Salt-marsh foraminifera and their potential for sea-level studies in the North Sea region

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This thesis is dedicated to my son Wilhelm Müller-Navarra, to my boyfriend Tobias Giese, to my mother Christiane Steusloff-Müller-Navarra, to my father Sylvin H. Müller-Navarra, and to my siblings Moritz, Annika, and Charlotte.

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Coastlines are determined by natural processes (such as wind, waves, tides, sea-level fluctuations) and man-made interventions (dike and dam building, agriculture usage). Coastlines include intertidal and salt-marsh ecosystems, vulnerable to all these processes. Salt marshes react by waxing or waning, mainly determined by varying marine submergence. This enables studies on ecosystem changes which are archived in salt-marsh sediments, for example on past sea-level fluctuations. One proxy for studying these fluctuations is based on salt-marsh foraminifera. Salt marshes are densely populated by indicative foraminiferal assemblages. They are indicative, because, ideally, foraminiferal assemblages are vertically zoned with respect to the tidal frame, although this zonation can be also triggered by other environmental parameters, such as salinity, or be modified due to human influence.

In the frame of this thesis, the distribution and ecology of modern benthic foraminifera were studied in three North Sea salt marshes located at the Bay of Tümlau, (Eiderstedt peninsula, Germany), at Rantum (Sylt Island, Germany), and at Sønderho (Fanø Island, Denmark). The latter two marshes are natural coastal (Rantum) and tidal-creek (Sønderho) marshes while the marsh of Bay of Tümlau was anthropogenically altered until 1985 CE. All above-named marshes are situated in an area where storm tides occur regularly during the winter season. To encompass the full range of the environmental conditions, each salt-marsh surface was sampled for foraminiferal analyses and for environmental parameters, including salinity, pH, and grain size, along a number of transects reaching from the upland to adjacent tidal flats. In all marshes, station elevation relative to local benchmarks was measured and local tides were assessed. Fossil foraminiferal assemblages in a sediment section from the Bay of Tümlau were analyzed to study the salt-marsh development during the last century relative to water-level changes and man-made influences.

The foraminiferal analyses of the anthropogenically altered Bay of Tümlau salt marsh showed that the agglutinated taxa *Entzia macrescens*, *Trochammina inflata*, and *Miliammina fusca*, and the calcareous species *Quinqueloculina* sp. dominate the vegetated salt marsh. In contrast, the tidal flat, tidal channels, marsh ponds and ditches are characterized by calcareous species, among which *Elphidium williamsoni* is dominant in the ponds, while *Elphidium excavatum*, *Haynesina germanica*, and *Ammonia batava* dominate the tidal flats and ditches. However, their distribution patterns lack a clear separation between low, middle
and high marsh assemblages. The modern foraminiferal distribution in this salt marsh is modified due to drainage (ditching), and is further modulated by storm-tide sedimentation, as surface samples were taken three months after a storm tide. The different intertidal and marsh species occupy specific niches linked to ecosystem stability and the combined influence of marine submergence, substrate (i.e., grain size), pH, and likely food sources. The faunas in the Bay of Tümlau salt marsh show no consistent relation to water-level gradient, restricting the applicability of foraminiferal reference data sets from human-interfered salt marshes for relative sea-level reconstructions.

In the natural Rantum and Sønderho salt marshes the same species such as in the ditched marsh were found. Additionally, the high-marsh zones are dominated by *Balticammina pseudomacrescens* and *Entzia macrescens irregularis*. In these marshes, the modern foraminiferal distributions show a separation between low, middle, and high marsh faunas and, hence, a relation to the frequency and duration of marine submergence. But they also show an inter-site variability, which can be related to environmental differences (e.g., salinity and pH) and different flooding dynamics of the coastal salt marsh (Rantum) and the tidal-creek salt marsh (Sønderho). In order to assess the predictive ability of the foraminifera from these salt marshes for relative sea-level estimates for the southeastern North Sea coastal region, different transfer functions were established. These are based on the widely applied, standardized water-level index (SWLI, dimensionless quantity [1]) approach, and on three flooding parameters (i.e., duration of submergence (DoS [%]), mean submergence time (MST [minutes]), and flooding frequency (FF [%])). Results indicate that the SWLI approach performs well and that the approaches based on flooding parameters offer a suitable addition for assessing relative sea-level estimates in the North Sea region, and to assess storm-tide induced sedimentation. A comparison of the different approaches shows a variable precision for tide-level reconstructions along the elevational gradient because flooding parameters and elevation are non-linear correlated.

The above described observations are transferred to a salt-marsh sediment section to investigate the man-made and natural salt-marsh development at the Bay of Tümlau. This sediment section provides a high-resolution archive of sea-level changes and storm-tide events, as well as coastal management processes such as ditching and diking of the past 170 years. After completion of a dike in 1935 CE and until the area became a nature reserve in 1985 CE, the environment changed from a former tidal flat to a salt marsh. Sedimentation was controlled by both tides and storm tides; and overall accretion kept pace with ongoing sea-level rise. During storm tides, reworked calcareous tests of tidal-flat foraminifera were
ABSTRACT

transported onto the salt-marsh surface together with siliciclastic sediments characterized by a symmetrical grain-size distribution. Application of foraminiferal transfer functions indicates that i) periods of higher mean submergence time can be correlated to major storm tides, and ii) the vertical accretion of marsh sediments was enhanced after the marsh became nature reserve in 1985 CE, which leads to a return of natural vegetation and reduction of submergence frequency. Supra-tidal conditions are indicated by a nearly abrupt occurrence of *B. pseudomacrescens*, a species that is adapted to only occasional submergence during storm tides. This observation suggests a high resilience of natural developing salt marshes to ongoing regional sea-level rise.
KURZFASSUNG


gesteuert. Zudem wurde die Marsch ca. drei Monate nach einer Sturmflut beprobt, was die Foraminiferenverteilung ebenfalls beeinflusst hat. Des Weiteren beeinflussen andere natürliche Faktoren wie die Korngrößenzusammensetzung, der pH-Wert, der Salzgehalt und offenbar die Nahrungsverfügbarkeit und -art die Foraminiferenverteilung. Diese Beobachtungen zeigen, dass anthropogen veränderte Marschen ungeeignet sind, um anhand der rezenten Foraminiferenvergesellschaftung als Referenzdatensatz Aussagen über relative Meeresspiegeländerungen in der Vergangenheit machen zu können.


Die entwickelten Transferfunktionen wurden auf ein hochauflösendes Sedimentprofil aus der Tümlauer Bucht angewandt, um die zeitliche Entwicklung der Marsch in den letzten
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Salt marshes fringe coastlines worldwide. They develop in relatively calm coastal areas, for example in estuaries, at back-barrier islands, and in protected bays where sedimentation dominates (Allen, 2000). Natural salt marshes are characterized by a dense halophytic plant cover that allows to separate the salt marsh into different zones such as low, middle and high marsh (Hobbs, 2012). Such salt-mash zones develop relative to sea level, because sedimentation on marshes depends on the amount of tidal submergence (Harrison and Bloom, 1977; Orson et al., 1985; Reed, 1990; Allen, 1990; Karle and Bartholomä, 2008; Kirwan and Megonigal, 2013; Leonardi et al., 2018). This circumstance makes salt marshes an excellent sediment archive to study tide and sea-level variations far beyond instrumental records (Hobbs, 2012; Barlow et al., 2013; Nikitina et al., 2015). The relation of the position of the salt-marsh surface relative to tidal datums (e.g., mean high water) is indicated by specific foraminiferal assemblages (Horton, 1997; Shennan, 2000; Kemp et al., 2017a).

In addition to sediment input by regular high waters, storm tide-induced sedimentation enhance marsh growth unrelated to regular tidal inundation (Allen, 1990). Several centimeters of sediment can be deposited during a single storm event (Zedler and West, 2008). A further factor influencing sedimentation processes in salt marshes is the modification or creation of salt marshes by humans (Rozsa, 1995). This is, for example, the case for most marshes of Europe, North America and Japan which are anthropogenic-influenced since centuries (Adam, 2002). Some of these non-natural salt-marsh regions are densely populated today. For example, the cities Boston, San Francisco, Amsterdam, and Tokyo expanded into former salt marshes (Gedan et al., 2009). Those anthropogenic fostered marshes may drown when land reclamation stops (Orson et al., 1985) and relative sea level keeps rising. An opposite example is that marshes also can outpace sea-level rise, when anthropogenic interferences on marshes completely ended such as observed in the Bay of Tümlau, located at the southeastern North Sea coast (Müller-Navarra et al., subm.) (Chapter 4).
1.1 Intertidal foraminifera: A proxy for water-level reconstructions

Foraminifera are single-celled organisms with calcareous or agglutinated tests that are preserved in sediment archives. Modern intertidal, and thereby particularly, salt-marsh foraminifera show a distinct vertical zonation with respect to the tidal frame, and, hence, along the submergence gradient (Scott and Medioli, 1978). Therefore they can be used to quantitatively predict past water levels in salt marshes (Horton and Edwards, 2006). In general, salt marshes are dominated by agglutinated taxa, while adjacent tidal flats are dominated by calcareous taxa (Fig. 1.1). At the North Sea coast, dominant taxa in high marshes are *Entzia macrescens* and *Balticammina pseudomacrescens*, middle marshes comprise *E. macrescens* together with *Miliammina fusca*, and low marshes are dominated by *M. fusca* and *E. macrescens*. Most abundant tidal-flat taxa are *Elphidium excavatum*, *Elphidium williamsoni* and *Haynesina germanica* (Fig. 1.1) (Müller-Navarre et al., 2017) (Chapter 3). Although several studies confirm this strong vertical zonation in natural salt marshes (review in Barlow et al. 2013), the study of de Rijk and Troelstra (1997) reveals that in human altered salt marshes the foraminiferal zonation is mainly triggered by salinity changes and independent of tidal submergence, and also Müller-Navarra et al. (2016) (Chapter 2) discussed, that modified salt-marsh morphology due to ditching, determines the foraminiferal assemblages in human-driven change in salt marshes. In addition,

**Fig. 1.1.** Sketch of a salt-marsh profile. Different salt-marsh zones are indicated by distinctive foraminiferal assemblages within the tidal frame. MTL: mean tide level, MHW: mean high water.
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environmental variables such as food availability (Müller-Navarra et al., 2016), as well as seasonality (Buzas, 2015), determine the foraminiferal distribution.

In salt marshes where foraminifera show a distinct vertical zonation with respect to the tidal frame, foraminifera-based transfer functions are applied. These transfer functions use the relationship between the foraminiferal distribution and the environmental variable of interest (i.e., elevation) (Kemp and Telford, 2015) to predict paleo-marsh elevations relative to tides with site-specific prediction potentials, ranging from centimeters to decimeters (Varekamp and Thomas, 1998; Barlow et al., 2013, Kemp and Telford, 2015; Ruiz et al., 2015; Barnett et al., 2016). Studies, which successfully used transfer functions to predict paleo-marsh elevations, include salt marshes located at the coasts of the US (e.g., Wright et al., 2011; Kemp et al., 2015; Kemp et al., 2017a), Canada (Barnett et al., 2016), Iceland (Gehrels et al., 2006), Portugal (Leorri et al., 2011), Denmark (Gehrels and Newman, 2004), South African (Strachan et al., 2016), UK (Horton and Edwards, 2005), and Germany (Müller-Navarra et al., 2017) (Chapter 3).

One constraint influencing the prediction potential of foraminiferal-based transfer functions are processes related to the taphonomic preservation of foraminiferal tests. For example, a selective preservation of agglutinated taxa and an early diagenetic dissolution of calcareous taxa has been observed (Goldstein and Watkins, 1999; Patterson et al., 2004; Berkeley et al., 2007). Calcareous tests, for example, have no preservation potential in acidic salt marshes. On the other side, agglutinated foraminifera secrete acid mucopolysaccharide (tectin) to build their test, which is resistant to dissolution in acidic marshes (Lipps, 1973), but tectin is prone to bacterial degradation (Goldstein and Watkins, 1999). Species that are prone to bacterial degradation include *Miliammina fusca* and *Ammobaculites* spp. (Goldstein and Watkins, 1999), while species such as *Trochammina inflata* and *Haplophragmoides* spp. are most likely preserved (Goldstein et al., 1995).

Another constraint is, that for regional water-level reconstructions based on the assemblages in different salt marshes, inter-site comparability between different tidal ranges is needed. Initially, Horton (1997) solved this by developing the standardized water level index (SWLI) to standardize marsh elevations relative to tidal datums in British marsh sites. This approach is valid for marshes where submergence is linearly correlated to elevation along the sampled tidal frame (Horton, 1997), i.e., for marshes with insignificant meteorological impacts on the tide level. However, as discussed by Woodroffe and Long (2010), standardizing by using arbitrary tidal datums in the SWLI formula, especially in sites with a low tidal range, result in a non-linear relation between tidal submergence and
elevation. This issue is addressed in just a few studies (Gehrels et al., 2001; Müller-Navarra et al., 2017) (Chapter 3), although this non-linear relationship was observed, whenever submergence times were calculated (Leorri et al., 2011; Francescangeli et al., 2017).

This is particularly of importance in micro-tidal environments that are mostly prone to meteorological impacts (Hobbs, 2012), those are assumed to deliver the most precise sea-level reconstructions (Barlow et al., 2013). Another issue of the SWLI approach is that tidal datums are non-stationary (Gerber et al., 2016; Kemp et al., 2017a, Müller-Navarra et al., subm.) (Chapter 4) and the influence of non-stationary tidal datums is not entirely understood for long-term, century-scale relative sea-level reconstructions (Kemp et al., 2017a). Further constraints are storm-related sedimentation and the impact of human activity on the salt-marsh development relative to water level, which may result in biased water-level reconstructions. For example, Kemp et al. (2015) used a foraminifera-based transfer function to reconstruct a relative sea-level rise in a salt marsh of Long Island Sound (USA), which is nearly entirely ditched (Redfield, 1972; Harrison and Bloom, 1977) and where dredged sediments were dumped on marsh surface (Rozsa, 1995), and storm tides arose nearly every winter season (Gornitz et al., 2001).

1.2 Study areas
The southeastern North Sea coast (Fig. 1.2) encompasses Europe’s largest intertidal region, the Wadden Sea (~86,000 km²), including major areas of salt marshes (~460 km²) (Common Wadden Sea Secretariat (CWSS), 2010). The younger geological history of the North Sea region is related to Pleistocene ice-sheet waxing and waning with associated sediment.
deposition as well as erosion during transgressional and regressional periods. The German North Sea coast provides one of the most pronounced sedimentation areas of the entire North Sea region (Zeiler et al., 2000; Milbrandt et al., 2015). First North Sea salt marshes are formed at 7,500 cal before present (BP) (Streif, 2004) or since at least 6,000 cal BP (Shennan et al., 2000).

In the present southeastern North Sea coastal region basically two distinct types of salt marshes exist. The Frisian Islands and the North Sea Danish coast are mainly characterized by almost naturally-developed sandy to muddy open-coast and estuarine back-barrier marshes with meandering tidal creeks, located on the sheltered, landward sides of coastal barrier islands and spits. These marshes are characterized by a relatively high degree of biotic variation and form about 40% of the total marsh area in the entire Wadden Sea (CWSS, 2010). In contrast, the German coastal region is mainly characterized by

Fig. 1.3 A and B: Bay of Tümlau during low water, C: benchmark in Sønderho, D: Sønderho marsh during low water, E: Rantum marsh during low water, F: Sampling at Rantum marsh. A, B: H.A. Winkelbauer, C: M. Paul, D: author, E, F: Y. Milker
human altered open-coast mainland marshes with artificial drainage systems (Stock, 2011). These typically muddy or sandy systems are characterized by a flat topography, show relatively little biotic variation, and adjoin exposed tidal flats (Pye and French, 1993).

Anthropogenic influence on salt marshes started in the medieval period, and since then they were modified for land reclamation purposes (Meier, 2004). These man-made modifications include ditching, to reclaim land and diking to protect land against storm tides (Meier, 2004), as well as dumping of dredged sediments onto marsh surfaces (Rozsa, 1995). This man-made influence contributes to ‘coastal squeezing’ (Doody, 2004) (Fig. 1.2) and significantly contributes to salt marsh development unrelated to sea-level fluctuations (Nydick et al., 1995, Varekamp and Thomas, 1998; Gedan et al., 2009, Hartig et al., 2002), and also alter marsh vulnerability to sea-level fluctuations and storm tides. Nowadays, progresses in ‘coastal release’ are ongoing: dikes are opened in the foreland of former salt marshes, e.g., at the Scheldt estuary (Belgium) (Temmerman et al., 2013) or at Lower Saxony (Germany) (pers. comm. A. Groeneveld, Wadden Sea National Park) to enhance sedimentation ratios and to increase flooding areas at the coast. A few salt marshes are nature reserve today such as parts of Bay of Tümlau, Schleswig-Holstein, or entire barrier islands of the North Sea coast, for example Fanø, Denmark. In this thesis, three different salt marshes were studied: one site is located in a non-natural developing marsh at the Eiderstedt peninsula (Bay of Tümlau), two sites are located in a natural developing salt-marsh on the protected landward sides of
Sylt and Fanø islands (Fig. 1.2, Fig. 1.3). They will be characterized in further detail in the following.

**The Bay of Tümlau salt marsh**

This salt marsh is located on Eiderstedt peninsula, at the North Frisian coast of the German North Sea (Fig. 1.2, Fig. 1.3, and Fig. 1.4). The Bay of Tümlau itself is a remnant of a former tidal stream (Ehlers, 1988). Two intra- to subtidal sandy barrier ridges fringe the bay since around 1878 CE (Hofstede, 1997). The Bay of Tümlau has been successively diked for coastal protection and land-reclamation purposes since 1100 AD (Meier, 2004). The hinterland of the bay was diked in 1933–1935 CE and the salt marsh was ditched every three to seven years (pers. comm. LKN.SH, 2017) until the region became nature reserve in 1985, and an United Nations Educational, Scientific and Cultural Organization (UNESCO) world heritage site in 2009. Today, ditches are filled with sediment and natural salt-marsh vegetation returns (Fig. 1.5). Within the salt marsh, isolated, stagnant, un-vegetated ponds have developed. Besides the artificial drainage system, naturally meandering tidal channels drain the marsh area. The dike itself prevents migration of the salt marsh further landwards, and therefore, the marsh is eroding laterally forming a cliff at the transition to the tidal flat. Historic maps show that the study area was tidal flat in 1919, and that first salt-marsh patches were present in 1943 (Königlich Preußische Landes-Anstalt, 1878; Preußische Landesaufnahme, 1943). Today, the salt marsh exhibits zones of low, middle and high marsh areas, as defined by plants (Müller-Navarra et al., 2016) (Chapter 2). The salt marsh of the Bay of Tümlau mainly consists of low marsh environments with a few patches of high marsh. The low marsh is characterized by vascular plant associations comprising *Triglochin maritima*, *Plantago maritima*, *Atriplex portulacoides*, *Limonium* sp., and *Agrostis stolonifera*.

![Figure 1.6: Storm tides at “Tümlauer Hafen” tide gauge (green dots) and Cuxhaven tide gauge (open circles) since 2001. Shown are values above 1.5 m mean high water (MHW).](image)
The low marsh/tidal flat transition is sparsely vegetated with *Salicornia europaea, Puccinella maritima* and *Spartina* sp. (Stock et al., 2005). The salt-marsh vegetation close to the studied erosional cliff includes *Artemisia maritima, Carex extensa, Halimone portulacoides*, and *Glaux maritima*, hence represents a high-marsh zone.

The tide gauge “Tümlauer Hafen” located at the Bay of Tümlau (Fig. 1.4; gauge number 110016, operating since September 2001) falls dry during low water preventing the calculation of the exact tidal range. Tidal datums of “Tümlauer Hafen” tide gauge are: 2.0 m Normalhöhennull (NHN), highest astronomical tide (HAT), 1.59 m NHN, mean high water springs (MHWS), 1.44 m NHN, mean high water (MHW), and 1.19 m NHN, mean high water neaps (MHWN). The modern salt-marsh surface lies above MHWS, thus it is only inundated during storm tides. Flooding parameters (mean submergence time, flooding frequency, and duration of submergence) become non-linear to elevation above 1.3 m NHN due to winds (compare Chapter 4). During the winter season, storm tides arise frequently, with storm-free years being exceptional cases (Fig. 1.6) (Tomczak, 1952; Dangendorf et al., 2014). Between 1843 and 2013, a total of 582 storm tides were recorded at Cuxhaven tide gauge, in the vicinity to the Bay of Tümlau (Müller-Navarra et al., subm.) (Chapter 4). The storm tides deliver sediment from the eroded salt marsh and the adjacent tidal flat to the salt-marsh surface (Schürch et al., 2014).

**The Sønderho salt marsh**

The Sønderho salt marsh is situated on the island of Fanø in the Danish North Sea region. The entire island of Fanø is a nature reserve. Those sediments originate partly from the northern end of Sylt (Davis, 1994) and generate a seaward progradation of the coast of Fanø (Davis, 1994). The studied tidal-creek salt marsh of Sønderho is situated on the
southern edge of the island, in the direct vicinity of the urban area of Sønderho, in front of a dike (Fig. 1.7). It has a N-S extension of around 1 km length and a W-E extension of around 500 m. The Sønderho salt marsh can be divided into a high, middle and low marsh on the basis of vascular plants. Dominant vascular plants in the high marsh are *Festuca rubra* and various Poaceae. The middle marsh is characterized by *Spartina* sp., *Glaux maritima*, *Puccinellia maritima*, and *Bolboschoenus maritimus*. Within the middle marsh, a bog with *Phragmites australis* has been observed that is flooded regularly during high waters. The low marsh is characterized by Poaceae species, *Salicornia europaea*, *Spartina* sp. and *Puccinellia maritima*. In the tidal flat area, around mean high water neaps (MHWN), *Salicornia* spp. is growing. Pedersen (1953/54) described the flora of Fanø in detail. Tidal datums of Sønderho are: HAT: 1.13 m NHN, MHWS: 0.80 m NHN, MHW: 0.75 m NHN, and MHWS: 0.62 m NHN (Müller-Navarra et al. 2017) (Chapter 3).

**The Rantum salt marsh**

The Rantum salt marsh is located on the island of Sylt, which is the largest North Frisian Island, at the northeastern part of the German North Sea coast (Fig. 1.6). Postglacial Holocene sea-level rise, longshore currents and isostatic vertical movements determine the shape of this island (Bayerl and Higelke, 1994). Its west side, open to the North Sea, is strongly influenced by erosional processes that affect the beaches due to storms, storm tides, tides, longshore currents and breaking waves (Lamprecht, 1957). In contrast, the eastern side is protected from erosional processes, allowing sediment to accumulate. The studied open-coast back barrier salt-marsh region is situated at the south-eastern end of the island, near the small village of Rantum (Fig. 1.7). The study area is situated in front of dunes and fringes and has an N-S extension of around 1 km length and a W-E extension of around 100 m. The Rantum salt marsh can be divided into high marsh, middle marsh and low marsh zones on the basis of vascular plants. The vegetation of the high marsh is dominated by *Agrostis stolonifera* and *Festuca rubra* with a few *Limonium vulgare*. The middle marsh is dominated by *Atriplex portulacoides* and the low marsh by *Salicornia europaea*. Tidal datums of Rantum are: HAT: 1.59 m NHN, MHWS: 1.26 m NHN, MHW: 1.12 m NHN, and MHWS: 1.26 m NHN (Müller-Navarra et al. 2017) (Chapter 3).
1.3 Research questions
This study aims to shed light on North Sea salt-marsh development relative to sea-level fluctuations by using salt-marsh foraminifera. To understand the different environmental factors determining the salt-marsh ecosystem, these three research questions were defined:
1) What determines foraminiferal distribution in an anthropogenic modified salt marsh?
2) What are the environmental factors controlling the foraminiferal distributions in natural salt marshes and can foraminiferal-based transfer functions be used to reconstruct tidal and relative sea level variations in the past?
3) What are the man-made and natural impacts on salt-marsh sedimentation and development on centennial time scales?

1.4 List of papers and related contributions
Chapters 2 and 3 are based on publications in peer-reviewed journals, and chapter 4 is based on an article that is submitted to a peer-reviewed journal. Adjustments of the articles (including figures, tables, and journal related typesetting) were made for purpose of consistency in this monographic thesis. Acknowledgements concerning chapters 2 to 4 indicate contributions of persons excluding the co-authors.


The first author designed the realization, did the field work, the foraminiferal analysis and data evaluation, wrote the chapter and generated the figures. Contributions of the Co-Authors: The second and the third author contributed to the typesetting of the manuscript, did the submission, modified the text concerning minor revisions suggested by the editorial board of the journal, and did the re-submission because the first author was in parental leave during the submission process.

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The first author designed the realization, did the field work, the foraminiferal analysis and data evaluation, wrote the chapter and generated the figures. Contributions of the Co-Authors: Technical discussions and advices mostly concerning the statistics were given by Y. Milker, who also helped to implement moderate revision suggested by the editorial board of the journal. Y. Milker and G. Schmiedl enhanced the writing style of the manuscript.

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Schmiedl shortened the length of the manuscript to fulfill the requirements of *Estuarine, Coastal and Shelf Science* before the initial submission.

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2 NATURAL AND ANTHROPOGENIC INFLUENCE ON THE DISTRIBUTION OF
SALT-MARSH FORAMINIFERA IN THE BAY OF TÜMLAU, GERMAN NORTH SEA

*This chapter is mainly based on Müller-Navarra et al., 2016*

2.1 Introduction
Salt marshes represent the transition zone between terrestrial and marine ecosystems and are characterized by strong physical, biogeochemical and biological gradients (Allen, 2000). Many salt marshes are increasingly altered by local human influences such as land reclamation, diking, and grazing. In this context, a better understanding of the stability and resilience of salt-marsh ecosystems to human interference and ongoing sea-level rise appears essential (Kirwan and Megonigal, 2013).

Benthic foraminifera are abundant in salt marshes world-wide and their tests are readily transferred into the sedimentary archive. The distribution patterns of salt-marsh foraminifera in naturally developed coastal intertidal environments are closely related to gradients in salinity, pH, grain size, and tidal range, allowing for the characterization of different ecological niches (e.g., Bradshaw, 1968; Scott and Medioli, 1978, 1986; Alve and Murray, 1999; Edwards et al., 2004b; Wright et al., 2011). These gradients are, in turn, closely related to the distance from the coast and hence, to the tidal frame. Accordingly, salt-marsh foraminifera show a distinct vertical zonation relative to the tidal frame (Scott and Medioli, 1978; Gehrels, 1994; Horton et al., 1999a) making them precise indicators for past relative sea-level changes. In this context, transfer functions have been developed to quantify the relationship between modern foraminifera and tidal level (Barlow et al., 2013; Kemp and Telford, 2015), which are then applied to foraminiferal assemblages in fossil records (e.g., Guilbault et al., 1995; Edwards et al., 2004a; Gehrels et al., 2006a, 2012; Horton and Edwards, 2006; Kemp et al., 2013b).

In coastal wetlands influenced by human activities, the hydrodynamic conditions, morphology and ecological zonation of salt marshes can be severely altered due to the impact of ditches and dikes (Vincent et al., 2013). However, little information is available on

the foraminiferal fauna from these altered ecosystems. The distribution of foraminifera in human-influenced salt marshes seems to be mainly controlled by salinity (de Rijk, 1995; de Rijk and Troelstra, 1997). Salt marsh ecosystems along the southeastern North Sea coast have experienced a long history of human interferences including diking and land reclamation since medieval times, and transfer to pastures accompanied by intense ditching and poldering (Meier, 2004). The distribution of foraminifera in a largely natural-grown salt marsh in Ho Bugt, western Denmark exhibited a zonation closely related to tidal elevation and pH, while salinity appeared less important (Gehrels and Newman, 2004). The small-scale patchiness and population dynamics of foraminifera were studied in a salt marsh of the Schleswig-Holstein west coast by Lehmann (2000). This study revealed three main foraminiferal assemblages associated with specific vegetation units and confined to the lower, middle and upper supra-littoral line. The faunas exhibited significant species-specific spatial and seasonal changes in standing stock and test size, likely responding to the seasonal temperature and vegetation cycle.

The present study provides the first detailed inventory of foraminifera from a German North Sea salt marsh and adjacent tidal flat ecosystems in the Bay of Tümlau (Germany). The studied salt marsh has experienced poldering, ditching and dike construction in the past, and parts are still impacted by sheep grazing, altering the natural elevation profile and vegetation succession. We hypothesize that these anthropogenic impacts influence foraminiferal distribution patterns and vertical faunal zonation. We also aim to test if modern faunas from this area can serve as reliable reference data sets for the reconstruction of past sea-level changes based on fossil faunas from regional salt-marsh sediment archives.

2.2 Material and methods
Surface sediments were sampled along three transects (D, E, F) across the salt marsh of the northeastern Bay of Tümlau in April 2013 (Fig. 1.4). Transects were installed in the ditched salt marshes and cover a range of intertidal habitats (i.e., tidal flats to salt-marsh environments). Our new data set is accompanied by a previous study (Ottmar, 2012) based on a sampling campaign in March 2011 in the northwestern Bay of Tümlau (A, B, C; Fig. 1.4). The results of Ottmar (2012) mainly refer to faunas from the tidal flat, marsh ponds and ditches, and thus we use it for evaluation of the whole range of foraminiferal habitats in the discussion chapter.

A total of 43 surface sediment samples were collected along Transects D, E, and F using a metal frame measuring 10 cm x 10 cm length by 1 cm depth for foraminiferal analysis. All samples were preserved in a rose Bengal solution (2 g rose Bengal per liter,
96 % ethanol) on the sampling day to separate living (rose Bengal stained) individuals from
dead (unstained) individuals (Walton, 1952). Additional surface sediment samples were
taken for salinity and pH measurements, and grain-size analyses. Measurements of salinity
and pH samples were performed corresponding to the standard DIN ISO 10390: 2005-12.
For this purpose, 10 g dry sediment of each sample were shaken for one hour in 25 ml
demineralized water, and subsequently the solution rested for one hour. The measurement
was performed in the suspension using a hand held multi-meter (Multi 340i Set). Samples
for grain-size analysis were treated for a couple of weeks with H2O2 to dissolve the organic
content. Grain-size analyses were performed with a laser diffraction particle-sizer (Sympatex
HELOS/KF Magic), using apertures of 0.5–3500 µm.

All sites were surveyed with a manual leveling system, referring to a geodetic
reference point approximately 1 km east of the sampling area (UTM32 WGS84: 477968 E,
6027295 N; Fig. 1.4). Heights were calculated using laser scan data of the salt-marsh
surface obtained in 2010 by LKN.SH. After determination of the wet volume, samples were
wet-sieved over 500 µm and 63 µm sieves to separate larger organic particles (>500 µm)
and material smaller than 63 µm. The 63–500 µm residue of each sample was split into
equal aliquots using a wet splitter after Scott and Hermelin (1993). The samples were
counted wet because drying of samples may result in under-representation of fragile
agglutinated species (e.g., Scott and Medioli, 1980b; de Rijk, 1995). All stained and non-
stained benthic foraminifera were counted under a stereo-microscope until a minimum
number of 200 non-stained tests were found. Only tests with bright red staining were
considered alive at the time of collection (Murray and Alve, 2000). The residues >500 µm
were examined for foraminifera before being disregarded. The identification of the
foraminiferal taxa was mainly based on the publications of Hofker (1977), Gehrels and
Newman (2004), and Horton and Edwards (2006). For documentation purposes, images
from most of the modern species were created using a Zeiss Leo VP 1455 scanning electron
microscope.

For the multivariate statistical analyses, we used dead assemblages to integrate
seasonal and temporal fluctuations in the populations (e.g., Buzas, 1968; Murray, 1982;
Horton, 1999; Murray and Alve, 2000). For classifying the general distribution of the salt-
marsh fauna, we applied a hierarchical clustering method. To define groups (clusters) on
the basis of the mean distance between objects in each group, we used the unweighted pair
group average (UPGMA) algorithm. The distance metric was selected according to the
cophenetic correlation, which is the linear Pearson correlation between the original matrix
and the dissimilarity matrix (e.g., Legendre and Birks, 2012). We finally used the Chord dissimilarity (Overpeck et al., 1985) distance measure, which is a common metric for quantitative community data (Simpson, 2012). Cluster analysis was carried out with the PAST software package, version 2.15 (Hammer et al., 2001). Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) was performed to test whether species in the modern samples exhibit a unimodal or linear response along an environmental gradient. The test revealed a gradient length of 2.4 standard deviation (SD) units (first axis), indicating a more unimodal species response (Birks, 1995). Consequently, Canonical Correspondence Analysis (CCA; Ter Braak, 1986), based on a unimodal species-environment relationship was used to further analyze the relationships between the foraminiferal species and the environmental parameters elevation, salinity, pH, and grain size [silt and clay = mud (<63 µm) content]. A data set containing only species with a relative abundance of 1 % in at least two samples was used in the analyses and environmental parameters were standardized. For both DCA and CCA, we used the software package CANOCO, version 4.5 (Ter Braak and Smilauer, 2002; Leps and Smilauer, 2003). We calculated the Pearson coefficients between the environmental parameters (grain size, salinity, pH, elevation) and species relative abundances to determine the linear (inter-) correlations between the biotic and abiotic factors using the PAST software package, version 2.15 (Hammer et al., 2001).

2.3 Results

2.3.1 Environmental parameters

The elevation of the tidal flat stations ranges between 1.4–1.8 m NHN and the elevation of the salt-marsh stations is 1.79–2.02 m NHN in the study area. At sample sites of Transects D, E, and F, pore-water salinity varied from 1.71–12.74 g kg⁻¹ (Fig. 2.1; Suppl. S 1.1). Higher salinities (4.03–12.74 g kg⁻¹) were measured in the tidal flat and lower salinities (1.71–8.06 g kg⁻¹) in the salt marsh. In the tidal flat, pH varied from 8.05–8.18 while in the salt marsh, pH varied from 7.54–8.14 and generally decreased landwards. Typically, the salt-marsh environments are characterized by muddy substrate (mud content 41.5–98.3 %), and the tidal flat environments by sandy to muddy substrate (mud content 32.6–75.1 %) (Fig. 2.1, Suppl.S1.1).

2.3.2 Foraminiferal distribution

The most abundant live taxa include Entzia macrescens and Quinqueloculina sp. in the salt marsh of Transect D [Station (St.) D1–D13] and Haynesina germanica in the mudflat of Transect F (St. F14, F15). A total of 29 different foraminiferal taxa, partly grouped by genus,
were distinguished in the dead fauna. The higher salt marsh (St. D1–D11, E1–E8, F1–F9) is dominated by the miliolid *Quinqueloculina* sp., and the agglutinated taxa *E. macrescens*, *Miliammina fusca* and *Trochammina inflata*. The tidal flat and lower salt-marsh environments (St. D12–D16, E9–E12, F10–F15) are dominated by the calcareous *H. germanica*, *Elphidium excavatum*, *Elphidium williamsoni*, and *Ammonia batava* (Figs. 2.1, Plate 1). Associated abundant taxa (3–10 % of the total fauna) of salt marsh and tidal flat environments are *Ammonia* cf. beccarii, *Nonion depressulum*, and *Nonion* sp. 1, while rare taxa (with 3 % of the total fauna) include *Balticammina pseudomacrescens*, *Bolivina* spp., *Bolivina variabilis*, *Bulimina* spp., *Buliminella borealis*, *Cibicides* spp., *Cornuspira involvens*, *Paratrochammina haynesi*, *Stainforthia fusiformis*, *Textularia* spp., *Tiphotrocha comprimata*, and *Trochammina ochracea* (Suppl. S1.2). In the higher parts of the salt marsh, relative abundances of agglutinated taxa are 76–87 % for *E. macrescens*, 1–34 % for *T. inflata* and 1–23 % for *M. fusca* (Fig. 2.1). The relative abundances of the calcareous *Quinqueloculina*

![Fig. 2.1 Distribution of relative dead abundances of important salt marsh and tidal flat foraminifera along the studied transects D, E, and F of the Bay of Tümlau.](image-url)
sp. increase with increasing distance from the coastline and exhibit a maximum of 40 % at Transect F (St. F3; Fig. 2.1). The abundances of other calcareous taxa (mainly *H. germanica*, *E. excavatum*, *E. williamsoni*, and *A. batava*) range from 0–40 % in the higher salt marsh with some local peak occurrences at St. D2, D5, E3 and F3 and increasing towards the tidal flat (Fig. 2.1).

In the tidal flat, channels and lower parts of the salt marsh, *H. germanica*, *E. excavatum*, *E. williamsoni* and *A. batava* are the dominant taxa and comprise 40–68 % of the total fauna counted. *Elphidium williamsoni* and *H. germanica* have a relative abundance of up to 16 % and 68 %, respectively. The occurrence of *E. excavatum* is mainly restricted to the tidal flat and lowermost salt marsh environment (St. E10–E12, D14–D16, F10–F15) where it comprises 10–46 % of the total fauna. *Ammonia batava* also commonly occurs in the tidal flat and lowermost salt marsh (St. D14–D16, E10, E11, F11–F15), with relative abundances of up to 10 %. None of the species show a strong linear correlation to elevation, with Pearson correlation coefficient of -0.49–0.42.
2.3.3 Results of the multivariate statistical analysis

Cluster analysis revealed two main clusters, representing the separation between salt marsh and tidal flat faunas (Fig. 2.2). Cluster I contains nearly all stations from higher marsh environments, and mainly comprises the salt-marsh taxa *E. macrescens*, *T. inflata*, *M. fusca*, and *Quinqueloculina* sp.. Cluster II contains all mud flat and lowest marsh stations, and higher salt marsh Station D5. This cluster is characterized by the calcareous taxa *H. germanica*, *E. excavatum*, *E. williamsoni*, *A. batava*, and *N. depressulum* (Fig. 2.2). The first axis of the CCA analysis explains 33% and the second axis explains 4.3% of the total variance of the data set. Both axes are significant at the 95% confidence level (*p*-value, 0.05). Substrate and elevation are negatively related and pH is positively related to the first axis, salinity is positively related to the second axis (Fig. 2.3). The calcareous species *E. excavatum* and *H. germanica* (and to a lesser extent, *A. cf. beccarii* and *N. depressulum*) and the agglutinated species *P. haynesi* (and to a lesser extent *Textularia* spp.) are positively related to pH and negatively related to mud content of the substrate and to elevation. Agglutinated taxa *E. macrescens* and *T. inflata* are positively related to both elevation and mud content. *Cornuspira involvens*, *Quinqueloculina* sp. and *M. fusca* show a positive correlation to mud content and salinity, and *A. batava*, *S. fusiformis* and *Cibicides* spp. (and to a lesser extent *E. williamsoni* and *T. ochracea*) to salinity and pH (Fig. 2.3).
CHAPTER 2

2.4 Discussion

Benthic foraminifera, especially agglutinated species, in naturally developed salt marshes commonly exhibit a close relationship to the tidal frame, as it is shown for salt marshes worldwide (e.g., Scott and Medioli, 1978; Scott and Leckie, 1990; Gehrels and Newman, 2004; Horton and Edwards, 2006; Hawkes et al., 2010; Kemp et al., 2012; Engelhart et al., 2013b; Milker et al., 2015b). This zonation reflects the specific gradients created by the semi-diurnal tidal submergence, and related physical, biogeochemical and biological parameters. In this respect, the distribution of the different foraminiferal species is controlled by the specific requirements and tolerance levels to substrate type, pH, elevation with respect to the tidal frame, and to a lesser extent, salinity (Horton et al., 1999b, 2000; Edwards et al., 2004b; Gehrels and Newman, 2004; Horton and Murray, 2007). The natural morphology of the salt marsh in the Bay of Tümlau has been distorted by ditching and related drainage (see discussion below). As a consequence, the salt marsh faunas lack a clear relationship to the tidal frame. Instead, the CCA identified substrate type (grain size) and pH, as well as elevation, as the most important environmental parameters (Fig. 2.3). The majority of calcareous species were restricted to the tidal flat and lower marsh environments, where they are positively related to pH and negatively related to muddy substrate and elevation. In the Bay of Tümlau, *E. excavatum*, *H. germanica* and *A. batava* dominate the sandier substrates in the lowest marsh and tidal flat, where an average pH of 8.1 and salinities of up to 14 were recorded. However, in this environment, salinities can reach up to 30 during the summer months (BSH, survey in 1995). These species also occur in tidal channels and artificial ditches in the Bay of Tümlau (Ottmar, 2012; Fig. 2.4). They are known to tolerate a wide range of salinities but appear sensitive to heavy metal and hydrocarbon pollution (Armynot du Châtelet and Debeney, 2010). These species are characteristic of shallow marine environments of the southern North Sea (Jarke, 1961; Murray, 1992) and are also typical for the German Bight and near-coastal ecosystems under estuarine influence (Wang, 1983; Schönfeld et al., 2013). *Ammonia batava* and closely related *Ammonia tepida* are very common in organic-rich littoral and coastal settings (Alve and Murray, 1999; Hayward et al., 2004; Armynot du Châtelet et al., 2009) and are able to survive and reproduce even under oligohaline (1.2–1.5) conditions (Wennrich et al., 2007).

*Elphidium excavatum* occurs with different morphotypes in a wide range of shelf and coastal habitats of the Arctic, North Atlantic, North Sea, and Baltic Sea (Feyling-Hanssen, 1972; Schönfeld and Numberger, 2007). This species has also been recorded from near-shore sands and intertidal marshes (summary in Feyling-Hanssen, 1972) and from the
In the western Baltic Sea, where its main reproductive cycle was related to feeding and growth during the spring bloom (Schönfeld and Numberger, 2007). *Haynesina germanica* has been recorded in low marsh environments with salinities of up to 35 in Chichester Harbour, UK (Swallow, 2000). In the near-coastal ecosystems of the southeastern North Sea, *H. germanica* shows some affinity to estuarine influence (Wang, 1983), which may also explain its persistence in some salt-marsh sites of the Bay of Tümlau. A dominance of this species at higher elevation relative to *A. tepida* and *E. excavatum* was also documented in Aiguillon Cove on the French Atlantic coast (Armynot du Châtelet et al., 2009). *Elphidium williamsoni* is a common species of the tidal flat in the Bay of Tümlau (Fig. 2.2), but also occurs in the salt marsh. In the western part of the Bay of Tümlau, this species was found to be dominant on relatively sandy substrates in stable ponds on the salt marsh, where it constitutes up to 90% of the total foraminiferal assemblage (Ottmar, 2012).

The CCA results suggest a negative relationship of *E. williamsoni* to mud content and positive relation to salinity (Fig. 2.3), but other factors such as specific food sources may also play a role. A similar correlation of *E. williamsoni* to sandy substrate and salinity was previously reported from an estuarine environment in southwestern Spain (Ruiz et al., 2005). Agglutinated species *E. macrescens* and *T. inflata*, which occur in high numbers in the salt marsh, are positively related to elevation and muddy substrate and negatively related to pH. Both species are cosmopolitan (e.g., Hawkes et al., 2010; Engelhart et al., 2013b; Fatela et al., 2014; Hayward, 2014) and are associated with marsh plants. Specifically, *E. macrescens* flourishes epiphytically on decaying Carex-leaf debris (Alve and Murray, 1999). In the Bay of Tümlau, highest abundances of these species appear in the vegetated and high marsh areas, which are inundated only during storm floods and often exhibit particularly low pH values. *Trocchammina inflata* can live at the extreme limits of tidal influence (Hayward, 1993) and has been observed in the higher marshes of the North American Pacific and Atlantic coasts (Hawkes et al., 2010; Engelhart et al., 2013b; Kemp et al., 2013a). It has also been found on the North Sea coast of the UK where it inhabits the high and middle marshes (Horton and Murray, 2007). Laboratory experiments indicate a grain-size dependency of *T. inflata*, with a relation to silty substrates (Matera and Lee, 1972).

*Quinqueloculina* sp. and *M. fusca* are also found in the salt-marsh environments of the Bay of Tümlau, where they are positively correlated to muddy substrate and occur within a salinity range of 3–8 g kg⁻¹. Both taxa seem to favor the same microhabitat with an affinity to muddy substrate (Lee et al., 1969). Commonly, the relative abundances of *Quinqueloculina* sp. and *M. fusca* exhibit a slight land-ward increase, however, elevated
numbers can also be observed locally in lower marsh environments. Similar distribution patterns have also been reported from other regions (e.g., Gehrels, 1994; de Rijk and Troelstra, 1997; Kemp et al., 2013b). Alve and Murray (1999) described *M. fusca* as typically representative of the seaward edge of salt marshes. *Miliammina fusca* has been reported from high and middle marsh environments from a salt marsh in the UK (Swallow, 2000; Horton and Murray, 2007), from low marsh and tidal flat environments along the US Pacific coast (Jennings and Nelson, 1992; Hawkes et al., 2011; Engelhart et al., 2013; Milker et al., 2015a, b) and from tidal flat environments of New Zealand (Hayward, 1993). These studies mentioned salinity as the main controlling factor of this species.

### 2.4.1 Taphonomy and fossilization potential of foraminiferal faunas

The loss of calcareous species can influence the accuracy of sea-level estimates when a modern data set, including calcareous species, is applied to fossil samples where the calcareous species have been dissolved. In the study area, calcareous species dominate the tidal flat, but also occur in different salt-marsh environments, where they account for up to 40 % of the foraminiferal fauna, and are even more abundant in marsh ponds of the western Bay of Tümlau (Ottmar, 2012). Early diagenetic dissolution of calcareous tests has been observed in many salt marshes (e.g., Scott and Medioli, 1980a; Horton et al., 1999b; Berkeley et al., 2007, 2009; Hawkes et al., 2010; Engelhart et al., 2013b; Milker et al., 2015a, b) and has been attributed to pH values lower than 7.2 (Berkeley et al., 2007).

![Schematic transect across the salt marsh of the Bay of Tümlau integrating the results of the present study and Ottmar (2012). The various salt marsh environments include natural and grazed vegetated areas, ponds, and artificial ditches. Each environment is characterized by distinct benthic foraminiferal taxa. The vegetated salt marsh areas are preferentially inhabited by agglutinated taxa and miliolids, lacking a clear internal zonation relative to the tidal frame. Tidal flats and ditches are characterized by calcareous taxa. The species *E. williamsoni* is particularly abundant in marsh ponds.](image-url)
Laboratory experiments revealed that at a pH of 5.0, complete dissolution of calcareous tests occurred within one day, and identified a pH window of 2 to 9.5 at which some foraminifers can exist (Bradshaw, 1968). In our study area, pH values were always higher than 7.2, and in seaward direction, pH increased to values above 8 in April 2013. Similar values were measured in March 2011 in the western Bay of Tümlau (Ottmar, 2012). The relatively high pH values relative to naturally developed salt marshes is likely a reflection of the intense ditching and grazing that prevents the development of a natural vegetation succession and related acidification of salt-marsh soils. Hence, the pH range in the study area does not affect foraminiferal test dissolution and favors the occurrence and long-term preservation of calcareous taxa in sub-surface salt-marsh sediments.

The fossilization potential of agglutinated foraminiferal taxa is influenced by physical destruction of tests by wave action during storm tides, repeated drying of empty tests, compaction, or by bacterial degradation of test cement in subsurface sediments (e.g., Goldstein et al., 1995; Goldstein and Watkins, 1999; Culver and Horton, 2005). Tests of *E. macrescens* appear particularly prone to degradation, as indicated by decreasing numbers in subsurface sediments from the Fraser River delta, British Columbia (Jonasson and Patterson, 1992). In other salt-marsh areas, agglutinated tests have been reported to be well preserved (e.g., Scott and Medioli, 1980b, 1986). High rates of test degradation have also been documented for *M. fusca* (Goldstein and Watkins, 1999; Murray and Alve, 1999), while tests of *T. inflata* appear to be more robust (J. Gauthier, pers. comm.). Based on preliminary results from sediment cores from the Bay of Tümlau, agglutinated taxa provide to be well preserved in subsurface sediments indicating a high fossilization potential for these foraminifera in our study area.

### 2.4.2 Small-scale spatial variability of salt-marsh foraminifera

The integration of our results with those of an earlier study (Ottmar, 2012) allows for an assessment of small-scale spatial differentiation of environments and foraminiferal assemblages in the Bay of Tümlau salt marsh. The salt-marsh meadows are internally subdivided by artificial ditches and natural ponds, the latter being particularly frequent in the northwestern part of the study area (Ottmar, 2012). The marsh pond assemblages mainly consist of *E. williamsoni* and *E. excavatum* that are even more abundant in the ponds than in the adjacent tidal flats (Fig. 2.4). Notably, *E. williamsoni* is most dominant in the ponds sampled along transects A and B, where it accounts for up to 90% of the total assemblage and exhibited unusually high standing stocks of up to 160 live individuals per 10 cm$^3$ in March 2011 (Ottmar, 2012). The high numbers of *E. williamsoni* in the ponds can be
attributed to the specific feeding strategy of this species. Lopez (1979) documented a higher uptake rate of chloroplasts by *E. williamsoni* relative to *E. excavatum*. Obviously, *E. williamsoni* benefits from the rich and stable algal communities that are present in marsh ponds. The ditches and natural tidal channels are also inhabited by calcareous taxa, mainly by *E. excavatum* and *H. germanica* (Ottmar, 2012). In the ditches, both taxa are related to relatively sand-rich substrates, free of vegetation, similar to conditions in the tidal flat environments.

These findings are relevant for future sampling strategies, particularly with respect to naturally developed, un-ditched salt marshes, where the number of ponds is usually much higher when compared to ditched marshes (LeMay, 2007). The documented small-scale differences have a direct influence on the quantitative interpretation of modern assemblages and establishment of transfer functions for sea-level reconstructions. In future studies, these issues could be addressed by a wider spatial sampling, instead of sampling along single transects, in order to capture all microhabitats. In addition, lateral shifts of channels and ponds are likely documented in sediment cores and related faunas, which may result in erroneous sea-level estimates.

### 2.3.3 Anthropogenic impacts on the distribution of foraminifera

The foraminiferal distribution patterns in the Bay of Tümlau reflect the specific morphology of the salt marsh, which lacks the usual landward increase in elevation but instead slightly rises towards its seaward end (Fig. 2.1). The local salt marsh was ditched for land reclamation purposes and ditches are still visible as linear features (compare Fig. 1.3); some areas now have developed naturally as part of nature reserves (compare Fig. 1.5). To the landward side, the salt marsh is further bordered by a dike, which protects the hinterland from storm floods. The dike prevents the lateral migration of the salt marsh and thus the development of a natural succession with a low, middle, and high marsh. As a consequence, only a few high marsh and middle marsh areas can be found (Stock et al., 2005) and the transition to the tidal flat is regularly represented by erosional edges.

These processes, superimposed by the compaction of the muddy substrate of the salt marsh by desiccation and capillary suction stress (Brain et al., 2011), modified the hydrology of the salt marsh and the drainage process. Further drying following rare flooding events (storm tides) has resulted in subsidence of older parts and an overall concave cross profile with rising edges (LeMay, 2007; Stock, 2011). Similar processes and morphologies have been documented for ditched salt-marsh areas along the northeast American coast (Vincent et al., 2013). Accordingly, only two main foraminiferal zones were observed in the
Bay of Tümlau, including a lowest marsh/ tidal flat zone, and a salt-marsh zone lacking a clear sub-zonation with respect to the tidal frame. The salt marsh zone is predominantly inhabited by agglutinated species, represented by Cluster I. The tidal flat and lowest marsh zone is inhabited by calcareous taxa, represented by Cluster II (Fig. 2.2). The artificial alteration of the salt-marsh morphology for drainage results in a distortion of the tidal frame, so that the salt marsh is only submerged during storm tides (van der Molen, 1997). Consequently, the foraminiferal distribution in the Bay of Tümlau is not primarily controlled by semi-diurnal tidal submergence and, hence, elevation is similar to that previously described by de Rijk and Troelstra (1997) for a ditched salt marsh in Massachusetts (USA). These authors mentioned pore water salinity as an important parameter acting on the foraminiferal distribution in these human-altered salt marshes.

Sheep grazing in parts of the salt marsh in the Bay of Tümlau has resulted in a reduction of the floral diversity, accompanied by a modified trapping of suspended sediment (Stock, 2011), and likely an alteration of the biogeochemical processes in the soils. The grazed parts of the salt marsh (particularly at Transect D) are dominated by a monospecific *Agrostis stolonifera* community. However, it seems that this monospecific plant community does not have any influence on the foraminiferal distribution in the study area because their distribution along transect D is similar to that of the other transects (Fig. 2.1). Comparable monospecific grass communities are typical for grazed marshes (Kiehl et al., 1996). Interestingly, this grass species is still dominant in some of the currently protected and non-grazed areas of Transects E and F. This suggests an extensive recovery period for natural floral secondary succession (Kiehl et al., 1996). The ditching, diking and grazing processes altered the salt-marsh morphology in the Bay of Tümlau, preventing the development of distinct floral and foraminiferal zones in equilibrium with the tidal frame. To date, the natural zones have not yet established in areas that have not been grazed for at least several years. Our results confirm the study of de Rijk and Troelstra (1997) and Mills et al. (2013), who concluded that the topography plays a crucial role for the vertical zonation of intertidal foraminifera relative to the tidal frame. A tight and distinct vertical zonation is restricted to salt marshes with a regular landward-rising topography (Scott and Medioli, 1980b). As a future perspective, regular monitoring of benthic foraminiferal and floral successions in the Bay of Tümlau would be useful to assess the recovery potential of human-altered salt marshes, and to provide information on the response of these ecosystems to the impact of sea-level rise.
3 APPLICABILITY OF TRANSFER FUNCTIONS FOR RELATIVE SEA-LEVEL RECONSTRUCTIONS IN THE SOUTHEASTERN NORTH SEA COASTAL REGION BASED ON SALT-MARSH FORAMINIFERA

This chapter is mainly based on Müller-Navarra et al., 2017*

3.1 Introduction
Salt marshes represent the tidally influenced transition zone between marine and terrestrial ecosystems and are important habitats with characteristic plant and animal life. They are natural buffering zones against tides and storm tides, and hence are a valuable component of coastal protection in connection with relative sea-level rise (Möller et al., 2014). In this context, the vertical development and lateral shift of salt marshes in relation to long-term changes of relative sea level need to be better understood (van de Plassche et al., 1992; Kirwan and Murray, 2007; Deegan et al., 2012; Balke et al., 2016; Kirwan et al., 2016).

One aspect in understanding salt-marsh development is to study salt-marsh foraminifera and their relation to the tidal influence. It has been shown that in natural salt marshes certain species are found in specific zones relative to the tidal frame (e.g., Horton and Edwards, 2006). This vertical distribution of salt-marsh foraminifera with respect to the tidal frame is controlled by changing environmental parameters such as pH, salinity and grain size (e.g., Phleger, 1970; Horton and Edwards, 2006; Hawkes et al., 2011) or by food availability (Shaw et al., 2016). Scott (1977) reported that individual foraminiferal species occur in a characteristic and limited range of habitats around their particular environmental optimum. The first recognition of this relationship dates back to the work of Phleger and Walton (1950) and Phleger (1954), who studied salt-marsh foraminifera from Massachusetts and the Mississippi Delta area. They described the restriction of certain indigenous species to marsh areas and stated that salt-marsh foraminifera can be used to reconstruct the history of old salt marshes. Two decades later, Scott (1976) and Scott and Medioli (1978) used salt-marsh foraminifera as proxies to reconstruct former tide levels in Nova Scotia, North America. Scott (1977) concluded that foraminiferal assemblages could be used to accurately locate tidal datums (e.g., mean high water) in a marsh sequence. Since the first

observations, this relationship has been confirmed in many studies around the world. In more recent times, foraminifera-based transfer functions are widely applied to reconstruct relative sea-level changes by using elevation relative to the local tidal frame as a proxy for sea level in salt marshes. Such transfer functions were initially applied by Imbrie and Kipp (1971) and were for example also used to reconstruct paleoenvironmental changes in lakes using diatoms to reconstruct pH (Renberg and Hellberg, 1982). Guilbault et al. (1995) were the first who used transfer functions to reconstruct paleo-elevations based on foraminifera in a salt marsh at Vancouver Island (Canada). Ter Braak and Prentice (1988) were the first to use unimodal-based Weighted Averaging (WA) techniques and Ter Braak and Juggins (1993) introduced a combination of unimodal (WA) and linear partial least squares (PLS) methods to improve the performance of transfer functions. These methods were subsequently applied in a number of studies, confirming the applicability of intertidal foraminifera for relative sea-level reconstructions, e.g. in the UK (Gehrels, 1999a, b; Horton et al., 1999a, b; Barlow et al., 2013), at the US Atlantic coast (Gehrels, 2000; Edwards et al., 2004; Engelhart and Horton, 2012; Kemp et al., 2012; Kemp et al. 2017a,b), at the Atlantic coast of SW Europe (Leorri et al., 2010), at the North Sea coast (Gehrels and Newman, 2004), in Iceland (Gehrels et al., 2006a), in Tasmania (Callard et al., 2011), in southern Africa (Strachan et al., 2016), and along the Adriatic Sea (Shaw et al., 2016). Until today, the establishment of a regional transfer function for the southern North Sea region is hampered by the rare occurrence of naturally developed coastal ecosystems. Most salt marshes and the associated floral and faunal zonation of this region were largely altered in the past by anthropogenic impacts such as draining and sheep grazing (Müller-Navarra et al., 2016) (Chapter 2). Since the establishment of the Wadden Sea National Park in 1985, protected salt marshes are able to develop more naturally again.

It has been argued that the duration of submergence, which is a function of elevation relative to the tidal frame and the height of the tides reaching this elevation, determines the foraminiferal distribution in salt marshes (van der Molen, 1997; Horton and Edwards, 2006; Balke et al., 2016). However, the local tidal-induced duration of submergence has been rarely addressed in salt-marsh studies although Horton and Edwards (2006) and others stated that information about the local tidal regime may improve the resolution of reconstructions of the local relative sea level by reducing scatter in the modern taxa-elevation relationships, and that sample elevation can be considered to be a general indicator of flooding frequency. Gehrels (2000) and Gehrels et al. (2001) used the flooding and height normalization for their training data sets but found a moderate correlation
between flooding duration and the modern foraminiferal distribution in southern UK and Maine (USA) salt marshes; however, the relationship improved significantly when other microfossil groups (diatoms and amoebae tests) were included. Further, Kemp and Telford (2015) reported a non-linear relationship between elevation and tidal inundation in the highest marsh. And Wright et al. (2011) discussed the difficulties obtaining information on local tidal datums and developed the principle of the highest occurrence of foraminifera (HoF) to avoid problems concerning the local tidal information, especially at elevations in the upper tidal regime. These results underline the necessity to quantify the influence of local flooding and tide level on the foraminiferal distribution and to test the usefulness of these parameters for relative sea-level reconstructions.

The aim of our study is to develop a first regional transfer function for the southern North Sea coastal region that can be used to reconstruct past relative sea-level changes in southern North Sea salt marshes. For this, we investigated the foraminiferal distribution along four surface transects in two recently naturally-grown back-barrier island salt marshes in the southeastern North Sea region and calculated duration of submergence, flooding frequency, and submergence time based on local tide gauge data. We developed and compared different regional transfer functions by using (1) the widely applied standard water level index (SWLI [1]) approach and (2) approaches on the flooding parameters duration of submergence (DoS [%]), mean submergence time (MST [min]), and flooding frequency (FF [%]) to quantify the relationship between the foraminiferal distribution, elevation within the tidal frame, and flooding parameters. We further address the difficulties in depicting the local tidal conditions in each salt marsh, by using tidal datums from permanent tide gauges installed in the direct vicinity.

3.2 Material and methods

3.2.1 Sampling methodology, foraminiferal investigations and measurement of environmental parameters

We collected a total of 47 modern surface sediment samples (100 cm² by 1 cm deep) along three E-W orientated cross-marsh transects at Rantum (Sylt) (SyRa I 1–12, SyRa II 1–12, and SyRa III 1–9), and one NW-SW orientated transect at Sønderho (Fanø) (Sø 1–14) in September 2014 and June 2014, respectively (compare Fig. 1.7 A, B), accordingly to the sampling methodology described in Chapter 2.2. In both areas, sample stations were placed in a line perpendicular to the coast. A total of 33 samples were taken along the three transects at Rantum and a total of 14 stations along one transect at Sønderho. All transects include samples from upland to the tidal flat. At each station, we took a further set of samples
for foraminiferal and grain size analysis, and for salinity and pH measurements. The sediment samples for foraminiferal analysis were preserved using a solution of 50 % ethanol and 50 % demineralized water, stained with rose Bengal (2 g rose Bengal per liter ethanol (96 %)) on the sampling day, to distinguish between stained (living) and unstained (dead) foraminifera (Walton, 1952; Murray and Bowser, 2000). We investigated only the dead foraminiferal species to avoid a seasonal bias of the foraminiferal record (Culver and Horton, 2005). All samples for foraminiferal investigations were wet-sieved over 500 µm (to remove larger plant material) and 63 µm sieves and then the 63–500 µm fraction was split into aliquots using a wet-splitter (Scott and Hermelin, 1993) as described by Horton and Edwards (2006). Samples were counted wet to prevent drying of the organic residue, which may result in consolidation or “pancaking” (de Rijk, 1995). If present, a minimum of 200 unstained foraminifera were counted under a stereo-microscope. We identified the foraminiferal taxa based on illustrations and descriptions of Hofker (1977), Gehrels and Newman (2004), Horton and Edwards (2006), Filipescu and Kaminski (2008), Wright et al. (2011), and Milker et al. (2015a, b).

Measurements of salinity and pH followed the standard DIN ISO 10390: 2005-12. For one hour, 10 g of dry sediment of each sample was shaken in 25 ml demineralized water. After one-hour resting, measurements were performed in the suspension with a hand-held multi-meter (Multi 340i Set). For the grain size measurements, we treated the samples with H₂O₂ for two weeks to dissolve the organic components. The grain size analyses were carried out with a laser diffraction particle-sizer (Sympatex HELOS/KF Magic).

### 3.2.2 Elevation measurements

All land-fixed horizontal and vertical geodetic datums of the sample stations and of the station where we made water level measurements at Sønderho were levelled to a local benchmark (Fig. 1.7 A, B). The local benchmarks at Sønderho (triangulation station 135-16-00001) and at Rantum (triangulation station 1115 001 06) were used to obtain the heights of the sample points and the height of the station for the water level measurements by using a roving receiver. We used Real Time Kinematic (RTK) with GPS and GLONASS satellites, because using both significantly improves the accuracy of positioning results (Wang, 1999). Post-processing was conducted using the Leica Geo Office 8.3 software package. Processed horizontal and vertical accuracy of the sample stations is better than 0.01 m. The Danish height system is slightly different to the German height system, therefore, all
geodetic datums of the sample points at Sønderho were transformed to NHN using equation 3.1 (Schmidt, 2000) in order to have a consistence reference datum for the calculations.

3.2.3 Tide-gauge and water-level measurements

Tide-level data for Rantumdamm, 3.2 km north from the Rantum transects, for the period of May 13, 1996 to December 31, 2015 were provided by the Federal Maritime and Hydrographic Agency (BSH) on a resolution of 10-minute tidal curves and with a completeness of tidal data of 99.21 %. Tidal datums are calculated based on these tide-level data (Table 3.1). As the low water at this site is not adequately represented at the Rantumdamm tide gauge (in around 15 % of the 10-minute tidal data, this tide gauge falls dry), we estimated mean low water (MLW), and local mean tide level (MTL) by using four nearby tidal stations: Hörnum harbor (distance to Rantum salt marsh: 8.5 km), Osterley (distance to Rantum salt marsh: 67 km), Föhrer Ley Nord (distance to Rantum salt marsh: 15 km), and Amrum Odde (distance to Rantum salt marsh: 13.5 km). Tidal datums for Sønderho were calculated using data of the tide gauge of Esbjerg provided by the Danish Meteorological Institute (DMI) for the period of October 01, 1997 to May 31, 2016 and on a resolution of 10-minute tidal curve and with a completeness of tidal data of 99.25 %. We have further made water level measurements of high-water heights relative to a benchmark.

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**Fig. 3.1** Tidal curves of Esbjerg and Ribe Kammersluse permanent tide gauges during twelve days (May 15 to May 27, 2016). Dots represent own measurements during every second high water at Sønderho. The Esbjerg tide gauge data was chosen to fit best to the tidal conditions found at Sønderho salt marsh. The small figure shows the difference between Esbjerg, Ribe and own observations on 19 May at afternoon.
installed at Sønderho, for two weeks from May 15 to May 26, 2016 and used these water level measurements to calculate tidal datums for Sønderho. Phase difference between high water (time of slack water) of Sønderho and Esbjerg were recorded.

The water level measurements were made near to the landing bridge of Sønderho, at a distance of 120 m from the sampled transect. We put a flagstone at the sea bed during low water and measured the elevation of its surface with the RTK-GPS device. We then measured water levels above the flagstone during high waters. During low water, the tidal creek of Sønderho is isolated from the open sea due to a sand barrier offshore the tidal creek; and hence low waters could not be measured at Sønderho. We measured water levels during high water once a day on twelve consecutive days. Our observations were then compared to the data of the two nearest tide gauges: the Esbjerg tide gauge (12.8 km distance) and Ribe Kammersluse tide gauge (11.9 km distance).

The comparison of the two tidal curves shows that the Ribe Kammersluse tide gauge is less comparable to the tidal conditions of Sønderho (Fig. 3.1). Therefore, we used the data of the Esbjerg tide gauge and reduced Esbjerg tidal data by approximately 4 %, which was calculated from the difference of 3 cm ± 1.8 cm between the high water of Sønderho and the high water of Esbjerg during the 12 days period (Equation 2.3). Mean low water (MLW) or MSL of Sønderho is not represented in the field, because the tidal creek is

<table>
<thead>
<tr>
<th>Tidal datums</th>
<th>Rantumdammm [m NHN]</th>
<th>Sønderho [m DVR90]</th>
<th>Esbjerg [m DVR90]</th>
</tr>
</thead>
<tbody>
<tr>
<td>HAT</td>
<td>1.59*</td>
<td>1.15*</td>
<td>1.20</td>
</tr>
<tr>
<td>MHWS</td>
<td>1.26</td>
<td>0.82*</td>
<td>0.88</td>
</tr>
<tr>
<td>MLWS</td>
<td>-1.10*</td>
<td>-0.90</td>
<td></td>
</tr>
<tr>
<td>MHWN</td>
<td>0.97*</td>
<td>0.65*</td>
<td>0.68</td>
</tr>
<tr>
<td>MLWN</td>
<td>-1.00*</td>
<td>-0.70</td>
<td></td>
</tr>
<tr>
<td>MHW</td>
<td>1.12</td>
<td>0.77</td>
<td>0.80</td>
</tr>
<tr>
<td>MTL</td>
<td>0.03*</td>
<td>-0.01*</td>
<td>-0.01</td>
</tr>
<tr>
<td>MLW</td>
<td>-1.06*</td>
<td>-0.79*</td>
<td>-0.82</td>
</tr>
<tr>
<td>LAT</td>
<td>-1.33*</td>
<td>-1.23*</td>
<td>-1.31</td>
</tr>
<tr>
<td>MSL</td>
<td></td>
<td>0.09</td>
<td></td>
</tr>
</tbody>
</table>

Tidal datums for the permanent tide gauge of Rantumdammm, delivered by the Federal Maritime and Hydrographic Agency (BSH), (data* are calculations). For Sønderho, measured and calculated data* using the tidal datums of the Esbjerg tide gauge, are delivered by the Danish Meteorological Institute (DMI), are calculated by the BSH, and are calculated by using the R-code TideTables. HAT: highest astronomical tide, MHWS: mean spring high water, MLWS: mean spring low water, MHWN: mean neap high water, MLWN: mean neap low water, MHW: mean high water, MTL: mean tide level, MLW: mean low water, LAT: lowest astronomical tide, MSL: mean sea level, NHN: Normalhöhennull, and DVR90: “Dansk Vertikal Reference 1990”. Difference between DVR90 and m NHN: 2.1 cm (Equ. 3.1).
regularly cut off from the open sea tidal dynamics during low waters (see above). All measurements include meteorological effects such as local wind strength and direction.

\[ \text{NHN} = \text{DVR90} - 0.021 \text{ m} \quad (\text{Schmidt, 2000}) \quad (3.1) \]

\[ \text{tidal datums}_{\text{Sønderho}} = 0.96 \cdot \text{tidal datums}_{\text{Esbjerg}} \quad (3.2) \]

For calculations of the tidal datums for Rantum, Esbjerg and Sønderho (except for the neap and spring datums) and for the tidal curves we used the R package (R-Core-Development-Team, 2016) TideTables (Müller-Navarra and Müller-Navarra, 2017). These calculations were compared with tidal datums of the BSH and the DMI. All calculations are based on tidal analysis and predictions of the most recent 18.6 years of water-level observations (observation period) by means of harmonic representation of inequalities (Müller-Navarra, 2013). We defined the duration-of-submergence (DoS) as the percentage of the observation period during which the elevation point is flooded, the mean submergence time (MST [min]) is the mean duration at which the elevation point is flooded after the water level has reached this point, and the flooding frequency (FF) is the percentage of all tidal cycles within the observation period that reached or surpassed the elevation point (van der Molen, 1997; Davis Jr. and Dalrymle, 2011; personal communication, S. Müller-Navarra, BSH). Calculations of the flooding parameters are made using the web application ‘Salt-marsh submergence’ (Müller-Navarra and Müller-Navarra, 2017).

\[ \text{MST} = \overline{\Delta t^j} = \frac{\sum_{i=1}^{m} \Delta t^j_i / m^j}{\text{min}} \quad \text{with} \quad \Delta t^j_{1,i} = t^j_{2,i} - t^j_{1,i} \quad \text{[min]} \quad (3.3) \]

\[ \text{DoS} = 100 \cdot \frac{\sum_{i=1}^{m} \Delta t^j_i}{(n \cdot 10 \text{ min})} \quad [\%] \quad (3.4) \]

\[ \text{FF} \approx 100 \cdot \frac{m^j / k}{\%} \quad \text{with} \quad k = 2 \cdot \left( n - 1 / (1.030501d \cdot 144d^{-1}) \right) \quad (3.5) \]

\( m^j \): total number of submergence events of the \( j \)th transect point.
\( i \): index, numbering the events of submergence
\( j \): index, numbering the site elevation points
\( n \): total number of water level observations
\( k \): estimate of the total number of high waters covered by the time series. With 1.030501 being one mean lunar day and 144 equals the number of 10-minute observations per solar day. Because the local tides are semidiurnal, values are multiplied by 2.
Since the completeness of the time series reaches almost 100 %, the parameters MST, DoS and FF are approximated sufficiently with the equations below (Equations 3.3, 3.4, and 3.5). For the determination of MST, submergence events with data gaps in the time series were excluded before calculation. The local tidal data of Sønderho (Esbjerg data modified according to Equation 3.2) and Rantum provided the basis for all these calculations. A schematic sketch is shown in Fig. 3.2 and the elevation related to DoS, MST, and FF is presented in Fig. 3.3.

3.2.4 Investigating the modern species-environment relations
To address potential effects of environmental variables other than elevation relative to tidal datums and flooding parameter on the foraminiferal distribution (Juggins, 2013), we used Canonical Correspondence Analysis (CCA; Ter Braak, 1986). Before applying CCA, we tested whether the species response is linear or unimodal along elevation by using Detrended Canonical Correspondence Analysis (DCCA; Hill and Gauch, 1980). For CCA and DCCA, we used relative abundance data and the software package CANOCO, version 4.5 (Ter Braak and Smilauer, 2002). A total of 40 samples from the Sønderho and Rantum salt marshes were used, because samples with less than 50 individuals were excluded from
the combined modern set (n=7; SyRa I 1, SyRa I 2, SyRa I 12, SyRa II 11, SyRa II 12, Sø 1, and Sø 2).

In order to determine the influence of elevation and the flooding parameters on the foraminiferal assemblages, we further applied one-way Non-Parametric Multivariate Analysis of Variance (NPMANOVA, 9999 permutations) (Anderson, 2001). The same modern data set as described above was used. For this approach, the samples were numerically coded to four categories (tidal flat, low marsh, middle marsh, high marsh to upland transition) and we used the Bray-Curtis dissimilarity (Bray and Curtis, 1957) as the distance metric. For calculations, the software package Past (version 2.17; Hammer et al., 2001) was used. To classify the distribution of foraminifera in the combined modern data set, we performed Cluster Analysis by using the unweighted pair group average (UPGMA) algorithm to define clusters (groups) and the Bray-Curtis similarity as distance metric. Cluster analysis was carried out with the software package PAST (version 2.17; Hammer et al., 2001).

3.2.5 Development of the transfer functions

We developed different regional transfer functions based on 1) SWLI as an equivalent for elevation and 2) the flooding parameters DoS, MST, and FF as a function of elevation, in order to test to what extent the foraminiferal distribution is individually influenced by these parameters and to assess their individual predictive accuracy. SWLI was calculated using equation 3.6 (Hawkes et al., 2011; Horton, 1997), standardizing each elevation to the heights of mean high water (MHW) and mean high water springs (MHWS).

\[
SWLI = \frac{\text{sample elevation} - \text{MHW}}{\text{MHWS} - \text{MHW}} \quad [1] \quad (3.6)
\]

We used MHW and MHWS (capturing 5% of the samples) because both datums are represented in the study areas. The vertical range between MTL and MHW (capturing 10% of the samples) or MLW and MHW (capturing 97% of the samples) could not be used, because MLW is not represented at the sample sites. The modern data set for the transfer functions consists of a total of 40 samples from both study areas, which is an appropriate training set (Kemp and Telford, 2015), but also will be increased in number in future studies. We developed the transfer functions by using the widely applied unimodal-based Weighted Averaging (WA) technique with inverse deshrinking (Ter Braak and Juggins, 1993) where the modern relationship between the training set (Y) and the environmental variable of interest (X) is statistically modelled and the resultant transfer function can then be used to predict the variable of interest in a fossil record (Birks, 1995; Kemp and Telford, 2015). We
used bootstrapping (1000 cycles) to calculate the coefficient of determination ($R^2_{\text{boot}}$) between observed and predicted SWLI, and flooding parameters, and the root mean squared error of prediction (RMSEP), which is a measure of the predictive precisions of the transfer function. For all approaches, we used the software package C2 (Juggins, 2007).

### 3.3 Results

#### 3.3.1 Tidal inundation

We found that the tidal datums of the tide gauge of Esbjerg are valid for Sønderho, with a slight modification of phase and water level, which is based on our observational data of high water heights at Sønderho (Fig. 3.1). We observed a phase difference in high water time (time of slack water), with high water occurring 20 minutes earlier in Sønderho compared to Esbjerg and a mean height difference of the observed heights of high water of 3 cm ± 1.8 cm lower in Sønderho compared to the high water heights in Esbjerg (Fig. 3.1).

The tidal curves are not perfectly sinusoidal-shaped (Fig. 3.3). In a sinusoidal-shaped tidal curve, the position of the 50-%-duration of submergence equals the elevation of MSL and MTL. In a non-sinusoidal-shaped tidal curve, differences between MTL and MSL are calculated by using a correction factor (which is 0.4539 for List (Sylt)) (Wahl et al., 2011). Under this assumption, MTL roughly equals the MSL, because the difference of MSL and MTL at the northern German North Sea coast is around 3 cm (Wahl et al., 2011). Locally, MSL slightly differs from the 50-%-duration of submergence in both salt marshes. The observed height of Sønderho at 50-%-duration of submergence is 0.16 m NHN, while the calculated MSL is 0.10 m NHN (equivalent to 52.3 % duration of submergence; Fig. 3.3). The height of Rantum at 50-%-duration of submergence is 0.10 m NHN while the calculated MSL is -0.02 m (equivalent to 52.9 % duration of submergence; Fig. 3.3).

Compared to a sinusoidal-shaped curve, the position of the true MSL of Sønderho differs by 6 cm, and the MSL of Rantum differs by 12 cm.

#### 3.3.2 Environmental parameters

The elevation range of the salt-marsh stations at Rantum is between 2.25 m and 0.38 m relative to NHN, which corresponds to a total range of 1.87 m (Fig. 3.3 A–C). Pore-water salinity fluctuates between 0.02 g kg$^{-1}$ in the upper salt marsh and 19.7 in the low marsh and tidal channel. pH values at Rantum range between approximately 6.3 and 8.4. Grain size analysis for Rantum reveal a nearly monotonic sandy succession with the exception of transect SyRa I, where the high marsh to middle marsh transition is characterized by muddy sediment
The elevational range of the salt-marsh stations at Sønderho is between 2.00 m and 0.41 m relative to NHN, which corresponds to a total range of 1.40 m (Fig. 3.3 C, Suppl. S2.2). Pore-water salinity at Sønderho fluctuates between 2.9 in the high and low marsh and 20.6 g kg\(^{-1}\) in the tidal creek. pH is around 4 in the middle marsh and increases towards the low marshes to up to 8. Grain size analyses for Sønderho reveal sandy high marsh, muddy middle marsh and sandy low marsh and tidal channel sediments.

### 3.3.3 Foraminiferal distribution in the studied transects

We found a total of 16 different foraminiferal taxa in the Rantum and Sønderho salt marshes (Fig. 3.4 A–D, Suppl. S2.1). Agglutinated taxa are the most abundant taxa in both salt marshes. Calcareous taxa only show higher occurrences in the tidal flat stations of Sønderho, while at Rantum the calcareous taxa are randomly distributed over the whole transects. The main agglutinated species comprise *Entzia macrescens*, *Miliammina fusca*, *Balticammina pseudomacrescens*, and *Ammobaculites* spp. and the main calcareous species comprise *Quinqueloculina* sp. and *Elphidium excavatum*. Species of minor relative abundance include *Ammonia batava*, *Haynesina germanica*, *Elphidium williamsoni*, *Ammodiscus* spp., irregular forms of *E. macrescens* (*Entzia macrescens* irregular, Plate 2), *Trochammina ochracea*, and *Haplophragmoides* sp.

In general, the relative abundance of *Ammobaculites* spp. and *E. excavatum* increases with decreasing elevation and increasing duration of submergence, while the relative abundance of *B. pseudomacrescens* and *E. macrescens* increases with increasing elevation and decreasing duration of submergence. We found foraminifera (i.e., *B. pseudomacrescens*, *E. macrescens*, and *T. inflata*) in places where duration of submergence is very low with 0.19 % DoS (equivalent to 135.3 minutes per event) at SyRa III 1 (Fig. 3.4 A–D). Among the most important species, the high marsh at Rantum is dominated by *E. macrescens* (up to 72 % at transect SyRa I), the middle marsh is dominated by *M. fusca* (up to 82 % at transect SyRa I, sample 8), and the low marsh by *Ammobaculites* spp. (up to 83 % at SyRa I, sample 11) (Fig 3.4 A–C). The foraminiferal record of samples 10 and 11 (transect SyRa I) almost exclusively consists of *Ammobaculites* spp.. *Balticammina pseudomacrescens* occurs in the high and middle marsh, with a relative abundance of up to 26 % in the high marsh of SyRa III. *Entzia macrescens*\(^{\text{irregular}}\) has a maximum relative abundance of 20 % in the high marsh.
APPLICABILITY OF TRANSFER FUNCTIONS

Fig. 3.4 A–B Environmental parameters and foraminiferal distribution along the transects SyRa I (A) SyRa II (B) and SyRa III (C) in Rantum (Sylt) and along the transect in Sønderho (Fanø) (D). Shown are elevation, flooding parameters, salt-marsh zonation defined by plant associations, main foraminiferal species, and environmental parameters (UL: upland, LM: low marsh, MM: middle marsh, HM: high marsh, TF: tidal flat, DoS: duration of submergence, FF: flooding frequency, MST: mean submergence time.
Fig. 3.4 C–D Figure caption on p. 37.
Calcareous taxa are less abundant along transects SyRa I and SyRa III, while SyRa II has a high relative abundance of calcareous taxa with *Quinqueloculina* sp. (up to 26% in the high marsh), *E. williamsoni* (up to 12% in the low marsh) and *E. excavatum* (sample Sø 8) (Fig 3.4 D). *Entzia macrescens* has its highest relative abundance (48%, sample Sø 10) in the low marsh; it then decreases rapidly towards the tidal creek. Also *Trochammina inflata* has its highest relative abundance in the low marsh, with up to 18%. The relative abundances of the calcareous species *E. excavatum*, *E. williamsoni* and *A. batava* increase towards the tidal creek to up to 61% (sample Sø 13), 16% (sample Sø 14), and 16% (sample Sø 13), respectively. We found that the vertical distribution in both marshes are almost comparable for those species that are present in both marshes, reflecting the influence of similar environmental conditions, and indicating that both data sets can be combined (Fig 3.5).

Cluster Analysis revealed four clusters (Fig. 3.6). Cluster I contains calcareous foraminifera (*E. excavatum* (up to 61%) and *E. williamsoni* (up to 17%)). This assemblage is found at the edge to tidal flat region of Sønderho. Cluster IIa is dominated by *B. pseudomacrescens* (with up to 78–89%) present at the landward end of the salt marsh of Sønderho above MHWS. Cluster IIb, predominantly located between MTL and MHWS, is dominated by *E. macrescens* (7–72%) and *M. fusca* (with up to 39%). In Cluster IIc, predominantly located below MTL, *Ammobaculites* spp. and *M. fusca* are the most dominant

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**Fig. 3.5** Optima and tolerances of the species found in both study areas and in the combined modern data set.
species with up to 90% and up to 80%, respectively. This cluster further comprises *B. pseudomacrescens* (around 45%) and *E. macrescens* (around 72%).

3.3.4 Species-environment relationships

The DCCA revealed a gradient length of 2.06 standard deviation (SD) units for SWLI, 2.31 for MST, 3.00 for DoS, and 2.63 for FF for the first axis, respectively, indicating a unimodal species response to elevation and the flooding parameters (Hill and Gauch, 1980; Birks, 1995).

We consequently applied CCA to determine the influence of elevation and other environmental parameters (i.e., flooding parameters, grain size, pH and salinity) on the foraminiferal distribution in...
the study area (Fig. 3.7). Results show that 19.1% of the variance of the species data is explained by the first axis and 13.8% by the second axis (Table 3.2). Duration of submergence, flooding frequency and SWLI, as well as sand content are more closely related to axis one. Mean submergence time and pH are related to axis 2, and salinity to both axes one and two. *Balticammina pseudomacrescens*, and to some extent *E. macrescens*, are related to higher elevations and *Ammobaculites* spp. to lower elevations and higher DoS, FF and sand content. Salinity and pH seems to have little control on the foraminiferal distribution due to their short gradient lengths at the studied sites, but it seems that *E. williamsoni*, *H. germanica*, *E. excavatum* and *A. batava* have a relation to higher pH and/or salinity. Duration of submergence and FF equals SWLI, with increasing DoS and FF equivalent to decreasing SWLI. One-way NPMANOVA showed that all flooding parameters and SWLI have a significant ($p<0.05$) influence on the foraminiferal assemblages in the tidal flat, low, middle, and high-marsh areas (Table 3.3). MST has a slightly higher influence on the foraminiferal assemblage (highest $F$ value) than the other parameters, and is therefore used in Chapter 4.

| Table 3.2: Results of the Canonical Correspondence Analysis |
|-----------------|--------|--------|--------|--------|
| Axes            | 1      | 2      | 3      | 4      |
| Eigenvectors    | 0.49   | 0.36   | 0.30   | 0.08   |
| Species-environment correlations | 0.90   | 0.75   | 0.79   | 0.62   |
| Cumulative percentage variance of species data | 19.1 | 32.9 | 44.8 | 48.2 |
| Cumulative percentage of species-environment relation | 38.2 | 66.1 | 90.0 | 96.8 |

| Table 3.3: Results of the one-way NPMANOVA |
|-----------------|--------|--------|--------|--------|
| SWLI | FF | MST | DoS |
| Total sum of squares | 9.88 | 8.46 | 2.30 | 9.25 |
| Within-group sum of squares | 2.83 | 2.30 | 0.55 | 2.63 |
| $F$ | 4.43 | 4.76 | 5.66 | 4.48 |
| $p$ | <0.001 | <0.001 | <0.001 | <0.001 |

*FF*: SWLI: Standard water-level index [1], DoS: duration of submergence [%], MST: mean submergence time [min], FF: flooding frequency [%].
We used a Weighted Averaging (WA, inverse deshrinking) to establish our transfer functions. We run an initial transfer function and found two samples having residuals of >2.5 times of standard deviation in the residuals (Sø 3 and Sø 14). Those samples are located at the upper (2.0 m NHN) and lower (0.41 m NHN) edge of the elevational gradient, contain a nearly monospecific assemblage (\textit{B. pseudomacrescens} and \textit{E. excavatum} are dominant, respectively). These samples were excluded for the development of the final transfer function for SWLI following Juggins and Birks (2012). For the DoS- and MST-transfer functions, all 40 samples were included as in this analysis all samples having residuals of <2.5 times of standard deviation. For the FF-transfer function we found two samples having residuals of >2.5 times of standard deviation in the residuals (SyRa III 8 and SyRa III 9; both samples contain nearly monospecific assemblages with \textit{Ammobaculites} spp.), which were excluded for the development of the final transfer function using FF. Residuals are slightly structured, as being observed by others (Kemp and Telford, 2015) (Fig. 3.8). Samples at the lower end of the elevation gradient are partly over-predicted, while samples at the upper end are partly under-predicted (Fig. 3.8). The root-mean squared error of prediction (RMSEP) is 2.77 SWLI for the transfer function based on SWLI. This is equivalent to an error range of approximately 0.23 m, when assuming a linear relationship between elevation and tidal

<table>
<thead>
<tr>
<th>Method</th>
<th>1) SWLI [1]</th>
<th>2) DoS [%]</th>
<th>3) MST [min]</th>
<th>4) FF [%]</th>
</tr>
</thead>
<tbody>
<tr>
<td>RMSE</td>
<td>2.07</td>
<td>6.95</td>
<td>29.93</td>
<td>19.49</td>
</tr>
<tr>
<td>(R^2)</td>
<td>0.76</td>
<td>0.67</td>
<td>0.62</td>
<td>0.63</td>
</tr>
<tr>
<td>(R^2_{\text{boot}})</td>
<td>0.65</td>
<td>0.52</td>
<td>0.47</td>
<td>0.48</td>
</tr>
<tr>
<td>RMSEP</td>
<td>2.77</td>
<td>9.1</td>
<td>38.52</td>
<td>24.95</td>
</tr>
</tbody>
</table>

Performance of the standardized water level index (SWLI), the duration of submergence (DoS), mean submergence time (MST), and flooding frequency (FF) transfer function approaches used in this study. RMSE: apparent root mean squared error; \(R^2\): squared correlation between inferred and observed values; \(R^2_{\text{boot}}\): cross-validated (bootstrapped) squared correlation between predicted and observed values; RMSEP: cross-validated root mean squared error of prediction. RMSEP for SWLI was converted to meters by multiplying the RMSEP value with the range between MHW and MHWS, RMSEP for DoS and FF was converted into meters by using Fig. 3.3, MST was converted to meters by: \(\text{RMSEP [cm]} = \text{height difference [cm]} \cdot (\text{RMSEP [minutes]} / \text{time [minutes]} \cdot \text{height difference})\). RMSEP conversion from minutes to meters are done by using the results of calculations from the web application 'Salt-marsh Submergence'.

Table 3.4: Performance of the transfer function approaches using the weighted averaging model (inverse deshrinking)
parameters, i.e. flooding parameters (Horton, 1997). In our study areas the flooding parameters are non-linearly related to elevation. Therefore, we calculated the change in precision segment-wise (Fig. 3.9), because the SWLI formula was developed by Horton (1997) on the assumption on MST being linearly related to elevation. The RMSEP for the transfer function based on DoS is around 9.1 % duration of submergence (Table 3.4), which is equivalent to an error range of 0.30 m cm around MTL to 0.29 cm between MHW and MHWS, and of 1.3 m at the upper tidal frame where observed DoS is around 0.2 %. The RMSEP for the transfer function based on MST is 38.52 minutes, which is equivalent to 0.12 m between MTL and MHW and 0.53 m between MHW and MHWS, but higher than 1.0 m above MHWS. The RMSEP for the transfer function based on FF is 24.95 %, which is equivalent to 0.20 m around MTL and 0.35 m between MHW and MHWS, but also higher than 1.0 m above MHWS (Fig.3.9).

3.4 Discussion

3.4.1 Foraminifera and their relation to elevation and tidal regime in salt marshes
We observed a relation of intertidal foraminifera to elevation and the flooding parameters. Canonical correspondence analysis showed that *B. pseudomacrescens* and *Ammobaculites* spp. have the strongest relation to elevation (and to the flooding parameters), with *B. pseudomacrescens* preferring higher elevations (lower flooding durations) and
Ammobaculites spp. preferring lower elevations (higher flooding durations). Salinity, pH and substrate (i.e., grain size distribution) influence the foraminiferal distribution only to a minor degree. One-way

Non-Parametric Multivariate Analysis of Variance (One-way NPMANOVA) showed that the flooding parameters and elevation have a significant influence on the foraminiferal distribution, with MST having a slightly higher influence. Regarding the individual distribution of the most dominant species at our salt-marsh sites, we found B. pseudomacrescens to be dominant in the high marsh and E. macrescens and M. fusca to be dominant in the low and middle marsh together with Ammobaculites spp.. Calcareous species (E. williamsoni, E. excavatum, H. germanica and A. batava) are mainly restricted to low marsh and tidal flat environments except of Quinqueloculina sp., which also occurs in the middle marsh. Minor occurrences of Haplophragmoides spp. in the high marsh and T. ochracea in the middle marsh were observed. Specifically, we found E. macrescens irreglar in the high marsh of Rantum (samples SyRa II 1 and SyRa III 2 with elevations between 0.80 to 1.0 m above MHWS).

The morphology of E. macrescens irreglar is comparable to juvenile forms of Trochamminita irregularis. Trochamminita irregularis has been considered endemic to Pacific salt marshes (Engelhart et al., 2013a) and was only once described in European high salt marshes, i.e., at the North Sea coast (Halebüll, 58 km southeast of Rantum) and the Baltic Sea coast (Bottsand) by Lehmann (2000). We speculate that the irregular growth of E. macrescens (as also observed for T. inflata; Plate 2) is the consequence of environmental stress, i.e., extremely low salinity in the high marsh of Rantum. During the sampling period, salinity was between 0 and 8 g kg\(^{-1}\) at those stations in the Rantum salt marsh where we observed high amounts of E. macrescens irreglar with up to 19 % of the total assemblage. Further, DoS and MST were very low with 0.42 and 2.12 % and 139.3 and 135.15 minutes, and FF was around 2 and 11 % at these stations. This suggests that irregular tests of E. macrescens increase at elevations where mainly storm tides influence foraminiferal distribution. For B. pseudomacrescens, this observation is also valid, but to a stronger degree for the Sønderho salt marsh, where B. pseudomacrescens was found to be most abundant (around 90 % on the total assemblage) at low salinity stations, where no E. macrescens irreglar was detected while at Rantum, abundances of B. pseudomacrescens remain below 30 % at low salinity stations. This observation shows, that the vertical distribution of E. macrescens irreglar has to be investigated in more detail. De Rijk and Troelstra (1999) observed E. macrescens (their T. macrescens) to be more abundant at
stations with higher salinity in the Great Marshes (Massachusetts, USA) but other studies showed that this species is more dominant at the upper edge of the intertidal zone and it sometimes occurs as a monospecific assemblage (e.g., Kemp et al., 2017b and references therein) but the occurrence of a high amount of deformed specimens were, to our knowledge, never reported. We note, that future studies regarding the individual ecological preference of salt-marsh foraminifera and their reaction to environmental stress are necessary.

*Miliammina fusca* has its highest occurrence in the middle marsh, both at Rantum and Sønderho. In the tidal-creek salt marsh of Sønderho, *M. fusca* has been observed at stations with a duration of submergence below 10 % that is located approximately 1 m above MTL. There it is restricted to a muddy substrate, low pH values and salinities around 20 g kg\(^{-1}\). In other coastal areas, it occurs in the tidal flat and low marsh (e.g., Hawkes et al., 2010; Kemp et al., 2012; Milker et al., 2015a, b), and it is often considered as a typical indicator species of lower marsh environments (e.g., Engelhart et al., 2013b) and of clayey substrate (du Chatelet et al., 2008).

Apart from the general foraminiferal distribution, we also observed differences between the tidal-creek marsh of Sønderho and the coastal marsh of Rantum. As already mentioned, *B. pseudomacrescens* is dominant in the high marsh of Sønderho, where the duration of submergence remains below 5 %, but has a low relative abundance in the middle and high marsh of Rantum. It has been also found to be dominant in the high marsh at Ho Bugt (Gehrels and Newman, 2004), situated approximately 10 km north of Fanø. In the Pacific region, *B. pseudomacrescens* is mainly restricted to middle and high marsh environments (e.g., Hawkes et al., 2010; Engelhart et al. 2013b; Kemp et al. 2013c; Milker et al. 2015a, b). We assume that *B. pseudomacrescens* is indicative for a reduced marine influence, which raises the question, whether mainly the tidal regime influences its distribution. Other studies reported a high relative abundance of *B. pseudomacrescens* in modern salt marshes in southeastern Canada, southwestern Alaska and Newfoundland (Wright et al., 2011; Kemp et al., 2013c; Barnett et al., 2016). It is rare in Connecticut in the surface record, but common in the fossil record there (Gehrels and van de Plassche, 1999).

*Balticammina pseudomacrescens* is also common in Maine, New Jersey, North Carolina and Massachusetts (de Rijk, 1995; Edwards et al., 2004; Kemp et al., 2009; Wright et al., 2011; Kemp et al. 2012). These observations suggest that this species has a preference for cool climates (Kemp et al., 2013c), where it occurs nearly monospecific in the high marsh (Kemp et al., 2017d). The near-monospecific occurrence of *B. pseudomacrescens* in the
high marsh of Sønderho can also arise from environmental stress (e.g., low duration of submergence of less than 5 % and low salinities of around 8 at the highest stations). However, high percentages of living B. pseudomacrescens are observed in modern low marsh environments, influenced by more brackish rather than marine conditions in Oregon (Milker et al., 2015b) and in modern salt-marsh areas of Massachusetts, characterized by mean salinities ranging between 10 and 22 g kg\(^{-1}\) (de Rijk, 1995). These observations imply that salinity and tidal submergence as well as climate may exert an important control on the distribution of B. pseudomacrescens.

*Entzia macrescens* and *T. inflata* have their highest occurrences in the low marsh of Sønderho (at around 12 % DoS) just around the seaward end of the *Phragmites australis* plant zone. At Ho Bugt, Denmark, a low marsh peak of *E. macrescens* was observed, too (Gehrels and Newman, 2004). In Rantum, this species reach its highest relative abundance in the high marsh where the duration of submergence is between 0.42 % and 0.74 %. *Entzia macrescens* has been observed in areas where the tides drain the salt marsh regularly (Gehrels and van de Plassche, 1999), but also at stations with higher salinity and at higher elevations relative to the tidal frame (Horton et al., 1999a, b; de Rijk, 1999; Shaw et al., 2016; Kemp et al., 2017c). Thomas and Varekamp (1991) described *T. inflata* as an indicator species for time of exposure in salt marshes in Connecticut. Both species are also found in low to high marsh environments in many other salt marches (e.g., Hawkes et al. 2010; Engelhart et al. 2013b; Milker et al. 2015a, b). We further found *Ammobaculites* spp. to be dominant in the tidal flat and low marsh environments of Rantum, where salinity varies between 4 and 10 g kg\(^{-1}\), whereas it is absent in Sønderho. In Rantum it is highly correlated to duration of submergence because we found this taxon at stations, which are flooded between 29 and 40.4 % of the time. *Ammobaculites* spp. was also found in marshes with low salinity (0 to 15 psu; Murray, 2014) and generally in subtidal settings (Kemp et al., 2009). Lehmann (2000) observed *Ammobaculites* spp. to be widely distributed in brackish waters and low marshes at the North Sea coast. Calcareous species (*E. williamsoni, E. excavatum, H. germanica, A. batava* and *Quinqueloculina* sp.) are mainly restricted to the lowest tidal-creek marsh areas and the adjacent tidal flat, characterized by sandier conditions and a relatively high duration of submergence of up to 35 % in Sønderho. On the other side, calcareous tests have also been observed in the higher marsh in Rantum at stations that are flooded in at least 0.47 % of the time (Suppl. 2.1). These might be allochthonous tests.

In other salt marshes, e.g., in North America, calcareous taxa are rapidly dissolved post-mortem due to highly organic, and therefore acidic conditions (e.g., Kemp et al., 2009;
Hawkes et al., 2010, 2011; Milker et al., 2015a, b). Post-mortem dissolution of calcareous tests is obviously not an issue in the tidal-creek salt marsh of Sønderho. Dissolution may not explain the absence of calcareous taxa in the low marsh of Rantum, where pH is around 6 to 8. In accordance with other studies (Gehrels and Newman, 2004; Horton and Edwards, 2006) calcareous species are obviously not indicative for tidal flat and low marsh environments of Rantum. In contrast, calcareous taxa characterize the tidal flat and low marsh in the Bay of Tümlau (Eiderstedt peninsula, located south of Sylt), where they show an increase in abundance with reducing distance to the coast line, as well as high abundances in salt-marsh ponds and channels (Müller-Navarra et al., 2016) (Chapter 2).

3.4.2 The usefulness of extracting local tidal information from salt-marsh regions for transfer-function development

The prerequisite for accurate relative sea-level reconstructions and prediction of vertical positions relative to a local datum is a thorough understanding of the relationships between the environmental parameters (in this case the tidal regime) and the foraminiferal distribution. Most reconstructions of past relative sea-level changes refer to tidal datums of permanently installed tide gauges that have records over a sufficient time period (i.e., a minimum of 18.6-year period is assumed according to Pugh, 2014) to calculate SWLI. This procedure allows for addressing the individual tidal regime in each salt marsh and to combine foraminiferal data from different sites to a regional data set under the assumption that these tidal datums are valid for the individual salt marshes (Horton and Edwards, 2005). However, tide gauges, which fulfill these requirements are rarely found in the direct vicinity of salt marshes used for relative sea-level studies, as they are mostly run for coastal protection purposes and ship traffic at places where they should experience the full tidal range. Furthermore, tidal datums are local datums because tides may be distorted by local bathymetry and weather conditions (van der Molen, 1997; Scherer et al., 2000; Hobbs, 2012) when the water column decreases. Hence, the approach using tidal datums from permanently installed tide gauges does not incorporate local tidal conditions that may differ from that of the reference tide gauge.

Our study shows that own tidal observations are necessary to select the most suitable permanent tide gauge for the assessment of the relation between the local tidal regime and the distribution of salt-marsh foraminifera. We observed differences in high water heights of 3 cm ± 1.8 cm between the permanently installed Esbjerg tide gauge and high water height measurements in Sønderho, which is around 10 % of the precision for the SWLI and MST approaches. Further, tidal curves for intertidal areas are far from being perfectly
sinusoidal-shaped. In both studied salt marshes, MTL slightly differs from the 50-%-duration of submergence by around 2%, which results in a difference between the locally observed and calculated MTL level by 6 and 12 cm in Sønderho and Rantum, respectively. This value is significant when paleo-marsh elevation relative to mean tide level is reconstructed with a vertical error less than 10 cm as it was shown by, e.g., Kemp et al. (2011). There are only a few other studies that used local tidal data in order to address local conditions in a salt marsh. For example, Gehrels et al. (2000) used a correction factor to address the difference in tidal heights between local tidal heights and tidal heights measured by a permanent tide gauge stations. Also Edwards et al. (2004) installed tide gauges on the marshes and linked them to permanent tide stations. Hawkes et al. (2010) used a tidal numerical model, based on official tide gauges and showed that there is a difference between the modeled and real tidal nodes, but these differences were not tested by field measurements. These and our findings imply that, whenever possible, on-site tidal measurements should be made to calibrate tidal datums from permanently installed tide gauge stations so that they match the local conditions in salt marshes under consideration such as Kemp et al. (2017c) did for a salt marsh on the North Atlantic coast of the US. Although direct field measurements are time-consuming, they can be realized by using electronic tide gauges (van der Molen, 1997; Anisfeld et al., 2016; Kemp et al., 2017c) or simply by using leveled flagstones at the sea bed and a ruler, as we did in Sønderho. When the high water data of the nearest permanent tide gauge is comparable to that in the investigated salt marsh, a short measurement period of around 14 days over a neap and spring modulation of the tidal amplitude (which lasts 14.77 days; Pugh, 2014) appears sufficient. The advantage of measuring local tidal parameters is, that permanent tide gauges can then be adjusted for the marsh site of interest, and local flooding parameters for individual salt marshes can be calculated. Finally, each salt-marsh region can be individually assessed in terms of tidal influences.

3.4.3 Advantages and disadvantages of the transfer-function approaches using SWLI and flooding parameters

It is widely accepted, that the tidal influence determines the foraminiferal distribution in salt marshes (e.g., Horton and Edwards, 2005; Kemp and Telford, 2015; Strachan et al., 2016). Commonly, salt-marsh foraminifera are assumed to be vertically distributed relative to the tidal frame and elevation is a linear approximation of tidal influence (Wright et al., 2011). Accordingly, the distribution of foraminifera in intertidal environments is a direct function of altitude with the flooding parameters as the most important factors (Horton et al., 1999b).
Consequently, most studies used elevation, converted into SWLI (a linear approximation of tidal influence) as established by Horton (1997), for the development and application of a regional transfer function (e.g., Horton and Edwards, 2006; Wright et al., 2011; Kemp et al., 2017c; Kemp et al., 2017a), and showed that intertidal foraminiferal assemblages can be used as precise relative sea-level indicators.

Different studies used different upper tidal datums such as HAT or MHHW to convert elevation into SWLI units. Using upper tidal limits constrained by tidal datums do not necessarily capture the complete species response curve in a study area and neglect local meteorological effects on water level, and, hence, on the foraminiferal distribution. Therefore Wright et al. (2011) used the highest occurrence of foraminifera (HoF), reflecting the upper limit of marine influence to reduce extrapolation, to capture the complete species response curve, and to align the uppermost samples, which increased the precision of their transfer function. At Sønderho, HoF coincides with the upper marine limit (upper marine limit is at around 2.00 m NHN). Above this limit, flooding parameters are zero in value (compare Suppl. S2.2). At Rantum (SyRa I), the highest occurrence of foraminifera is around 60 cm below the recorded upper marine limit calculated by the flooding parameters, and hence HoF not necessarily reflects the upper marine limit. Such barren zones free of foraminifera were also described by others (e.g., Haslett et al., 2001) in areas with macro-tidal ranges. To summarize, assessment of the upper tidal datum level of a salt marsh should ideally be calculated based on local flooding parameters. The calculation of local flooding parameters for each sampling point provides an alternative approach to that of using SWLI when more than one site is incorporated into a modern data set used for sea-level reconstructions, especially in salt marshes where meteorological effects determine the water level.

In our study, we used the SWLI approach and alternative approaches, based on flooding parameters, to compare their elevation-prediction precision for the southern North Sea coastal region. We found a good and comparable precision for all approaches between MTL and MHW (Fig. 3.9). When assuming a linear correlation between MST and elevation which is fundamental for the SWLI approach (Horton, 1997), precision is comparable to that of the SWLI approach (Fig. 3.9). The MST approach may be more reliable in the study areas because local water levels are highly determined by storm tides. On the other hand, due to the non-linearity in the upper tidal regime between DoS, MST and FF and elevation, precision decreases to around ±1.0 m, while the SWLI approach shows constant precisions at this vertical position.
Canonical Correspondence Analysis reveals that MST is less important for the foraminiferal distribution than the other flooding parameters and SWLI. But this is not in coincidence with the one-way NPMANOVA results, which reveal that MST has a slight higher influence on the foraminiferal assemblage than the other parameters. MST shows the mean duration of time a elevational level is flooded after the water level has reached this point, while DoS and FF are percentages of the observation period (here: 19 years) and are running along the same environmental gradient as SWLI. Storm tides may not impact environmental changes calculated with FF, DoS, and SWLI, but storm tides have influences on the mean submergence time (by increasing the submergence time), which might increase salinity, especially in temperate climate regimes were precipitation, and to a lesser extent evaporation controls salinity in the sediment. To our knowledge, these observations were not made in other salt-marsh areas because of the lack of compiled flooding parameters. Likewise, de Rijk (1995) observed a strong correlation between salinity and foraminiferal distribution but did not consider flooding parameters.

The non-linearity between flooding parameters and elevation is, because the geometry of the tidal curve is severely influenced by the weather conditions, as also Allen (1990) described for the elevation above extreme tides. The flooding approaches can be generally used to reconstruct relative tide-level changes in the southern North Sea region with changing values along the salt-marsh gradient (Fig. 3.9). The SWLI-approach allows for the establishment of a regional transfer function by making several sites with varying tidal regimes comparable (e.g., Horton et al., 1999a, b). This method uses station elevation data measured in the field (Kemp et al., 2017a), and tide gauge data taken from a nearby permanent tide gauge or derived from tide-level models (Hawkes et al., 2010; Wright et al., 2011; Barlow et al., 2013). However, there are some
restrictions when using this approach for relative sea-level estimates. For example, different studies used different tidal datums (such as MLLW, MTL, MHW, and MHHW or MHWS) to convert elevation into SWLI (e.g., Horton and Edwards, 2006; Kemp and Telford, 2015) but incorporating tidal datums such as MLLW and MLW into the SWLI equation is sometimes impossible when low waters are not represented at the studied site, as it was found at our studied sites. But using upper tidal datums such as MHW and MHWS (as we did) needs extrapolation between samples that were taken below and above these datums, which reduces precision.

Another restriction is the changing precision (RMSEP) when using different tidal datums in the SWLI equation as also reported by Woodroffe and Long (2010). This should be considered when assessing the reconstruction potential and error estimation of transfer functions, especially when the reconstruction precision is high (i.e., below 10 cm) (Barlow et al., 2013). The main problem in using MTL (or MLLW and MLW) is that these tidal datums are without fundamental connection to the salt-marsh development at our studied sites, and hence do not directly influence the distribution of foraminifera in the marshes. Low waters are not adequately represented in the studied coastal and tidal-creek salt marshes, because the lower salt-marsh surface lies above this level (up to 1.3 m at Sønderho and up to 0.6 m at Rantum) and only some higher low waters were recorded at the Rantum tide gauge. Based on this under-recorded local low water data of Rantum, MLW cannot adequately be calculated. Calculation of an artificial MLW for Rantum can be done by extrapolating tide levels from other nearby tide gauges (Reichs-Marine-Amt, 1917) and for Sønderho by using the tide gauge data of Esbjerg with the established correction-factor of around 3 cm, but these estimates are only approximate values. Water level measured by tide gauges are sensitive to wind conditions, for example, the MHW position within the tidal frame has a standard deviation of 0.41 m for observational data (Müller-Navarra, 2013).

Similarly, also the HAT vertical position can be easily surpassed by storm tides. In the flooding parameters, storm-tide water levels are included, that is why the floodings are not restricted to the HAT level, and instead it surpassed this level by around 80 cm (high marsh at Sønderho) and by around 0.66 m at Rantum. To circumvent potential biases of the SWLI-approach due to required extrapolations or by using approximate tidal datums, the flooding approaches may be applied as an addition to the SWLI approach. The flooding approaches also enable comparison of more than one site when different tidal conditions are present, as the SWLI approach does. Although there is consensus that the vertical foraminiferal distribution in salt marshes can be related to flooding parameters (see above),
their direct influence has only rarely been studied. One exception is the study of Gehrels et al. (2001), who reported a moderate relation between duration of tidal flooding and the foraminiferal distribution. Specifically, they described a non-linear relationship (comparable to our DoS approach) between flooding duration and elevation relative to the tidal frame, especially in the high marsh. The authors used the piece-wise sinusoidal tidal curve for their calculations of the tidal flooding, which may partly explain the weak relation. Although the use of a sinusoidal tidal curve has been considered to be a valid approach (Wright et al., 2011; Balke et al., 2016), it does not describe the flooding parameters adequately in our study area, because the local salt-marsh morphology and wind regime significantly alters the tidal curve and local tidal datums.

An advantage of a detailed knowledge of the local tidal regime is that flooding parameters, when plotted relative to elevation, make any estimates of HoF redundant. The flooding parameter shows the highest elevation of tidal influence and therefore vertical sampling resolution could be adjusted in the field. Sampling strategies concerning the detection of HoF by searching for foraminifera under a microscope is time consuming and sometimes it is impossible to capture HoF due to sampling concerns, while the flooding parameters are easily calculated. One restriction of the application of the DoS, MST and FF approach is that they badly perform for elevations at the upper tidal limit where the relationships between DoS, FF, and MST, and elevation become non-linear. The flooding approaches are useful to investigate the suitability of a particular salt marsh for past tide-level reconstructions by increasing the knowledge on local water level and the related foraminiferal distribution. In each salt-marsh region, the detection of the upper limit of tidal influence is possible by calculating the flooding parameters and, foraminiferal distribution above a certain tide level is determined by storm tides.
4 NATURAL AND ANTHROPOGENIC IMPACTS OF SALT-MARSH EVOLUTION IN THE SOUTHEASTERN NORTH SEA DURING THE PAST CENTURY

This chapter is mainly based on Müller-Navarra et al., submitted*

4.1 Introduction

The southeastern North Sea is frequently impacted by storms and it experienced the most and highest storm tides of the entire North Sea coast during the past centuries (Tomczak, 1952). Hence, storm-tide protection management is crucial for densely populated regions such as the German North Sea coast, especially since regional sea-level rise at a present rate of around 2 mm yr⁻¹, as recorded by the Cuxhaven tide gauge (Dangendorf et al., 2014). In this context, it is essential to understand the function of salt marshes in attenuating storm-tide energy and their long-term resilience to storm tides with respect to lateral and surface erosion and sediment deposition (e.g., Karimpour et al., 2017). In the light of rising sea level, the superimposed impacts of tides, storm tides and waves on North Sea coasts are still not well understood (Arns et al., 2017), although this issue and its importance for coastal defense strategies are discussed since a long time (Grossmann, 1916; Schelling, 1952).

Storm tides occur during nearly every winter season at the North Sea coast (Gerber et al., 2016). Severe storm tides repeatedly impacted the coastal region in the past and led to dike failures, losses of marsh areas and numerous casualties. Examples include the so-called ‘Grote Mandränke’ in 1362 CE (Lamb, 1991; Meier, 2004) but also more recent storm floods in 1962 CE and 1976 CE (Zitscher et al., 1979; Gerber et al., 2016). On the other hand, storm tides deliver large amounts of suspended sediment to the salt marsh where it is trapped by the vegetation cover (Turner et al., 2006; Schürch et al., 2014; Fagherazzi, 2014; Leonardi et al., 2018). This frequent sediment input allows vertical growth of the marsh to supra-tidal conditions, while tidal flooding during regular high waters and local plant growth and decay alone cannot supply the amount of material needed to outpace sea-level rise (Stumpf, 1983). Results from southern North Sea marshes elsewhere revealed that the accretion rate of the low salt marsh was proportional to mean storm strength, while in the high salt marsh it was mainly controlled by storm frequency (Schürch et al., 2012).

Tidal flats and salt marshes are densely populated by foraminifera, which exhibit a distinct vertical zonation relative to the tidal frame because they respond to gradients in pH, salinity, substrate and submergence time (e.g., Scott and Medioli, 1978; Horton et al., 1999; Müller-Navarra et al., 2016, 2017) (Chapter 2, 3). Accordingly, salt marshes provide an important tool for the reconstruction of past sea-level changes and the detection of paleo-storm tides in salt-marsh deposits (e.g., Kortekaas and Dawson, 2007; Scott et al., 2003). Storm layers contain re-deposited calcareous foraminifera from tidal flats that can be used as a proxy for storm-tide events in non-acidic marsh deposits.

This study analyses the evolution of a salt marsh from the southeastern North Sea during the last approximately 170 years, with particular focus on the response to storm tides and major anthropogenic influences, including dike construction and ditching. Our study is based on micropaleontological, granulometric and geochemical investigations of a well-dated sediment succession, in comparison with historical information and tide-gauge data.

4.2 Material and methods

4.2.1 Marsh sampling

The elevation of the cliff surface at site TB13-1 (UTM32 WGS84 478981E 6022981N) was leveled to a trigonometric point (triangulation station 161803110, Fig. 1.4) by a roving receiver using real time kinematic with global positioning system (GPS) and global navigation satellite system (GLONASS). Post-processing of raw data was done using the software Geo Office 8.3 (Leica). Sediment sampling was conducted on August 14, 2013 by using a total of 15 U-channels (each 108 cm long, 1.6 cm wide and 1.6 cm deep). The U-Channels were pushed into the cleaned erosional face of the salt-marsh cliff enabling the coverage of undisturbed, vertical successions. In the laboratory, the sediment successions were described, photographed and three sediment sections were sliced into 1 cm aliquots, each with a volume of around 2.56 cm³, for the analyses of grain size, foraminifera, and age dating.

4.2.2 Age dating

A total of 38 samples were taken to establish an age model. The sediment samples were gamma-counted for $^{210}\text{Pb}$, $^{226}\text{Ra}$, $^{214}\text{Pb}$, $^{241}\text{Am}$ and $^{137}\text{Cs}$ on a planar broad energy GE detector (CANBERRA), and $^{210}\text{Pb}_{\text{supported}}$ ($^{226}\text{Ra}$), and $^{210}\text{Pb}_{\text{unsupported}}$, were calculated accordingly. The CRS model (constant rate of supply model) by Appleby and Oldfield (1978) was applied to develop the sediment chronology and to calculate mass accumulation rates (MAR). The CRS model assumes the rate of supply of $^{210}\text{Pb}_{\text{unsupported}}$ from the atmosphere.
remains constant over the entire period of time. In consequence, the $^{210}$Pb$_{\text{supported}}$ activity of the sediment varies directly proportional to the sedimentation rate, i.e., high sediment accumulation means lower activity in the sediment due to dilution and vice versa. The sediment further contains $^{210}$Pb$_{\text{supported}}$, which is constantly produced by decay of its radioactive precursors in the lithogenic components. In order to confirm the $^{210}$Pb-based age model, Cesium ($^{137}$Cs) and Americium ($^{241}$Am) were measured and used as time markers as well (Pennington et al., 1973; Hardy et al., 1973). $^{137}$Cs has strongest peaks in 1963 CE (fallout of nuclear test debris), which marks the end of the atmospheric bomb tests, and in 1986 CE due to the Chernobyl accident. The $^{241}$Am independent time marker forms by decay of $^{239}$Pu, originating from fallout of atmospheric nuclear-weapons tests debris and marks the period of nuclear tests from 1952-1963 CE, with the strongest signal in 1963 CE. $^{241}$Am is immobile in the sediment and therefore a more reliable than the more mobile time marker $^{137}$Cs (Ehlers et al., 1993). Errors in the sediment age estimates are represented by the 1-sigma counting error for the activities. Errors for MAR and sediment age are calculated with error propagation. The estimated errors are ±10 years and >±50 years in the upper and lower parts of the section, respectively (compare Fig. 4.2).

4.2.3 Estimation of water-level differences

To account for the storm-tide history in the Bay of Tümlau, we calculated the water-level difference between the tide gauges Tümlauer Hafen and Cuxhaven. The water-level difference is determined by the wind-induced surge differences (Fig. 4.1) using the comparative method of Tomczak (1952). This method considered wind strength and direction as being the second most important drivers of water level after tides. Hourly geostrophic winds of the triangle List-Emden-Hamburg (DWD, pers. comm. B. Tinz) were used to calculate wind strength (10-m-wind) during high waters (Luthardt and Hasse, 1983); wind data are given for 48,373 number of cases, recorded between September 25, 2001 and December 31, 2016. Based on these data a table of mean water-level differences between Cuxhaven and Tümlauer Hafen for different wind strengths and directions can
be estimated. These data allow for the extrapolation of storm-tide heights at the Bay of Tümlau beyond the available local record. Wind data beyond the digital measuring period have been consulted using hand-written local wind protocols of signal-station books (Wagner et al. 2016); here, e.g. for the estimation of storm-tide water level at Bay of Tümlau in the year 1941 CE.

4.2.4 X-Ray-core scanning
Scanning X-Ray Fluorescence (XRF) spectroscopy was performed at an ITRAX Core Scanner with a chromium tube applying a generator setting of 30 kV (30 mA), a step size of 260 µm, and a measuring time of 15 seconds per step size. The ln(Zr/Rb) ratio was used as proxy for particle-size variation following Dypvik and Harris (2001). Spectral analyses were carried out on the ln(Zr/Rb) record with AnalySeries, version 2.0 (Paillard et al., 1996). The ln(Zr/Rb) records for the two defined time intervals 1935–1985 and 1986–2013 were rescaled with \[ \Delta t = 0.02 \text{ yrs} \] (Suppl. S3.5).

4.2.5 Grain-size analyses
Prior to grain-size measurement, all samples for grain-size analysis were treated with H₂O₂ to oxidize the organic matter and subsequently sieved using a 2000 µm sieve. Samples were then suspended in water with addition of a 0.05-%-solution of Na₄P₂O₇·10H₂O as a dispersant agent. The particle-size distributions of the samples were determined by means of a Sympatec Helos/KF Magic laser diffraction particle sizer (measuring range 0.5-3500 µm). Grain-size statistics was calculated using GRADISTAT (Blott and Pye, 2001) and are based on the graphical measures (Folk and Ward, 1957).

4.2.6 Foraminiferal analyses and application of transfer functions
For foraminiferal analyses, 106 samples were wet sieved over 63 µm and 500 µm sieves. The fraction 63-500 µm was divided into equal aliquots by using a wet-splitter after Scott and Hermelin (1993) and by using the procedure described in Horton and Edwards (2006). Around 200 specimens per sample were counted under a stereomicroscope. The identification of foraminiferal taxa was based on Gehrels and Newman (2004), Horton and Edwards (2006), and Milker et al. (2015).

Regional transfer functions based on standardized water level index (SWLI) and on mean submergence time (MST) as published in Müller-Navarra et al. (2017) (Chapter 3) were applied using the R software (version 3.4.1.; R-Development-Core-Team, 2017), and the R-package “rioja” (version 0.9-5; Juggins, 2017). SWLI for the training set was calculated by standardizing each elevation to MHW and MHWS. MST for the training set was calculated...
as the mean time over which the marshes were flooded based on 10-minute tidal observation using the web application “Salt-marsh submergence”. To account for the storm-tide history in the Bay of Tümlau, we calculated the water-level difference between the tide gauges “Tümlauer Hafen” and Cuxhaven which is determined by the wind-induced surge differences (for further details on the MST approach see Chapter 3).

4.2.7 Significance tests of transfer-function results

In order to test whether or not the fossil assemblages have modern analogues, we used the modern analogue technique (MAT; Hutson, 1980). We have chosen the five closest modern analogues (Kemp and Telford, 2015) in the modern data set and the squared chord distance (Overpeck et al., 1985) as the distance metric. Calculations were done using the R-package “analogue” (version 0.17-0; Simpson, 2007; Simpson and Oksanen, 2017). Dissimilarity calculation between modern surface samples and fossil samples showed that 15 samples out of 106 samples (9.4 %) lacked a modern analogue and were excluded from analysis.

We tested the significance of our SWLI and MST reconstructions by applying the random transfer-function test (Telford and Birks, 2011). The random transfer-function test calculates the explanatory significance of a transfer function by comparing its proportion of explained variance with that of alternative models (n=999) trained on random environmental data by using redundancy analysis (van den Wollenburg, 1977). We used redundancy analysis due to gradient length of 2.81 standard deviations (calculated by Detrended Correspondence Analysis) of the fossil data along the first axis (Hill and Gauch, 1980). Reconstructions, whose explained variance in the fossil data exceeds 95 % of that of the random models are considered to have a significant explanatory value. For calculations, we used the R packages “palaeoSig” (version 1.1-3; Kemp and Telford, 2015), “rioja”, and “vegan” (version 2.4-3; Oksanen et al., 2017).

4.3 Results

4.3.1 Age model

The \(^{210}\text{Pb}_{\text{unsupported}}\) declines quasi exponentially down to zero with depth (Fig. 4.2, Suppl. S3.3). According to its half-life of 22.6 years this indicates a sediment age of ca. 120 years at 100 cm depth. The surface sample contains very little \(^{210}\text{Pb}_{\text{unsupported}}\) because of the dominance of macro-plant remains. In the upper 15 cm of the section \(^{210}\text{Pb}_{\text{unsupported}}\) varies strongly between 18 and 5 suggesting strong variability in the mass accumulation rates (Fig. 4.2). The \(^{210}\text{Pb}_{\text{supported}}\) activity, which represents the \(^{210}\text{Pb}\) of lithogenic origin, varies between 39.5 Bq·kg\(^{-1}\) and 16.5 Bq·kg\(^{-1}\) throughout the succession. It represents the
sedimentary background value, which is constantly produced by decay of its radioactive precursors in the lithogenic components of the sediment, and therefore remains largely constant in steady, undisturbed environments. The variability of $^{210}$Pb$_{\text{supported}}$ at site TB13-1 therefore indicates changing sources of sediment, e.g., due to storm tides. The distinctive $^{241}$Am peak around 62 cm depths can be associated with the year 1963 CE and implies the absence of substantial bioturbation. $^{137}$Cs shows two peaks, one of which is located at 62 cm depth confirming the time of highest fallout of $^{137}$Cs and $^{241}$Am in 1963 CE. The upper $^{137}$Cs peak at 33 cm depth most likely originates from the Chernobyl reactor accident in 1986 CE. The age model based on $^{210}$Pb$_{\text{unsupported}}$ deviates by five to seven years from the age indicated by the $^{137}$Cs and $^{241}$Am markers (Fig. 4.2). The average atmospheric deposition of $^{210}$Pb in the North Sea is 42 Bq·m$^{-2}$·y$^{-1}$, with a total flux into the sediment of 150 Bq·m$^{-2}$·y$^{-1}$ (Beks, 1997). Our measured annual average lead flux in the core is 141.1 Bq·m$^{-2}$·y$^{-1}$, which is in perfect agreement with literature value. The calculated mass accumulation rates (MAR) are an estimate of sedimentation rates. All MAR values in the sediment deposited prior to approximately 1950 are affected by high uncertainties. The MAR shows two major peaks at 15 cm and 49 cm depths with 13.5 and 8.3 g cm$^{-2}$ year$^{-1}$, respectively, where the $^{210}$Pb$_{\text{unsupported}}$ activities are very low (Fig. 4.2). By the CRS model high MAR is calculated when, $^{210}$Pb$_{\text{unsupported}}$ activities in core sections are comparably low. This consequently indicates dilution of the atmospheric $^{210}$Pb signal by large amounts of deposited material. An alternative interpretation is the re-

Fig. 4.2 Age-dating of the sediment succession based on excess of $^{137}$Cs, $^{241}$Am, and excess $^{210}$Pb, and derived mass accumulation rates (MAR) and CRS (constant rate of $^{210}$Pb$_{\text{unsupported}}$ supply) age model. Error bars represent the 1-sigma counting error for $^{137}$Cs and $^{210}$Pb activities and CRS years are calculated with error propagation.
deposition of old material (>120 years) that contains no $^{210}$Pb$_{\text{unsupported}}$ delivered during storm tides. Similar $^{210}$Pb$_{\text{unsupported}}$ anomalies were observed in a Danish salt marsh and assigned to storm tides (Andersen et al., 2011).

### 4.3.2 Estimated heights of storm tides in the Bay of Tümlau

The storm-tide heights exhibit significant differences between tide gauges “Tümlauer Hafen” and Cuxhaven since 2001 CE suggesting comparable deviations for the time interval beyond the measurement period. During westerly and southwesterly winds, water levels are higher in the Bay of Tümlau relative to Cuxhaven. Highest positive water-level differences occur under southwesterly winds with $\geq 10$ Bft (0.61 m ± 0.03 m difference) and highest negative water-level differences under northwesterly winds with $\geq 8$ Bft (-0.22 m ± 0.28 m difference) (Suppl. S3.4). For example, the storm tide of 2002 CE (during southwesterly winds) was around 0.30 m higher in the Bay of Tümlau, while the storm tide of 2007 (during northwesterly winds) was around 0.30 m lower (compare Fig. 1.6).

### 4.3.3 Distribution of foraminifera

A total of 24 foraminiferal taxa were identified. The most common species comprise *Entzia macrescens*, *Haynesina germanica*, *Ammonia batava*, *Elphidium excavatum*, *Balticammina pseudomacrescens*, *Trochammina inflata*, and *Elphidium williamsoni* (Fig. 4.3, Suppl. S3.1). Total foraminiferal numbers range between 634 (at 90 cm depth) and 29 individuals per 1 cm$^3$ sediment (at 3 cm depth) with lowest numbers in the surface interval (0–7 cm). The lowermost part of the section, deposited around 1840 CE, is dominated by *E. macrescens* (37 %) and *E. excavatum* (37 %). The lower and middle parts of the section, between 1840 and 1932 CE, are dominated by calcareous taxa, mainly comprising *E. excavatum* (up to 80 %), *H. germanica* (up to 50 %), and *A. batava* (up to 20 %). Between approximately 1935 CE (dike completion) and 2002 CE, the fauna is alternately dominated by agglutinated (mainly *E. macrescens*) and calcareous taxa, respectively. Intervals with almost 100 % *E. macrescens* are centered on around 1940, 1970, and 1980 CE, and alternate with intervals dominated by *E. excavatum*, *H. germanica* and *A. batava* (the calcareous tidal-flat fauna). Since 2002 CE until recent times, the most abundant species are *B. pseudomacrescens* (with up to 70 %) and *E. macrescens* (with up to 50 %) together with *T. inflata* (with up to 10 %), (the agglutinated salt-marsh fauna) (Fig. 4.3). Furthermore, two species groups were distinguished, the allochthonous storm-tide foraminifera (i.e., calcareous tidal-flat taxa), and the autochthonous salt-marsh foraminifera (i.e., agglutinated taxa).
Fig. 4.3 Distribution of foraminiferal taxa, grain size, and XRF data in sediment succession TB13-1 plotted versus CRS years. Displayed are relative abundances of agglutinated and calcareous tests and of the most abundant foraminiferal species. Stippled horizontal lines mark completion of dike in 1935 and foundation of the Wadden Sea National Park in 1985 CE.
4.3.4 Grain-size distribution and trace elements

The mean grain size ranges between 15 and 95 µm and the coarse tail of the grain-size spectrum (90\textsuperscript{th} percentile) between 80 and 200 µm. Both parameters are highly variable in sediments deposited between 1840 and 1965 CE (particularly from 1935–1970 CE) and subsequently show a gradual coarsening towards recent years (Fig. 4.3). The grain-size spectrum is symmetrical to fine skewed with values between $-0.5$ to $0$ phi, displaying pronounced and partly abrupt fluctuations across the whole section (Fig. 4.3, Suppl. 3.2).

The $\ln(Zr/Rb)$ record ranges between approximately 0 and 3 and reveals a strong variability on yearly to multi-decadal time scales with pronounced maxima (Fig. 4.3). After dike completion in the 1935 CE, the $\ln(Zr/Rb)$ ratio exhibits a gradual increase coinciding with the observed coarsening upward of the section. Since around the early 1980s CE, the $\ln(Zr/Rb)$ ratio is characterized by high-frequency fluctuations, centered at periods of 1.6, 2.4, and 4.8 years. This is contrasted with the time interval 1935 CE to 1985 CE, where the $\ln(Zr/Rb)$ ratio exhibits significant power centered at periods of 2.7 and 16.7 years (Fig. 4.4).

4.3.5 Results of the transfer-function application

The application of the transfer functions on the fossil foraminiferal record reflects changes in paleo-marsh elevation of ~0.5 to 1.3 m MHW, using non-stationary MHW for each year (mean uncertainty of ± 0.44 m), and changes in mean submergence time (MST) of ~139 to 250 min (mean uncertainty of ± 40 min) (Fig. 4.5). Prior to the dike completion in 1935 CE, estimated salt-marsh elevation was ~0.8 m MHW and MST ~244 min, lacking any significant fluctuations. Elevation was around 0.7 m MHW between 1960 CE and 1986 CE and increased to ~1.3 m MHW in recent years, (present-day elevation of the marsh surface of around 0.70 m MHW) (Fig. 4.5). For stationary MHW, the reconstruction changed slightly (Fig. 4.6).
A first temporary MST increase occurred from 1935–1942 CE, and since 1960 CE, MST fluctuated strongly between 137 and 252 min with constantly low values since around 2002 CE.
Reconstructions based on the SWLI approach are not significant while the reconstructions based on the MST are significant at the 95% level (Fig. 4.7). Although the reconstructed paleo-marsh elevations are plausible, changes in elevation of more than 0.3 m between two successive years are questionable. These values are related to the high percentages of *B. pseudomacrescens* in the uppermost part of the succession and refer to the interval where elevation and MST become non-linearly related to submergence, above the MHW height (Fig. 4.8).

4.4 Discussion

4.4.1 Salt-marsh submergence and elevation changes

The evolution of salt-marsh elevation and submergence during the past ~170 years allows for distinguishing three main periods, which are tightly connected to human interferences. In the first period, prior to dike completion in 1935 CE, a tidal-flat system was established at site TB13-1, with a vertical position of the surface of around 0.70 m above MHW and MST of around 250 min per tidal cycle (Fig. 4.5). This interpretation of a tidal-flat system is underlined by the dominance of the calcareous taxa *A. batava*, *E. excavatum* and *H. germanica*, which are characteristic for modern tidal flat and subtidal environments with variable salinity and substrate (e.g., Müller-Navarra et al., 2016; Francescangeli et al., 2017) (Chapter 2). This fauna does not record information on the influence of storm tides although the skewness of the grain-size distribution reveal variable depositional energy during this period (Fig. 4.3). During the second period, between dike completion in 1935 CE and establishment of the Wadden Sea National Park in 1985 CE, a ditched and grazed salt marsh is established, as indicated by the intermittent dominance of *E. macrescens*, which is
typical for the middle to high marsh (Horton et al., 1999; Müller-Navarra et al., 2016) (Chapter 2). MST decreased to ~150 min within two years after dike construction. But the pausing of ditching during the Second World War and early post-war years (between 1939 and 1952 CE; Wohlenberg, 1954) was accompanied by marsh degradation and a return to tidal flat environments as reflected by the transient predominance of calcareous taxa (Fig. 4.3).

In the following time, the alternation between agglutinating and calcareous taxa represents a ditched salt marsh, which was regularly submerged during high tide and storm tides and susceptible to the re-deposition of tidal flat foraminifera during phases of enhanced storm-tide activity. While reconstructed elevation only slightly increased to ~0.7 m MHW, MST fluctuates between 140 and 250 min (Fig. 4.5). Ditching and grazing led to a distortion of the salt-marsh morphology and associated flooding dynamics and ecological zonation (Vincent et al., 2013; Müller-Navarra et al., 2016) (Chapter 2). As a consequence, ditched salt marshes are more frequently flooded during high tides and the sedimentary record responds sensitively to phases of storm tides as also reported by Schürch et al. (2012).

The third period, between 1985 and 2013 CE, is characterized by the progressive natural evolution of the salt marsh, where former ditches are filled with sediment and the natural vegetation zonation and drainage system gradually returns. Since 2002 CE, high abundances of *B. pseudomacrescens*, a high-marsh indicator (Gehrels and Newman, 2004; Müller-Navarra et al., 2017) (Chapter 3), imply supra-tidal conditions. Reconstructed elevation is ~1.3 m MHW and MST is remarkably decreased to ~139 min, indicating that marsh became supra-tidal and therefore, sedimentation is driven by storm tides only (Fig. 4.5).
4.4.2 Vertical salt-marsh accretion, lateral erosion, and resilience to sea-level rise

Vertical salt-marsh accretion rates at site TB13-1 are 14.0 mm yr\(^{-1}\) during the phase of ditching and grazing (~1960–2002 CE) and 11.3 mm yr\(^{-1}\) in recent years when the marsh is only submerged during storm tides. These values are similar to those reported from other salt marshes of the German North Sea coast (Schürch et al., 2012; Nolte et al., 2013) and demonstrate the potential of both ditched and natural marshes to outpace the present rate of sea-level rise of ~2mm yr\(^{-1}\) in the southeastern North Sea (Dangendorf et al., 2012), even when considering the effects of sediment autocompaction (Allen, 2000; Bartholdy et al., 2010). Highest accretion rates in the Bay of Tümlau appear between ~1960 and 2002 CE, a period of enhanced tidal submergence and storm-tide induced sedimentation. This is contrasted by reconstructed vertical accretion rates (Fig. 4.8), where highest rates are indicated since 2002 driven by storm-tide sedimentation only. In fact, high accretion rates in a back-barrier salt marsh 57 km north of the site have been shown to coincide with high inundation levels caused by increased storm activity during the 1980s and 1990s CE (Schürch et al., 2012).

However, the increasing elevation gradient between the tidal flat- and the salt-marsh surface may enhance the erosive impact of incoming storm-tide waves (Leonardi et al., 2018). In the Bay of Tümlau, the retreating cliff developed since the 1960s. Aerial photographs of 1969 CE show that the erosional cliff of the ditched marsh was located approximately 300 m further westward than today (LKN.SH, 2016), suggesting a mean local retreat of around 6 m yr\(^{-1}\), which appears to have decelerated during recent years (Stock et al., 2005). The stabilization of salt-marsh retreat is also indicated by the recent development of a pioneer marsh next to the cliff face, indicated by occurrence of Salicornia spp. and patches of Spartina anglica. A similar evolution has been documented for UK salt marshes although the feedbacks between lateral marsh erosion and regeneration are not yet fully understood (Allen and Haslett, 2014). The eastward shift of the cliff face is likely one reason for the observed long-term coarsening upward of the sediment, which reflects the lateral gradient in depositional energy across the salt-marsh platform leading to a proximal-to-distal fining of the sediments (Schürch et al., 2012; Leonardi et al., 2018). In this context, vegetation contributes to wave attenuation and enhances accretion of sediment during storm tides (Cearreta et al., 2013; Möller et al., 2014; Leonardi et al., 2018), where coarse grains are particularly trapped by naturally developed salt-marsh vegetation (García-Artola et al., 2017). Additionally, the advancing depletion of fine-grained sediment in the tidal flats of the Wadden Sea may have also contributed to the observed coarsening at site TB13-1. This
process has been attributed to the interruption of the normal energy gradient by the landward dike, impeding the lateral shift of intertidal facies zones under the influence of sea-level rise (Flemming and Nyandwi, 1994). Our observations support previous findings, that naturally developed salt marshes are quite resilient to sea-level rise and storm impacts (Leonardi et al., 2018). However, on a long run, coastal squeeze (Doody, 2004) due to the fixed position of the dikes may foster lateral erosion of the salt marsh and calls for sustainable coastal protection measures including creation of space for a landward shift of intertidal zones and ecosystems.

4.4.3 Depositional model of a ditched salt marsh and identification of storm-tide layers

The salt-marsh sediments deposited during the time of regular ditching and early years of protection (between ~1960 and 2002 CE) show distinct alternations in the dominant foraminiferal groups and the skewness of the grain-size distribution. This suggests that changes in MST were accompanied by changes in the transport and deposition of allochthonous (calcareous) foraminiferal tests and clastic components. Between ~1960 and 1985 CE, intervals with dominant calcareous tests correspond to an almost symmetrical grain-size distribution, while intervals with dominant autochthonous agglutinated tests correspond to fine skewed grain-size spectra (Fig. 4.9). The dominance of symmetrical to fine skewed grain-size populations and the absence of coarse skewed sediments suggests deposition during suspension settling and absence of fast tidal currents at site TB13-1, as also observed by Rahman and Plater (2014) in UK marshes.

Based on these observations, we propose a depositional model for the ditched marsh in the Bay of Tümlau, which is closely linked to deposition during both regular high tides and storm tides (Fig. 4.9). During phases of prevailing high tides and associated lower MST, sediment suspension is fine skewed and the reworking and displacement of coarser grains from the tidal flat and cliff face is limited as indicated by the dominance of
autochthonous agglutinating salt-marsh taxa and low abundance of reworked calcareous tests. During storm tides, increased shear stress on the tidal flat enhances the mobilization and suspension of coarser grains. The suspension load consists of single clastic particles, sediment aggregates and flocculated material (Christiansen et al., 2000), and is subsequently transported to the salt marsh where it is trapped by the vegetation (Fagherazzi et al., 2013; Brandon et al., 2014; Rahman and Plater, 2014; Chaumillon et al., 2017).

Various studies also reported the mobilization of fine-grained material during storm tides, and subsequent mud enrichment in storm-tide deposits of salt marshes (Reineck and Singh, 1975; Bartholdy, 2012). Goodbred and Hine (1995) observed re-suspended near-shore sediments with variable grain-size distribution, showing a mineralogical similarity between storm-tide deposits and underlying marsh sediments. These observations suggest that the grain-size characteristics and composition of a storm-tide layer is controlled by the regional effects of sediment sources (erosion of tidal-flat and former salt-marsh deposits), MST, and vegetation cover. In the Bay of Tümlau, re-deposition of coarser particles was increased during storm tides as reflected by the shift from a fine-skewed to a symmetrical grain-size distribution (Fig. 4.3). The associated accumulation of tidal-flat foraminifera at site TB13-1 may get further enhanced by selective winnowing of calcareous tests on the tidal flats (Horton et al., 2005). Allochthonous calcareous foraminifera have been previously used

**Fig. 4.9** Depositional models for salt marshes under storm-tide and regular high-tide conditions, respectively. Symmetrical and fine skewed grain-size distribution is displayed for both conditions. Calcareous taxa are the tidal flat indicative taxa, agglutinated taxa are the salt marsh indicative taxa. Plus: increasing, minus: decreasing ratio.
as indicator for storm layers in US Atlantic salt marshes (Scott et al., 2003; Hippensteel et al., 2013). However, this storm-tide proxy is restricted to salt marshes, which are not influenced by early diagenetic dissolution of calcareous tests (e.g., Jonasson and Patterson, 1992). In the Bay of Tümlau, fossil calcareous foraminifera exhibit pristine tests and lack signs of dissolution confirming their general applicability as storm-tide indicator.

The presence of coarse siliciclastics in the salt-marsh deposits, indicative for storm-tide layers, is also reflected by the \( \ln(\text{Zr/Rb}) \) ratio, because zirconium is enriched in the coarse-grained sediment fraction in form of zircon, while rubidium is mainly concentrated in clay minerals (e.g., Dypvik and Harris, 2001; Croudace and Rothwell, 2015). Spectral analyses of the high-resolution \( \ln(\text{Zr/Rb}) \) time series of sediment succession TB13-1 revealed decadal changes (centered at a period of 16.7 years, Fig. 4.4) for the time interval between 1935 and 1985 CE. These changes are particularly expressed in the 1970s to 1990s and are also illustrated by repeated alternations between calcareous and agglutinated test dominance (Fig. 4.3). Storm-tide reconstructions for the North Sea based on water-level observations display substantial inter-annual to decadal variability and display increased storminess for the time between ~1970 and 1995 CE (Dangendorf et al., 2014). This period can be linked to phases of predominant positive NAO index (Hurrell et al., 2003; Dangendorf et al., 2012, 2014). Similarly, in the Bay of Tümlau, the estimated phases of increased MST (up to ~240 min) during this period can be generally associated with local storm tides above 2.90 meter MHW, including severe storm tides in 1962, 1976, 1981, 1990, and 1995 CE. However, an exact (by the year) assignment of the sediment and tide gauge data is inhibited by the dating errors of the sediment succession (Fig. 4.5).

Although the recorded changes at site TB13-1 likely reflect the variability of storminess and associate changes in MST and sedimentation dynamics, disturbance of the natural sedimentation by ditching cannot be excluded. Unfortunately, no records of past ditching schemes of the salt marsh in the Bay of Tümlau exist, but ditching in more recent times was conducted every three to seven years (personal communication LKN.SH, 2016). Consequently, displacement of sediment from the ditches onto the top of the salt marsh may account for some of the observed multi-annual variability in calcareous test abundance and grain size characteristics before ditching was terminated in 1985 CE.

The time interval between 1985 and 2013 CE, i.e., after foundation of the National Park and protection of the salt marsh, lacks a systematic correlation between the proportion of allochthonous foraminiferal tests and sediment skewness, hinting to a gradual change in the depositional regime. The \( \ln(\text{Zr/Rb}) \) record exhibits annual to multi-annual variability
(centered at periods of 1.6, 2.4, and 4.8 years) suggesting that the salt marsh has been flooded only during storm-tide events. This conclusion is corroborated by the dominant appearance of *B. pseudomacrescens*, which is indicative for a supratidal salt-marsh habitat (Müller-Navarra et al., 2017) (Chapter 3).
5 CONCLUSIONS

The distribution of modern foraminifera was studied in three southeastern North Sea coastal salt-mashes were studied. Two of these salt marshes develop naturally and one is influenced by human activity. This thesis specifically addressed the effect of anthropogenic modifications and the natural development on the salt-marsh foraminiferal assemblages. It also investigated the effects of wind on local tidal parameters, and developed different transfer functions to reconstruct tidal and relative sea-level variations in the past. Further, a sediment section was investigated to analyze the development of a salt marsh at the German North Sea coast, which was influenced by storm-tide sedimentation and by human inferences, during the last 170 years. The research questions raised above (Chapter 1.3) can be answered as follows:

What determines foraminiferal distribution in an anthropogenic modified salt marsh?

To answer this question, the modern foraminiferal distribution in human-influenced salt-marsh environments of the Bay of Tümlau at the German North Sea coast was investigated. Based on cluster analysis, two main foraminiferal assemblages were distinguished: an internally undifferentiated salt-marsh assemblage dominated by the agglutinated species Entzia macrescens, Trochammina inflata and Miliammina fusca and the miliolid Quinqueloculina sp., and a lowest marsh/tidal flat assemblage dominated by the calcareous species Haynesina germanica, Elphidium excavatum, and Ammonia batava. Canonical Correspondence Analysis revealed that the foraminiferal distribution is mainly influenced by substrate type, pH and elevation, and to a lesser extent by salinity. Among the most common species, H. germanica, E. excavatum and A. batava are mainly related to higher proportions of sand in the sediments and to higher pH values, while E. macrescens, T. inflata, M. fusca and Quinqueloculina sp. are mainly related to finer-grained substrate and lower pH. In contrast to organogenic-dominated salt marshes, pH did not drop significantly below 7.5 in the tidal flat and salt-marsh areas in the Bay of Tümlau. Consequently, greater preservation of calcareous species is found, than in acidic salt marshes.

The morphology, hydrology and vegetation of the salt marsh in the Bay of Tümlau has been significantly altered by human influence, including ditching and sheep grazing, and by the landward dike for coastal projection. As a consequence, the salt marsh has a weakly developed concave morphology with rising edges, thus lacking a continuous landward rise in elevation and associated foraminiferal and vegetation zonation. Our results demonstrate
that single transects of modern benthic foraminiferal samples in human-interfered salt marshes, particularly with a small elevation range, do not provide reliable reference data sets for the establishment of transfer functions and application in sea-level reconstructions. The presence of ditches, tidal channels, and ponds creates a high level of small-scale variability of ecosystems and associated foraminiferal faunas within the salt marsh. This underlines the need of a wider spatial sampling to record all microhabitats in anthropogenic-influenced salt marshes.

What are the environmental factors controlling the foraminiferal distributions in natural salt marshes and can foraminiferal-based transfer functions be used to reconstruct tidal and relative sea level variations in the past?

This question was addressed by the study of the modern distribution of salt-marsh foraminifera of two naturally grown salt marshes at Rantum (Sylt) and Sønderho (Fanø), southeastern North Sea coast. The foraminiferal distribution in the studied salt marshes shows a vertical zonation with respect to the tidal frame. The highest marsh regions are dominated by *Balticammina pseudomacrescens* and *Entzia macrescens*. *Balticammina pseudomacrescens* is more abundant in the tidal-creek Sønderho marsh and *E. macrescens* is more abundant in the coastal Rantum marsh, which is probably the result of regional differences in flooding and therefore changes in salinity. The middle marsh is dominated by *Miliammina fusca*. The low marsh to tidal flat of the coastal marsh is dominated by *Ammobaculites* spp. and of the tidal-creek marsh by *Elphidium excavatum*.

Field measurements of tidal parameters in Sønderho showed that there is a difference in high water heights of 3 cm ± 1.8 cm between the permanently installed tide gauge Esbjerg and high-water height measurements in Sønderho. We further found that the tidal curves, calculated for the studied salt marshes, are not perfectly sinusoidal-shaped so that MSL slightly differs from the 50 %-duration of submergence in both salt marshes, by 6 and 12 cm in Sønderho and Rantum, respectively, which is significant for relative sea-level reconstructions on a centimeter scale. These results imply that, whenever possible, on site measurements should be performed to calibrate tidal datums from permanently installed adjacent tide gauge stations so that they are in better accordance with the local conditions in a salt marsh.

Different transfer functions, based on elevation (converted into SWLI), and on duration of submergence (DoS), mean submergence time (MST), and flooding frequency (FF) were developed to test to test their prediction precision. We showed that all approaches
perform well with a precision of around 0.23 m for the SWLI approach. Precisions ranged from 0.12 m to 1.30 m for the MST, DoS and FF approaches. It was further demonstrated that using flooding approaches in addition to the SWLI approach provide further insights into the marsh development by considering the local tidal regimes. The upper limit of water level can be accurately evaluated by using local flooding parameters. The flooding approaches account for meteorological effects on the water level, which become especially important at supra-tidal elevations of micro-tidal marshes, where currently the high precision sea-level reconstructions based on salt-marshes originate from.

What are the man-made and natural sedimentation impacts on the development of a salt marsh on centennial time scales?

Foraminiferal, sedimentological and geochemical data as well as foraminiferal-based transfer functions were used to study the temporal development of a human-influenced salt marsh in the Bay of Tümlau (southeastern North Sea coast), and to detect the imprint of storm tides in the resulting marsh succession. The establishment of the salt marsh was fostered by the construction of the dike in the years 1933 to 1935 CE. In the ditched and grazed salt-marsh between approximately 1955 and 1985 CE (and during the early years of natural protection until ~2002), storm-tide layers are indicated by a marked increase of re-deposited calcareous tidal-flat taxa (i.e., accounting to ~70 % of the total fauna), symmetrical grain-size distribution (skewness of around -0.1 to 0 phi), and a reconstructed mean submergence time (MST) of around 250 minutes.

In contrast, sediments deposited during regular high tides contain mainly autochthonous agglutinated taxa and have negatively skewed sediments (-0.3 to -0.5 phi). The presence of coarse siliciclastics, reflected by ln(Zr/Rb) ratios, reveal decadal changes, centered at a period of 16.7 years, that are particularly expressed in the 1970s to 1990s and display substantial inter-annual to decadal variability in storminess linked to phases of a predominant positive NAO index. Since around 1965 CE, the salt-marsh reveals a coarsening upward. This long-term change likely reflects the advancing depletion of fine-grained sediments in the source area of the mud flats and the lateral progression of the salt-marsh cliff. The natural, non-ditched salt-marsh, which established around the year 2002 CE, is dominated by agglutinated taxa (including the high marsh indicator B. pseudomacrescens) and MST is declined to 139 min, reflecting the establishment of a stable high marsh 1.3 m above MHW, resilient to sea-level rise and storm impacts. However, the fixed position of the hinterland dike has fostered the lateral erosion of the salt-marsh edge,
and may contribute to marsh geometry in the future. Vertically, marsh growth outpace sea-level rise since 2002 CE. This underlines the need of marsh monitoring in forelands of dikes to evaluate the best practice for dike reinforcement under rising sea-level scenarios.
A1: Taxonomic information on all species mentioned in the text.

<table>
<thead>
<tr>
<th>Species</th>
<th>References</th>
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<tbody>
<tr>
<td><em>Trochammina inflata</em> (Montagu, 1808)</td>
<td>Hofker, 1977, p. 230, Pl. 1 Fig.5, Gehrels and Newman, 2004, p. 102, Pl. 1, Fig. Q-T, Horton and Edwards, 2006, p. 68, Pl. II, Fig. 8a-d</td>
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<td><em>Miliammina fusca</em> (Brady, 1870)</td>
<td>Milker et al. 2015a, p. 5, Pl. 1, Fig. 25 and 26</td>
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<td><em>Balticammina pseudomacrescens</em> (Brönnimann, Lutze and Whittaker, 1989)</td>
<td>Milker et al. 2015a, p. 5, Pl. 1, Fig. 1 and 2, Wright et al. 2011, p. 58, Fig. A1/1a-1d, Horton and Edwards, 2006, p. 64, Pl. I, Fig. 1a-1d</td>
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<td><em>Entzia macrescens</em> (Brady, 1870)</td>
<td><em>Jadammina macrescens</em> in Müller-Navarra et al., 2016, p. 65, Fig. 5.5, Filipescu and Kaminski, 2008</td>
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<td><em>Ammobaculites</em> spp.</td>
<td>Horton and Edwards, 2006, p. 72, Pl. IV, Fig. 20a-20b</td>
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<td><em>Elphidium williamsoni</em> (Haynes, 1973)</td>
<td>Horton and Edwards, 2006, p. 72, Pl. IV, Fig. 16a, 16b</td>
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<td><em>Elphidium excavatum</em> (Terquem, 1857)</td>
<td>Horton and Edwards, 2006, p. 72, Pl. IV, Fig. 21a-21b</td>
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<td><em>Haynesina germanica</em> (Ehrenberg, 1840)</td>
<td>Horton and Edwards, 2006, p. 70, Pl. III, Fig. 10a-10c and 11a-11c, Milker et al. 2015a, p. 5, Pl. 1, Fig. 25 and 26</td>
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<td><em>Ammonia batava</em> (Hofker, 1951)</td>
<td>Horton and Edwards, 2006, p. 66, Pl. II, Fig. 9a, 9b</td>
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<td><em>Ammonia cf. beccarii</em> (Linné, 1758)</td>
<td><em>Streblus beccarii</em> in Hofker, 1977, p. 249, Pl. 6, Fig. 4; Milker and Schmiedl, 2012, p. 117, Fig. 27.1–2</td>
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<td><em>Trochamminita</em> spp.</td>
<td>Appendix A2, Plate 2, Fig. 5-10</td>
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<td><em>Quinqueloculina</em> sp.</td>
<td>Wright et al. 2011, p. 59, Fig. A2/7a-7h</td>
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<td><em>Entzia macrescens</em> irregular</td>
<td>Wright et al. 2011, p. 59, Fig. A2/7a-7h</td>
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<td><em>Haplophragmoides</em> sp.</td>
<td>Horton and Edwards, 2006, p. 242, Pl. 2, Fig. 26; Milker and Schmiedl, 2012, p. 81, Fig. 19.25–26</td>
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<td><em>Bolivina variabilis</em> (Williamson, 1858)</td>
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<td><em>Bolivina</em> spp.</td>
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<td><em>Bulimina</em> spp.</td>
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<td><em>Cibicides</em> spp.</td>
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<td><em>Buliminella borealis</em> (Haynes, 1973)</td>
<td>Hofker, 1977, p. 240, Pl. 4, Fig. 22</td>
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<td><em>Cornuspira involvens</em> (Reuss, 1850)</td>
<td><em>Cyclogyra involvens</em> in Hofker, 1977, p. 233, Pl. 2, Fig. 5; Milker and Schmiedl, p. 44, Fig. 12.1</td>
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<td><em>Stainforthia fusiformis</em> (Williamson, 1858)</td>
<td>Horton and Edwards, 2006, p. 74, Pl. 3, Fig. 13a–b</td>
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<td><em>Tiphotrocha comprimata</em></td>
<td>Wright et al., 2011, p. 59, Fig. A2/1a–i</td>
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<tr>
<td>(Cushman and Brönnimann, 1948)</td>
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<tr>
<td><em>Nonion depressulum</em></td>
<td>Hofker, 1977, p. 254, Pl. 8, Fig. 3; Milker and Schmiedl, 2012, p. 81, Fig. 19.25–26</td>
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<td>Nonion sp. 1</td>
<td>2012, p. 112, Fig. 25.17–18</td>
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<td>Ammodiscus spp.</td>
<td>Wright et al. 2011, p. 59, Fig. A2/6a-6c</td>
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<td>Paratrochammina haynesi</td>
<td>Gehrels and Newman, 2004, p. 102, Pl. 1, Fig. N-P</td>
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<tr>
<td>Trochammina ochracea</td>
<td>Gehrels and Newman, 2004, p. 102, Pl. 1, Fig. J-M</td>
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Plate 1 Scanning electron micrographs of characteristic foraminiferal taxa of salt marsh and tidal flat environments of the Bay of Tümlau, German North Sea coast. 1 Miliammina fusca (side view), 2 Trochammina inflata (spiral side), 3 T. inflata (umbilical side), 4 Entzia macrescens (spiral side), 5 E. macrescens (apertural view), 6 Cornuspira involvens (side view), 7 Quinqueloculina sp. (side view), 8 Quinqueloculina sp. (side view), 9 Bolivina variabilis (side view), 10 Buliminella borealis (side view), 11 Stainforthia fusiformis (side view), 12 Haynesina germanica (side view), 13 H. germanica (side view), 14 H. germanica (apertural view), 15 Ammonia batava (spiral side), 16 A. batava (umbilical side), 17 Elphidium excavatum (side view), 18 E. excavatum (side view), 19 E. excavatum (apertural view), 20 Elphidium williamsoni (side view), 21 E. williamsoni (side view). Scale bar is 60 µm.
Plate 2 Light microscope photographs of selected foraminiferal taxa from the North Sea coast (Number 4, 5, 6 and 9 are from Bay of Tümlau (see Müller-Navarra et al., 2016)), all other individuals are from the study areas. 1a, 1b and 4b *Miliammina fusca* (side view), 2a *Trochammina inflata* (spiral side), 2b *T. inflata* (umbilical side), 3a *Trochammina inflata*, irregular specimen (spiral view), 3b *T. inflata*, irregular specimen (umbilical view), 5 to 10 *Entzia macrescens*, irregular, (5, 6, 7, 9, 10b spiral view and 8, 10a umbilical view). Scale bar is 100 μm.
A3: References


Juggins, S., 2013. Quantitative reconstructions in palaeolimnology: new paradigm or sick science? Quaternary Science Reviews 64, 20–32.


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SUPPLEMENTS

S1.1: Census counts, Chapter 2
S1.2: Environmental parameter, Chapter 2
S2.1: Census counts, Chapter 3
S2.2: Environmental parameter, Chapter 3
S3.1: Census counts, Chapter 4
S3.2: Grain-size data, Chapter 4
S3.3: Age model, Chapter 4
S3.4: Water-level differences, Chapter 4
S3.5: XRF-data, Chapter 4

(All supplements can be found in the attached compact disc.)
Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass die vorliegende Dissertationsschrift von mir, Katharina Müller-Navarra, verfasst wurde und ich keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, den

__________________________

Katharina Müller-Navarra