Wetlands
https://doi.org/10.1007/s13157-018-1089-3

ORIGINAL RESEARCH

Biogeochemical Characteristics of the Last Floating Coastal Bog Remnant in Europe, the Sehestedt Bog

Gijs van Dijk[1,2] · Christian Fritz[2,3] · Nicko Straathof[4] · Bas van de Riet[1,5] · Niels Hogeweg[5,6] · Sarah F. Harpenslager[2,7] · Jan G. M. Roelofs[1,2] · Karl-Ernst Behre[8] · Leon P. M. Lamers[2,1]

Received: 9 January 2017 / Accepted: 1 October 2018
© Society of Wetland Scientists 2018

Abstract

With the current risks caused by sea level rise and increased extreme weather events, the study of natural coastal systems has never been more important. Erosion and anthropogenic forcing led to disappeared of the majority of coastal bogs in Europe. Here, we report on case study of a unique bog remnant still under influence by seawater which floats during storm floods. We investigated biogeochemical characteristics and discuss mechanisms that influence buoyancy, which is of vital importance for the conservation of the bog and can provide insights into the functioning of coastal bogs and potential consequences of future sea level rise. The studied area is characterized by a steep salinity gradient and marine clay deposits provide the 'hinge' that allows the upper peat layers to float. Our results show out that buoyancy is driven by a combination of factors: the density differences, desiccation along the edges and methane production. If the ability to float is reduced in coastal bogs, the impact of erosion and the sum of several other processes (i.e., peat decomposition, salt stress, clay sedimentation, internal eutrophication and reduced methanogenesis) can cause a shift in environmental conditions and lead to loss of this unique habitat and its characteristic species.

Keywords Salinity · Raised bog · Buoyancy · Sehestedter Aussendeichsmoor · Coastal wetland

Introduction

The study of natural coastal systems has gained importance with the current risks caused by sea level rise, anthropogenic forces and increased extreme weather events (Herbert et al. 2015). The appearance and functioning of many natural coastal ecosystems, including coastal bogs have been affected by erosion and anthropogenic forcing. As a result, the majority of coastal bogs in Europe has either disappeared or become isolated from the sea.

Many coastal bogs, although located in coastal areas, have been formed during periods of high groundwater influence (due to regression phases of the North Sea or the formation of elevated levees) and subsequently developed into rainwater-fed bogs over time. Some bogs, however, started (partially) under salt marsh-like conditions, in which increased influence of freshwater created suitable conditions for swamp formation, resulting in the formation of fen peat (from 8000 to 4000 BP). This fen peat, formed by plants such as *Phragmites sp.*, *Typha* spp., *Carex* spp. and *Sparganium* spp. developed into alder and birch carr forests and eventually into raised bog as the influence of rainwater increased (Behre and Kucan 1999; Bakker and Smeerdijk 1982; Pons 1992; Vos 2015).

✉ Gijs van Dijk
g.vandijk@b-ware.eu

[1] B-WARE Research Centre, Radboud University Nijmegen, P.O. Box 6558, 6503, GB Nijmegen, The Netherlands

[2] Aquatic Ecology and Environmental Biology, Institute of Water and Wetland Research, Radboud University, P.O. Box 9010, 6500, GL Nijmegen, The Netherlands

[3] Centre for Energy and Environmental Studies, University of Groningen, Nijenborgh 6, 9747 Groningen, The Netherlands

[4] Natuurmonumenten, P.O. Box 9955, 1243, ZS 's Graveland, The Netherlands

[5] Landschap Noord-Holland, P.O. Box 222, 1850, AE Heiloo, The Netherlands

[6] PWN, P.O. Box 2113, 1990, AC Velserbroek, The Netherlands

[7] School of Biological and Chemical Sciences, Queen Mary University of London, E1 4NS, London, UK

[8] Lower Saxony Institute for Historical Coastal Research, P.O. Box 2062, 26360 Wilhelmshaven, Germany

Published online: 26 October 2018

These coastal raised bogs became influenced by salt water in a later stage due to rising seawater levels, tectonic plate motion, flooding events and anthropogenic influences. Examples of such former bogs include peat remnants in the Doggersbank in the North Sea (Reid 1913; Gaffney et al. 2007) and peat remnants along the Thames valley and the British east coast (Reid 1913). In former times (4000–1000 BP), these large coastal bog complexes were often directly influenced by the sea along the seaside during later stages in their evolution (some only during storm floods, others more often). From roughly 1000 years AD onwards, anthropogenic influence on coastal bogs increased. North-western European coastal bogs became disconnected from marine influence by dike construction, were drained for agricultural use or turf extraction (Pons 1992), or used for salt exploitation after burning (called 'selnering' which has been described for a series of locations along the Wadden Sea coast (Borger 1992; Van Geel and Borger 2002; Behre 2005; Leenders 2013)). Many of these anthropogenic activities have probably enhanced the vulnerability of coastlines and coastal bogs to flooding. The majority of the North-western European coastal bogs therefore became eroded, drained or exploited and often lost direct hydrological connection with their surroundings. The remaining inland peatlands in coastal regions are often remnants of former large coastal bogs and include large parts of the North-western part of the Netherlands and Germany. The present paper reports on a case study of the last raised bog remnant in Europe still under direct marine influence. On a global scale there are more examples of large coastal bog complexes with saline/marine influences, such as coastal bogs along the bay of Fundy in the region of Maine (United States of America), New Brunswick (Canada) and Nova Scotia (Canada) (Damman 1977; Breathnach and Rochefort 2008).

Knowledge of the functioning of natural coastal bog remnants is important, not only for management and restoration of these sites, but also for the conservation of coastal wetlands, as they are likely to experience increased salt water influence and erosion due to rising sea level and increasing anthropogenic pressure (Herbert et al. 2015). At present, however, large European coastal peatlands have either been lost or modified to such an extent that they can no longer serve as a reference for restoration projects.

In North-western Germany, however, a remnant of a former large bog along the coast is still present. This area (Sehestedter Aussendeichsmoor or Schwimmendes Moor) is a small raised bog remnant on the seaside of the dike. The history and deterioration of the study area have been described in detail (Künnemann 1941; Behre and Kucan 1999; Behre 2005, 2007b). These studies reported that edges of the bog remnant become buoyant during storm floods, thus reducing salinity/marine influence on bog vegetation.

So far, however, little attention has been paid to the biogeochemical functioning of these bog remnants. Enhanced salinity is known to have large consequences for the functioning of bogs (Herbert et al. 2015), including redox processes in the peat soil. Examples of these include enhanced sulfate reduction (Herbert et al. 2015), which affects the iron and phosphorus cycle (Smolders et al. 2006; Lamers et al. 2013), and reduced methanogenesis (Weston et al. 2006), which might also influence gas production and buoyancy (Smolders et al. 2002; Strack et al. 2005). Salinity is also known to influence the availability of nutrients such as ammonium (NH_4, Rysgaard et al. 1999; Weston et al. 2006) and phosphorus (P, Weston et al. 2006; Van Dijk et al. 2015) and can have a negative influence on bog vegetation since many bog species are sensitive to increased alkalinity and higher ionic concentrations (e.g. Clymo and Hayward 1982; Wilcox and Andrus 1987; Hájek et al. 2006). In the present paper, we focus on how biogeochemical soil and pore water characteristics of the bog remnant change over the gradient from sea to land. Special attention is paid to both horizontal and vertical biogeochemical gradients in the bog and how these might influence its functioning, species composition and the buoyancy of the remnant. Results presented in the present paper will help to better understand the functioning of coastal bogs under the influence of salinity with implications for future conservation of these systems under the current threats caused by a changing climate.

Material and Methods

Site Description

The Sehestedter Aussendeichsmoor or 'Schwimmendes Moor' (German for swimming or floating peatland; further called Sehestedt Bog) is a raised bog remnant of a former extensive raised bog formed behind an elevated levee along the coast in the Jade Bay in North-West Germany (Fig. 1). Peat formation started with swamp and minerotrophic peat accumulation during the regression phase in the North Sea between 1500 and 1000 B.C., when a shift occurred from marine to brackish and freshwater conditions (Behre 2003, 2005, 2007a). During further succession minerotrophic fens and alder woods developed, which eventually became a raised bog dominated by peat mosses (*Sphagnum* spp.) during the next regression of the North Sea by the end of the last century B.C. (Behre 2003, 2007a). At the beginning of the thirteenth century, storm surges broke through the elevated levee, which caused large erosion, of bogs behind the levee and started the formation of the Jade Bay (Behre 2005). During several centuries the bogs eroded away and the Jade Bay extended far beyond its present size. Although several storm floods led to major erosion, the coastal bog had a special resistance to flooding: during storm tides the seaward side of the bog starts to float, which prevents the bog being flooded and reduces erosion (Behre 2005).

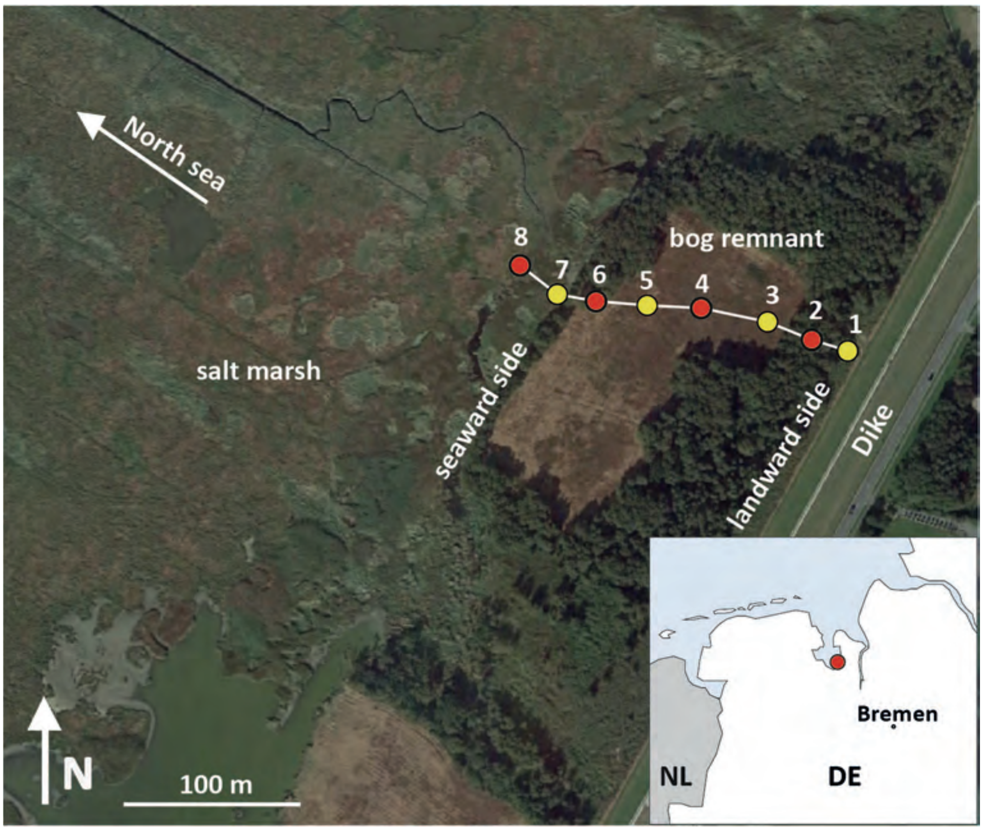

Fig. 1 Aerial picture of the northern part of the Sehestedt Bog (©Google Earth), showing the study transect (yellow dots indicate depth profile sites). The sea is on the western side of the dike. At the right bottom a map of the Northwestern region of Germany in white, in grey the north east of the Netherlands, the red dot indicates the study area

During the last centuries however a large proportion of the bog was eroded during storm floods. In 1725, a dike was built across the bog, leaving the inland part of the bog sheltered from the influence of the sea. The bog area outside the dike covered an area of 165 ha in 1725, which was reduced by erosion to 107 ha in 1820, to 21 ha in 1932 and to a present area of about 9.5 ha (Behre 2005). The bog remnant is boarded with an 9 m high dike on the South-eastern side and salt marsh vegetation at the north-western side and is surrounded by a small band of reed (*Phragmites australis*) along the edges of the bog (see Fig. 1). The remnant harbors a vegetation composition characteristic to raised bogs (*Sphagnum* spp., *Andromeda polifolia* and *Vaccinium oxycoccos*) as well as spreading bush vegetation of *Myrica gale*, *Calluna vulgaris*, *Erica tetralix* and Birch wood (*Betula pubescens*). The bog remnant is surrounded by salt marshes at the sea side.

According to Behre (2005), this is the last remaining European raised bog remnant subjected to marine influence during storm tide and storm floods. When high storm floods exceed 1.6 m above high tide the bog starts to float. The bogs ability to float during storm tides, however, prevents the inundation of the bog by salt water (according to Behre 2007b) the bog was reported to become buoyant several times in recent years). Although in the past other coastal bogs have been known that were able to float, the study area is now the last remaining European coastal bog where this phenomenon occurs.

Field Sampling

In October 2012, vegetation surveys and electric conductivity (EC) depth profiles were made on eight locations along a transect between the salt marsh and the dike (Fig. 1). At four locations (nr. 2, 4, 6 & 8 in Fig. 1) along the transect, soil, pore water and pore water gas samples were taken at different depths (from 0 to 4.5 m of depth below the surface). Three of the four sampling locations were taken on the bog itself (nr. 2, 4 and 6) and one (nr. 8) on the salt marsh (Figs. 1 and 2). Vegetation surveys were carried out in 2 × 2 m squares using the Braun-Blanquet scale (Braun-Blanquet 1964) on all eight locations along the transect (Fig. 1). EC depth profiles where also carried out on all eight locations with a conductivity sensor (WTW®, Germany) connected to the tip of a steel pole to enable measurements up to 2 m of depth.

Anaerobic soil pore water samples and gas samples were collected using 5 cm ceramic cups (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands) connected via teflon tubes to vacuumed syringes. Additional sediment pore water samples were collected for pore water methane (CH_4) and sulfide (H_2S) analyses by connecting vacuum 12 ml glass exetainers (Labco exetainer®, High Wycimbe, UK) (with 0.5 ml of 1 M HCl to preserve the sample) to the same ceramic cups. Uncompressed soil samples (every 10–25 cm, depending in the soil profile) were obtained using a Russian peat corer (Eijkelkamp Agrisearch Equipment, Netherlands),

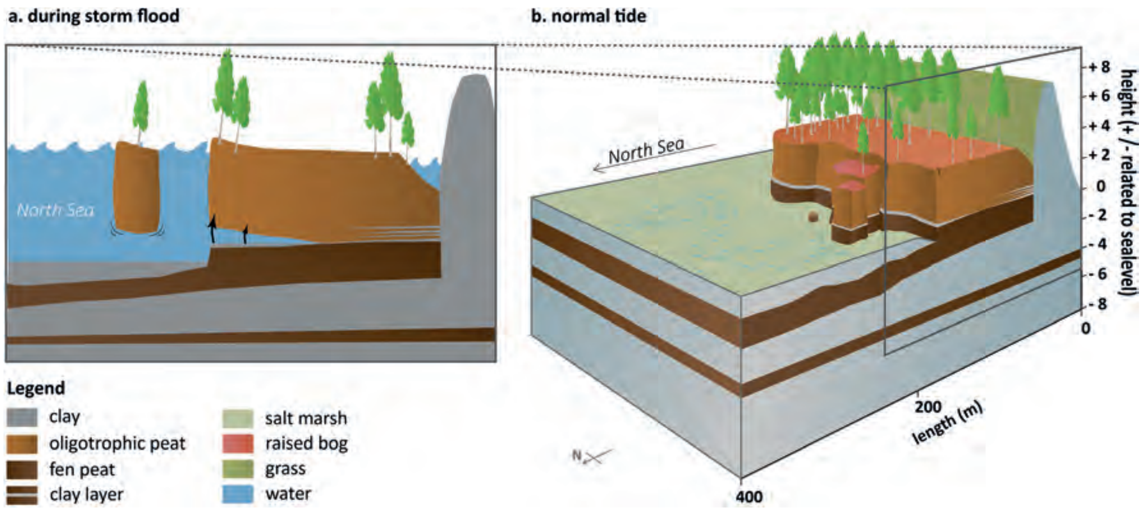

Fig. 2 Schematic overview of the area, based on data of the present paper and data from Behre (2005), scales in meters (length and high ± sea level). a. is the area during a storm flood when a part of the bog is floating. b. is the area under normal conditions

immediately put into sealed plastic bags, transported at 4 °C to the laboratory and stored at 4 °C until further analysis (i.e. bulk density, organic matter content and chemical composition). Peat type and origin were determined based on Meier-Uhlherr et al. (2011) and compared with data obtained by Behre (2005).

Chemical Analyses

Surface and Pore Water Analysis

The pH of surface water and pore water samples was measured using a combined pH electrode with an Ag/AgCl internal reference (Orion Research, Beverly, CA, USA) and a TIM800 pH meter. Alkalinity was measured by titration to pH 4.2 with 0.01 M HCl using an ABU901 Autoburette (Radiometer, Copenhagen, Denmark). Prior to elemental analyses, 10 ml of each sample was stored at 4 °C with 0.1 ml HNO_3^- to prevent metal precipitation. For the analyses of phosphorus (P), calcium (Ca^{2+}), magnesium (Mg^{2+}), iron (Fe^{2+}), sulfur (S), potassium (K^+) and aluminium (Al^{3+}) inductively coupled plasma spectrophotometry (ICP-Optical Emission Spectrometer, Thermo Scientific iCAP 6000 Series ICP) was used. To determine nitrate (NO_3^-), ammonium (NH_4^+), ortho-phosphate (o-PO_4^{3-}), sodium (Na^+), potassium (K^+) and chloride (Cl^-) concentrations, 20 ml of each sample was stored at −20 °C until they were analyzed colorimetrically with an Auto Analyzer 3 system (Technicon Instruments Corp., Tarrytown, NY, USA), using ammonium molybdate for o-PO_4^{3-} (Henriksen 1965), hydrazine sulfate for NO_3^- (Technicon 1969) and salicylate for NH_4^+ (Grasshoff and Johannsen 1977). Concentrations of Na^+, K^+ and Cl^- were determined with a Technicon Flame Photometer IV Control (Technicon Corporation). Concentrations of CH_4 and H_2S were measured in the headspace (after removing the vacuum with N_2 gas) of the exetainers using gas chromatography and recalculated for the water volume using Henry's constant. CH_4 concentrations were measured in the headspace were analyzed using a Hewlett-Packard 5890 gas chromatograph (Avondale, California) equipped with a flame-ionization detector and a Porapak Q column (80/100 mesh) operated at 120 °C with N_2 as carrier gas. H_2S concentrations analyzed using a 7890B gas chromatograph (Agilent Technologies, Santa Clara, USA) equipped with a Carbopack BHT100 glass column (2 m, ID 2 mm), flame ionization (FID) and flame photometric detector (FPD).

Soil Analysis

Dry weights and bulk densities of soil samples were measured by drying a known volume at 70 °C until constant weight, whereas organic matter content was determined by loss-on-ignition (4 h, 550 °C). Total element concentrations (Mg, S, Fe, Ca, P) of soil samples were determined by digesting 200 mg of dried (24 h, 70 °C) and homogenized sample in 4 ml concentrated HNO_3 and 1 ml 30% H_2O_2 (Milestone microwave MLS 1200 Mega). Samples were analyzed by ICP, as described above. Total nitrogen (N) and carbon (C) concentrations were measured with a CNS analyzer (Model NA 1500; Carlo Erba Instruments, Milan, Italy).

Results

Soil Characteristics

The bog comprises a 3–4 m thick peat layer situated on marine clay (Fig. 2). We found large differences in surface level between the three bog profiles and the salt marsh profile (Figs. 1 and 2). The peat layer consists of about

1 m of fen peat (*Phragmites*, *Carex*) on top of the marine clay basis. On top of this minerotrophic peat layer, a *Sphagnum* dominated ombrotrophic peat layer of about 2–3 m is present. Underneath the whole raised bog, especially on both the seaward and the landward edge of the bog, small clay layers (varying in thickness) are intercalated at the transition between the fen peat and ombrotrophic peat. On the landward side (loc. 2), five thinner bands (of 1–15 cm) of clay are present, while on the seaward side only one thicker clay layer (30 cm) is present. In the interior of the bog (loc. 4), clay bands between the two peat types are very thin. On the salt marsh, a top layer of more than a meter of marine clay is present with a peat layer underneath (Fig. 2). This peat layer consists of about 1.5–2 m of decomposed peat with a small clay band in the middle. Underneath this peat layer, marine clay is present again (Fig. 2). Organic matter content of the soil samples clearly indicates the difference between the bog peat (O.M. > 95%), fen peat (O.M. 80–90%) and clay (O.M. < 25%) layers (Figs. 3 and 4).

Soil and Pore Water Chemistry

The elemental composition of the pore water and soil show comparable depth gradients (see Table 1). Although there are clear signs of slightly increased salinity levels in the top of the peat profile (0.3–0.5 mS cm^{-1}, versus 0.1–0.2 mS cm^{-1} at 0.5–1 m of depth), the bog interior is dominated by rainwater intrusion indicated by several parameters (Table 1) and EC depth profiles (Figs. 5 and 6). Pore water Cl^- concentrations differ between the edges and the interior of the bog, with higher salinity in the top layer of the profile on the edges, especially at location 2 at the landward side (increasing up to 1–5 mS cm^{-1} in the root zone, Figs. 5 and 6). In the salt marsh on the seaside of the bog, high salinity levels were found (up to 330 mmol Cl l^{-1} (Table 1) and 30 mS cm^{-1} (Fig. 6)). In the bog interior (loc. 4), conditions remain acidic and ombrotophic (pH < 4.5, alkalinity 0.1 or lower and < 10 µmol Cl l^{-1}) to >3 m below the surface. The top 50 cm showed low pore water pH (3.2 to 4) and alkalinity (<0.05 meq l^{-1}) levels. These low pH and alkalinity conditions were maintained to depths of around 2 m. Only at greater depths (> 3 m), especially in fen peat layers, pH increases to values around 6.5 and alkalinity reaches 15 meq l^{-1}. Pore water nutrient concentrations (total phosphorus, $P_{(tot)}$, and NH_4^+; Table 1)) are relatively low (≈ 10 µmol l^{-1} $P_{(tot)}$ and ≈ 25 µmol l^{-1} NH_4) close to the surface of the bog itself but increase with depth. At greater depths (> 2 m), pore water of both the bog and the salt marsh higher nutrient concentrations were found (factor 5–20 times higher as concentrations found in the root zone of the bog interior). Pore water nitrate (NO_3^-) concentrations were low (< 5 µmol l^{-1} at all locations at all depths. Total pore water P and NH_4^+ concentrations correlate with pore water Cl^- concentrations (Fig. 5a.) and increased with depth. Sites with low salinity show low pH values (around 4) and lower pore water bicarbonate (HCO_3^-) concentrations (Fig. 5b.). Higher pore water total S and H_2S concentrations are only present at locations with high Cl^- concentrations (Fig. 5c.). Pore water CH_4 and H_2S concentrations varied throughout the bog and depth profiles. The highest CH_4 concentrations were found when H_2S concentrations were low (< 1 µmol l^{-1}) and salinity was low (Fig. 5d.). Pore water CH_4 concentrations were highest in the deeper layers of the bog profile and at 50 cm depth in the salt marsh (Table 1). H_2S was almost absent (< 1 µmol l^{-1}) in the bog interior and increased on the landward side of the bog and underneath the salt marsh (Table 1).

Total Na, Ca and S concentrations in the soil profiles (Fig. 3) show differences in marine influence within the peatland. The upper layers of the bog interior are characterized by low marine influence (chloride concentrations <10 mmol/l) and oligotrophic conditions. In the fen peat layers and around clay bands marine influence is clearly indicated by increased Na, Ca and S concentrations (Fig. 3). On the edges of the bog (loc. 2 and 6), Na and to a lesser extent S and Ca concentrations are present higher in the soil profile, on the seaward side (loc. 6) up to 2 m and on the landward side (loc. 2) even up to 1 m below surface level. Deeper in the marine clay layer Na concentrations decrease again.

Vegetation

The Sehestedt bog harbors a combination of vascular plant and bryophyte species characteristic for both communities of raised bogs, wet heathlands and salt marshes (Fig. 7). On the interior of the bog remnant (loc. 3–6) a species community characteristic for raised bogs and wet heathlands (Oxycocco-Ericion) is present with relatively high abundance (25–50% cover) of heather like species (*Calluna vulgaris*, *Erica tetralix* and *Vaccinium oxycoccos*) and peat mosses. Less abundant but characteristic bog species found were *Eriophorum vaginatum* and *Narthecium ossifragum* (both <5% cover and few individuals) and some peat mosses (*Sphagnum magellanicum*, *Sphagnum papillosum* and *Sphagnum rubellum* (all *Sphagnum* spp. mosses were found in low cover (< 5%)). Along the edges of the bog, plant species characteristic for raised bogs are absent, and a mixture of minerotrophic vegetation is present with dominance of *Phragmites australis, Festuca rubra*, *Urtica dioica*, *Calamagrostis epigejos* and *Elytrigia atherica* (Fig. 7). Location 8 is characterized by salt marsh vegetation, including *Bolboschoenus maritimus, Triglochin maritima, Aster tripolium, Atriplex portulacoides, Spartina anglica, Puccinellia maritima* and *Suaeda maritima* and do show no similarity with the vegetation on the bog (Fig. 7). Along the edges of the bog (including seaward) a small *Betula pubescens* forest is present. On the raised bog itself a

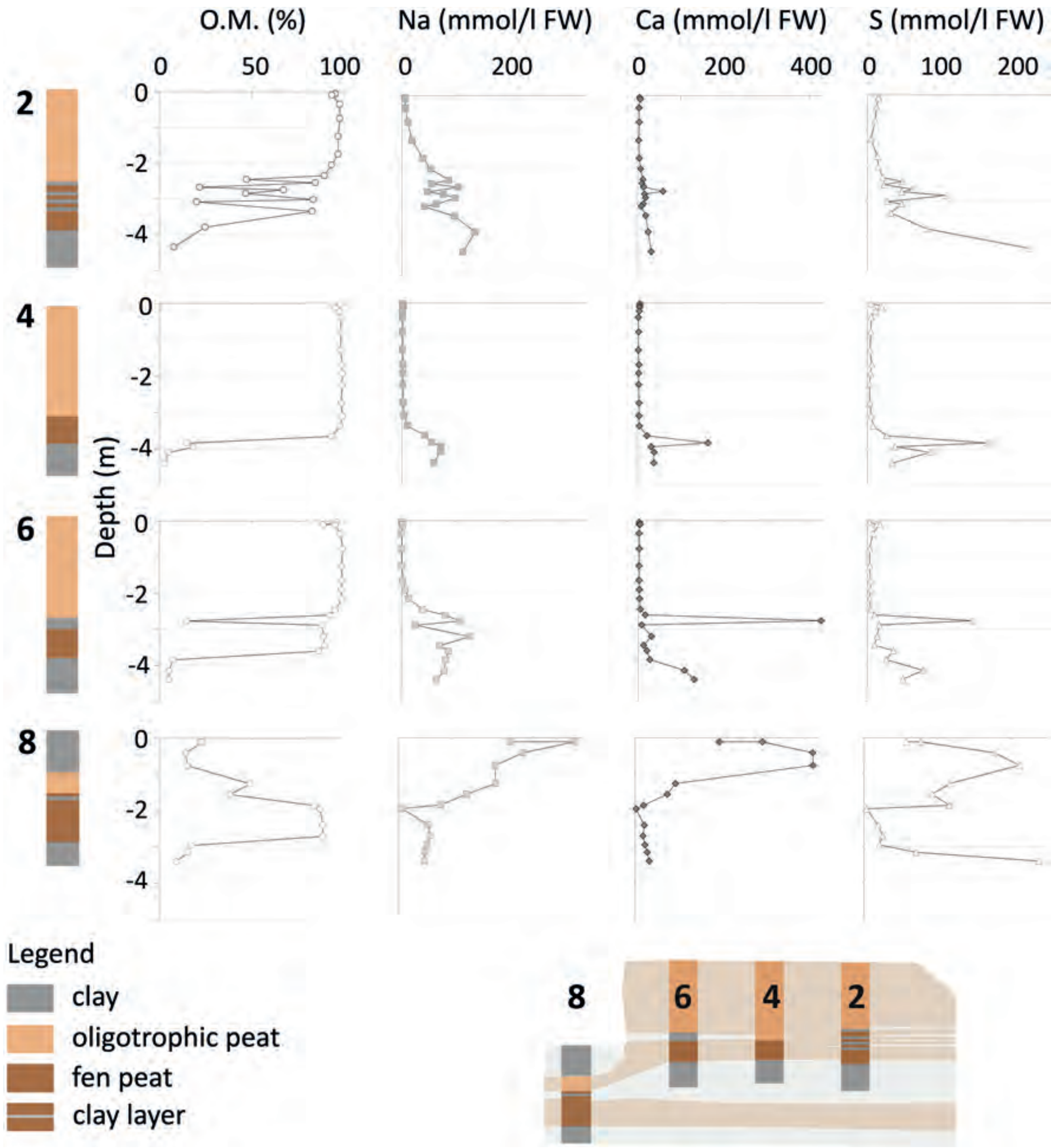

Fig. 3 Depth profiles of chemical soil characteristics of locations 2 (landward), 4, 6 and 8 (seaward), from the left to the right; organic matter content (%), and total sodium, calcium and sulfur concentration, all in mmol/l FW. On the right, soil types are shown: light brown = ombrotrophic peat, dark brown = fen peat, and grey = clay. Note that profiles are presented in meters below surface level, while surface levels differ per location, nr. 2, 4 and 6 are on the bog, 3–4 m above sea level, nr. 8 is at the salt marsh, 0–0.5 m above sea level

large number of *Betula* seedlings are present and patches where *Myrica gale* is dominant.

Discussion

Biogeochemical Functioning of Floating Coastal Bogs

The present study describes a rare and atypical combination of an oligotrophic raised bog remnant with marine influences around its edges. Surprisingly, however, biogeochemical conditions in the bog remnant still support raised bog and heather-like vegetation. The high abundance of heather-like species and low abundance of peat mosses, however, indicate signs of desiccation. The bog remnant shows strong horizontal and vertical biogeochemical gradients as a result of saltwater intrusion from the edges. As peat mosses, and bog vegetation in general, are very sensitive to high alkalinity and high ionic concentrations such as enhanced salinity (Clymo and Hayward 1982; Wilcox 1984, 1986; Wilcox and Andrus 1987; Hájek et al. 2006; Harpenslager et al. 2015), the ombrotrophic peat layers are clearly from older origin

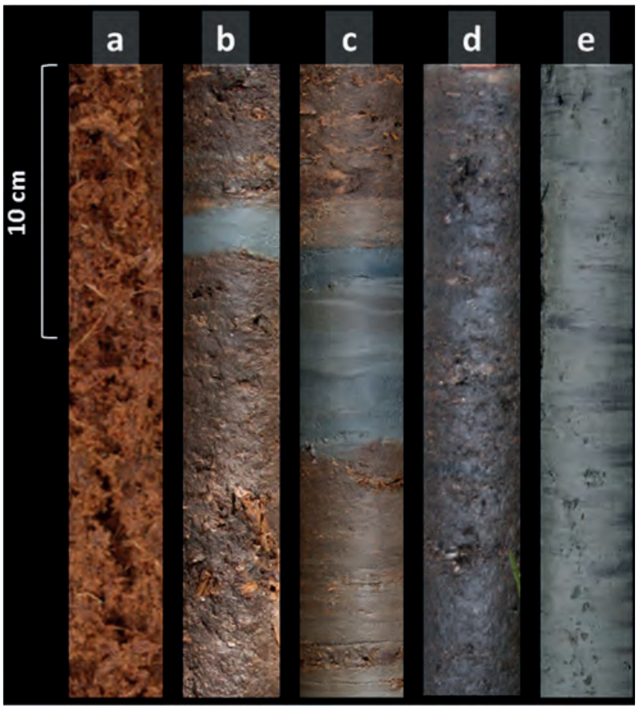

Fig. 4 Photos of different sediment types found in the soil cores, **a** ombrotrophic peat, **b** thin clay band of 'intercalated clay' in ombrotrophic peat, **c** thick clay band in fen peat, **d** fen peat, **e** marine clay. Photos by G. van Dijk

(4000–1000 BP, (Behre 2005)) and have been formed under rainwater dominated conditions. Enhanced salinity levels found in the ombrotrophic peat layer are a result of saltwater intrusion from the sides during storm tides and salt spray on the surface. Increased salinity influence from the sides also led to increased sulfur input in ombrotrophic peat layer. Enhanced salinity in the ombrotrophic peat layer is a result of saltwater intrusion from the edges during storm tides, most likely due to sea spray or partial temporary flooding add the edges during storm tide. Increased salinity also led to higher sulfur input in the ombrotrophic peat layer. Storm tide can increase the marine influence on the bog. Furthermore, the bog remnant directly borders a salt marsh, which harbors brackish to saline conditions (pore water chloride concentrations in the rhizosphere of the salt marsh (330 mmol Cl l^{-1}) are close to seawater concentrations (450–550 mmol Cl l^{-1})).

This unique high salinity on a raised bog soil can have large biogeochemical consequences, with potential effects on the S, Fe, P, N and C cycles (Herbert et al. 2015). The seawater induced sulfur input, along with a higher alkalinity, would have led to increased SO_4^{2-} reduction in anaerobic peat layers and enhanced peat mineralization (Lamers et al. 1998). Enhanced sulfate reduction (indicated by high H_2S concentrations in the peat profile along the edges of the bog) will have caused internal nutrient mobilization (Lamers et al. 2002; Smolders et al. 2006),

Table 1 Chemical pore water composition at four depths for 4 locations along the transect. Note that concentrations are given in different units

loc.	depth cm	pH	alk meq l^{-1}	EC mS cm^{-1}	CO_2 mmol l^{-1}	HCO_3	CH_4 µmol l^{-1}	H_2S	Fe	Ca mmol l^{-1}	S	Na	Cl	P µmol l^{-1}	NO_3	NH_4
2	-12	3.1	< 0.1	1.0	0.3	< 0.1	0.3	0.2	23.6	0.3	0.5	4.7	6.3	9.2	1.4	24.8
	−52	3.5	< 0.1	0.6	4.0	< 0.1	683.4	0.4	25.3	0.1	0.1	2.6	3.3	4.6	2.4	84.3
	−202	4.6	0.2	7.8	9.4	0.1	805.3	73.0	29.8	0.6	2.2	53.3	57.8	8.6	0.8	481.6
	−332	6.7	17.5	18.0	6.6	15.2	308.4	876.2	2.4	4.7	22.8	152.5	26.1	109.2	0.9	816.5
	−402	6.8	15.5	16.2	5.8	15.1	579.8	445.2	3.1	4.5	7.8	134.4	101.8	79.1	3.4	1013.6
4	−12	3.5	< 0.1	0.2	1.5	< 0.1	0.3	0.2	10.6	0.1	0.5	4.1	4.2	5.3	1.4	27.3
	−52	4.0	< 0.1	0.1	2.4	< 0.1	187.2	0.3	14.7	0.0	0.1	1.6	1.8	2.9	1.3	82.8
	−202	4.5	0.1	0.1	3.7	0.1	775.7	0.4	4.6	0.0	0.1	0.6	0.6	1.8	3.3	159.7
	−317	4.4	0.1	0.9	5.4	0.1	930.2	0.9	27.1	0.1	0.1	5.8	7.0	8.3	0.8	368.0
	−402	6.8	10.7	8.5	4.1	10.1	505.9	0.8	3.4	3.1	0.1	51.0	55.7	123.1	2.7	658.2
6	−12	3.6	< 0.1	0.2	1.0	< 0.1	0.3	0.3	12.2	0.0	0.2	2.1	1.9	12.6	1.7	20.4
	−52	3.9	< 0.1	0.1	2.2	< 0.1	83.9	0.3	6.8	0.0	0.1	0.7	0.8	2.6	1.5	27.1
	−202	4.1	< 0.1	14.9	5.5	< 0.1	3203.6	0.8	16.6	0.1	0.0	4.1	5.3	4.9	0.5	373.6
	−332	6.5	14.4	15.2	9.6	11.9	1848.8	0.6	300.4	4.1	0.0	83.5	99.6	278.2	1.1	1683.7
	−402	6.7	7.9	0.9	3.8	7.6	681.7	0.7	229.4	2.8	0.0	63.8	75.5	43.5	5.1	795.9
8	−12	7.0	25.7	38.3	4.7	18.0	97.4	86.7	14.6	10.0	10.2	255.7	328.4	189.0	4.8	196.4
	−52	7.1	25.0	32.1	5.5	28.7	8070.9	0.8	5.1	9.4	0.7	221.3	273.7	450.8	2.8	1667.5
	−152	6.2	7.5	26.3	19.7	13.5	602.5	1.4	2.6	9.2	0.1	177.9	227.2	275.5	1.2	2351.3
	−202	6.3	6.8	8.6	7.9	6.1	607.2	0.6	1372.6	4.7	0.1	48.6	63.0	4.9	3.9	1574.2
	−302	6.3	6.7	x	6.2	4.7	22.1	0.5	1476.6	5.2	0.1	51.4	72.2	25.2	1.1	1780.3

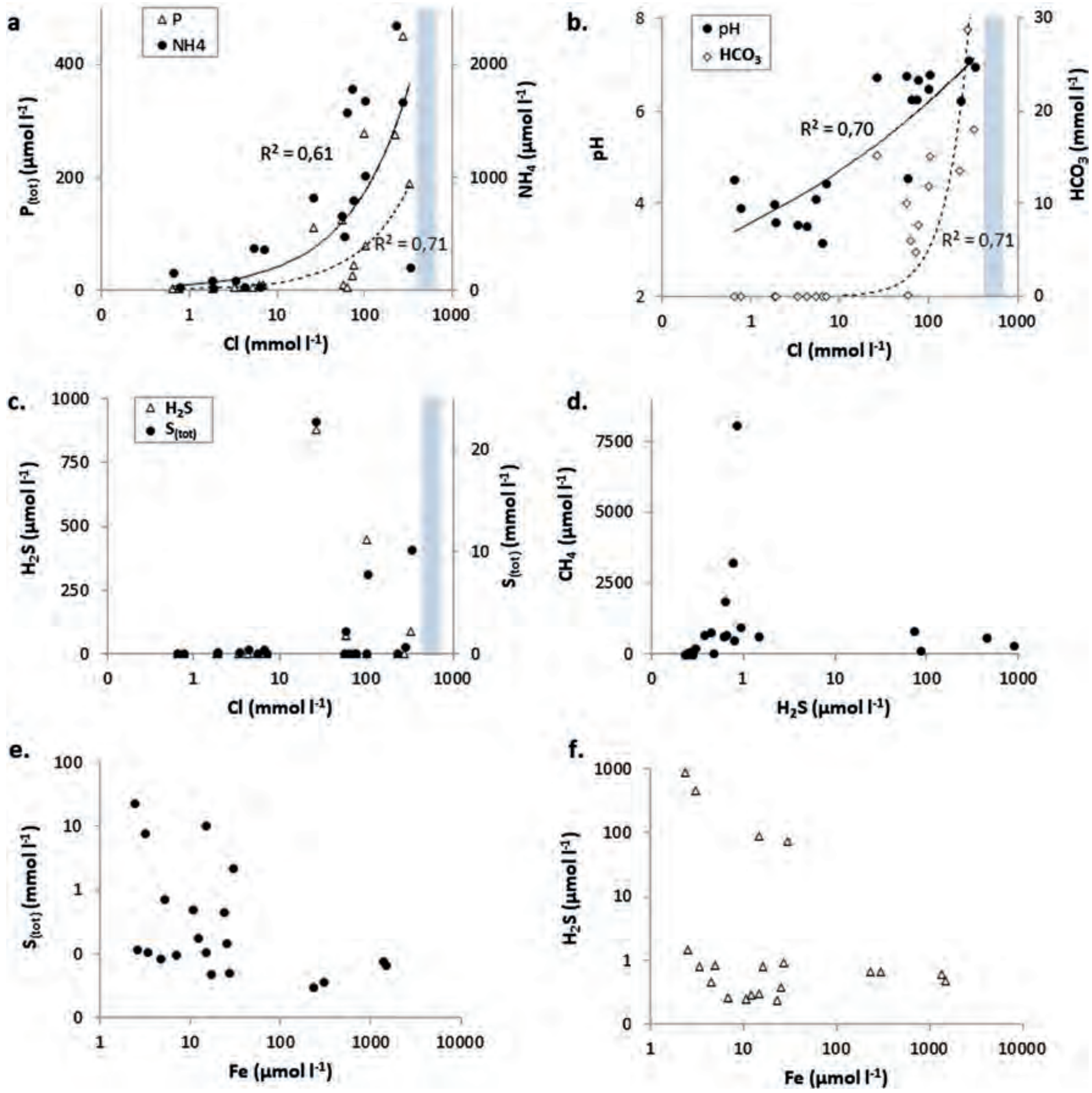

Fig. 5 Correlations between different pore water characteristics for all locations sampled. Note that the horizontal axis presents a log scale. **a** Chloride to total phosphorus (in triangles) on the left axis and ammonium (filled circles) on the right axis. **b** Chloride to pH (filled circles) on the left axis and bicarbonate (filled circles) on the right axis. **c** Chloride to sulfide (triangles) on the left axis and total sulfur (filled circles) on the right axis. **d** sulfide to methane on the left axis. **e** iron to total sulfur on the left axis. **f** iron to sulfide on the left axis. In blue the average chloride concentration of sea water is shown in **a, b** and **c**

as is also indicated by the correlation between both Cl and SO_4^{2-} and nutrient concentrations of NH_4^+ and P (Fig. 5). Enhanced SO_4^{2-} reduction in peat soils is also known to reduce methanogenesis (CH_4 production), as SO_4^{2-} reduction is thermodynamically more efficient than methanogenesis (Segers 1998; Smolders et al. 2002). The toxic end product of SO_4^{2-} reduction, H_2S, might even further reduce methanogenic activity. Additionally, increased ionic concentrations as a result of seawater intrusion, can temporarily enhance NH_4^+ availability due to cation exchange (i.e. Weston et al. 2006; Ardón et al. 2013; Van Dijk et al. 2015). The seawater influence along the edges of the bog might therefore not only cause osmotic stress for occurring vegetation but can also lead to enhanced competitive advantage of graminoids, trees and species like *Urtica dioica* due to nutrient mobilization, at the expense of more oligotrophic species (i.e. *Sphagnum* mosses). This effect has also been observed along the sides of the bog (Fig. 7). The ability of the bog remnant to float during storm tide reduces the influence of seawater intrusion and flooding with seawater. For the functioning and future conservation of the oligotrophic conditions characteristic for raised bogs, the ability to float during storm tide is of vital importance for the bog remnant.

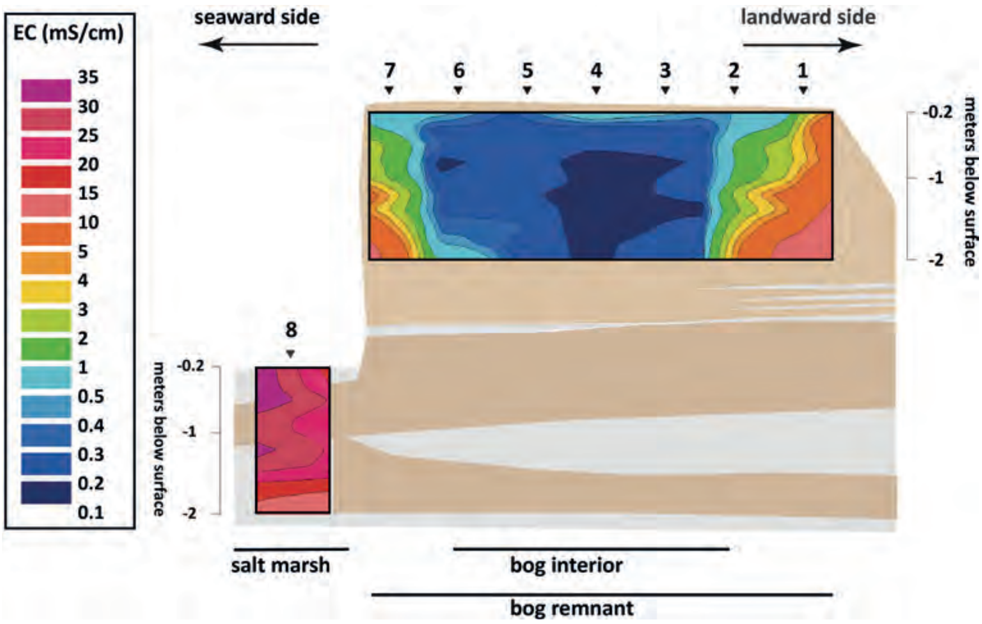

Fig. 6 Depth profile of interpolated electric conductivity measurements (in mS/cm) in the soil along a transect from location 1 to 8, (see Fig. 1)

To Float or Not to Float

The ability of an entire bog remnant to float is a special phenomenon which did occur in more coastal peatlands in the past. In literature, descriptions can be found of floating bigger or smaller bog segments, during high storm tide. During a large flood in 1509, for example, a large section of a bog floated 15 km eastward from the Dutch west side of the Dollard Estuary to German shore, carrying 12 cattle. In the 18th and 19th century observations were made of floating bogs including small wooden houses and trees (Behre 2005 and references within). The bog remnant of the present study only fully floats during high storm floods (in some winters several times; in 2006 there was a strong storm flood, splitting the bog remnant in two

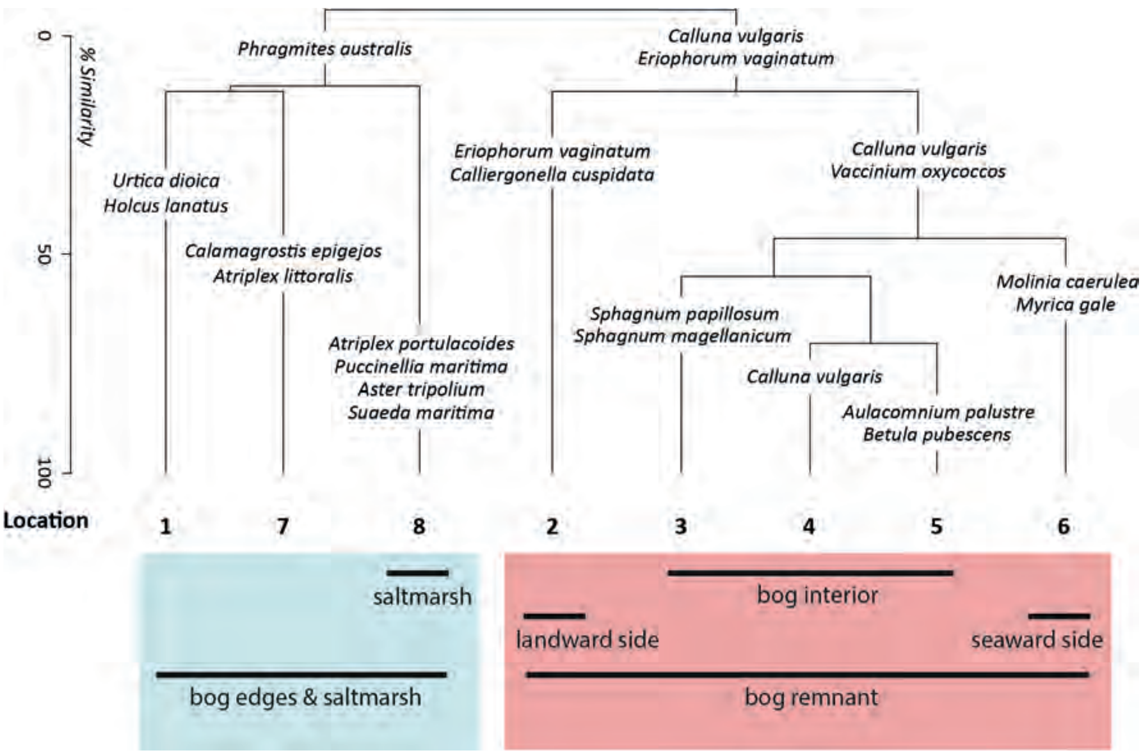

Fig. 7 Vegetation composition clustered in a dendrogram based on similarity in species occurrence. Under the figure the locations of the vegetation surveys are indicated (for locations see Fig. 1)

parts; Behre 2005 & Behre 2007b) when mean high water levels increase up to >1.6 m above average seawater level (during storm tide) (Künnemann 1941; Behre 2005). If the remnant does not float during high storm tide it will be flooded, which didn't occur so far (see Fig. 2).

The buoyancy of the bog remnant is probably caused by a combination of mechanisms and processes. First, one potential mechanisms could be the difference in densities between the freshwater in the bog peat and the seawater (1000 versus 1025 kg/m^3), as in growing, *Sphagnum*-dominated raised bogs the water content is about 95–98%, the density can be a mechanisms of influence. Secondly the buoyancy of a peat column is limited by the weight of the unsaturated peat that is compacting underlaying water saturated peat layers (e.g. Fritz et al. 2008). The extra weight from desiccation and trees can cause additional compaction, especially along the edges of the bog by increasing shear stress and potential for erosion of edges. Drainage of the entire remnant will reduce the buoyancy of the bog remnant. High water levels upon intensive rainfall, decompressed peat ('Mooratmung') and open bog-vegetation can enhance the potential to float. Thirdly the buoyancy of a peat soil is influenced by entrapped gas bubbles (Lamers et al. 1998; Smolders et al. 2002; Strack et al. 2005), which often partly consist of CH_4 originating from in-situ methanogenesis (Tokida et al. 2005). Other gasses present in bubbles in the pore water that provide buoyancy can be nitrogen (N_2) gas, carbon dioxide (CO_2) or even H_2S. Pore water CH_4 concentrations (0.5 to >1 mmol CH_4 l^{-1}) found in the present study can facilitate buoyancy (Smolders et al. 2002; Kellner et al. 2004). Methanogenesis is influenced by several factors such as temperature, pH and salinity; especially due to the presence of oxidized sulfur components in saline water (Williams and Crawford 1984; Dunfield et al. 1993; Smolders et al. 2002; Weston et al. 2006; Chambers et al. 2011; Aben et al. 2017). Bubbles are formed when pore water CH_4 concentrations are oversaturated, which is often determined by temperature, decreased air pressure and increased salinity (Strack et al. 2005; Tokida et al. 2007). Decreased air pressure during storm tide combined with flood water pressure from the edges might lead to temporary CH_4 oversaturation, bubble formation and enhanced buoyancy during storm tide. Behre (2005) has also described observations of escaping gasses from the floating peat layer during storm flood.

Enhanced salinity and its associated SO_4^{2-} enrichment might reduce methanogenesis on the bog and thereby decrease buoyancy on the longer term. Increased salinity is also found to increase hydraulic conductivity in soils, especially in peat soils due to the combined effect of pore dilation and suppressed methanogenesis (Ours et al. 1997; Hoag and Price 1997; Kettridge and Binley 2011; Van Dijk et al. 2017). One can, however, only speculate whether an altered hydraulic conductivity in salinity-affected edges of the bog will stimulate or reduce buoyancy of the bog remnant. We propose/ conclude that the low bulk density of undecomposed peat and the formation of entrapped gas bubbles (e.g. CH_4, N_2, CO_2) provide conditions for peat floatation. Sea water intrusion in contrast is likely to increase bulk density and reduce bubble formation and volume.

Deposition of Clay Layers within the Peat Body

As a consequence of the buoyancy of the bog, several small layers of so-called 'turn-up clay' (or 'Klappklei' or 'intercalated clay layer') were deposited during floating events and stabilized the peat layer underneath (Fig. 4.). In former times, this phenomenon occurred in several coastal peatlands along the North Sea coast, where bands of younger marine clay were found deposited within peat layers of older origin (i.e. Baeteman 1981; Behre 2005; Groenendijk and Vos 2013). The Sehestedt bog does not always float entirely during every high storm flood. Often, only the edges float (Behre 2005), turning them into a sort of natural levee. The peat cores in the present study underline these observations, as clay layers became thinner and fewer from the edges in to the direction of the bog interior. These clay bands were mainly deposited at the transition from minerotrophic to ombrotrophic peat soil. The location of these clay bands indicates that only the ombrotrophic part of the bog floats and that the deeper fen peat layer does not. The peat profile might easily break at the transition between the two peat layers due to differences in bulk density. When a clay layer is deposited, the ability of the peat layer underneath to float will be reduced. According to Künnemann (1941) the southernmost part of the bog had been covered with a layer of clay during a flooding event in 1914 and had not floated since then.

Where Salt Marshes and Raised Bog Meet

The impact of the combined effect of salinity, severe erosion and desiccation do not predict a bright future for the conservation of the Sehestedt Bog. The ability to float has been shown to be vital for maintaining environmental conditions for raised bog-associated species composition. It did function as a natural levee in former larger coastal bogs, protecting the bogs hinterland. Seawater intrusion during storm tides would most likely enhance erosion along the edges due to e.g. reduced buoyancy and increased peat decomposition. Behre (2005) reported that the inland edge of the bog floated less, which corresponds with the anthropogenic disturbances on this side of the bog.

On top of the impact of salinity and erosion, other factors such as enhanced atmospheric N deposition and desiccation, also threaten the conservation of vegetation communities on the bog remnant. Increased N deposition and desiccation will lead to a shift to dryer and nutrient enriched conditions with increased abundance of graminoids, trees and shrubs. The cover of trees (mainly *Betula pubescens*) has increased in the last century (in 1936 almost no trees were present on the bog remnant, Behre 2005), which could have been caused by prohibition of grazing, drainage and atmospheric nitrogen deposition (Lamers et al. 2000; Limpens et al. 2003; Tomassen et al. 2003). An increasing number of trees might deteriorate the bog by (1) enhancing evapotranspiration, (2) decreased buoyancy due to increase of weight and (3) erosion along the sides, creating cracks in the bog remnant which will enhance drainage and desiccation.

Since the Sehestedt Bog is still under direct marine influence during storm tides, it forms a unique system characterized by a gradient from a raised bog to a salt marsh. This coastal bog remnant can give a remarkable insight in the historical functioning of coastal wetlands and functions as a reference site. It is however very small and it is expected that a combination of factors including drainage, desiccation, salinization and erosion during storm tide may result in the disappearance of the remnant. Predicted future sea level rise, estimated from 0.2 to more than 1 m by the year 2100 (Vermeer and Rahmstorf 2009; Albrecht et al. 2011; Church et al. 2013) and potentially higher flood events (Rhein et al. 2013) might even accelerate the erosion of the bog. Even though it seems too late for the Sehestedt bog, this study on its biogeochemical and hydrological functioning can be used to help management of coastal bogs and peatlands to understand the impacts of future erosion, sea level rise and salinization on these systems.

Acknowledgements The authors would like to thank Rüdiger Schuhmann and Heinz-Hermann Kathmann from Nationalparkverwaltung Niedersächsisches Wattenmeer in Wilhelmshaven for granting permission to sample and for providing additional information of the area. The authors would like to thank P. van der Ven and J. Eygensteyn for assistance in the laboratory.

References

Aben RCH, N Barros, E van Donk, T Frenken, S Hilt, G Kazanjian, LPM Lamers, ETHM Peeters, JGM Roelofs, LN de Senerpont Domis, S Stephan, M Velthuis, DB Van de Waal, M Wik, BF Thornton, J Wilkinson, T DelSontro, S Kosten (2017) Cross continental increase in methane ebullition under climate change, nature communications 8, Article number: 1682, https://doi.org/10.1038/s41467-017-01535-y

Albrecht F, Wahl T, Jensen J, Weisse R (2011) Determining sea level change in the German bight. Ocean Dynamics 61:2037–2050

Ardón M, Morse JL, Colman BP, Bernhardt ES (2013) Drought induced saltwater incursion leads to increased wetland nitrogen export. Global Change Biology 19:2976–2985

Baeteman C (1981) De Holocene ontwikkeling van de westelijke kustvlakte (België). PhD Thesis. Vrije Universiteit Brussel, Faculteit Wetenschappen, Vakgroep Geologie: Brussel. 297 pp.

Bakker M, Van Smeerdijk DG (1982) A palaeoecological study of a Late Holocene section from “Het Ilperveld”, western Netherlands. Review of Palaeobotany and Palynology 36: 95–163

Behre KE (2003) Eine neue Meeresspiegelkurve für die südliche Nordsee: Transgressionen und Regressionen in den letzten 10.000 Jahren. Probleme der Küstenforschung im südlichen Nordseegebiet 28:9–63

Behre KE (2005) Das Moor von Sehestedt. Landschaftsgeschichte am östlichen Jadebusen – Oldenburger Forschungen NF 21:1–145

Behre KE (2007a) A new Holocene Sea-level curve for the southern North Sea. Boreas 36(1):82–102

Behre KE (2007b) Die Auswirkungen der Wintersturmfluten 2006/2007 auf das Sehestedter Außendeichsmoor (SO-Jadebusen). Drosera:17–24

Behre KE, Kucan D (1999) Neue Untersuchungen am Außendeichsmoor bei Sehestedt am Jadebusen – Probleme der Küstenforschung im südlichen Nordseegebiet 26: 35–64

Borger GJ (1992) Draining—digging—dredging: the creation of a new landscape in the peat areas of the Low Countries, 153–157 in Verhoeven JTA ed., Fens and bogs in the Netherlands: vegetation, history, Nutrient Dynamics and Conservation, Dordrecht

Braun-Blanquet J (1964) Pflanzensoziologie. Grundzüge der Vegetationskunde ,3. Aufl. Berlin, Wien, New York

Breathnach C, Rochefort L (2008) Revegetation of bare peat substrates: the case of a saline bog, New Brunswick. Pp. 3718–376 in proceedings of the 13th international peat congress: after wise use? The future of peatlands, volume 1: Oral presentations, Tullamore, Ireland, 8–13 June 2008. C. Farrell & J. Feehan (eds.). International Peat Society, Jyväskylä, Finland

Chambers LG, Reddy KR, Osborn TZ (2011) Short-term response of carbon cycling to salinity pulses in a freshwater wetland. Soil Science Society of America Journal 75:2000–2007

Church JA et al. (2013) Sea level change. Cambridge University press, Cambridge

Clymo RS, Hayward PM (1982) The ecology of Sphagnum. In A.J.E. Smith (ed.), Bryophyte ecology, 229–289. Chapman Hall, London

Damman AWH (1977) Geographical changes in the vegetation pattern of raised bogs in the bay of Fundy region of Maine and New Brunswick. Vegetatio 35:137–151

Dunfield P, Knowles R, Dumont R, Moore TR (1993) Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. Soil Biology and Biochemistry 25:321–326

Fritz C, Campbell DI, Schipper LA (2008) Oscillating peat surface levels in a restiad peatland, New Zealand – magnitude and spatiotemporal variability. Hydrological Processes 22(17):3264–3274

Gaffney V, Thomson K, Fitch S (eds.) 2007, Mapping Doggerland: the Mesolithic landscapes of the southern North Sea, Archaeopress, Oxford

Grasshoff K, Johannsen H (1977) A new sensitive method for the determination of ammonia in sea water. Water Research 2:516

Groenendijk H, Vos P (2013) Early medieval peatbog reclamation in the Groningen Westerkwartier (northern Netherlands). Settlement and Coastal Research in the Southern North Sea Region (SCN) 36:136–156

Hájek M, Horsák M, Hájková P, Díte D (2006) Habitat diversity of central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. Perspectives in Plant Ecology, Evolution and Systematics 8:97–91

Harpenslager SF, Van Dijk G, Kosten S, Roelofs JGM, Smolders AJP, Lamers LPM (2015) Simultaneous high C fixation and high C emissions in Sphagnum mires. Biogeosciences, 12, 4739–4749

Henriksen A (1965) An automated method for determining low-level concentrations of phosphate in fresh and saline waters. Analyst 90:29–34

Herbert ER, Boon P, Burgin AJ, Neubauer SC, Franklin RB, Ardón M, Hopfensperger KN, Lamers LPM, Gell P (2015) A global perspective on wetland salinization: ecological consequences of a growing threat to freshwater wetlands. Ecosphere 6(10):206 https://doi.org/10.1890/ES14-00534.1

Hoag RS, Price JS (1997) The effects of matrix diffusion on solute transport and retardation in undisturbed peat in laboratory columns. Journal of Contaminant Hydrology 28:193–205

Kellner E, Price JS, Waddington JM (2004) Pressure variations in peat as a result of gas bubble dynamics. Hydrological Processes 18:2599–2605

Kettridge N, Binley A (2011) Characterization of peat structure using X-ray computed tomography and its control on the ebullition of biogenic gas bubbles. J Geophys Res 116 (G01024)

Künnemann C (1941) Das Sehestedter Moor und die Ursachen seiner Zerstörung – Probleme der Küstenforschung im südlichen Nordseegebiet 2: 37–58

Lamers LPM, Van Roozendaal SME, Roelofs JGM (1998) Acidification of freshwater wetlands: combined effects of non-airborne sulfur pollution and desiccation. Water, Air, and Soil Pollution, 105, 95–106

Lamers LPM, Bobbink R, Roelofs JGM (2000) Natural nitrogen filter fails in polluted raised bogs. Global Change Biology 6(5):583–586

Lamers LPM, Falla SJ, Samborska EM, Van Dulken LAR, Van Hengstum G, Roelofs JGM (2002) Factors controlling the extent of eutrophication and toxicity in sulfate-polluted freshwater wetlands. Limnology and Oceanography, 47, 585–593

Lamers LPM, Govers LL, Janssen ICIM, Geurts JJM, Van der Welle MEW, Van Katwijk MM, Van der Heide T, Roelofs JGM, Smolders AJP (2013) Sulfide as a soil phytotoxin—a review. Front Plant Sci 4:268

Leenders KAHW (2013) Verdwenen venen. Een onderzoek naar de ligging en exploitatie van thans verdwenen venen in het gebied tussen Antwerpen, Turnhout, Geertruidenberg en Willemstad (1250–1750) Picture Publichers, Woudrichem, The Netherlands

Limpens J, Berendse F, Klees H (2003) N deposition affects N availability in interstitial water, growth of Sphagnum and invasion of vascular plants in bog vegetation. The New Phytologist 157:339–347

Meier-Uhlherr R, Schulz C, Luthart V (2011) Steckbriefe Moorsubstrate. HNE Eberswalde (Hrsg.), Berlin

Ours DP, Siegel DI, Glaser PH (1997) Chemical dilation and the dual porosity of humified bog peat. Journal of Hydrology 196:348–360

Pons LJ (1992) Holocene peat formation in the lower parts of the Netherlands. In Verhoeven JTA (ed.), Fens and bogs in the Netherlands: vegetation, history, Nutrient Dynamics and Conservation. Kluwer Academic Publishers, Dordrecht: 7–79

Reid C (1913) Submerged forests. Cambridge University Press, Cambridge

Rhein M et al (2013) Observations: ocean. Pages 255–310. In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Rysgaard S, Thastum P, Dalsgaard T, Christensen PB, Sloth NP, Rysgaard S (1999) Effects of salinity on NH_4^+ adsorption capacity, nitrification, and denitrification in Danish estuarine sediments. Estuaries 22(1):21

Segers R (1998) Methane production and methane consumption: a review of processes underlying wetland methane fluxes. Biogeochemistry 41:23–51

Smolders AJP, Tomassen HBM, Lamers LPM, Lomans BP, Roelofs JGM (2002) Peat bog restoration by floating raft formation: the effects of groundwater and peat quality. Journal of Applied Ecology 39:391–401

Smolders AJP, Lamers LPM, Lucassen ECHET, Van der Velde G, Roelofs JGM (2006) Internal eutrophication: how it works and what to do about it - a review. Chemistry and Ecology 22(2):93–111

Strack M, E Kellner JM Waddington (2005) Dynamics of biogenic bubbles in peat and their effects on peatland biogeochemistry. Global Biogeochemical Cycles, 19, GB1003

Technicon (1969) Industrial method 33–69W, nitrate + nitrite in water. Technicon Autoanalyser methodology (ed. Technicon), pp. 1–2. Technicon Corporation, Karrytown

Tokida T, Miyazaki T, Mizoguchi M, Seki K (2005) In situ accumulation of methane bubbles in a natural wetland soil. European Journal of Soil Science 56(3):389–396

Tokida T, Miyazaki T, Mizoguchi M, Nagata O, Takakai F, Kagemoto A, Hatano R (2007) Falling atmospheric pressue as a trigger for methane ebulltion from peatland. Global Biogeochemical Cycles, 21, GB2003

Tomassen HBM, Smolders AJP, Lamers LPM, Roelofs JGM (2003) Stimulated growth of Betula pubescens and Molinia caerulea on ombrotrophic bogs: role of high levels of atmospheric N deposition. Journal of Ecology 91:357–370

Van Dijk G, Smolders AJP, Loeb R, Bout A, Roelofs JGM, Lamers LPM (2015) Effects of salinization on nitrogen, phosphorus and carbon biogeochemistry of coastal freshwater wetlands; constant versus fluctuating salinity levels. Biogeochemistry 126:71. https://doi.org/10.1007/s10533-015-0140-1

Van Dijk G, Nijp JJ, Metselaar K, Lamers LPM, Smolders AJP (2017) Salinity-induced increase of the hydraulic conductivity in the hyporheic zone of coastal wetlands. Hydrological processes, https://doi.org/10.1002/hyp.11068

Van Geel B, Borger GJ (2002) Sporen van grootschalige zoutwinning in de Kop van Noord-Holland. Westerheem 51:242–260

Vermeer M, Rahmstorf S (2009) Global Sea level linked to global temperature. Proceedings of the National Academy of Sciences USA 106:21527–21532

Vos PC (2015) Origin of the Dutch coastal landscape. Long-term landscape evolution of the Netherlands during the Holocene, described and visualized in national, regional and local palaeogeographical map series. PhD thesis Utrecht University. Deltares, Utrecht / Bakhuis, Groningen, 359 p

Weston NB, RE Dixon, SB Joye (2006) Ramifications of increased salinity in tidal freshwater sediments: Geochemistry and microbial pathways of organic matter mineralization Journal of Geophysical Research, 111

Wilcox DA (1984) The effects of NaCl deicing salts on Sphagnum recurvum. Environmental and Experimental Botany 24:295–304

Wilcox DA (1986) The effects of deicing salts on vegetation in Pinhook bog, Indiana. Canadian Journal of Botany 64(4):865–874

Wilcox DA, Andrus RE (1987) The role of Sphagnum fimbricatum in secondary succession in a road-salt impacted bog. Canadian Journal of Botany 65:2270–2275

Williams RT, Crawford RL (1984) Methane production in Minnesota peatlands. Applied and Environmental Microbiology, 1266-1271