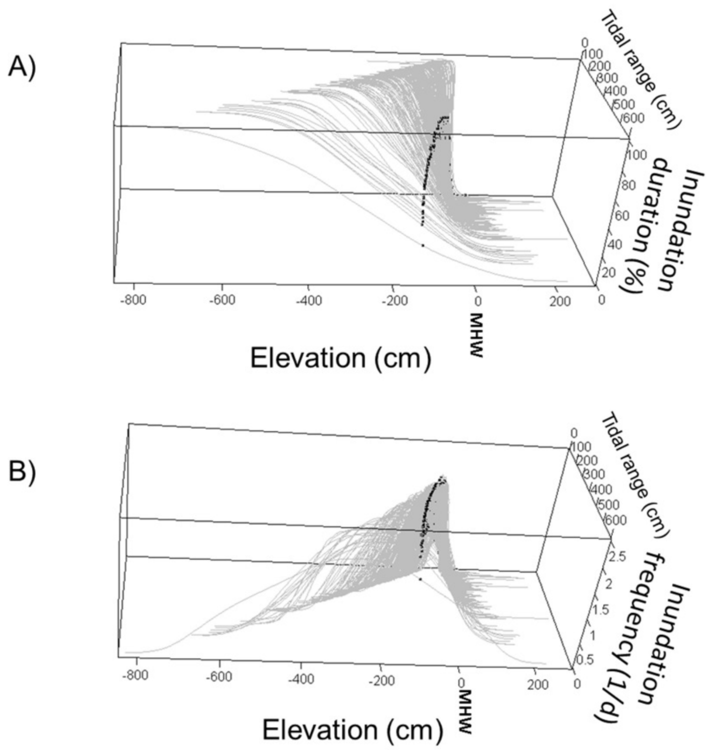
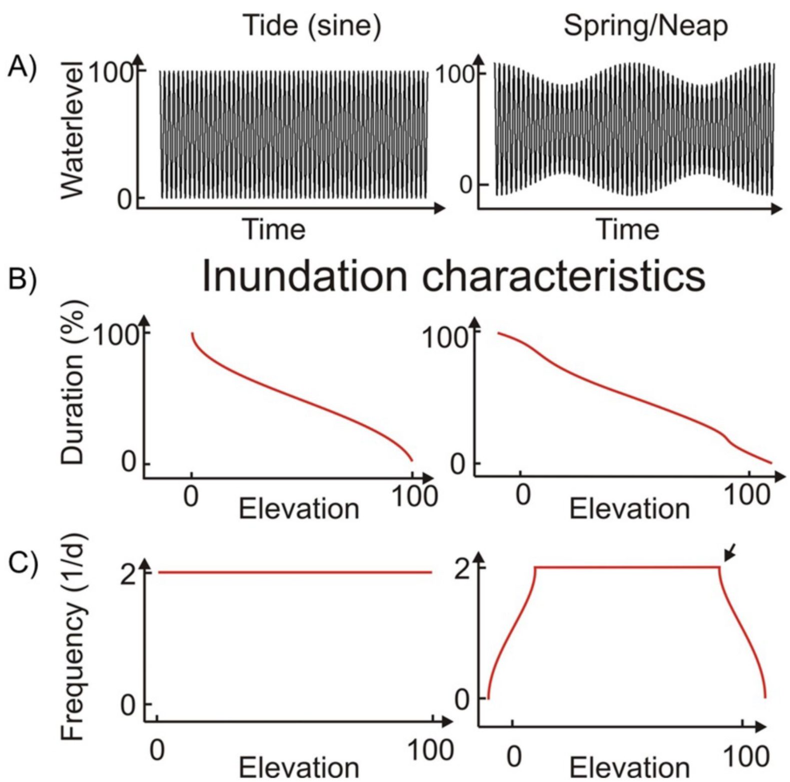

A)
Tidal range (cm)
0
100
200
300
400
500
600
Inundation duration (%)
100
80
60
40
20
0
-800
-600
-400
-200
0
200
MHW
Elevation (cm)
B)
Tidal range (cm)
0
100
200
300
400
500
600
Inundation frequency (1/d)
2.5
2
1.5
1
0.5
0
-800
-600
-400
-200
0
200
MHW
Elevation (cm)

Fig. 7


Tide (sine)
Spring/Neap
A)
Waterlevel
100
0
Time
100
0
Time
B)
Inundation characteristics
Duration (%)
100
0
0
Elevation
100
100
0
0
Elevation
100
C)
Frequency (1/d)
2
0
0
Elevation
100
2
0
0
Elevation
100