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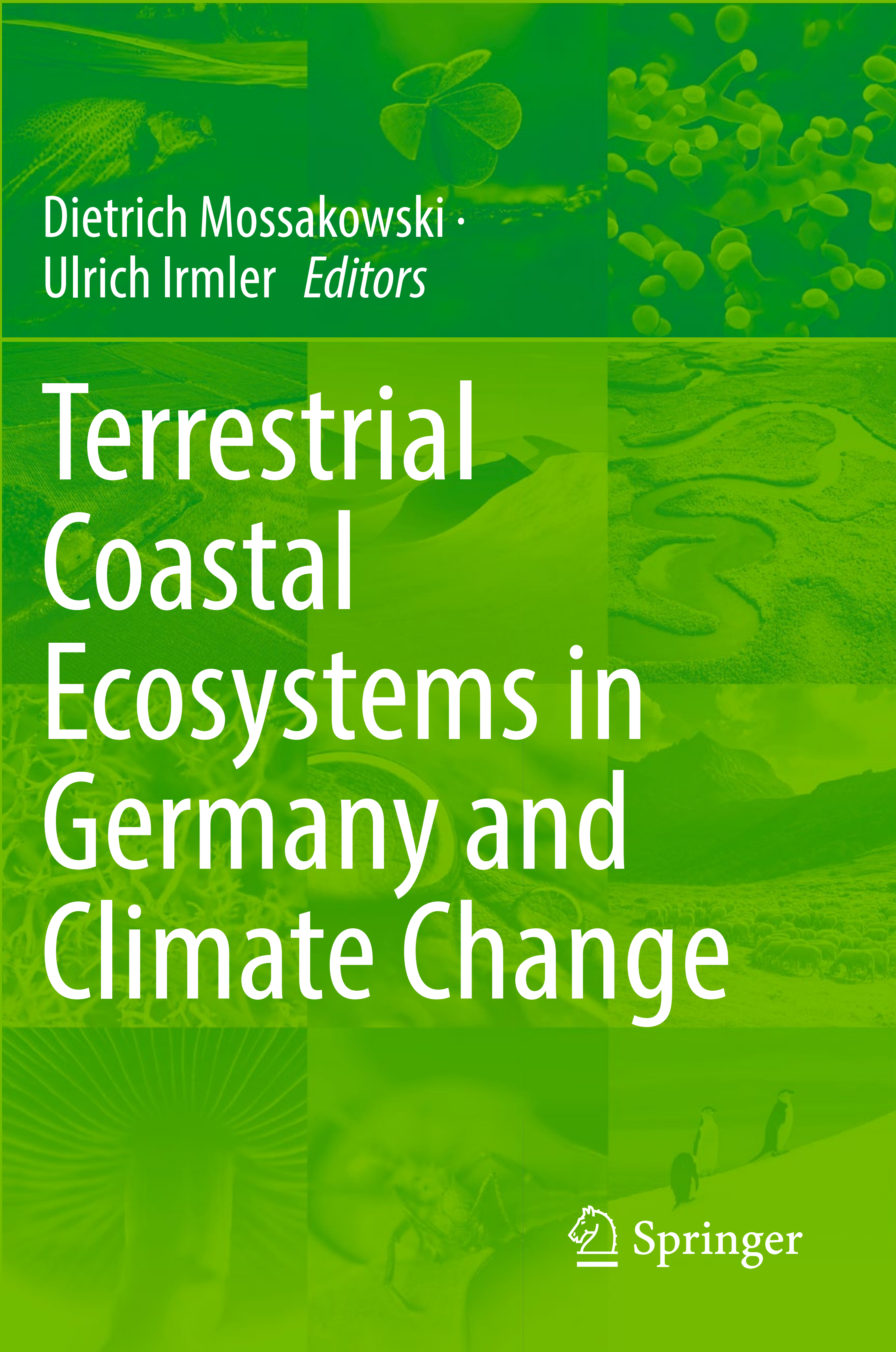

Dietrich Mossakowski ·
Ulrich Irmler *Editors*

Terrestrial Coastal Ecosystems in Germany and Climate Change

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Terrestrial Coastal Ecosystems in Germany and Climate Change

Springer

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Preface

With the beginning of the 1990s, the human impact on climate with increasing temperature and rising sea level became more evident. These severe future predictions were the motivation to initiate a large investigation program by the German Bundesministerium für Bildung und Forschung (BMBF: Ministry for Education and Research) with the aim of finding solutions to the impacts of the increasing global temperature with warmer climate also in Germany. The whole packet of scientific projects goes by the name "Klimafolgenforschung" (consequences of climate change). For the northern German states, the sea level rise was in the foreground of interest because at the coast the increase of the sea level will have extreme consequences at the usually flat coasts with adjacent plain hinterland. Thus, the Federal State of Germany represented by the BMBF started together with the four northern countries, Lower Saxony, Bremen, Schleswig-Holstein, and Mecklenburg-Vorpommern, a scientific program: Consequences of the climate dependent impacts on non-regenerable ecosystems at the North and Baltic Sea coast. Finally, scientific groups of the four universities, University of Oldenburg, University of Bremen, University of Kiel, and the University of Greifswald, formed a scientific network with the aim of investigating the increase of temperature and the sea level rise in the coastal ecosystems that include plants, vegetation, soils, and faunal elements. Overall, ten research groups were partners in this network that lasted three years from 1997 to the end of 1999.

The philosophy of ecosystem research was the background for the selection of the individual scientific projects. On the one hand, at least most important elements of coastal ecosystems should be reflected by the research. On the other hand, the two gradients developed at the coast should be included: the west–east gradient that also represents a climate gradient with a warmer and moister Atlantic climate in the West and a dryer, more continental climate in the East and the elevation gradient from the sea level to higher elevations on differently formed coastal ecosystems. Additionally, the North and the Baltic Sea differed tremendously by the environmental factors: North Sea with expressed tides and the influence of partly enormous west winds and Baltic Sea without remarkable tides and influenced more by eastern winds. As the large area and variety of ecosystems on both coasts makes it impossible to investigate all parts of the coasts in high extensities, the working groups agreed to exclude beaches from their projects and to concentrate on salt grassland and on dunes. As coastal ecosystems were already in the focus of the research groups before this investigation started, only those parts should be considered which were not studied before. The research should:

1. Reflect the west–east changes with respect to the temperature increase and the potential extinction or invasion of plants and animals
2. Focus on the changes of the elevation gradient and the differences between the North Sea and the Baltic Sea
3. Also consider results from experimental studies to support and explain ecological results from field studies
4. Also investigate solutions to avoid harmful consequences for the foreland biocenoses at both coasts, e.g., is de-embankment a practical solution to help foreland plants and animals to survive
5. Exclude beaches and cliff coasts because it would blast the financial potential of the project
6. Also exclude problems of grazing because these impacts were studied already sufficiently in former research networks (e.g., research to the National Park of the Wadden Sea)

In addition to the results found by the abovementioned research network, few chapters are included that were not directly part of projects. They complete some aspects of historical changes, in particular, if datasets are needed that also include data from long-term investigations.

Unfortunately, after finishing the project with the usual final reports, some responsible scientists passed too early or became sick, which prevents the intention to quickly realize a comprehensive book with the main results of the scientific network. Therefore, we are grateful to Springer for giving us now the opportunity to publish the results in the series *Ecological Studies*. Additionally, we are much obliged to the German BMBF and the four northern German states for the financial support as well as the four universities to give us the needed equipment for the research, such as cars, laboratories, or facilities for the experiments. Many official agencies helped us with data or permissions for field studies necessary for our research, e.g., sea levels for both coasts, temperature data in the past, or projections of climate development in the study area. These were Lower Saxony Service for Water Economy and Coastal Preservation (NLWK), Norden, gauge data of the coast between Bremen and Cuxhaven provided by Johannes Chittka (NLWKN, Stade), of the North Sea coast in Schleswig-Holstein by bureau of rural areas, Büsum, for the Baltic Sea coast of Schleswig-Holstein by the Agency for Water and Shipping Affairs, Lübeck, of the Baltic Sea coast near Greifswald by the Federal Agency for Sea Shipping and Hydrography (BSH), Rostock, German Weather Service, and the administrations of the National Parks “Niedersächsisches Wattenmeer,” “Schleswig-Holsteinisches Wattenmeer,” “Vorpommersche Boddenlandschaft.”

Our sincere thanks are also due to the following colleagues: Ralph Annutsch (BSH, Hamburg) and Hans von Storch (MPI for Meteorology, Hamburg) for providing and helping with the prediction of climate change scenarios, Susanne

Armstrong (ABG), Stefan Beese (Nationalpark Mecklenburg-Western Pomerania), Thomas Buss (Amt für Wasserwirtschaft, Abteilung Hochwasserschutz, Planung WS 31, Hamburg), Maartens Jans (team investments—Seascheldt division, Antwerpen: sigmaplan, Begique), StALU Vorpommern, Greifswald, pers. comm. 2011 for information on de-embankment sites, Heinz-Christian Fründ for detailed information on his study sites, Matthias Grünwald and Julien Pétillon for providing their original data, and Günter Mühlner (Untere Naturschutzbehörde Kreis Wesermarsch) for information on Kleinensieler Plate. Heinrich Krummen, Jaderberg, for providing the basics of the maps indicating the study sites at Borkum and Wangerooge. Hans-Bert Schikora for the identification of spiders from Mellum and Wursten Coast. Dipl. Ing. Raimund Kesel to provide his leveling data of Wursten Coast. Hans Turin for his kindness to allow the use of his distribution maps, Stephan Gürlich for allowance to use his Estuary-Elbe-Maps, and to Mieczysław Stachowiak who kindly entrusted us his point maps of Polish *Pogonus* species.

Furthermore, many institutes of the four universities helped with their equipment but were not partners in the research network.

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November 2021

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Part I

Introduction and Description of Study Area

1 Introduction

Gerhard Weidemann, Ulrich Irmler, and Dietrich Mossakowski

Abstract

Coastal zones at the German North Sea and the Baltic Sea were essentially caused by climate changes in the past. Humans have affected the dynamics of these systems by coastal protection and land reclamation. The salt marshes are regarded as one of the most natural ecosystems in Central Europe. At the same time, their function for coastal protection is in danger. As well as dunes, they are characterised by extreme abiotic conditions for plants and animals. Changes of abiotic conditions induced by climate change will affect the function and ecosystem services of coastal ecosystems, i.e. primary production, mineralisation, and soil development. These functions will especially affect the social subsystem, since the usability of the ecosystems for agriculture, coastal protection, water extraction, and tourism is directly concerned.

Author "Gerhard Weidemann" has died before the publication of this book.

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The changes of coastal zones at the German North Sea and the Baltic Sea are generated by the Holocene transgressions and coast-forming processes, which were essentially caused by climate changes in the past. Humans have affected these dynamics by coastal protection and land reclamation projects for almost 1000 years (Behre 1993). Human settlement has adapted to the ecological systems, but also depends on them. Due to current climate changes, shifts in these systems will hence affect the socio-economic system as well (Schernewski et al. 2011). Therefore, knowledge about climate-dependent changes of the biotic communities and ecosystems at our coasts is of elementary interest as a prerequisite for predictions.

Climate change is amplified by humans and is primarily caused by increased CO_2-concentrations in the atmosphere, reinforcing the greenhouse effect, which results in a temperature rise. As a consequence, the sea level rises due to the melting of glaciers and ice caps (eustatic effect) and a thermal extension of the seawater (steric effect) (Sterr 1998a). Further relevant effects on the climate include seasonal changes of temperature and precipitation, a change of main wind directions and velocities, and an increase of extreme weather situations, e.g. storms and heavy rains (Sterr 1998b; IPCC 2001). In consequence, main coastal morphological processes, such as erosion and sedimentation, may change (e.g. Hofstede 2011; Bobertz et al. 2005). How single components of climate change or the whole climate complex will affect supralittoral communities may be deduced from the specific conditions to which they are adapted.

Salt marshes are semi-terrestrial biotopes of surf-protected areas with silty, peaty, or sandy sediments, which are frequently inundated by salt water. Therefore, they are inhabited by highly specialised biota, which are more or less tolerant against flooding and salt (Ranwell 1972; Packham and Willis 1997). Under natural conditions, salt marshes and salt meadows are zonal ecosystems that are determined by flooding and salt drift. At the North Sea, the extent of the zones depends on the frequency and altitude of the tides that govern the duration of floods and the concentration of salt. In addition, storm surges are of high importance. At the Baltic Sea coast, where tides are not existent or without relevance, wind or irregular storm events alone effect flooding and salt content. The decline of salt in the west-east gradient of the Baltic Sea changes the salt marshes from salt meadows with biota similar to the North Sea to nearly fresh water conditions as found on the grassland of the hinterlands. Due to the utilisation of these habitats and their limited extension, they are severely endangered. Today, the salt marshes are regarded as one of the most natural ecosystems in Central Europe. At the same time, their function for coastal protection is also in danger.

Living conditions in dunes are also characterised by extreme abiotic conditions (Ranwell 1972; Boorman 1977; Packham and Willis 1997). The main factor in this regard is wind, which causes high substrate mobility especially in early phases of dune development. Salt is transported by wind into the dune area in decreasing intensity with increasing distance from the beach. Dunes are exposed to strong insolation that is combined with a low water holding capacity and sand instability, which leads to extreme hydrological conditions with frequent drying of the surface-near layer. Accordingly, coastal dunes are inhabited by a stress-adapted community, which tolerates substrate movement and sanding-up as well as a lack of nutrients and frequent dryness. Due to their geomorphologic activity and biotic regeneration potential, young dunes, in particular, are highly dynamic ecosystems. Older dunes, too, have a high regeneration potential under natural conditions. Coastal salt marshes and salt meadows as well as coastal dunes are of great relevance for both nature and coastal protection. Thus, the question must be raised concerning the effects that an accelerated climate change has on these ecosystems.

Due to sea level rise, the loss of coastal areas mainly depends on the speed of such changes and whether the accretion of salt marshes will keep pace with them or not. The succession of this process is also dependent on the chance to move further inland, which is only possible if the sea dikes are shifted further inland. Additionally, the involved organisms need broad tolerance amplitudes, or adapted ecotypes must evolve to cope with the fast change of ecological conditions.

The increase of storms will presumably lead to increased erosion and mobilisation of dunes. The translocation and regeneration of dunes depend on material supply and on the contribution of the biotic community to sand stabilisation (Koehler and Weidemann 1995), in particular, if higher CO_2 concentrations and temperatures intensify the growth of dune plants.

Finally, climate change may affect the geographic distribution of plants and animals. At the moment, it is hardly possible to assess what consequences this may have for the structure and function of coastal communities.

The hypothesised consequences of climate change on the biological systems of the German coasts have been studied in a compound research project, which intended to answer the following questions:

- Will a restructuring of the communities occur within habitats or will existing habitats pass through a translocation?
- How do both distribution areas and zones of plant and animal species, respectively, shift if the assumed climate change will occur according to the scenarios defined in Chap. 2?
- What do the distributional or zonal shifts mean for the ecosystems, and how will the ecosystems react to these shifts?
- How will the composition of the communities change and how will this change impact the ecosystems?
- What consequences are needed for the utility and protection of coastal habitats regarding these potential changes?

These superior questions were subdivided into subcomponents, each studied by two different approaches: (1) a comparative geographic approach and (2) experimental ecological analysis. We performed the geographic analyses by comparing the actual distribution of coastal plants and selected animal taxa in a west-east climate gradient with historic information on their distribution. Using this approach,

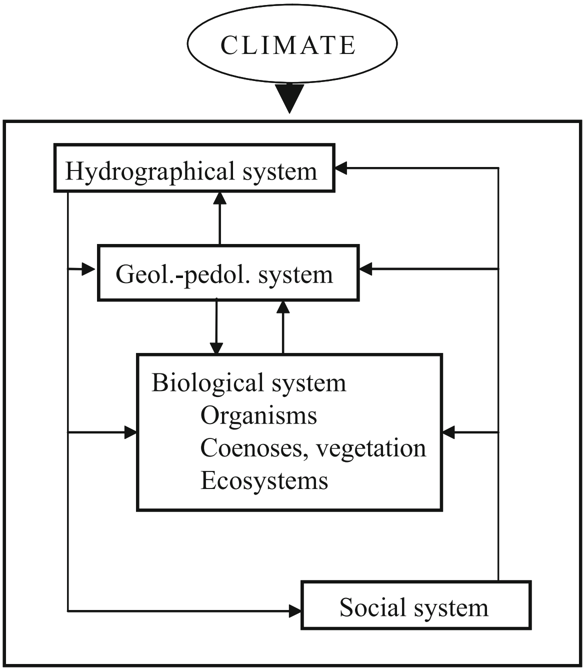

Fig. 1.1 The coastal system and subsystems as a background for the presented studies. Modified after: Forschungsleitplan 1994 (BMBF and Norddeutsche Länder 1994)

distributional shifts in the past were detected and expected shifts in the future assessed. The experimental approaches concentrate on the analyses of the consequences (1) of the sea level rise due to the extension of zones in the salt meadows under tidal and non-tidal conditions and (2) of the increase of extreme weather events and temperature, e.g. on the population of single species, on the vegetation, and on ecosystem processes like nutrient turnover, biogenic sand stabilisation, and soil development. The synthesis of the findings will enable an estimation of the consequences of accelerated climate change on the coastal ecosystems, i.e. on salt marshes and dunes, which are the basis for predictions and recommendations for planning coastal management in the future.

The concept of the compound project was described in the *General Research Plan of the Joint Project "Climate Change and Coast" of the Ministry of Research and the Northern German Coastal States/Forschungsleitplan zum Verbundvorhaben "Klimaänderung und Küste" des Bundesministeriums für Forschung und Technologie und der norddeutschen Küstenländer* (BMBF and Norddeutsche Länder 1994). According to this plan, the coastal systems are subdivided into hydrographical, geo-pedological, biological, and socio-economic subsystems. Between these functional subsystems, interrelations of different intensity exist. They are directly and indirectly affected by external climatic factors. The biological subsystem, which is the focus of the present project, was analysed on different levels of integration that are affected by the other subsystems as well as by climate (Fig. 1.1).

The predicted climate change will primarily affect organisms of the supralittoral coastal ecosystems. Increased and longer-lasting salt stress, increased temperatures, changed redox conditions, and heavier mechanical stress due to changed currents, wind, and sedimentation conditions will strain their ecological plasticity and adaptability. These factors affect competition ability and lead to the restructuring of the communities. This can be well observed, in particular, in the vegetation, since it distinctly forms the character of the landscape.

Furthermore, species may disappear if their tolerance limits have been exceeded, while other species that benefit from the new living conditions may immigrate or extend their range. These are important aspects for nature conservation. Finally, changes of abiotic conditions and the composition of biotic communities will affect the function and ecosystem services of coastal ecosystems, i.e. primary production, mineralisation, and soil development. These latter functions will especially affect the social subsystem, since the usability of the ecosystems for agriculture, coastal protection, water extraction, and tourism is directly concerned.

References

Behre K-E (1993) Die nacheiszeitliche Meeresspiegelbewegungen und ihre Auswirkungen auf die Küstenlandschaft. In: Schellnhuber HJ, Sterr H (eds) Klimaänderung und Küste. Springer, Berlin, pp 57–76

Bobertz B, Kuhrts C, Harff J, Fennel W, Seifert T, Bohling B (2005) Sediment properties in the western Baltic Sea for use in Sediment transport modelling. J Coast Res 21:588–597

Boorman LA (1977) Sand-dunes. In: Barnes RSK (ed) The coastline. Wiley and Sons, Chichester, pp 1561–1197

BMBF, Norddeutsche Länder (1994) Forschungsleitplan zum Verbundvorhaben "Klimaänderung und Küste" des Bundesministeriums für Forschung und Technologie und der norddeutschen Küstenländer

Hofstede J (2011) Climate change and the need for integrated coastal risk management in the Baltic Sea. In: Schernewski G, Hofstede J, Neumann T (eds) Global change and Baltic Costal Zones. Springer, Dordrecht, pp 93–102

IPCC (2001) Climate change 2001: impacts, adaption an vulnerability, 3rd edn. Cambridge University Press, Cambridge

Koehler H, Weidmann G (1995) Biogenic dune sand stabilization. In: Van Dijk HWL, Hurkmans WEG (eds) Management and preservation of coastal habitats. EUCC, Leiden, pp 83–98

Packham JR, Willis AJ (1997) Ecology of dunes, salt marsh and shingle. Chapman and Hall, London

Ranwell DS (1972) Ecology of salt marshes and dunes. Chapman and Hall, London

Schernewski G, Hofstede J, Neumann T (2011) Global change and Baltic Costal Zones. Springer, Dordrecht

Sterr H (1998a) Auswirkungen auf den Meeresspiegel. In: Lozan JL, Graßl H, Hupfer P (eds) Warnsignale Klima. Wissenschaftliche Auswertungen, Hamburg, pp 201–206

Sterr H (1998b) Gefährdung in den Küstenregionen. In: Lozan JL, Graßl H, Hupfer P (eds) Warnsignale Klima. Wissenschaftliche Auswertungen, Hamburg, pp 248–253

Climate Changes Along the German Coast

2

Michael Schirmer and Gerhard Weidemann

Abstract

The present coastal zones have been developed under specific climate, sea level and human activities. A changing climate will alter these mechanisms and dynamics and result in new physical, ecological and social conditions. IPCC tries to assess the changes to be expected due to rising greenhouse gas concentrations in its IPCC Reports. The research presented here is based on a compilation of climate change descriptors referring to the Second Assessment Report (1996). It defines three scenarios with 380 (standard) and 450 and 550 ppmv CO_2 in 2050 including estimations of mean temperature, sea level, tidal range, wind speed, duration and frequency of storm surges and precipitation in winter. In 2000, IPCC defined and published a new set of four emissions scenarios (A1, A2, B1, B2) which were used in the following Third and Fourth Assessment Reports (TAR 2001) and (AR4 2007), respectively. A comparison with our descriptors defined in 2000 reveals only minor differences and confirms the validity of our approach (Table 2.3), esp. with regard to the persisting trend matching the "worst case-scenarios". A downscaling by Klimabuero in 2011 confirmed similar prospects for the Baltic Sea and the North Sea.

Author "Gerhard Weidemann" regrettably has died before the publication of this book.

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2.1 Climate Change Assessments and Scenarios of the Year 2000 (IPCC 2nd Assessment Report)

The existent coastal zones are the outcome of former climate changes and their consequences, i.e. the resulting Holocene transgression and the subsequent processes that formed the coastal regions. For almost 1000 years, humans have interfered with these dynamics through activities such as coastal protection and land reclamation. The pattern of utilisation is adapted to the structure of these particular ecosystems, but also depends on them. Therefore, changes of the biological systems induced by climate change will also influence the socio-economic systems. Thus, knowledge of changes of coastal systems induced by climate is of increasing interest as a prerequisite for future prospects.

Climate change is a natural process enhanced by human activities. Human impact is primarily driven by an increase of CO_2 and other “greenhouse” gas (GHG) concentrations in the atmosphere. The reinforcement of the greenhouse effect, thus, results in an increase of temperatures. As a consequence of natural and human impacts, an increase of the sea level is triggered by melting glaciers and ice caps (eustatic effect) as well as by thermic expansion of marine water bodies (steric effect) (Sterr 1998a). As additional relevant consequences, Sterr (1998b) mentioned seasonal changes in temperature and precipitation, changes in the main direction of winds and their forces and an increase of extreme weather conditions like storms and heavy rains. In consequence, important components of processes that form coastal morphology, such as erosion and sedimentation, may alter. The estimates of climate scenarios published by the IPCC (1996; 2nd Assessment Report) in combination with their regional downscaling (von Storch et al. 1998) were taken as a baseline for field experiments and for the interpretation of the findings of our research groups (Table 2.1).

Table 2.1 Estimates made in 2000 for the year 2050: conditions under the assumption of secular trends and two different scenarios with human impact

	Secular trend	Human impact	
		Conservative estimate	High estimate
Scenarios	Standard	Scenario I	Scenario II
CO_2	380 ppmv	450 ppmv	550 ppmv
Temperature, annual mean	As nowadays	+1.5 K	+2.5 K
Sea level (mean height)	+15 cm	+35 cm	+55 cm
Tidal range	+10 cm	+ 20 cm	+30 cm
Wind/storms	As nowadays	+ 5%	+10%
Storm surges, duration and frequency	As nowadays	+10%	+15%
Precipitation in winter	As nowadays	+8%	+15%

Vestergaard (1997) published data for the Danish Baltic Sea coast. His estimates note an increase of the sea level by about 33–46 cm, a temperature rise of 2–5 K in winter and 1–3 K in summer and an increase of precipitation of 0–20%. Changes in wind conditions are of particular importance because the water level changes on the Baltic Sea coast are determined nearly exclusively by wind. Therefore, an increase of severe wind events by 10% and a possible change in wind direction will result in a higher frequency of inundations of flat shores and in more intensive erosion as well as material transport (Sterr 1993).

2.2 Climate Change Science: According to the State of the Art in 2011 (IPCC 2007, AR4 and Beyond)

Knowledge of climate change, its physical basis, expressions and impacts has considerably improved since the publication of the Second Assessment Report (SAR) in 1996 (IPCC 1996), on which the downscaling by von Storch et al. (1998) was based, at least in part. It referred to the IS92 emissions scenarios, which had been formulated in 1992. In the year 2000, IPCC defined and published a Special Report on Emissions Scenarios (SRES) (IPCC 2000) with a new set of emissions scenarios comprising a much wider range of possible greenhouse gas (GHG) emissions and a very complex set of possible technological and societal developments, resulting in a set of 40 storylines within four “families”.

The four families can be presented as follows (from Wikipedia):

A1. The A1 scenarios presuppose a more integrated world. They are characterised by:

- Rapid economic growth.
- A global population that reaches 9 billion in 2050 and then gradually declines.
- The quick spread of new and efficient technologies.
- A convergent world, i.e. income and way of life converge between regions. Extensive social and cultural interactions worldwide.

There are subsets to the A1 family based on the technological emphasis:

- A1FI has an emphasis on fossil fuels.
- A1B has a balanced emphasis on all energy sources.
- A1T has an emphasis on non-fossil energy sources.

A2. The A2 scenarios assume a more divided world. They are characterised by:

- A world of independently operating, self-reliant nations.
- Continuously increasing population.
- Regionally oriented economic development.
- Slower and more fragmented technological changes and improvements to per capita income.

B1. The B1 scenarios presuppose a world that is more integrated and more ecologically friendly. The B1 scenarios are characterised by:

- Rapid economic growth as in A1, but with rapid changes towards a service and information economy.
- A population rising to 9 billion in 2050 and then declining as in A1.
- Reductions in material intensity and the introduction of clean and resource efficient technologies.
- An emphasis is placed on global solutions to economic, social and environmental stability.

B2. The B2 scenarios assume a world that is more divided, but more ecologically friendly. The B2 scenarios are characterised by:

- A continuously increasing population, but at a slower rate than in A2.
- An emphasis on local rather than global solutions to create economic, social and environmental stability.
- Intermediate levels of economic development.

These actual SRES scenarios represent the uncertainties about future emission rates, the physical system and the driving forces. The Third Assessment Report (TAR; IPCC 2001) and the Fourth Assessment Report (AR4; IPCC 2007) use the SRES scenarios.

A comparison of the scenarios of the Second AR and of AR4 reveals the following differences:

- Atmospheric CO_2:
  - By 2010, the average atmospheric CO_2 concentration rose to ca. 390 ppmv (Dec. 2010) (co2now 2010) from ca. 361 ppmv in 1989, when v. Storch et al. (1998) published their downscaling.
  - This corresponds roughly to an increase by 13 ppmv per decade and would lead to ca. 440 ppmv CO_2 by 2050 if extrapolated linearly.
  - Between 1995 and 2005, the decadal increase rose to 19 ppmv and would lead to ca. 465 ppmv CO_2 by 2050 if extrapolated linearly (AR4, p. 2).
- Average global air temperature:
  - Best estimates for global average surface temperatures in 2090–2099 now range from +1.8 K (B1 scenario) to +4.0 K (A1FI scenario) (AR4, WG1 Table SPM.3, p. 13).
  - Using AR4 Fig. SPM.5, surface temperatures in 2050 could increase by +0.9 to +1.4 K (best guess +1.2 K) for the B1 scenario or by +2.4 to +6.4 K for the A1FI scenario (best guess +2.8 K).
  - Atmospheric 450 ppmv CO_2 equivalents (sum of GHG's) correspond to a best guess equilibrium surface temperature increase by +2.1 K, 550 ppmv to +2.9 K (IPCC 2007, Table 10.8) (*nota bene*: referring to the radiative forcing of CO_2 alone would reduce the temperature increase by ca. 0.5 K).

- Klimabuero (2011): Period 2036–2065:
  - *Nota bene*: downscaling is based on 12 different model runs using the SRES scenarios A1B, A2, B1 and B2 (the fossil intensive scenario A1FI ("worst case") was not included in the calculations).
  - North Sea coast: annual mean (reference period: 1961–1990): +1 K to +2 K (best guess: +1.6 K); summer: +1.1 K to +1.8 K.
  - Baltic coast: annual mean (reference period: 1961–1990): +1.1 to +2.3 K (best guess: +1.6 K); summer: +1.1 K to +1.8 K.
- Sea level:
  - IPCC 2007 calculates 20–80 cm higher sea levels for 2100 than today (with low to moderate contributions by melting glaciers).
  - An IPCC "Workshop on Sea Level Rise and Ice Sheet Instabilities" in 2010 (Stocker et al. 2010) stated that it is still too early to model future sea levels more precisely.
  - At present, global mean sea level rises are calculated with ca. 41 mm/year, hence >41 cm/100 years (satellite measurements) (Nerem et al. 2010).
  - A similar trend is documented for the German Bight, where the mean Tidal High Water rose between 1950 and 2005 with a rate of 41 cm/100 years (Jensen and Mudersbach 2007) (*nota bene*: this includes ca. 10 cm isostatic subsidence).
  - Assessments drawing on other calculations present higher values, e.g. Deltakommissie (2008): +0.2 to +0.4 m in 2050; Copenhagen (2009): at least double IPCC 2007 values, e.g. for the A1FI scenario >0.26 to >0.60 m in 2050; UK Climate Projections (UKCP 2009) estimates ca. 0.4–0.8 m by 2050 (High++ scenario).
  - In general, the sea level of the Baltic Sea has been following the upward trend of the North Sea level (Jensen and Mudersbach 2007) and will probably do so in the future (Zorita et al. 2010).
  - Further trends in the Baltic will strongly be subjected to changing precipitation patterns within the Baltic Sea catchment and postglacial isostatic processes (upward lift).
- Tidal range, wind/storms, storm surge durations and frequency, precipitation in winter:
  - A considerable increase of the tidal range due to greater coastal water depths has been documented by Jensen and Mudersbach (2007) and Schirmer (2010) for the German Bight.
  - Klimabuero (2011) estimates an increase of average wind speed for 2036–2065 (North Sea) in winter by −2% to +4% and 0% to +3% in autumn (*nota bene*: the "worst case" scenario A1FI is not included!) (Baltic coast winter: −1% to +4%, autumn 0% to +4%).
  - Maximum winter storm speed is estimated to change by −2% to +4% as well (0% to +3% in autumn) (Baltic coast winter: −1% to +4%, autumn +0% to +4%).
  - Stormy days may increase by −0.6% to +1.7% (winter) resp. 0% to +1.6% (autumn) (Baltic coast winter: −0.4 to +1.2, autumn +0.2 to +2 days).

Table 2.2 Compilation of calculated (scenario-based) and extrapolated trends and values for future sea levels (Mean Water MW) and Tidal High Water (MThw) in the Southern North Sea by 2050 (according to Schuchardt et al. 2008)

Source	Scenario/Data source	Parameter	Rise by 2050 (m)
IPCC (2007)	B1 (global)	MW	0.09–0.19 + x[a]
IPCC (2007)	A1B (global)	MW	0.11–0.24 + x[a]
IPCC (2007)	A1Fl (global)	MW	0.13–0.30 + x[a]
Rahmstorf and Richardson (2007)	3.4 mm/year per 1 °C increase (global)	MW	B1: 0.19–0.50 A1B: 0.29–0.75 A1Fl: 0.41–1.09
Jensen and Mudersbach (2007)	Time series of six German coastal gauges (linear extrapolation, basis 1950–2005)	MW	0.07–0.10
Jensen and Mudersbach (2007)	Ditto	MHW	0.21

[a] Unknown allowance for glacier melt

- Storm surge durations and frequency will probably increase in autumn and winter as compared to today, quantification being very limited: von Storch and Claußen (2009) estimate +30 to +110 cm storm surge heights by 2100, thus about +55 cm by 2050; up to now, an increase of storm surge duration and frequency is very likely but not calculable.
- Winter precipitation in North Germany will increase by +8% to +35% by 2050 (in summer +3% to −8%).

Table 2.2 provides a compilation of several recent estimations of possible sea levels in 2050.

2.3 Are the Climate Change Scenarios of 1998/2000 Still Valid and Applicable in 2010?

In general, the climate change assessments published by IPCC (2007) and other sources thereafter resulted in higher temperature and sea level calculations for the year 2100 than in the Second IPCC Report published in 1996 (IPCC 1996). Any climate change, however, still depends on the rate and amount of greenhouse gases emitted into the atmosphere. Therefore, we still have to formulate possible scenarios when assessing climate change impact as has been done in the beginning of this research project at the end of the 1990s. In the meantime, however, it has become

Table 2.3 Compilation of climate change descriptors defined in 1998 and 2010

	2010	Assessments as of 1998	
	Mean 2050, assessments as of 2010	Conservative estimate 2050	High estimate 2050
Scenarios		Scenario I	Scenario II
CO_2	440–465 ppmv	450 ppmv	550 ppmv
Temperature, annual mean	+1.2 to 2.8 K	+1.5 K	+2.5 K
Sea level (mean height)	+20 to +60 cm	+35 cm	+55 cm
Tidal range	No new data	+20 cm	+30 cm
Wind/storms	+4%	+5%	+10%
Storm surges, duration and frequency	Increase certain but not quantifiable	+10%	+15%
Precipitation in winter	+8% to +35%	+8%	+15%

evident that GHG emission rates are moving to the higher ("worse") SRES scenarios. Assuming that the physical basis for calculating global temperature from GHG concentrations (e.g. the radiative forcing) was and is still valid, we have to check for the proper labelling of a "conservative estimate" and a "high estimate" in 2050 (the "standard scenario" without human impact (Table 2.1) remains fixed). Table 2.3 combines the 1998 estimates for 2050 with the current 2010 state of climate change science.

Regarding Table 2.3, we must realise that the changes of climate and climate-dependent parameters formulated in 1998 are still consistent with the assessments of 2010. As far as parameters are quantified, the Conservative Scenario I describes a fairly moderate change of the future situation with a high degree of probability. It represents changes predicted by the B1, A1T, B2 and A1B scenarios, which is probably the most favourable scenario that can be reached after the disappointing results of the World Climate Congresses in Copenhagen 2009 and Cancun 2010.

The High Estimate Scenario II is still within the range of future climate change assessments; however, not as "high" and pessimistic as seen in 1998, but still appropriate to assess the impacts of a pronounced climate change on our coastal ecosystems.

2.4 The Climate Future of the German Coasts from the 2011 Perspective

As demonstrated above, the dimension of global climate change in the German coastal regions along the North Sea and the Baltic Sea still depends on the further accumulation of greenhouse gases in the atmosphere. The results of the downscaling published by the Norddeutsches Klimabuero (2011) show a fairly uniform shift in the average temperatures in the North Sea and the Baltic Sea coastal regions for 2036–2065 (3 decades centred around 2050). The fossil intensive scenario A1FI ("worst case"), however, was not included in the calculation. Regarding that the

Table 2.4 Maximum differences of seasonal mean temperatures and precipitation for 2036–2065 and 2071–2100 (Klimabuero 2011)

Region	North Sea Coast		Baltic Sea Coast	
Period	2036–2065	2071–2100	2036–2065	2071–2100
ΔT summer	+1.8 K	+4.8 K	+1.8 K	+5 K
ΔT winter	+2.8 K	+4.4 K	+3 K	+4.8 K
Δ precipitation summer	+5%	−43%	+2%	−38%
Δ precipitation winter	+30%	+51%	+39%	+64%

actual global emission rates are soaring and run along the highest SRES rates (and that the World Climate Conferences in Copenhagen and Cancun did not decide on any effective measures), we must assume that future temperatures, precipitation and the sea level rise will follow the upper values presented by the Klimabuero (2011).

Table 2.4 lists the upper values published by the Klimabuero (2011) separately for the North Sea and the Baltic Sea coasts, summer and winter and for 2050 (2036–2065) and 2085 (2071–2100).

On a long-term scale, it becomes evident that, based on the actual state of the art in downscaling, the medium- (2050) and long-term (2100) pessimistic assessments of climate change show a near-exponential increase in average temperature and a differentiated gradient. Until 2050, the actual trends continue, with winter temperatures rising faster than summer temperatures and winter precipitation increasing strongly.

These trends are very similar for the North Sea and the Baltic region. Regarding their water mass budgets, however, the enclosed Baltic Sea will react stronger to climate change than the open North Sea: the increase in winter precipitation and river discharge will probably provoke lower salinity in winter and spring and higher salinity in summer and autumn due to evaporation. On the other hand, the cold winters of 2009/10 and 2010/11 may signal a high variability of seasonal weather patterns with extreme events still possible.

Recent modelling of the consequences of the rapid decline of the arctic sea ice cover for the Northern European weather patterns (Petoukhov and Semenov 2010) shows that a distinct winter cooling is possible, if not probable, as an iceless arctic ocean feeds more energy into the atmosphere and displaces the traditional circulation patterns, favouring the transport of very cold Siberian air masses into Northwest Europe.

References

Cancun (2010) Report of the Conference of the Parties on its sixteenth session, held in Cancun from 29 November to 10 December 2010 https://unfccc.int/sites/default/files/resource/docs/2010/cop16/eng/07.pdf. Accessed Sept 2022

co2now (2010) What the world needs to watch. http://co2now.org/Current-CO2/CO2-Now/. Accessed Feb 2011

Copenhagen (2009) The Copenhagen diagnosis–updating the world on the latest climate science. In: Allison I et al (eds) The University of New South Wales Climate Change Research Centre (CCRC), Sydney, Australia. http://www.ccrc.unsw.edu.au/Copenhagen/Copenhagen_Diagnosis_HIGH.pdf. Accessed Jan 2011

Deltakommissie (2008) Working together with water–findings of the Deltakommissie. http://www.deltacommissie.com/doc/deltareport_full.pdf. Accessed Jan 2011

IPCC (1996) In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) Climate change 1995. Cambridge University Press

IPCC (2000) Emissions Scenarios. Nakicenovic N, Swart R (eds) IPPC special reports. Cambridge University Press, UK. http://www.ipcc.ch/ipccreports/sres/emission/index.php?idp=0. Accessed Jan 2011

IPCC (2001) Climate change 2001: impacts, adaptation and vulnerability. Cambridge University Press. http://www.grida.no/publications/other/ipcc_tar/. Accessed Jan 2011

IPCC (2007) Intergovernmental panel on climate change: climate change 2007: the physical science basis. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, USA. http://www.ipcc.ch/publications_and_data/ar4/wg1/en/contents.html

Jensen J, Mudersbach C (2007) Zeitliche Änderungen in den Wasserstandszeitreihen an den Deutschen Küsten. Berichte zur deutschen Landeskunde 81(2):99–112

Klimabuero (2011) Norddeutscher Klimaatlas. http://www.norddeutscher-klimaatlas.de/klimaatlas/2036-2065/jahr/durchschnittliche-temperatur/nordseekueste/grosstezunahme.html. Accessed Jan 2011

Nerem RS, Chambers DP, Hamlington B, Leben R, Mitchum GT, Phillips T, Willis J (2010) Observations of recent sea level change. In: Stocker et al. 2010, pp 145–146

Petoukhov V, Semenov VA (2010) A link between reduced Barents-Kara Sea ice and cold winter extremes over northern continents. J Geophys Res, 115 (D21). http://www.pik-potsdam.de/news/press-releases/global-warming-could-cool-down-temperatures-in-winter. Accessed Jan 2011

Rahmstorf S, Richardson K (2007) Wie bedroht sind die Ozeane? Fischer Verlag, Frankfurt am Main

Schirmer M (2010) Klimawandel: Folgen für Ems, Weser und Elbe. In: Fansa M, Ritzau C, Sander H-H, Brickwedde F (eds) Kalte Zeiten–Warme Zeiten: Klimawandel(n) in Norddeutschland. Schriftenreihe des Landesmuseums Natur und Mensch, vol 76, pp 72–79

Schuchardt B, Wittig S, Schirmer M (2008) Klimawandel und Ästuare. WWF Deutschland, Frankfurt/Main

Sterr H (1993) Der Einfluss von Klimavarianz auf die rezente Morphodynamik der deutschen Ostseeküste. In: Schellnhuber HJ, Sterr H (eds) Klimaänderung und Küste–Einblick ins Treibhaus. Springer-Verlag, Heidelberg, pp 153–173

Sterr H (1998a) Auswirkungen auf den Meeresspiegel. In: Lozán JL, Graßl H, Hupfer P (eds) Warnsignal Klima–Wissenschaftliche Fakten. Wissenschaftliche Auswertungen, Hamburg, pp 201–206

Sterr H (1998b) Gefährdung in den Küstenregionen. In: Lozán JL, Graßl H, Hupfer P (eds) Warnsignal Klima–Wissenschaftliche Fakten. Wissenschaftliche Auswertungen, Hamburg, pp 248–253

Stocker T, Dahe Q, Plattner G-K, Tignor M, Allen S, Midgley P (2010) Workshop Report. IPCC Workshop on Sea Level Rise and Ice Sheet Instabilities Kuala-Lumpur, Malaysia, 21–24 June 2010. http://www.ipcc.ch/pdf/supporting-material/SLW_WorkshopReport_kuala_lumpur.pdf. Accessed Jan 2011

UKCP09 (2009) UK climate projections. http://ukclimateprojections.defra.gov.uk/content/view/2009/500/. Accessed Jan 2011

Vestergaard P (1997) Possible impact of sea-level rise on some habitat types at the Baltic coast of Denmark. J Coast Conserv 3:103–112

von Storch H, Claußen M (eds) (2009) Klimabericht für die Metropolregion Hamburg, Hamburg. http://www.klimabericht-hamburg.de/hintergrund.html. Accessed Jan 2011

von Storch H, Schnur R, Zorita E (1998) Szenarien & Beratung. Anwenderorientierte Szenarien für den norddeutschen Küstenbereich. Abschlußbericht FKZ 01 LK 9510/0

Zorita E, Weisse R, Hunicke B, Albrecht F, von Storch H (2010) Sea level studies at GKSS, Germany. In: Stocker et al. 2010, pp 203–204

Coastal Landscapes of the North Sea and the Baltic Sea

3

Gerhard Weidemann

Abstract

The post-Pleistocene history of the German coasts is generally characterised by sea level rising, which was fast in the beginning and slower later. It was caused by the melting ice and a change of transgressions and regressions. Ca. 6000 years BP, human settlements at the coast began. Diking at the North Sea started in the eleventh century to protect the hinterland even against winter storm surges. Of the different ecosystems, salt marshes and sand dunes are widespread on both coasts. At the North Sea coast, salt marshes developed at the Wadden seaside of barrier islands and in front of sea dikes of the mainland. At the Baltic Sea coast salt meadows have developed in inundation areas at lagoons behind the beaches and in bights which were separated from the sea. Coastal dunes develop where sand is deposited on the beach by currents and surf, transported by frequent strong onshore wind, and finally deposited behind dead or living barriers. They occur almost along the entire North Sea coast. At the German coast of the Baltic Sea, dunes are only locally developed.

Author "Gerhard Weidemann" has died before the publication of this book.

As the author of this chapter passed away before it was submitted, D. Mossakowski and U. Irmler took over proofreading and act as contact persons for this chapter.

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3.1 Post-Pleistocene Development

Coastal landscapes are shaped by wind and sea. The effects of these forces may be destructive as well as constructive. By erosion, cliff coasts may be formed when Pleistocene moraines or geological older formations (Helgoland) are scraped off. On the other hand, salt marshes and dunes, main features along the southern coasts of the North Sea and the Baltic Sea, were accreted by sediments, which were transported by water or wind. Peat bogs grew up in low-lying areas with a high ground-water table. These coastal landscapes are geologically rather young. They developed as a direct or indirect consequence of postglacial climate changes and, during the last 6000 years, under the increasing influence of humans.

At the end of the late Vistula glaciations, about 10,000 years ago, the southern coast of the North Sea run north of the Dogger Bank. The sea level was about 65 m below the present level (Streif 1990). Between 8600 and 7100 years BP, the melting of the ice during the Holocene caused a fast (2 m/100 years; Streif 1993) rise of the North Sea from 45 to 15 m below the present sea level and a corresponding shifting of the coast line further inland. The later rise was slower and occurred in several steps (Dunkirk transgressions). From about 6000 to 3000 years BP, the sea level rose 0.3 m/100 years, on average, and during the last 3000 years, 0.11 m/100 years on average (Behre 1993). It was interrupted by temporary hiatuses and short regressions. These led to more or less intense peat and soil development in the coastal regions, which were subsequently covered by marine sediments. In the marshland formed in this way, Neolithic inhabitants settled on riverbanks (ca. 6000 years BP). Depending on the speed of transgressions and regressions and in adaptation to the different heights of storm surges, either ground level or mound settlements were built (Behre 1993; Meier 1994). At the same time, grazing and cultivation affected the surrounding ecosystems, including riverbank forests, bogs, and salt marshes. Finally, diking that started in the eleventh century exerted a long-lasting impact on the coast. Initially, only cultivated land was protected from storm surges by low ring dikes. But since the fourteenth century, a largely continuous coast-parallel dike line was established in order to protect the hinterland even against winter storm surges (Behre 1993, 2004; Meier 1994). Nevertheless, devastating storm surges repeatedly pulled out large areas from the hinterland (for an overview, see Streif 1990; Higelke 1998). Some of the bights could be recovered in the time following by reclamation measures, which continued into the twentieth century, and then closed again, while others were left lost (examples in Streif 1990). Especially in Northern Friesland, numerous settlements perished with the clay land in the fourteenth century (Harth 1992) (Fig. 3.1). The approximate shape of the North Frisian coast developed as a result of the second “great men drowning” (grote Manndränke) in 1634. Remaining islands after this large storm surge were Sylt, Amrum, and Föhr, with a Pleistocene core and parts of the former clay marshland; the islands of Pellworm and Nordstrand as well as 10 Holm islands, which are not diked up to the present, are only protected by low summer dikes (Schmidtke 1993). To date, the coastline is by no means durably stabilised.

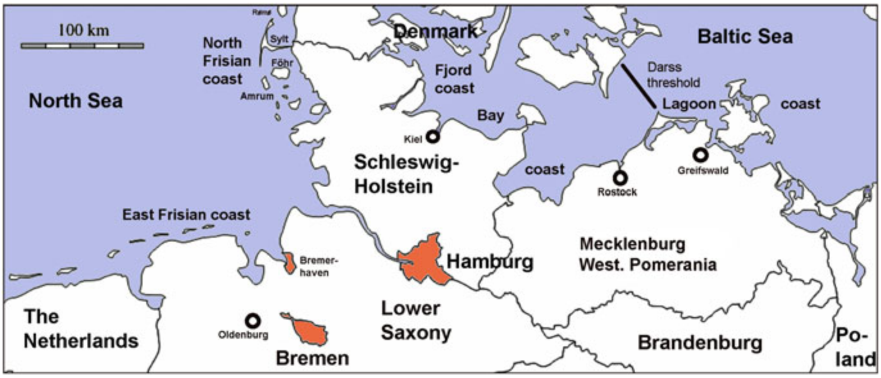

Fig. 3.1 Map of Northern Germany with the states adjacent to the North Sea and Baltic Sea and different types of coasts

At the earliest around 7500 years BP, the precursors of the (West) and East Frisian Islands developed at the edge of the Geest (the area of the late Pleistocene sands).

However, these nuclei were moved southwards with rising sea levels and covered by sediments, under which fossil peat and clay horizons were discovered (Streif 1990). The present shape of the chain of islands from West Friesland up to Sylt and the Danish islands Rømø and Fanø is an outcome of the tidal conditions. In the zone of high mesotides (tidal range between 2.0 and 3.5 m), a chain of barrier islands developed in front of the southern North Sea coast from coast-parallel beach ridges and sand plates. The development of dunes on these islands started in the thirteenth century (de Jong 1984; Streif 1990). However, many of them are much younger. Due to the dominating west winds, a west-east shift of sand forms the islands and their connection by sandbanks; the shape of the islands is still changing and the build-up of dunes lasts until today.

At the beginning of the Holocene, the Baltic Sea was a freshwater lake ("*Ancylus* lake"). Its highest level was 10–8 m below NN at approximately 9000 years BP. Therefore, the former coastline lay far from the present coastline of Schleswig-Holstein and Mecklenburg-Western Pomerania (Niedermeyer et al. 1987; Schmidtke 1993). When the run out started across the Darss threshold about 8700 years BP, large edge areas of the Baltic Sea felt dry, silted up, and peat developed. Between 7300 and 7000 years BP, a fast rise—about 15 m (i.e. 2.5 m/100 years)—of the Baltic Sea's level occurred. This caused widespread peat development due to the inundation of terrestrial areas near to the coast. Until 5700 years BP, the sea level rose slower by about 0.3 m/100 years. Thereafter, the level of the Baltic Sea has fluctuated just 1–2 m around the present level (Janke et al. 1993).

The present course of the German part of the Baltic Sea coast was reached 4000 years ago. Since the regular tidal range is low or not existent, mainly wind driven changes in water levels and alongshore sediment transport have shaped the coast. The coastal area, which consists almost entirely of Pleistocene moraine and melting water sand, has been formed according to its initial relief. Concerning the morphology and genesis, five coastal types can be differentiated along the German part of the southern coast of the Baltic Sea (Sterr et al. 1998): (1) the *fjord coast* along the western Kiel bight, which developed during the Littorina transgression (ca. 8000–4000 years BP) by the filling of glacier valleys and melting water channels, (2) the eastwards bordering *open-bay coast*, i.e. Hohwacht Bay, Lübeck Bay, and Wismar Bay, with former ice basins flooded during the Littorina transgression and subsequently smoothed by cliff erosion and coast-parallel material transport, whereby lateral bights were cut off by bars from the Baltic Sea, (3) the relative uniform *regularised* (moraine) *coast* of Mecklenburg between Rerik and Fischland, and (4 + 5) the adjacent eastern *Lagoon* (*Bodden) coast* of Western Pomerania with an *external coast* (4), which is exposed to the open sea, the regularised Bodden coast, and a more than five times longer *inner coast* (5) along the back side of islands and bars and the more or less cut off lagoons. The structure of the regularised coasts was also built by a combination of erosion and longshore material transport from the former southwest Baltic archipelago (Niedermeyer et al. 1987). To this day, the external coast is being set back by erosion, while the inner coast is silting up.

The (German) North Sea coast is diked along most of its total length. Therefore, coastal changes happen only in the foreland where sedimentation is frequently fostered by building creeks and brushwood groynes. However, the shortening of the coast by recent diking measures has strongly reduced the conditions for the growth of new foreland (Heydemann 1997). On the islands, the western ends are reinforced which are particularly at risk of erosion. Additionally, at many places attempts have been made to prevent seaside erosion by breakwaters. Where this fails, sediment from the marine offshore is pumped to the foreshore or to the beaches to deliver sand for dune development. Moreover, beaches may grow considerably within a few years by natural sediment supply at the seaside as well as at the island borders, thus enabling the development of primary dunes. To prevent dune erosion or to support dune growth, sand trapping fences are installed and dune grasses are planted (Streif 1993; Erchinger 1992).

Large areas of the coast of the Baltic Sea are more exposed to the direct influence of the sea than the mainland coast of the North Sea. Therefore, permanent erosion is especially observed at cliff coasts, amounting to 30–40 cm/years during the last five decades (Sterr et al. 1998). Massive reinforcements can be found only at coastal settlements and harbours. Dikes protect low-lying sections of the coast. Groynes are used to prevent longshore sediment transport, while fences and the planting of grasses serve to promote dune growth. As a rule, narrow beaches exist at the foot of cliffs and in front of dunes and dikes, which only broaden where bars join the beach.

3.2 Coastal Ecosystems

The different geological, geomorphologic, hydrological, and climatic conditions at the coasts of the North Sea and the Baltic Sea have led to the development of several very characteristic ecosystems. Due to their mostly limited size and quite restricted geographic distribution, at least under undisturbed conditions, they have high priority for nature protection measures. However, only two main ecosystem types were focused on in our research project, which are described in the following sections: salt meadows and sand dunes.

3.2.1 Salt Meadows

At the North Sea coast, salt marshes and salt meadows developed at the Wadden seaside of barrier islands and in front of sea dikes of the mainland from about 20 cm below the mean tidal high-water level (Ellenberg 1996). Continuous sedimentation, which is supported by dense vegetation, causes a rising of the terrain. With increased growth of salt marshes, the tidal inundation frequency and duration are reduced, salt is washed out from the soil, and the system becomes dryer. Depending on the relief, a sequence of zones or a mosaic of communities with different salt and flooding tolerance is developing. The composition of the biota depends on soil texture (sand, silt/clay, or peat) and to a high degree on the usual grazing by cattle (Heydemann 1983; Andersen et al. 1990; Meyer et al. 1995). Especially ungrazed salt marshes, which make up about 4900 ha in the National Park “Niedersächsisches Wattenmeer” (Bunje and Zander 1999) and about 6000 ha in the National Park “Schleswig-Holsteinisches Wattenmeer” (Gettner et al. 1998) are unique near-natural ecosystems and therefore require lasting protection. The protection is also necessary since the dike forelands absorb energy of storm tides and contribute to the stability of the dikes.

At the Baltic Sea coast with no noticeable tides and a changing Pleistocene relief of moraines and valleys in between, salt meadows have developed in inundation areas at lagoons behind the beaches and in bights which were separated from the sea. In the lagoon landscape of Mecklenburg-Western Pomerania, they resulted from cattle grazing of inundated coastal peatland and reeds. 90% of originally about 30,000 ha have been diked, drained, and cultivated (Holz and Eichstädt 1993). The few remaining near-natural sites with their specialised halotolerant flora and fauna need intensive protection (Müller-Motzfeld 1997).

3.2.2 Dunes

Coastal dunes develop where sand is deposited on the beach by currents and surf, transported by frequent strong onshore wind, and finally deposited behind dead or living barriers. Especially effective wind brakes are tussock grasses, such as *Ammophila arenaria*, and bushy therophytes and perennials like *Cakile maritima* or *Honckenya peploides* (Ellenberg 1996). On the lee side of them, initial or embryo dunes are built. When the plants grow with an increased accumulation of sand, e.g. with the presence of *Ammophila* plants, the dunes grow as well by the supply of sand. The stabilisation of the sand is an ecosystem process in which the root systems of the plants near the soil surface and its exudates play an important role. Moreover, bacterial mucus, dead organic matter, fungal hyphens, and filamentous algae as well as a diverse micro- and mesofauna support this process (on "organogenic dune formation", cf. van Dieren 1934; Koehler and Weidemann 1995).

Dunes occur almost along the entire North Sea coast from Hoek van Holland to Skagen. Due to different tide intensities, they are either located on the mainland as in the Netherlands and in Denmark (microtidal zone, compensatory coast), or offshore, e.g. on the West Frisian, East Frisian, and North Frisian barrier islands (mesotidal zone) (Ehlers 1994). Depending on the mainland or island situation of the dunes, not only climatic differences between them are observed, but they also differ in their accessibility for organisms. At the German coast of the Baltic Sea, dunes are only locally developed where enough space and sand were available on beach ridges and at the foot of cliffs. Similar to salt meadows, dunes, especially near-shore young white dunes, are near-natural ecosystems with a community that is adapted to the extreme conditions. They can be strongly disturbed by tourist impact with the effect that their conservation value as well as their coastal protection function is degraded (Schierding et al. 2011).

References

Andersen H, Bakker JP, Brongers M, Heydemann B, Irmler U (1990) Long-term changes of salt marsh communities by cattle grazing. Vegetatio 89:137–148

Behre K-E (1993) Die nacheiszeitlichen Meeresspiegelbewegungen und ihre Auswirkungen auf die Küstenlandschaft. In: Schellnhuber HJ, Sterr H (eds) Klimaänderung und Küste. Springer, Berlin, pp 57–76

Behre K-E (2004) Coastal development, sea-level change and settlement history during the later Holocene in the Clay District of Lower Saxony (Niedersachsen), northern Germany. Quat Int 112:37–53

Bunje J, Zander R (1999) Salzwiesenschutz im Nationalpark "Niedersächsisches Wattenmeer". In: Wattenmeer U (ed) 2: Wattenmeer zwischen Elb–und Emsmündung. Ulmer, Stuttgart, pp 126–127

De Jong JD (1984) Age and vegetational history of the Frisian Islands, the Netherlands. Geol en Mijnbouw 63:269–275

Ehlers J (1994) Geomorphologie und Hydrologie des Wattenmeeres. In: Lozan JL, Rachor E, Reise K, von Westernhagen H, Lenz W (eds) Warnsignale aus dem Wattenmeer. Blackwell, Berlin, pp 1–11

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen, 5th edn. Ulmer, Stuttgart

Erchinger HF (1992) Conservation of barrier dunes as a smooth, natural method of coastal protection on the East Frisian Islands, Germany. In: Carter RWG, Curtis TGF, Sheehy-Skeffington MJ (eds) Coastal dunes. Balkema, Rotterdam, pp 389–396

Gettner S, Heinzel K, Dierßen K (1998) Salzmarschen im schleswig-holsteinischen Wattenmeer. In: Wattenmeer U (ed) 1: Nordfriesisches und Dithmarscher Wattenmeer. Ulmer, Stuttgart, pp 86–87

Harth U (1992) Untergang der Halligen, 2nd edn. Christians, Hamburg

Heydemann B (1983) Das Ökosystem “Küsten-Salzwiese”–ein Überblick. Faunistisch-Ökologische Mitteilungen 5:249–279

Heydemann B (1997) Neuer Biologischer Atlas. Ökologie für Schleswig-Holstein und Hamburg. Wachholtz, Neumünster

Higelke B (1998) Das nordfriesische Wattenmeer seit dem Mittelalter. In: Wattenmeer U (ed) Bd. 1: Nordfriesisches und Dithmarscher Wattenmeer. Ulmer, Stuttgart, pp 32–33

Holz R, Eichstädt W (1993) Die Ausdeichung der Karrendorfer Wiesen–Ein Beispielprojekt zur Renaturierung von Küstenüberflutungsräumen. Natur und Naturschutz in Mecklenburg-Vorpommern 36:3–27

Janke W, Kliewe H, Sterr H (1993) Holozäne Genese der Boddenküste Mecklenburg-Vorpommerns und deren künftige klimabedingte Entwicklung. In: Schellnhuber HJ, Sterr H (eds) Klimaänderung und Küste. Springer, Berlin, pp 137–152

Koehler H, Weidemann G (1995) Biogenic dune sand stabilization. In: van Dijk HWL, Hurkmans WEG (eds) Management and preservation of coastal habitats. EUCC, Leiden, pp 83–98

Meier D (1994) Geschichte der Besiedlung und Bedeichung im Nordseeküstenraum. In: Lozan JL, Rachor E, Reise K, von Westernhagen H, Lenz W (eds) Warnsignale aus dem Wattenmeer. Blackwell, Berlin, pp 11–17

Meyer H, Fock H, Haase A, Reinke H-D, Tulowitzki I (1995) Structure of the invertebrate fauna in salt marshes of the Wadden Sea coast of Schleswig-Holstein influenced by sheep-grazing. Helgoländer Meeresuntersuchungen 49:563–589

Müller-Motzfeld G (1997) Küstenlebensräume des deutschen Ostseeraumes und deren Bedeutung für Biotop- und Artenschutz. Schriftenreihe für Landschaftspflege und Naturschutz 52:25–36

Niedermeyer R-O, Kliewe H, Janke W (1987) Die Ostseeküste zwischen Boltenhagen und Ahlbek. VEB H. Haack, Geographisch-Kartographische Anstalt Gotha

Schierding M, Vahder S, Dau L, Irmler U (2011) Impacts on biodiversity at Baltic Sea beaches. Biodivers Conserv 20:1973–1985

Schmidtke K-D (1993) Die Entstehung Schleswig-Holsteins, 2nd edn. Wachholtz, Neumünster

Sterr H, Schwarzer K, Kliewe H (1998) Holocene evolution and morphodynamics of the German Baltic Sea coast. Recent research advances. In: Kelletat DH (ed) German geographical research. The last decade. Institut für wissenschaftliche Zusammenarbeit, Tübingen, pp 107–134

Streif H (1990) Das ostfriesische Küstengebiet. Nordsee, Inseln, Watten und Marschen. Sammlung Geologischer Führer 57, 2nd edn. Bornträger, Berlin

Streif H (1993) Geologische Aspekte der Klimawirkungsforschung im Küstenraum der südlichen Nordsee. In: Schellnhuber HJ, Sterr H (eds) Klimaänderung und Küste. Springer, Berlin, pp 77–93

Van Dieren JW (1934) Organogene Dünenbildung. Martinus Nijhoff, Den Haag

Geography and Study Sites

4

Hans-Peter Blume, Wolfgang Dormann, and Dietrich Mossakowski

Abstract

The research areas of the joint project are described. Field studies were performed along a gradient at the coasts of the North Sea and the Baltic Sea from the island of Borkum in the west up to the Karrendorf Meadows at the western Pomeranian Bodden coast in the east. At the North Sea coast of Lower Saxony, the research areas were located on the East Frisian Islands of Borkum, Norderney, Wangerooge, and Mellum, and on the coast of Wursten near Cuxhaven, the west coast of Schleswig-Holstein on the foreshores of Friedrichskoog in southern Dithmarschen and Hedwigenkoog in northern Dithmarschen. In addition, bee studies were performed on the North-Frisian Island of Sylt. At the Baltic Sea coasts, the research areas were located at the Bay of Hohwacht in Eastern Holstein, on the peninsula of Darss/Zingst, and at the Greifswald Bodden in Western Pomerania.

While the zoological field work was restricted to individual locations along the geographical gradient, the evaluation of historical changes in floral composition included data of the whole range of the German coasts from the North Sea to the Baltic Sea covering a climate gradient separated into two floral regions.

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4.1 Introduction

The research areas of the joint project were situated at the coasts of the North Sea and the Baltic Sea along a gradient ranging from the island of Borkum in the west up to the Karrendorfer Wiesen at the western Pomeranian Bodden coast (*Vorpommersche Boddenküste*) in the east (Fig. 4.1).

At the North Sea coast of Lower Saxony, the research areas were located on the East Frisian Islands of Borkum, Norderney, Wangerooge, and Mellum, and on the coast of Wursten near Cuxhaven. Under the influence of tides, currents, waves, and wind, the East Frisian Islands have developed from intertidal sandy flats (*Sandplaten*) and beach ridges to sand dune islands (Semmel 1996). During the last 700 years, at least parts of the islands have translocated in a southeastern direction. The coast of Wursten is part of the northern marsh of the Weser River and was separated from the Elbe marshes by a terminal moraine of the Saalian glaciation, the Hohe Lieth at Cuxhaven-Sahlenburg.

At the west coast of Schleswig-Holstein, research areas were located on the foreshores of Friedrichskoog in southern Dithmarschen and Hedwigenkoog in northern Dithmarschen. The supratidal flats of all investigated parts of the coasts have developed only within a few decades under strong human influence after the

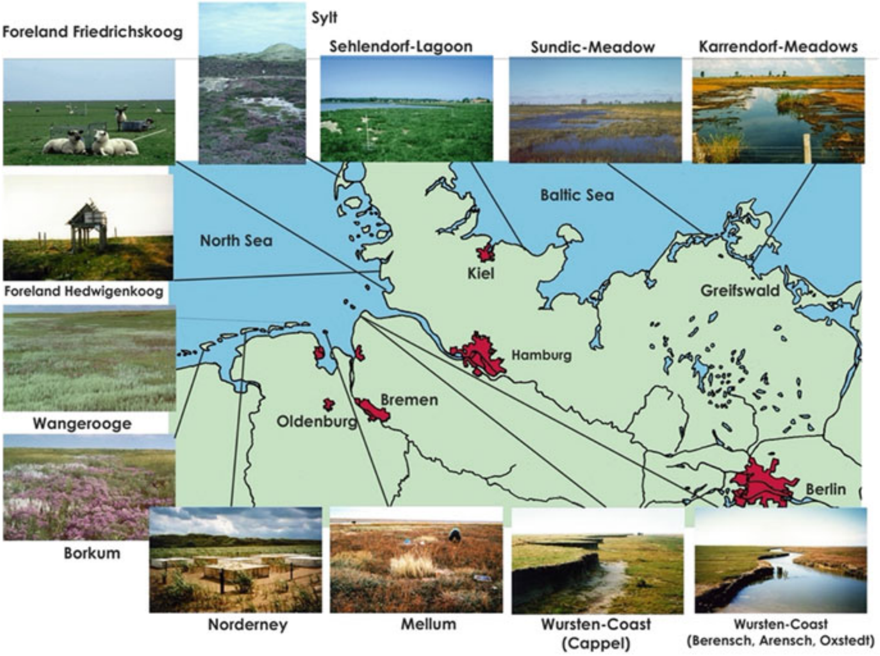

Fig. 4.1 Research regions in three Northern German Federal States: Lower Saxony, Schleswig-Holstein, and Mecklenburg-Western Pomerania

construction of fascines, beds, and creeks as well as after building dikes. In addition, the bee studies were performed on the North-Frisian Island of Sylt.

At the Baltic Sea coasts, the research areas were located at the Bay of Hohwacht in Eastern Holstein, on the peninsula of Darss/Zingst and at the Greifswalder Bodden in Western Pomerania. Barrier beaches, sand dunes, and lagoons with fens built up this so-called Bodden coast.

Presently, all these research areas are under nature protection. The areas at the North Sea belong to the national parks 'Niedersächsisches Wattenmeer' and 'Schleswig-Holsteinisches Wattenmeer', the areas of Zingst to the 'National Park Vorpommersche Boddenlandschaft', while the salt marshes near Sehlendorf in Holstein and the Karrendorfer Wiesen near Greifswald are separate nature reserves.

4.2 Research Area for the Study of Historical Changes in Floral Composition

The research area extends over the whole range of the German coasts from the North Sea to the Baltic Sea and covers a climate gradient separated into two floral regions (Fig. 4.2). The western part of the study area belongs to the Atlantic, the eastern part to the Central European floral region. The western part is characterised by relatively warm winters and cool and wet summers; the continental influence increases towards the eastern regions.

The historical changes in coastal vegetation are presented in Chaps. 9 and 10. Data from The Netherlands, Denmark, and Poland are included for taxa that have their boundary of distribution within these countries.

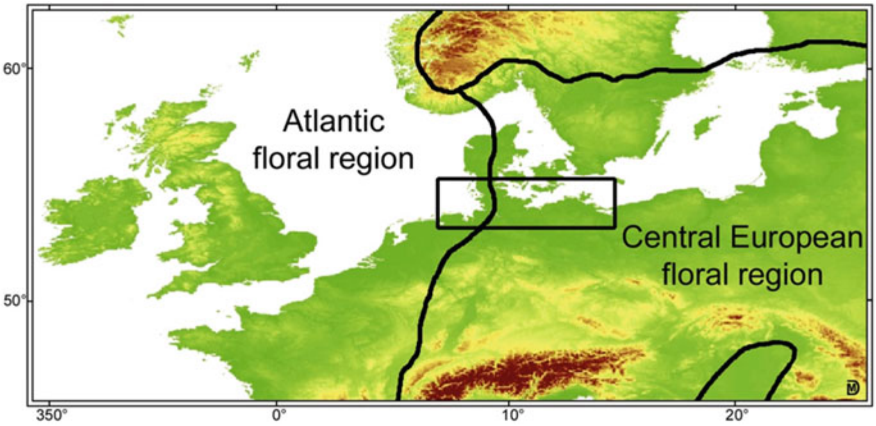

Fig. 4.2 Research area (rectangle) at the interface between Atlantic and Middle European floral regions (Image: according to Schröder (1998), modified)

4.3 Research Areas in a Geographical Gradient

According to the west-eastern geographical and climatic gradient, the study areas are described in geographical order from west to east (Fig. 4.1).

The East Frisian Islands are situated offshore the Lower Saxony mainland. Their development started with periodically flooded sand banks. Subsequently, sand was stabilised by pioneer vegetation that produced emerged, flood-free sand plates. Finally, the interplay of sand transport and stabilisation processes by organogenic dune development (Van Dieren 1934) resulted in the so-called old East Frisian Islands—in contrast to recent sand plates. The development of the East Frisian Islands started between the fifth and thirteenth centuries AD (Niemeier 1972; De Jong 1984; Ehlers 1986). Sandy beaches build up the seaside of the islands, while sedimentation at the backside produced salt marshes in the wind shadow.

In contrast to the mainland, a thin layer of silt on a sandy ground often builds up the salt marshes of the islands. They vary strongly due to elevation and soil composition. The vegetation is more diverse than at the mainland due to the poor nutrient content of the soil. The vegetation cover is often sparse (Erchinger 1985).

Borkum is the westernmost island of the German East Frisian Islands, with an area of 32 km^2 above the mean high-water level (MHW). It is strongly influenced by tourism. Salt marsh vegetation covers about 3 km^2 of the island. The research areas were located on the southern part of the island: one located in the ‘Ronde Plate’ near the southern beach, west of the dam between the harbour and the village, another one, called ‘Grüppenbeete’, is situated east of the dam in a salt marsh area with artificial creeks (Fig. 4.3).

The ‘Ronde Plate’ consists of barrier sands with overlying sand dunes separated by lagoons with tidal mud deposits. During the last decades, the barrier surface mainly changed into a very heterogeneous cover of halophytic vegetation (Peters 1996).

The investigation was executed on: (1) a diurnal flooded *lower salt meadow* upon a thin tidal mud deposit, 20–30 cm above the MHW level, (2) an *upper salt meadow* 50–70 cm above the MHW level, (iii) a saline fen 75–100 cm above the MHW level, and (4) a dune ridge 120–150 cm above the MHW level.

The salt marsh of the study area ‘Grüppenbeete’ is divided into a wet tidal marsh and a small low sand dune. The area is subdivided by small creeks and covered by dense halophytic vegetation. A *lower salt meadow*, 10–35 cm above the MHW level, an *upper salt meadow*, 40–50 cm above the MHW level, and a *sandy ridge*, 70–100 cm above the MHW level, were investigated.

Results of the zoological studies are found in Chaps. 14 and 15 and in the expert system in Chap. 27.

On the island of *Norderney*, a complex of different old dunes has developed. In 1992, the Lower Saxony Department for Water Economy and Coastal Protection (NLWK) levelled parts of an older dune valley, east of the village, and cultivated Marram grass (*Calammophila baltica*) for dune protection. The research area was a section of 200 m^2 of this field, located about 700 m south of the northern beach, and situated 260 cm above NN.

Fig. 4.3 Research areas (white rectangles) on the East Frisian Island of Borkum; (G): Salt marsh 'Grüppenbeete'; (R): Salt marsh and dunes 'Ronde Plate' (Images: (**a**): Satellite photograph: D-Sat2 top ware; (**b-d**): Satellite photographs: Google Earth; geographical coordinates: (G 1): 53°34′46.1″ N, 06°42′56.0″ E; (R 6): 53°34′05.7″ N 06°42′20.2)

On the Island of Norderney, the impact of climate change on biota and processes involved in dune stabilisation were studied experimentally (Fig. 4.4). The results are described in Chap. 17.

The field experiment was carried out on disturbed and levelled sands of an older dune. The soil is a transition between a Protic Arenosol with very low humus contents ('humusarmer Lockersyrosem') and a Eutric Arenosol (Normregosol) with already fully developed humus topsoil. Besides a very small humus accumulation, a decalcification of the primarily carbonate-poor dune sands and a moderate acidification have developed. Adjacent old dunes are also characterised by Arenosols with somewhat higher humus contents, while the valley soils among the dunes are gleyed as a consequence of a high groundwater level. The soils of the younger dunes near the coast have hardly developed, consisting of Protic Arenosols

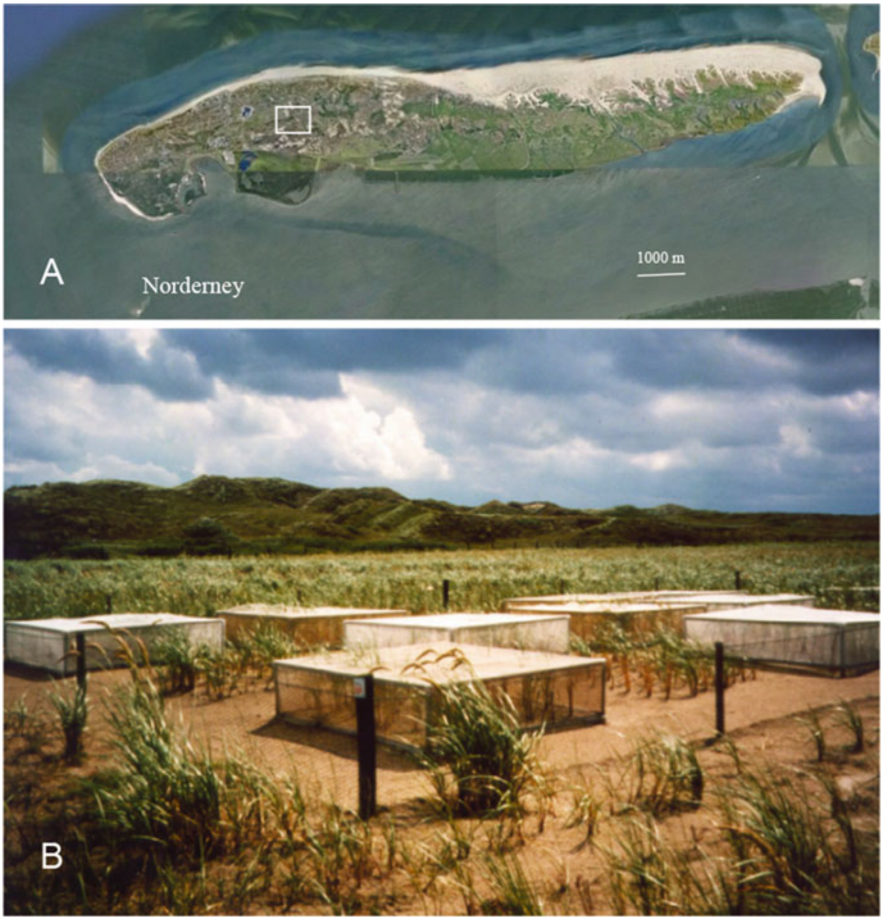

Fig. 4.4 Research area on the East Frisian Island of Norderney. (**a**): Location of the study site (white rectangle); the foreland of the mainland can be seen at the lower right corner; (**b**): Dune experimental area (Image: (**a**): Satellite photograph (Google Earth); (**b**): Photo by G. Weidemann; geographical coordinates: 53°43′08″ N, 7°11′38″ E)

with a minimal humus accumulation and an alkaline soil reaction. Although no salt content was measured, they might be sporadically influenced by salt spray. All plots are dry, aerated sites with low nutrient reserves and low (N, P) to moderate (Ca, Mg, K) contents of available nutrients.

Wangerooge is an island with an area of 7.9 km^2 above the MHW level and is extremely influenced by tourism. Salt marshes cover about 1.3 km^2 of this smallest island of the old East Frisian Islands. The research area is situated in the ‘Mittelaußengroden’ on the south part of the island. It is a sandy salt marsh complex, cut by artificially formed channels, which changes in the north to a dune complex. The research area includes two study sites (Fig. 4.5), which are located in the lower salt meadow at 20–35 cm above the MHW level, two sites in the upper salt meadow

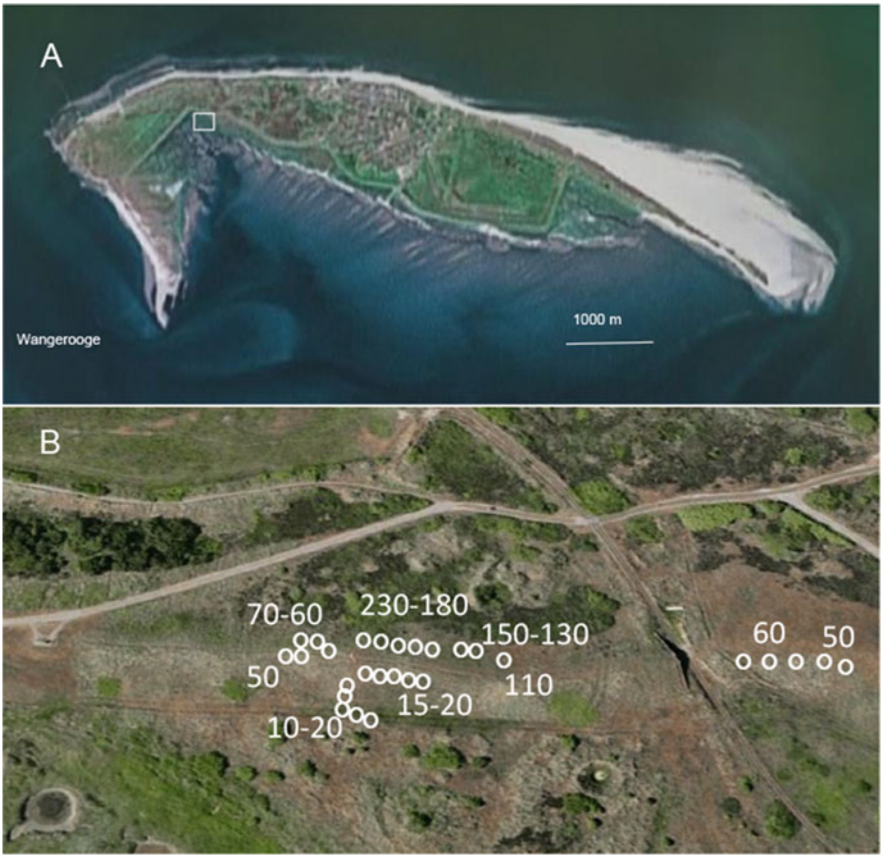

Fig. 4.5 Research area at the East Frisian Island of Wangerooge. (**a**): Location of the study site (white rectangle); (**b**): Arrangement of pitfall traps at 'Mittelaußengroden'. Numbers indicate elevation above the MHW level in cm (Images: Satellite photographs: Google Earth; geographical coordinates (10): 53°47′26.4″ N, 07°52′23.0″ E)

at 40–60 cm above the MHW level, and another one in the area of the lower dune at 100–120 cm above the MHW level.

Zoological results are presented in Chaps. 14 and 15 and in the expert system in Chap. 27.

The island of *Mellum* developed in the last 25 years of the nineteenth century at the apex of the Hohe-Weg-Watt between the Jade and Weser Rivers. It now has an area of 6.3 km^2 above the MHW level. Only ca. 4 ha in the southwest are protected against flooding by a ring dike that encloses a house as a shelter for scientists. The entire island is under nature protection. It has developed from sand reefs (Göhren 1975): mighty marine sands that, in the east, overlay Pleistocene glacial till and melt-water sands. In the flat area, they are overlain by thin tidal mud flats, while dunes overlay the higher area. The shape of the island has strongly changed during its existence (Sindowski 1979; Reineck 1987) and will change continuously in the future.

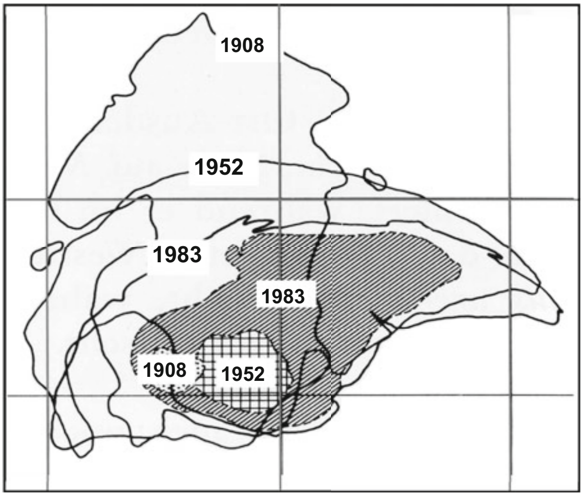

Fig. 4.6 Development of the total area (lines) and the grassland areas (hatchings) on the isle of Mellum (modified according to Kuhbier 1987)

The island was already mentioned in 1410 as a sand plate (Lang 1981; cited in Reineck 1987), but the strong storm floods in the sixteenth century destroyed it (Reineck 1987). In 1903, Mellum measured about 7 ha and was bordered by a high dune wall in the west with salt vegetation in its wind shadow (Schütte 1904; cited in Haeseler 1988). At that time, the island's shape had a north-south alignment, which shifted to a more west-east alignment at present. Green land vegetation was established in two periods: (1) at the end of the nineteenth century on the southern part of the island (Alte Mellum) and (2) at the beginning of the 1960s at the northern shore (Kuhbier 1987). Large dunes mainly characterised the northern, western, and southern parts, while extended salt marshes and many creeks were found in the eastern part (Fig. 4.6).

In the period from 1940 to 1942, an area of about 7.8 ha in the southwest was raised and diked for military purposes. During this development, soil and plants from the mainland and from the island of Wangerooge were introduced for camouflage. Therefore, species introduced by man and naturally colonising species can hardly be differentiated (Kuhbier 1987; Haeseler 1988).

The research areas are located at the salt marsh complex Alte Mellum (Mellum West) that was cut by several creeks, and 500 m to the east at the salt marsh complex Mellum East (Fig. 4.7).

The research area Mellum West is composed of: (1) a mixed Wadden area (10–50‰ sand) that lies 10–20 cm below the MHW level, (2) areas of the lower salt meadow that lie 0–40 cm above the MHW level, (3) an upper salt meadow that lies 50–80 cm above the MHW level, and (4) silt-poor beach wall sands that lie 100–120 cm above the MHW level. Near Mellum East, the following sites were studied: (1) a tidal marsh at 0 cm MHW, (2) a lower salt meadow that lies at 30 cm above the MHW level, and (3) a flat dune that lies 60–70 cm above the MHW level.

Results of the vegetation experiments are presented in Chaps. 18 and 19, results on zoological studies in Chaps. 14 and 15, and in the expert system in Chap. 27.

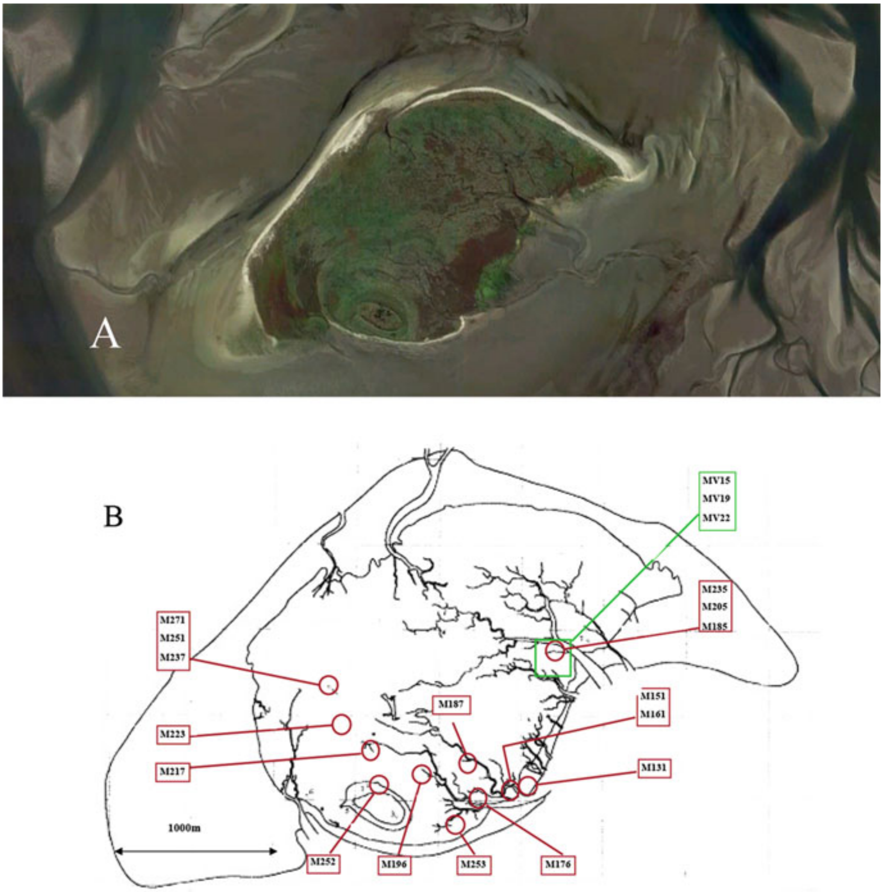

Fig. 4.7 The Island of Mellum is surrounded by tideways and sand flats. The first two digits of the site code indicate decimetre, minus 15 dm = elevation, e.g., M161, 16–15 = 1 dm = 10 cm above the MHW level (Images: (**a**): Satellite photograph at low tide: Google Earth; (**b**): Study sites for fauna (circles) and experimental vegetation study area (green square); geographical coordinates of the ring dike: 53°42′57″ N 08°08′43″ E)

In contrast to the Frisian Islands, the salt marsh sites of the mainland are exposed directly to the forces of the open North Sea, which provokes a stronger exposure to the flood regime.

The *Wursten Coast* is located 6 km southwest of Cuxhaven. The research areas are comprised of sheep pastures, a young salt fallow of the foreland, and a salt-influenced grassland along a large marsh creek system in the summer polder (*Sommergroden*). The salt marshes near Arensch, Berensch, Oxstedt, and Cappel-Neufeld have developed in front of a summer dike since 1854. This foreland (so-called *Außengroden*) is up to 2 km wide. The summer polder behind the summer dike is only open to tides in the wintertime. It is bordered further inland by dunes in the north (between Arensch and Berensch) and by a higher winter dike in the south (Fig. 4.8).

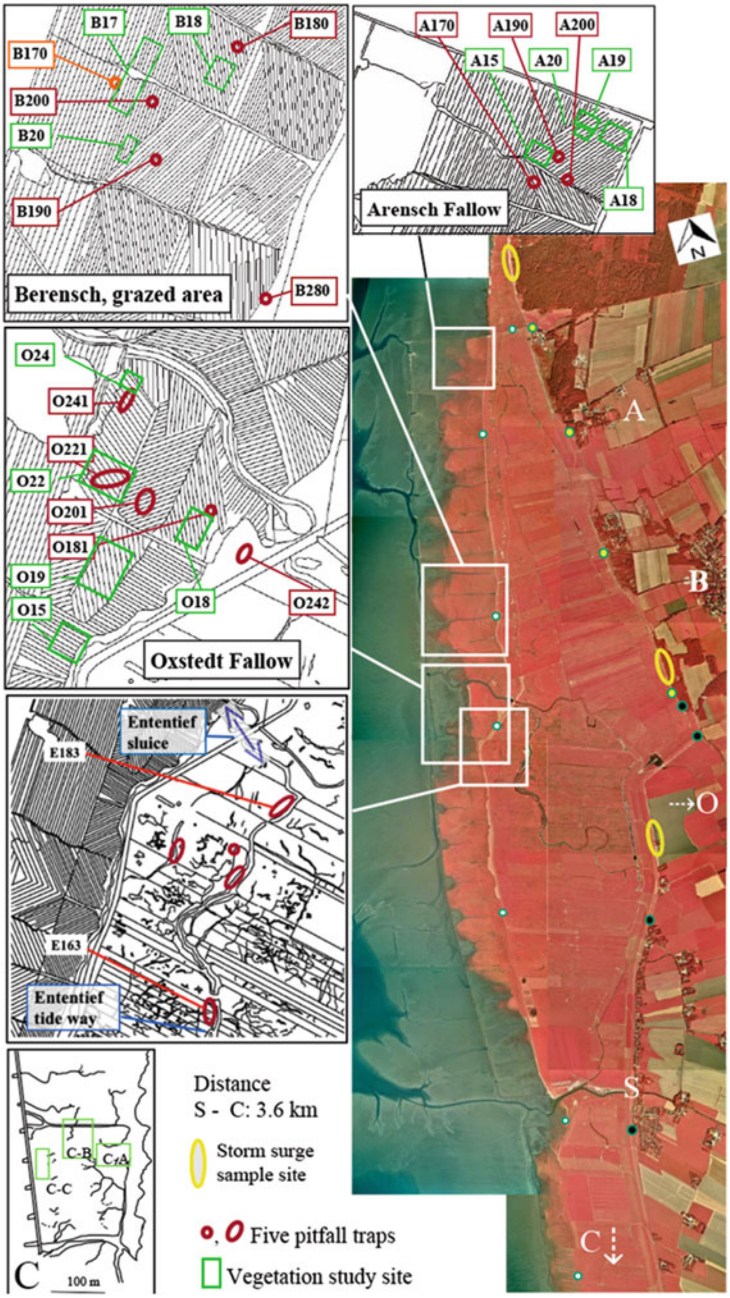

Fig. 4.8 Wursten Coast study sites for vegetation and arthropods. (A): Arensch; (B): Berensch; (O): Oxstedt; (S): Spieka-Neufeld; (C) Cappel-Neufeld. The summer dike is indicated by white, the main dike by black points, and the high dune by yellow ones. (C) represents a semi-natural salt marsh. Yellow oval indicates sampling sites at storm surge 'Kerstin' Image: Infrared colour photo from: Kinder et al. (2003) (With kind permission of the German Federal Agency for Nature Conservation (BfN), Bonn); geographical coordinates (B): 53°49′11″ N 8°35′28″ E; (C): 53°45′43″ N 08°31′37″ E)

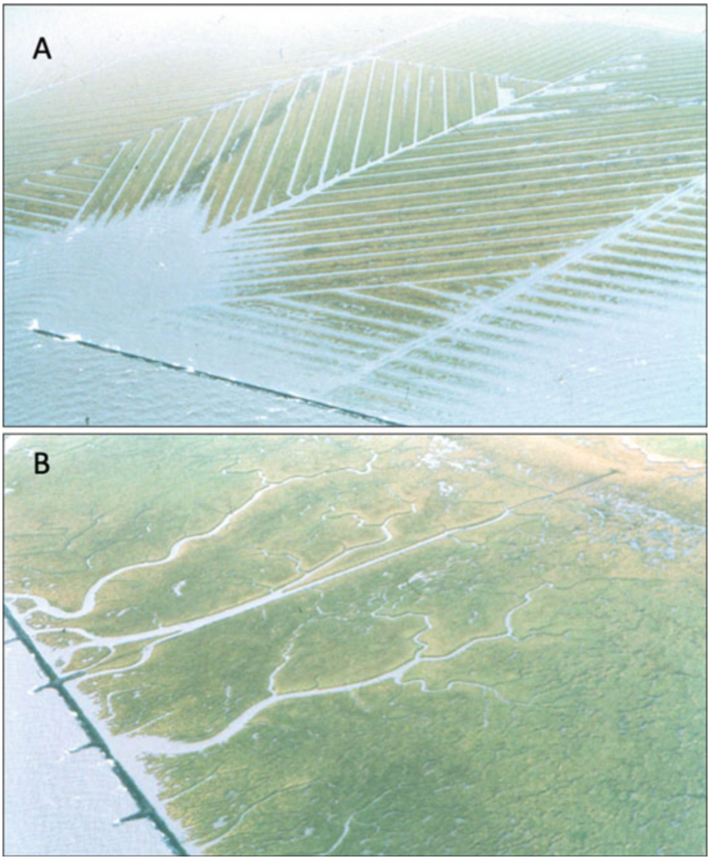

Fig. 4.9 Aerial photographs of the Wadden Sea coast at Wursten Coast. (**a**) Intensive managed salt marsh with ditches and groynes; (**b**) Semi-natural salt marsh with tide creeks. View from the open Sea (left side down)

Since 1932 (Stephan 1985), the sedimentation has been supported by fascines, beds, and ditches, which have been restored in 3–5 years intervals in front of Arensch, Berensch and near Oxstedt (Fig. 4.9a). This management successively elevated the salt marshes from a foreshore tidal level at 1.6 m above sea level (NN) to 2 m, on average, and to a maximum of 2.9 m above sea level. The sediments are mainly silty, calcareous, and humus. Since both the 1990s and the 1970s, the foreland in front of Arensch and Berensch and in front of Oxstedt, respectively, were no longer ditched regularly (Erchinger 1987). In consequence, the level of the outer part of the foreland ranges between +2.0 m and +2.5 m NN. At the seaside, the eulittoral zone begins immediately (<+1.6 m NN), whereas towards the inland, the foreland level decreases to about +1.85 m NN.

The salt marshes of Cappel-Neufeld are quite different. Although sedimentation lasted since the 1960s after building brushwood groynes, the effect on ditching was

Fig. 4.10 Research area at the foreland of Friedrichskoog. White circles indicate the locations of sampling stations (Image: Google Earth; geographical coordinates: 54°02′35″ N, 8°52′48″ E)

low (Grotjahn et al. 1982). While Müller (1961) only found *Spartina* and *Salicornia,* today the relief is characterised by natural meandering tidal creeks and areas with vegetation of upper salt marshes (Fig. 4.9b). The long-term impact of different agricultural use and of renaturation of salt marshes on the Wursten Coast was published by Kinder et al. (1995) and Främbs et al. (2000) (see Chap. 23).

Research areas were established in the lower wet salt marsh (1) ±10 cm beneath/ above MHW, (2) 20–30 cm above MHW, and (3) in an upper salt meadow 50–80 cm above MHW. Near Oxstedt, areas of the lower, middle, and higher salt grassland on the top of the summer dike at 80, 140, and 200 cm above MHW were included.

Results of the vegetation experiments are presented in Chap. 18, zoological results in Chaps. 14 and 15, and the expert system (27).

Near Edendorf in front of the *Friedrichskoog* (Meldorf Bay, southern Dithmarschen), faunal investigations in salt marshes were performed that are part of the National Park 'Schleswig-Holsteinisches Wattenmeer' (Fig. 4.10). Sandy-silty, calcareous, and humus sediments build up the salt marshes. Since the dike was constructed in 1854, sedimentation has caused an elevation of the foreland ranging between 1.6 and 3.0 m above NN. Furthermore, the construction of another dike at the Bay of Meldorf, constructed in 1978, enhanced sedimentation after the installations of fascines, beds, and wide ditches (Prange 1986).

Results of the vegetation experiments are presented in Chaps. 18 and 19, results on zoological studies in Chaps. 14, 15, and 21, and in the expert system in Chap. 27. The vegetation results originate from an area of the former ecosystem research programme (Stock et al. 1995) performed between 1987 and 1988, approximately 600 m east of the sites of the faunal research. Sheep grazing was excluded from these sites since 1988. They are elevated at 2.00–2.46 m above NN; the MHW level is 1.59 m above NN, and tide fluctuation is 3.5 m (Kiehl 1997).

The research area of the fauna was situated in the grazed salt grassland at: (1) 20–40 cm, (2) 60 cm (the three sites belong to the Puccinellietum maritimae vegetation), (3) 80 cm, (4) 100 cm (both sites with *Festuca rubra* association), and (5) 130–140 cm above the MHW level (Molinio-Arrhenateretea). The MHW level is at 1.59 m NN. The number of days with submergence ranged between 200 (±25) at the lowermost site to 8 (±4) at the uppermost site. Sheep grazing at all sites was amounted to 3–4 sheep ha^{-1} that equals 0.5 cattle ha^{-1}.

The zoological results are found in Chaps. 14 and 15 and in the expert system in Chap. 27.

At *Heedwigenkoog,* located approximately 20 km North of Friedrichskoog, the soil ecological heating experiments were executed. The dike separating the salt marsh from the foreland was built in 1936. Since that time, the high sedimentation rate built up a wide salt marsh, which now belongs to the National Park 'Schleswig-Holsteinisches Wattenmeer'. The experimental site is submerged by tides nearly 500 times year^{-1} (Fig. 4.11). The soils are described in more detail in Chap. 16 together with the results of the soil heating experiment. The main selection criterion was the homogeneity of the soil conditions. The slightly sandy marsh was covered by a lower salt marsh vegetation mainly built up by *Salicornia* and the grass *Puccinellia maritima* (Mueller et al. 1992).

The research area at the Baltic Sea in Schleswig-Holstein was located south of Hohwacht behind a barrier beach at the salt-water *Sehlendorf Lagoon* (Fig. 4.12). It is the only remaining lagoon with an existing connection to the Baltic Sea and covers 76 ha.

For decades, the barrier beach, partly covered with sand dunes, has been intensively used by tourism. In the past, the higher elevated sites of the research area were agriculturally used.

The research area has been under nature protection since 1976 in part and since 1985 in total. Presently, extensive grazing with cattle (Scottish Highland cattle) and periodically with horses is performed which equals approximately 0.5 cattle ha^{-1} (NABU 1992). In the research area, saline pastures with peat formation have developed at 20 cm, 30 cm, and 40 cm above sea level, salt-poor, fresh pastures at 60 cm, 80 cm, and 100 cm above sea level, and dry pastures at 100 cm and 150 cm above sea level.

The zoological results are presented in Chaps. 14 and 15 and in the expert system in Chap. 27.

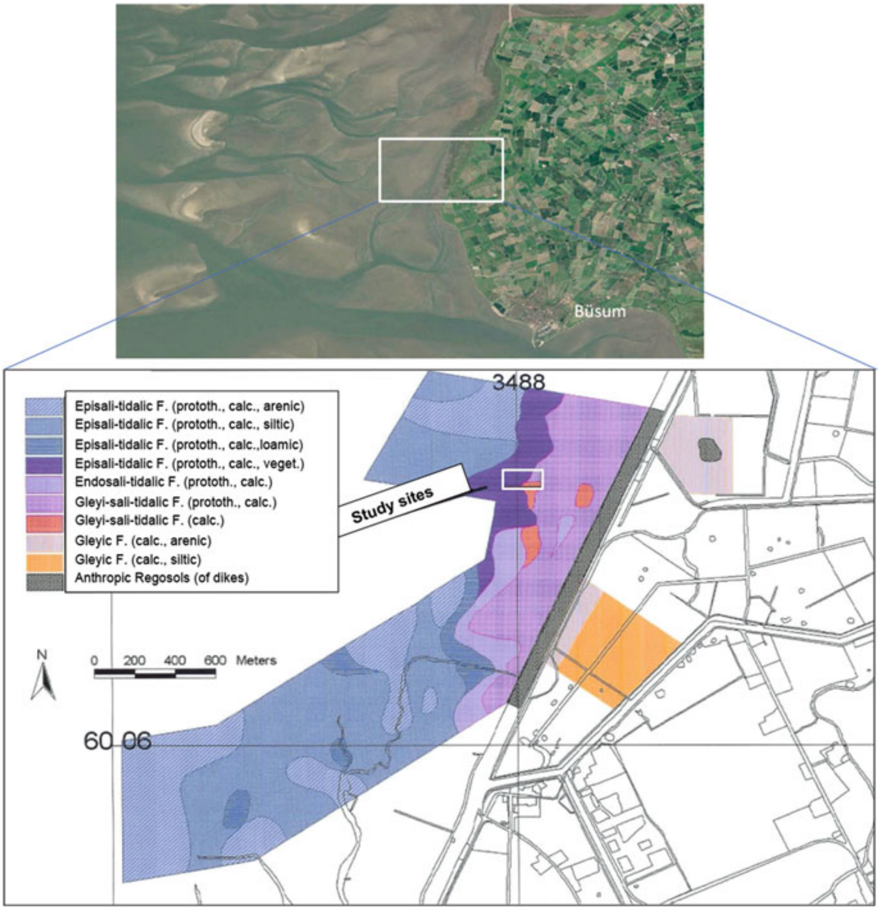

Fig. 4.11 Foreland at Heedwigenkoog with the research site for the soil heating experiment (white rectangle) (Image: Google Earth; geographical coordinates 54°11.62′ N, 8°48.84′ E)

The *Sundic Meadow* (Sundische Wiese) is located southeast of the Zingst Peninsula, which is an accumulation zone, presently increasing in an eastern direction (Fig. 4.13). The low elevated areas are composed of flooded fens and single beach walls, which have been partly diked. The Sundic Meadow was agriculturally used before 1990 on both sides of the dike. Additionally, there was a military training area. Since 1990, it has been extensively grazed with cattle. Salt marshes with peat formation were investigated at: (1) 30 cm, (2) 50 cm, and (3) 70 cm, fresh grassland (4) on the dike at 110 cm and (5) on a sandy beach wall at 160 cm above sea level.

Results of the zoological investigation are presented in Chaps. 14 and 15, and in the expert system in Chaps. 26 and 27.

The *Karrendorf Meadows* are part of a peninsula north-east of Greifswald that extends into the Greifswald Bodden (Fig. 4.14). Fens and mineral soils have been

Fig. 4.12 Research area at the Sehlendorf Lagoon (Hohwacht Bay of the Baltic Sea). White rectangle indicates the study site, points the sampling stations (Image: Satellite photograph: Google Earth; geographic coordinates: 54°18′45″ N, 10°40′34″ E)

developed on a former levelled moraine, which was flooded by seawater. After the construction of a dike, the Karrendorf Meadows were agriculturally used and fertilised. In 1988/1989, a last intensive ploughing was carried out. Since 1990, the area is under nature protection. After removement of the dike in December 1993, low elevated areas have been exposed to the influence of saline water. Since that time, the pastures have been extensively used for cattle grazing (Holz et al. 1996).

The research areas contain fens of a former foreshore at 15–25 cm above sea level with reed vegetation, fens under pasture at 20 cm, 40 cm, and 60 cm as well as mineral soils at 100 cm and 150 cm above sea level.

Results of the de-embankment are described in Chap. 25. Results of the zoological investigations are presented in Chaps. 14 and 15 and of both vegetation and zoology in the expert system in Chaps. 26 and 27.

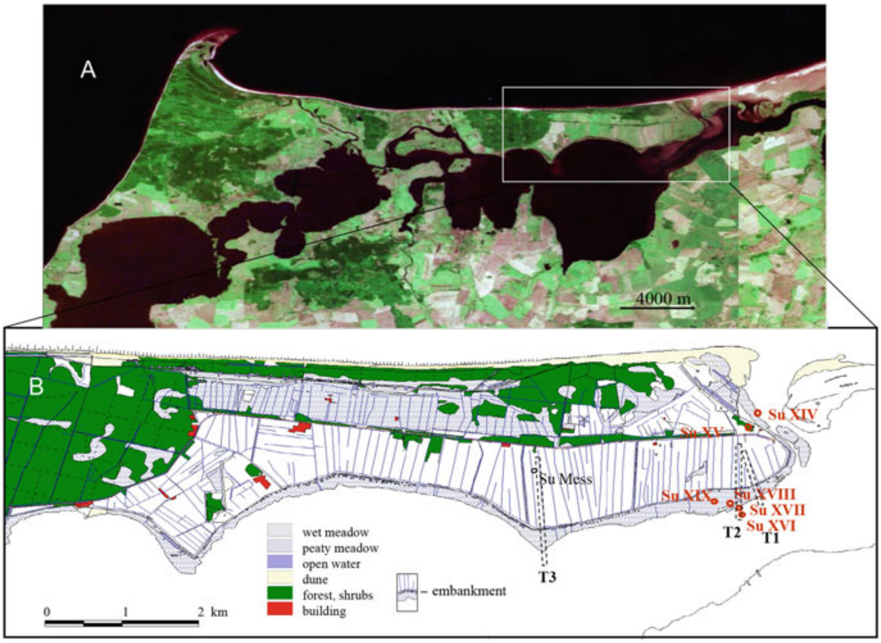

Fig. 4.13 Sundic Meadow at the Darß/Zingst Peninsula in Mecklenburg-Western Pomerania. SuMess: climate station of the Geographic Institute, University of Greifswald; (Images: (**a**): Satellite photograph: Google Earth; (**b**): faunal study sites (Roman numbers) and vegetation transects (T1–T3); geographical coordinates: 5°25′55″ N 12°55′07″ E)

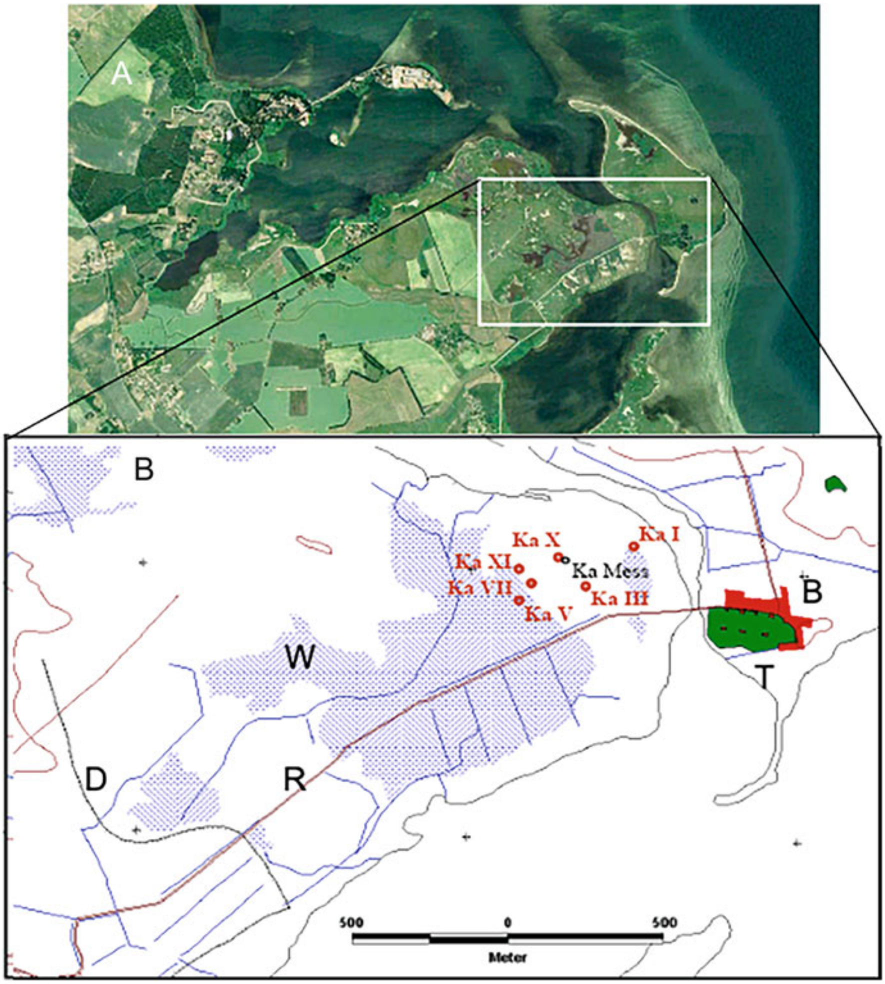

Fig. 4.14 Research areas at the Karrendorf Meadows northeast of Greifswald with the study sites (Images: (**a**): Satellite photograph: Google Earth; (**b**): Roman figures indicate zoological, letters vegetation study sites; (M): mesophilic grassland; (S): salt meadow; (p): pioneer vegetation. Capital letters indicate non-grazed, small type grazed sites. KaMes: climate station of the Geographic Institute, University of Greifswald. Geographical coordinates: 54°09′58″ N 13°24′20″ E)

References

De Jong JD (1984) Age and vegetational history of the coastal dunes in the Frisian Islands. The Netherlands Geol en Mijnbouw 63:269–275

Ehlers J (1986) Phasen der Dünenbildung auf den Inseln des Wattenmeeres. Berliner geographische Studien 20:27–38

Erchinger HF (1985) Dünen, Watt und Salzwiesen. Schutz und Erhaltung von Küste und Inseln, Tier- und Pflanzenwelt. Soltau, Norden

Erchinger HF (1987) Salzwiesenbildung und –erhaltung–Lahnungsbau und Begrüppung für den Küstenschutz. In: Kempf N, Lamp J, Prokosch P (eds) Salzwiesen: geformt von Küstenschutz, Landwirtschaft oder Natur? WWF-Deutschland Tagungsbericht 1. Husum, pp 279–296

Främbs H, Kinder M, Hielen B, Böhme B, Günther C-P, Rachor E, Cordes H, Mossakowski D (2000) Renaturierung salzbeeinflußter Lebensräume der Nordseeküste. In: Abschlußbericht des Salzwiesenprojektes Wurster Küste (1991–1999). Universität Bremen, Bremen

Göhren H (1975) Zur Dynamik und Morphologie der hohen Sandbänke im Wattenmeer zwischen Jade und Eider. Die Küste 27:28–49

Grotjahn M, Michelis H, Obert B, Stephan H-J (1982) Höhenentwicklung, Sediment, Vegetation und Bodenfauna in den Landgewinnungsfeldern beiderseits des Cappeler Tiefs (1957-1978). Jahresbericht Forschungsstelle für Insel- und Küstenschutz der Niedersächsischen Wasserwirtschaftsverwaltung (Norderney) 34:63–94

Haeseler V (1988) Entstehung und heutiger Zustand der jungen Düneninseln Memmert und Mellum sowie Forschungsprogramm zur Besiedlung durch Insekten und andere Gliederfüßer. Drosera 88:5–46

Holz R, Hermann C, Müller-Motzfeld G (1996) Vom Polder zum Ausdeichungsgebiet. Das Projekt Karrendorfer Wiesen und die Zukunft der Küstenüberflutungsgebiete in Mecklenburg-Vorpommern. Natur und Naturschutz in Mecklenburg-Vorpommern 32:3–27

Kiehl K (1997) Vegetationsmuster in Vorlandsalzwiesen in Abhängigkeit von Beweidung und abiotischen Standortfaktoren. Mitteilungen Arbeitsgemeinschaft Geobotanik Schleswig-Holstein und Hamburg 52, Kiel, 143 pp

Kinder M, Främbs H, Hielen B, Mossakowski D (2003) Regeneration von Salzwiesen in einem Sommergroden an der Nordseeküste: E + E- Vorhaben Salzwiesenprojekt Wurster Küste. Natur und Landdschaft 78:343–353

Kinder M, Kinder S, Mehrtes L, Vags I, Züghart W, Främbs H, Bach L, Albersmeyer J, Hassenstein W (1995) Salzwiesenprojekt Wurster Küste. Abschlußbericht zu den wissenschaftlichen Begleituntersuchungen 1992–1995. Im Auftrag der Projekt-Trägergemeinschaft und des Bundesamtes für Naturschutz (Bonn), Universität Bremen

Kuhbier H (1987) Oldeoog–die Alte Insel vor der Jade. Seekajak 8:11–14

Mueller K, Müller-Thomsen U, Unger G (1992) Bodenökologische Untersuchungen im Küstenbereich vor Hedwigenkoog (Norderdithmarschen) und Ergebnisdarstellung mit Hilfe des Geographischen Informationssystems ARC/INFO. Jahresbericht 1992 Forschungs-, Technologiezentrum Westküste, chapter 6.6, Kiel University

Müller CD (1961) Untersuchungen des Verlandungsfortschrittes beiderseits des Cappeler Tiefs. Jahresbericht Forschungsstelle für Insel- und Küstenschutz der Niedersächsischen Wasserwirtschaftsverwaltung (Norderney) 13:151–179

NABU (Naturschutzbund) (1992). Naturschutzgebiet Sehlendorfer Binnensee und Umgebung. Naturschutz im Kreis Plön, 2

Niemeier G (1972) Ostfriesische Inseln. In: Sammlung geographischer Führer 8. Borntraeger, Berlin

Peters M (1996) Vergleichende Vegetationskartierung der Insel Borkum und beispielhafte Erfassung der Veränderung von Landschaft und Vegetation einer Nordseeinsel. Dissertationes Botanicae 257:1–227

Prange N (1986) Die Bedeichungsgeschichte der Marschen in Schleswig-Holstein. Probleme der Küstenforschung im südlichen Nordseegebiet, A Lax, Hildesheim, pp 1–54

Reineck H-E (1987) Morphologische Entwicklung der Insel Mellum. In: Gerdes G, Krumbein W, Reineck H-E (eds) Mellum, Portrait einer Insel. Senckenberg-Buch 63. Kramer, Frankfurt a. M

Schröder F-G (1998) Lehrbuch der Pflanzengeographie. Quelle & Meyer, Wiesbaden

Schütte H (1904) Ein neu entstandenes Düneneiland zwischen Außenjade und Außenweser Jb. Ver Naturk Unterweser 03(04):31–42

Semmel A (1996) Geomorphologie der Bundesrepublik Deutschland, vol 5. F Steiner, Stuttgart

Sindowski K-H (1979) Zwischen Jadebusen und Unterelbe. Bornträger, Berlin, p 145

Stephan H-J (1985) Zur Vorlandsicherung an der Wurster Küste. Jahresbericht Forschungsstelle Norderney 36

Stock M, Kiehl K, Reinke H-D (1995) Salzwiesenschutz im schleswig-holsteinischen Wattenmeer. Grundlagen, Zielsetzungen und bisherige Umsetzungen. Abschlußbericht des Teilprojektes Ökosystemforschung A6.3 Schutz- und Managementkonzepte für Salzwiesen. Kiel, 126 pp

Van Dieren JW (1934) Organogene Dünen. Eine geomorphologische Analyse der Dünenlandschaft der West-Friesischen Insel Terschelling mit pflanzensoziologischen Methoden. Martinus Nijhoff, Den Haag

Climate and Weather Conditions Along the German Shores

5

Detlev Handelmann and Gerhard Weidemann

Abstract

The climate of the research area was derived from tables of the meteorological stations at the North Sea coast (Norderney, Cuxhaven, and St. Peter-Ording) and at the Baltic Sea coast (Kiel-Holtenau, Warnemünde, and Greifswald). Mean monthly air temperature and annual precipitation were derived from the datasets published by the German Weather Service (Deutscher Wetterdienst). To visualize the water balance from precipitation and evaporation, climate diagrams according to Walter and Lieth are presented for each observation station.

5.1 Climate Classification and Climatological Gradient

The general climate of the research area can be derived from the tables of six meteorological stations, three at the North Sea coast (Norderney, Cuxhaven, and St. Peter-Ording) and three at the Baltic Sea coast (Kiel-Holtenau, Warnemünde, and Greifswald), respectively (Figs. 5.1 and 5.2). Mean monthly air temperature and precipitation in the course of the year were derived from the data tables of the German Weather Service (Deutscher Wetterdienst 1997, 1998, 1999). To visualize the water balance from precipitation and evaporation, climate diagrams according to

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Author "Gerhard Weidemann" has died before the publication of this book.

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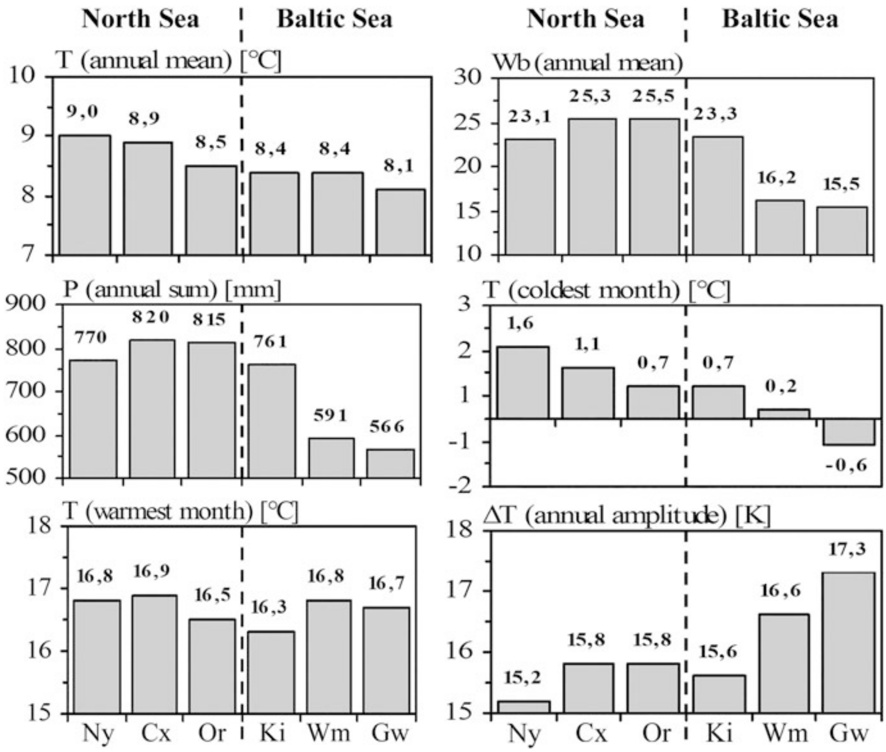

Fig. 5.1 Climate gradient along the German North and Baltic Sea coasts (mean values 1961–1990). Climatologic characteristics: *T* temperature, *ΔT* temperature amplitude, *P* precipitation, *Wb* water balance. Meteorological observation stations: *Ny* Norderney, *Cx* Cuxhaven, *Or* St. Peter-Ording, *Ki* Kiel-Holtenau, *Wm* Warnemünde, *Gw* Greifswald. The dashed vertical line divides North Sea and Baltic Sea stations

Walter and Lieth (1967) are presented for each observation station (Fig. 5.3). The climate diagrams are scaled in 10 °C-intervals for mean monthly temperature that equal 20 mm monthly precipitation. The distance between the curves of both temperature and precipitation roughly estimates the relation between precipitation input and evaporation output, which reflects the water balance. Positive values characterize humid conditions, while arid conditions are marked by negative values. A water balance of zero indicates the boundary of dryness.

The northern German coastal area is characterized by a temperate-warm humid climate with a cool season. At the climate stations mentioned above, the mean temperatures of both the warmest summer month and the coldest winter month range between 16.2 °C, 16.9 °C and 1.6 °C, −0.6 °C, respectively (Fig. 5.1). Due to the seasonally balanced distribution of precipitation, humid conditions exist throughout the year, i.e. the water balance is positive during the entire year. Regarding this combination of criteria, the German North Sea coast and the Baltic Sea coast are classified as Cfb-Climate according to the Köppen climate classification (Strässer 1998).

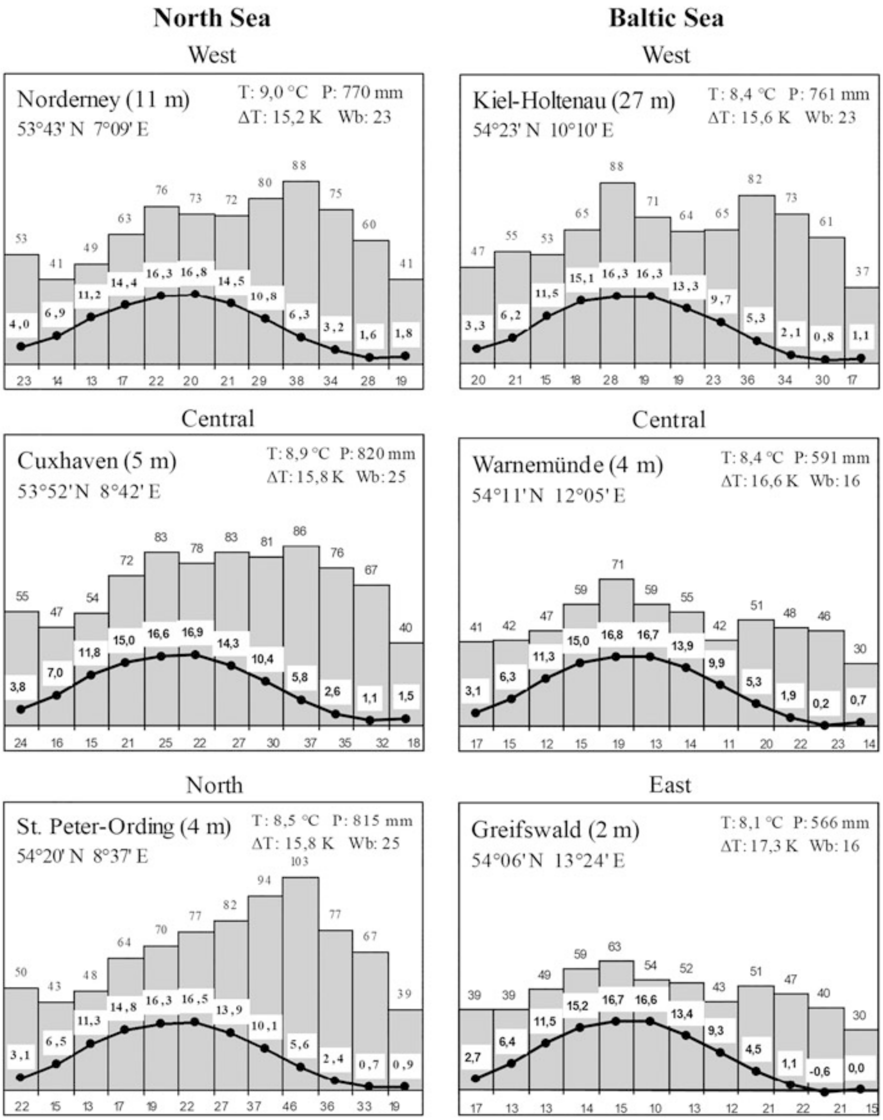

Fig. 5.2 Temperature, precipitation, and water balance along the German North Sea coast and the Baltic Sea coast (means 1961–1990). Long-term mean temperature [°C]: lines, precipitation sum [mm]: columns, water balance: figures at the abscissa, month: initials starting with March. *T* annual mean temperature, *ΔT* annual temperature amplitude, *P* annual precipitation, *Wb* water balance. Graph modified after Walter and Lieth (1967)

Depending on the west-east gradient of totally ca. 400 km distance and 6° 15′ geographic length, the stations cover a gradient from an oceanic to a continental climate (Figs. 5.1 and 5.2). The annual mean temperature decreases from Norderney to Greifswald, mainly due to colder winters of the more continental climate (Figs. 5.1 and 5.2). The annual amplitude of temperature (the difference between the warmest

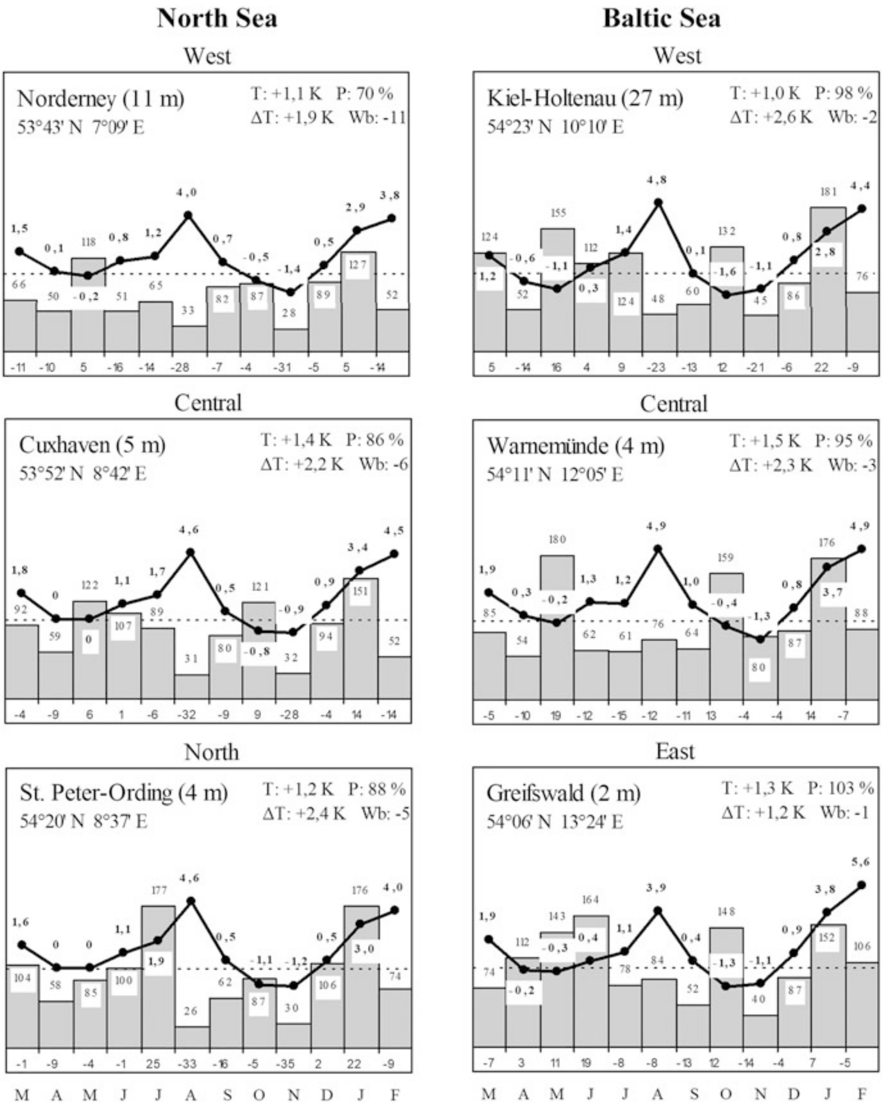

Fig. 5.3 Temperature, precipitation, and water balance from March 1997 through February 1998 (deviation from the long-term mean 1961–1990) at the German North Sea and Baltic coasts; the dotted line marks 100% of monthly precipitation, resp. zero deviation of monthly mean temperature (designations as Fig. 5.2)

and the coldest month) also documents continental climate manifestation (Blüthgen and Weischet 1980); it increases in eastern direction by about 2 K, with the steepest increase between Kiel and Warnemünde. The island of Norderney has the lowest amplitude and hence the mostly pronounced oceanic climate. Notably, oceanic climates are characterized by relatively high yearly sums of precipitation with a maximum in autumn (Blüthgen and Weischet 1980). The stations at the North Sea coast and at Kiel show this pattern, while the yearly sums of precipitation of Warnemünde and Greifswald with less than 600 mm are clearly lower and have their maximum during the summer months. The smaller water balance also indicates the dryer conditions during the whole year at these stations in contrast to those at the North Sea coast. Comparing the six stations, along the west-east climate gradient no continuous trend is revealed, whereas a steep change is marked at the 11° E geographical longitude between Kiel and Warnemünde (Fig. 5.1).

5.2 The Course of the Weather from March 1997 Through February 1998

Temperatures between both Kiel and Warnemünde were between 1.0 K and 1.5 K, respectively. Those above the long-term (30 years) annual mean indicate a markedly warm year (Fig. 5.3). While the temperatures in spring (March to May) were only slightly deviated from the long-term mean, the summer was very warm. In particular, in August, high monthly means with 20.5 °C (+3.9 K) at Greifswald and 21.6 °C (+4.9 K) at Warnemünde were reached. The autumn was slightly cooler than the long-term mean (−0.5 K). During the winter, extraordinarily high mean monthly temperatures were recorded. In January, they increased to +2.8 K at Kiel and +3.8 K at Greifswald above the long-term mean. Extreme deviations occurred in February; the maximum deviation of +5.6 K was measured at Greifswald. In spite of the mild winter, the temperature amplitude was increased to about 2 K which reflects a year with more continental climate than in the long-term mean.

In relation to the long-term mean, the annual precipitation sum was only 70% at Norderney and 88% at St. Peter-Ording (Fig. 5.3). The reduction of the water balance by 6–11 units also indicates an extraordinarily dry period. In contrast to the situation at the North Sea coast, precipitation sums and water balance at the Baltic Sea coast stations did not markedly deviate from the long-term mean. Seasonal precipitation and water balance were spatially and temporally heterogeneously distributed. May and January were above the long-term average indicating rainy and humid conditions at almost all observation stations. While precipitation and water balance during October were higher than the means at Cuxhaven and the Baltic Sea stations, Norderney and St. Peter-Ording had deficits. Due to minimal precipitation input, e.g. 26% at St. Peter-Ording, and high summer temperatures, an extremely dry phase during August occurred with mostly negative water balances. In spite of lowered mean monthly temperatures, November was also markedly dryer than the long-term average at all stations. April, September, December, and February were also relatively dry months. The remaining 3 months, e.g. June, showed a spatially heterogeneous pattern with partially marked differences between adjacent stations. Beside the raised temperature amplitude, the reduced precipitation illustrates the increased influence of continental weather situations, at least at the North Sea coast.

5.3 The Course of the Weather from March 1998 Through February 1999

At most observation stations, the mean temperatures showed only a slight deviation (+0.5 K) from the long-term mean, except at Kiel (Fig. 5.4). The temperature conditions are classified as balanced. On average, spring was 1.5 K to 2.0 K warmer than the long-term mean, while summer months were slightly cooler with 0 K to −1.0 K deviation. The autumn was characterized by a markedly cooler November: −2.6 K below the long-term mean at Norderney and −3.4 K at Greifswald. While the winter temperatures during December and February were relatively close to the long-term mean, January showed the most marked deviation with values between both +2.5 K and +3.4 K at St. Peter-Ording and Greifswald, respectively. Due to the temperate summer and mostly mild winter temperatures, the temperature amplitude was lowered by about 1.7 K compared with the long-term mean and shows a more oceanic character.

Along the German North Sea and Baltic Sea coasts, all stations revealed markedly higher precipitation sums than the long-term mean ranging between 119% at Greifswald and 145% at St. Peter-Ording (Fig. 5.4). Due to the temperate mean temperatures and the parallel running water balance, the observed period was classified as outstanding wet. Like in the foregoing year, precipitation showed a high variability in space and time. April, June, July, October, and February were spaciously rainy and wet. In particular, rainfall in October accounted to 15% and 25% of the long-term annual mean with peak values of 172 mm at St. Peter-Ording and 214 mm at Cuxhaven. In spite of high mean temperatures, April was markedly wetter than the long-term mean with water balance deviations of +7 at Greifswald and +45 at St. Peter-Ording. Supra-regionally, May was the driest month; slightly higher mean temperatures and reduced precipitation caused a reduced water balance at all observation stations. In September and January, water deficits were measured at most stations. However, no markedly dry periods, such as in the previous year, were found. March, August, November, and December showed balanced or regionally differently directed water balances. The higher precipitation combined with reduced temperature amplitudes indicates a predominance of cyclonal western weather.

5.4 The Weather Conditions from March to September 1999

The average temperatures during this 7-month period were markedly above the long-term mean, at Kiel by 1.3 K and at Warnemünde by 1.9 K (Fig. 5.5). Even the spring months were warmer than the average at all stations. During March and April, the mean temperatures ranged between +1.5 K and +2.3 K, whereas the May temperature increase was less than 0.5 K–1.3 K. The June temperatures differed only slightly from the long-term mean, but at mid- and late summer rather warm periods occurred. The mean temperature was 16.6 °C at Greifswald and 18.0 °C at Cuxhaven that

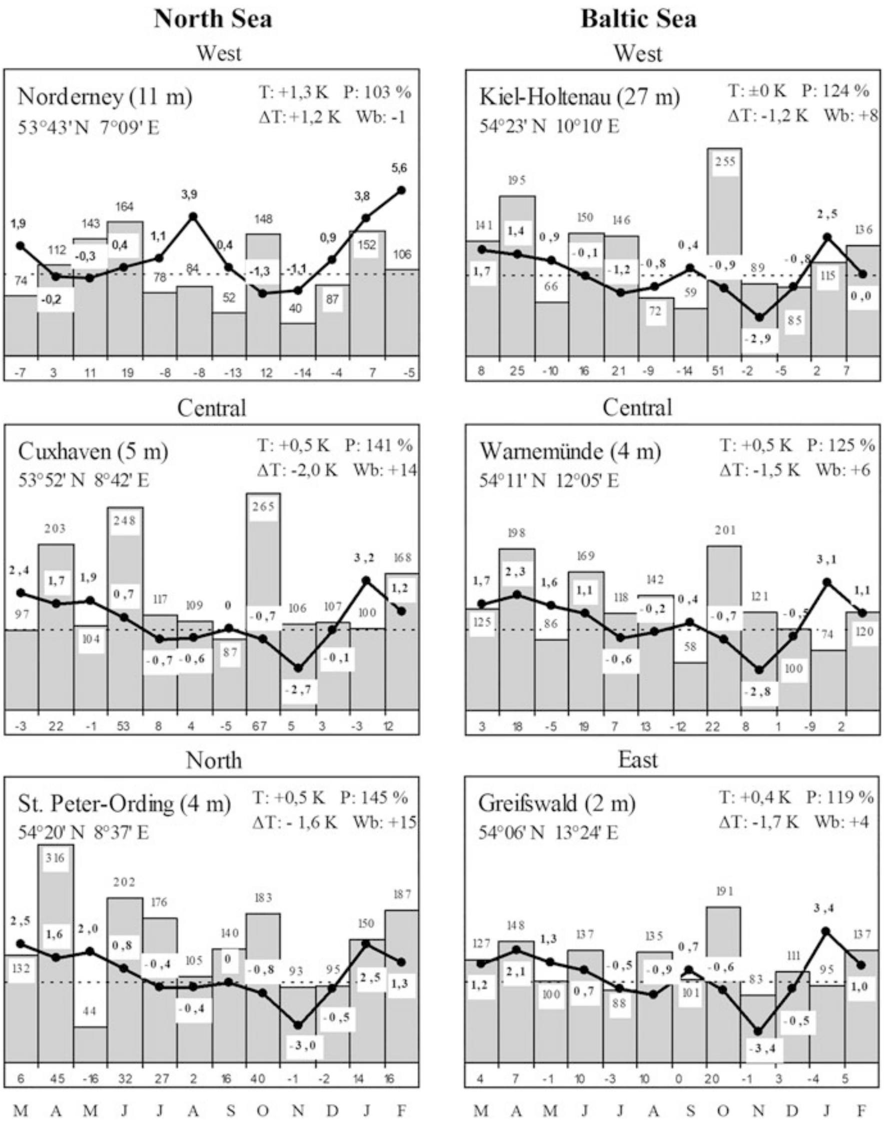

Fig. 5.4 Deviation of temperature, precipitation, and water balance of the period March 1998 through February 1999 from the long-term mean 1961–1990 at the German North Sea and Baltic coasts; the dotted line marks 100% of monthly precipitation, resp. zero deviation of monthly mean temperature (designations as Fig. 5.2)

deviated from the mean by +3.2 K and 3.7 K, respectively. Additionally, the July temperatures also documented the warm summer of 1999 with at least +1.8 K.

Between the observation stations at the North Sea and the Baltic Sea, the average precipitation sums and water balances were inhomogeneous (Fig. 5.5). In contrast to

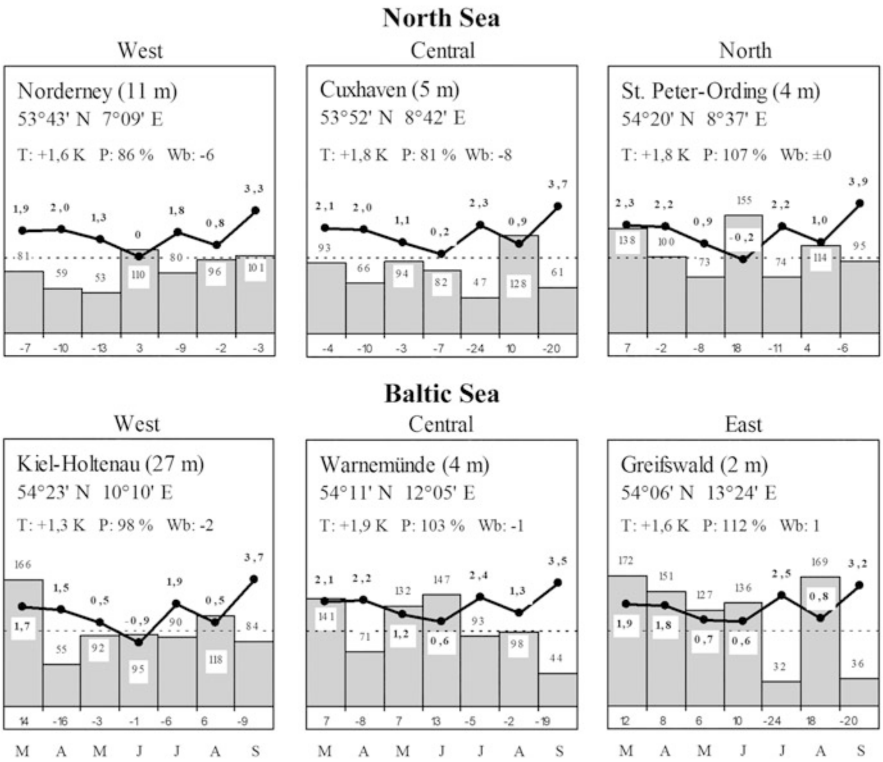

Fig. 5.5 Deviation of temperature, precipitation, and water balance of the period March through September 1999 from the long-term mean 1961–1990 at the German North Sea and Baltic coasts; the dotted line marks 100% of monthly precipitation, resp. zero deviation of monthly mean temperature (designations as Fig. 5.2)

Norderney and Cuxhaven with deficits in relation to the long-term mean, for both precipitation and water balances with 86–81% and −6 to −8, respectively, the values at St. Peter-Ording, Kiel, and Warnemünde were close to the mean. At Greifswald, precipitation reached 112% of the long-term mean combined with a compensated water balance. This means that the markedly high temperatures during spring and summer reveal water losses, in particular at the North Sea coast. Beside single exceptions, March and June were mostly rainy and wet, while April and especially July and September showed dry phases, at least regionally. In May and August, precipitation was within the range of the long-term mean or locally indifferent.

References

Blüthgen J, Weischet W (1980) Allgemeine Klimageographie, 3rd edn. Walter de Gruyter, Berlin. 887 pp

Deutscher Wetterdienst (ed) (1997) Monatlicher Witterungsbericht 45. Deutscher Wetterdienst, Offenbach/Main

Deutscher Wetterdienst (ed) (1998) Monatlicher Witterungsbericht. 46. Deutscher Wetterdienst, Offenbach/Main

Deutscher Wetterdienst (ed) (1999) Witterungsreport Daten. 1 (1–2). Deutscher Wetterdienst, Offenbach/Main

Strässer M (1998) Klimadiagramme zur Köppenschen Klimaklassifikation. Klett, Perthes, Cotta, Stuttgart. 95 pp

Walter H, Lieth H (1967) Klimadiagramm-Weltatlas. G. Fischer, Jena

Inundation Regimes of the German Coasts and the Impact of the Rising Sea Level

6

Stefan Seiberling and Wolfgang Dormann

Abstract

The sea water influence of coastal areas at the North Sea and the Baltic Sea is fundamentally different due to they respective tidal regimes and surface salinity. The tides at the North Sea amount to several metres, whereas tides at the Baltic Sea are mostly only a few centimetres as they are mainly influenced by wind and air pressure, but still influence the inundation frequency and the ground-water level of lower salt marshes. Additionally, weather events affect the inundation dynamics of elevation zones at both coastal regions in a similar way.

6.1 Introduction

The sea water influence of coastal areas at the North Sea and the Baltic Sea is fundamentally different due to the respective tidal regimes and surface salinity. Tidal fluctuations at the North Sea amount to several metres, whereas tides at the Baltic Sea are negligible but still influence the inundation frequency and the ground-water level of lower salt marshes. Additionally, weather events affect the inundation dynamics of elevation zones at both coastal regions in a similar way (see Chap. 5). Tidal dynamics and storm surges also have an impact on the development of soils and the topography of salt marshes (see Chap. 21).

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Besides the significant differences in surface salinity (see Chap. 7), the salt water inundations are responsible for the different biotic and abiotic conditions in the coastal ecosystems of the North Sea and the Baltic Sea. Due to the (micro)-tidal coasts of the Baltic Sea, no Tidal Mean High-Water Level (MHW) can be used to indicate the elevation of sites. Site elevation at the Baltic Sea is therfore referred to as NN (German Ordnance Map Level).

Different local inundation scenarios are necessary to assess the impact of rising sea levels on salt marshes of the meso-/macro-tidal North Sea coast and salt grasslands of the micro-tidal Baltic Sea coast. The GKSS Research Centre in Geesthacht, Germany, provided such scenarios for the study sites along the German Coast until the year 2050 (Storch et al. 1998).

6.2 Methods and Data

Based on a long-term time series of tidal gauges near the study sites (Fig. 6.1), scenarios were generated providing local deviations from the global sea level rise. The underlying temperature change of 1.7 °C lies within the 'high estimate' of the IPCC IS92a scenario (Houghton 2001 1229/id). For the calculation of the scenarios, the ECHAM4/OPYC3-model (Roeckner et al. 1999) with a spatial resolution of 250 km was applied, based on the IS92a emission scenario with a yearly CO_2-growth rate of 0.85%. As a monthly resolution was sufficient for the project requirements, the GKSS used a Canonical Correspondence Analysis (CCA). Therewith, empirical relations between large-scale atmospheric properties (pressure, temperature) and local target figures were detected to increase the spatial resolution. Thus, monthly quartiles for high water (HW) were calculated for the North Sea gauges of Borkum, Bremen, Bremerhaven, Cuxhaven, Emden, Husum, and Wilhelmshaven.

Fig. 6.1 Measurement stations with tidal gauges (●) at or near the study sites along the German Coast

The 7 pm-values of the tidal gauge 'Greifswald-Wiek' were used for the micro-tidal Baltic Sea.

Present observations and future scenarios were compared on a seasonal basis due to a mostly seasonal relation between variables at different scales. The predicted scenarios are related to the study sites along the North Sea (Storch et al. 1998). Because the North Sea and the Baltic Sea differ distinctly, tidal gauges are characterized in detail with one example each for the North Sea and the Baltic Sea.

6.3 Characterization of Inundation Regimes for the German Coasts

As outlined already in the introduction of this chapter, the inundation regimes differ fundamentally between macro-tidal coasts of the *North Sea* and micro-tidal coasts of the Baltic Sea. The inundation regimes of the eulittoral and lower supralittoral zones are evoked by luni-solar gravitational effects and centrifugal forces at the North Sea coast (semi-diurnal tides with ranges between ca. 2.5 m and 4.2 m at the German coast).

Meteorological conditions, atmospheric pressure, wind, and the time of occurrence can modify the height of individual tides (Brown et al. 2002). The inundation frequencies of the middle and upper supralittoral zones are driven mainly by meteorological forces (storm surges), with a modifying impact of luni-solar gravitational and centrifugal forces.

Furthermore, tidal ranges influence the ground-water level of coastal areas. Permanently high ground-water levels appear at the North Sea coast only in silty salt marshes.

The mainland salt marshes of the German North Sea coast show higher mean high-water (MHW) levels than the island salt marshes (Fig. 6.2). In contrast to the mainland coast, the tidal wave can pass the islands. The spreading of the tidal wave is held by the mainland coast piling up there.

While the flooding frequency approaches its maximum at 80 cm NN at the North Sea, the respective zones at the southern Baltic Sea are flooded almost exclusively in winter. The western parts of the Baltic Sea coasts are more affected by floods than the eastern parts. At Heiligenhafen, the 0 cm NN-level is immersed more than 25-times a month, with 15 floods per month being the random frequency for equally distributed wind directions without tidal influence. At Greifswald, the 0 cm NN is flooded only 18 days a month indicating mainly wind impact and a very low tidal influence.

The gauge of Spieka-Neufeld (Fig. 6.3), characterizing the North Sea tidal regimes, shows the characteristic sigmoid relation between flooding frequency and elevation. The zones below 60 cm NN are almost regularly flooded twice a day throughout the year. At higher elevations, an exponential decline is observed up to the annual MHW at about 160 cm NN. Elevations of 20 cm above the MHW (180 cm NN: height of spring tides) are flooded exclusively during wind and storm tides. Between 20 cm above the MHW and 0 cm MHW, flooding frequency

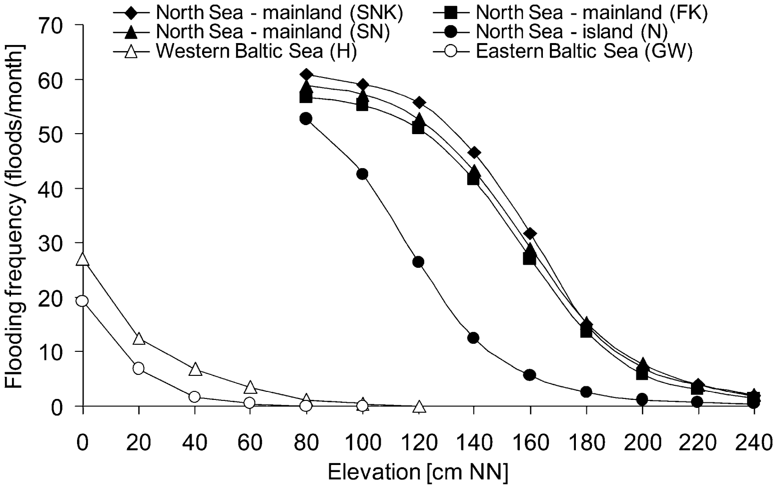


Fig. 6.2 Flooding frequency for study sites along the coast of the North Sea (80–240 cm NN) and the Baltic Sea (0–120 cm NN) between 1986 and 1996. The geographical specifications 'Eastern'/ 'Western' refer to the German coast. Tidal gauges: *GW* Greifswald-Wiek, *H* Heiligenhafen, *FK* Friedrichskoog, *N* Norderney, *SN* Spieka-Neufeld, *SNK* Sönke-Nissen-Koog

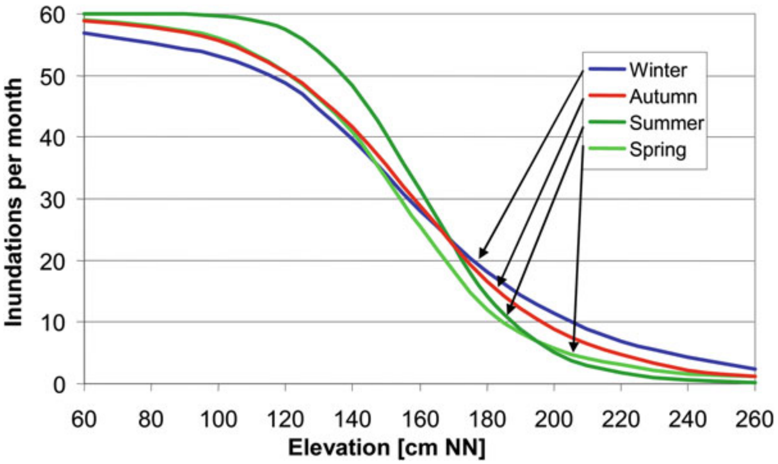
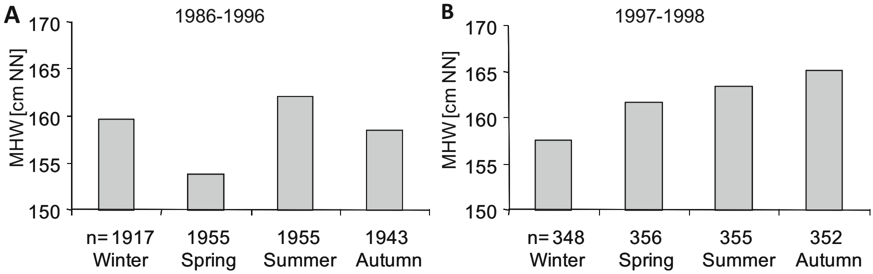


Fig. 6.3 Seasonal inundation of different elevations for the tidal gauge of Spieka-Neufeld (North Sea) during the period between 1986 and 1996

increases exponentially. Considering the modifying geomorphologic impact, the values are more or less similar for the whole mainland coast of the German North Sea. At the island of Norderney, the MHW is about 20 cm lower (Fig. 6.2).

At elevations lower than the MHW, the number of floods is highest in summer and lowest in winter, while at elevations above the MHW it is reversed. Thus, the pioneer-zones of salt marshes are flooded most frequently during the vegetation



A	Winter	Spring	Summer	Autumn	
Winter	–	–	–	–	
Spring	5.8	7.7	–	–	
Summer	–	-8.3	–	–	
Autumn	–	-4.6	3.7	–	B

- No significant difference

Fig. 6.4 (**a**) Seasonal mean high-water (MHW) levels at the tidal gauge Spieka-Neufeld (North Sea) for the decade from 1986 to 1996 and (**b**) for the study period from 1997 to 1998. Significant differences are observed in the MHW [cm] between seasons for the long-term period (**a**) and between study period and long-term values (**b**) ($p = 5\%$, ANOVA, Post hoc: Tamhane-T2)

period, while the lower, mid, and high salt marshes are submerged mainly in autumn and winter. Due to abundant storms, the highest tidal amplitude occurs in the winter season. The range between lowest and highest tide is more than twice as high in the winter than in the summer season (ca. 5 m compared to ca. 2.5 m).

Although extreme high tides occur in winter, with December being the month with the highest MHW, the long-term seasonal MHW is about the same in the winter and the summer. This is demonstrated in Fig. 6.4a for the period from 1986 to 1996. Spring shows the lowest values compared to the seasons from summer to winter. In the study period, the tides in spring were significantly higher than expected from the long-term values (Fig. 6.4b). The difference was about 8 cm. For the other seasons, there was no significant anomaly.

At the German *Baltic Sea* coast, tides only range between ca. 0.1–0.2 m. The number of inundations of the two littoral zones, hydro- and geo-littoral, are mainly affected by the strength and direction of the wind. The inundation dynamics are modified by the water discharge of the river mouths and by differences in air pressure over the Baltic Sea.

However, the micro-tidal ranges influence the inundation frequency and the ground-water level of coastal areas at the Baltic Sea. A low tidal range causes high ground-water levels in the salt grassland, particularly in the lower zone.

For the Baltic Sea, almost the same inundation scheme is seen as for tidal coasts (Fig. 6.5). As luni-solar tides are negligible, the mean water level (MWL) has a similar importance as the MHW of tidal coasts. The amplitude of the water level is

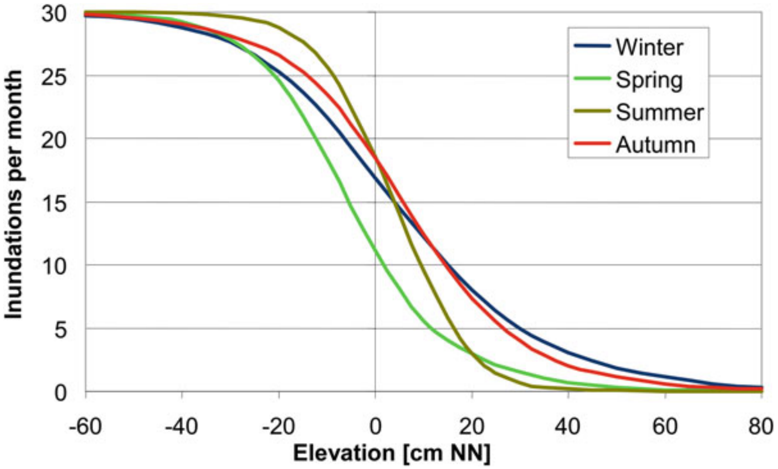


Fig. 6.5 Seasonal inundations of different elevations for the tidal gauge of Greifswald-Wiek (Baltic Sea) during the period from 1961 to 1990 (7:00 am-values)

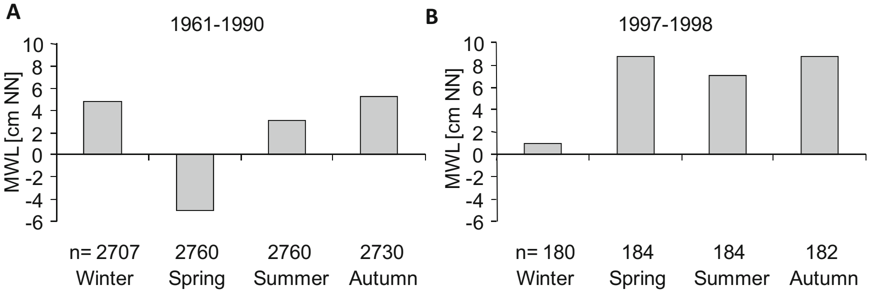
2.54 m during winter, which is twice as high as during summer (1.27 m). Salinity affects the vegetation only at levels up to 70 cm above the MWL (Krisch 1990). This landward boundary is exclusively flooded in winter. According to the weather stations east of Rostock, wind is mainly responsible for the inundation regime that is reflected in the positive correlation between wind speed and water level. Both factors show the same seasonal patterns (in descending order: winter 3.4 ± 0.6 Beaufort (Bft), autumn 3.1 ± 0.5 Bft, spring 3.1 ± 0.4 Bft, and summer 2.7 ± 0.4 Bft).

The magnitude of high inundations is influenced by the exposition of the coast. High waters are brought by northeastern winds through the opening of the Greifswalder Bodden towards the open sea, while west and southwest winds lower the water level. Serious storm surges are caused by strong west wind of about 15 days pushing waters of the North Sea through the Skagerrak and Kattegat followed by northeasterly winds, which push the water towards the coast. A future increase of such constellations is not expected (Beckmann and Tetzlaff 1999).

A more distinct, inter-seasonal differentiation of the inundation regime for the long-term reference period (1961–1990) is expected for the Baltic Sea tidal gauge ‘Greifswald-Wiek’, compared to the North Sea (Fig. 6.6a).

However, basic differences in the seasonal MWL are predicted. The maximum values occur in autumn, followed by winter, summer, and spring. Similar to the amplitude, the MWL depends on wind speed as well as wind direction. Furthermore, the exposition of the coast, ‘west’ for Spieka-Neufeld and ‘north-east’ for Greifswald-Wiek, in co-action with wind direction, generates deviations between seasonal distributions of the MWL (Baltic Sea) and the MHW (North Sea).

During the study period from 1997 to 1998 (Fig. 6.6b), summer and, in particular, spring showed higher MWL than expected from the long-term reference period.



A	Winter	Spring	Summer	Autumn	
Winter	–	–	–	–	
Spring	9.9	13.8	–	–	
Summer	0.1	-8.2	3.9	–	
Autumn	1.0	-10.4	-2.1	–	B

- : No significant difference.

Fig. 6.6 (**a**) Seasonal mean water levels (MWL) of the tidal gauge Greifswald-Wiek (Baltic Sea) from 1961 to 1990, and (**b**) for the study period between 1997 and 1998 (right side) (7:00 am-values). Significant differences in the MWL [cm] between seasons and the long-term period (**a**) and between study period and long-term values (**b**) ($p = 5\%$, ANOVA, Post hoc: Tamhane-T2)

Similar to the North Sea coast, higher inundation frequencies during the vegetation period at the Baltic Sea coast implicate changing abiotic conditions and higher stress for vegetation and animals.

6.4 The Impact of the Predicted Sea Level Rise on the Inundation Regime

The predicted sea level rise at the *North Sea* is affected by local and global components that differ in quality and quantity. Although the local contribution only weakly affects the MHW, it modifies the relative inundation frequency during the seasons (Fig. 6.7). The global sea level rise of 20 cm shifts the absolute inundation frequency by a proportionate rising magnitude, but has no effect on the relative inundation-elevation-scheme.

However, taking the global and the local sea level rise into account, the relative change in floods increases with the elevation, especially during spring and summer (Table 6.1 'local + global'). The absolute change, measured in additional flood events, reaches a maximum at the MHW (i.e. 1.6 m NN), with a mean increase of 16 floods per month. Whereas at 1 m below the MHW (i.e. 0.6 m NN), two additional floods per month will occur, it is only one additional flood at 1 m above the MHW (2.6 m NN). The pattern of the local component is more complex

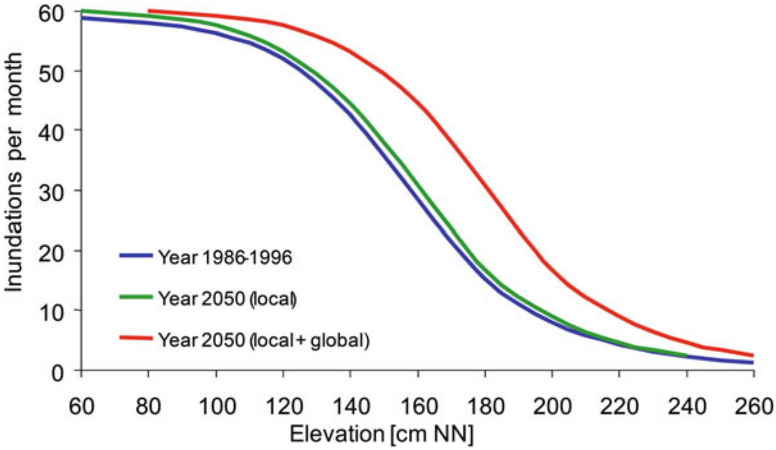


Fig. 6.7 Annual MHW for the tidal gauge Spieka-Neufeld (North Sea) for the long-term period from 1986 to 1996 and the scenario for 2050 (local and global effects)

Table 6.1 Local and global seasonal changes of the flooding frequency for the year 2050 in percent of the period between 1986 and 1996. Tidal gauge: Spieka-Neufeld (North Sea)

	cm NN	80	100	120	140	160	180	200	220	240
2050 (local)	Winter	3	3	2	7	12	13	23	27	16
	Spring	3	2	5	7	13	19	17	3	20
	Autumn	0	1	3	4	9	11	5	8	−25
	Year	1	1	−1	0	1	1	2	−6	−4
2050 (local and global)	Winter	5	7	12	25	52	74	80	102	108
	Spring	3	7	14	30	72	138	147	123	106
	Autumn	0	1	4	23	60	140	206	200	253
	Year	3	5	11	21	44	76	85	96	107

(Table 6.1 local). Compared to the present situation, a decrease is predicted depending on elevation and season as follows: summer: 240 cm NN, autumn: 120 cm, 220 cm, and 240 cm NN.

The seasonal inundation frequencies (Fig. 6.7), a fundamental attribute of the present inundation scheme, are modified by rising sea levels for the elevations between 1.2 m NN and 1.6 m NN. Consequently, the inundation frequency will be higher in spring than in autumn (Table 6.1). Another consequence of the seasonal change will be the sequence of inundation frequencies at 1.4 m NN. The order will shift from summer > autumn > spring > winter to summer > spring > winter > autumn in 2050. Referring to the present MHW level (1.6 m NN), winter in 2050 will have a higher inundation frequency than autumn.

The predicted changes for the *Baltic Sea* (Fig. 6.8) are comparable to the North Sea. In contrast to the North Sea, the local impact is too low to induce a change in the seasonal inundation pattern at different elevations, although different seasonal magnitudes of changes exist.

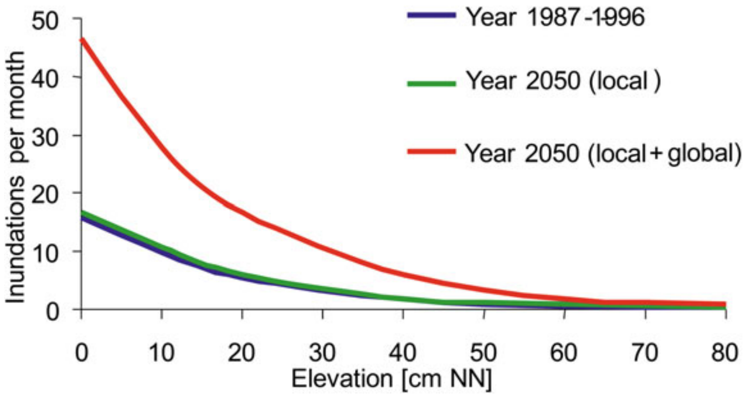


Fig. 6.8 Annual MWL for the tidal gauge Greifswald-Wiek (Baltic Sea) for the period from 1987 to 1996 (7:00 am-values) and the scenario for 2050 (local and global effects) for elevations above 0 cm NN

Table 6.2 Local changes of the seasonal flooding frequency predicted for the year 2050 in percent of the long-time period between 1986 and 1996 (7:00 am-values). Tidal gauge: Greifswald-Wiek (Baltic Sea)

cm > ML	0	10	20	40	60	80
Winter	0.27	0.31	0.33	0.16	0.19	0.47
Spring	0.32	0.56	0.88	0.69	0.03	−0.12
Summer	0.18	0.44	1.19	2.19	1.16	0.57
Autumn	0.12	−0.07	−0.13	−0.51	−0.16	−1.07
Year	0.19	0.23	0.25	0.02	0.08	0.12

According to the predictions of the local scenario (Table 6.2), the clearest changes relative to the present situation will occur in the summer-period. This season will be subject to higher hydro periods, whereas autumn will have lower inundation frequencies at all elevations above the MWL. In spring, the same is true for the higher salt grassland at 60 cm NN. During the whole year, only slight local impacts due to different seasonal trends are predicted.

The highest absolute changes are expected for the present MWL at 0 cm NN with an increase of 31 floods per month compared to merely 1 flood at 80 cm NN. Thus, the vegetation with the highest flooding tolerance will be subjected to the strongest increase in inundation. However, even a sea level rise of a few centimetres significantly affects freshwater communities.

References

Beckmann B-R, Tetzlaff G (1999) Veränderungen in der Häufigkeit von Sturmhochwassern an der Ostseeküste Mecklenburg-Vorpommerns und deren mögliche Ursachen. Die Küste 61:72–88

Brown E, Colling A, Park D, Phillips J, Rothery D, Wright J (2002) Waves, tides and shallow-water processes. Butterworth Heinemann in association with The Open University, Oxford, p 227

Houghton JT, Ding YH, Griggs DJ, Noguer M, van der Linden P, Dai X, Maskell M, Johnson C (2001) Climate change 2001: the scientific basis; contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Krisch H (1990) Ökologisch-soziologische Artengruppen und Pflanzengesellschaften im Geolitoral der Boddenküste (Ostsee). Phytocoenologia 19:1–28

Roeckner E, Bengtsson L, Feichter J, Lelieveld J, Rodhe H (1999) Transient climate changesimulations with a coupled atmosphere-ocean GCM including the tropospheric sulphur cycle. J Clim 12:3004–3032

Von Storch H, Schnur R, Zorita E (1998) Szenarien und Beratung: Anwenderorientierte Szenarien für den norddeutschen Küstenbereich. Abschlussbericht. BMBF Förderkennzeichen 01LK9510/0

The Surface Salinity of the North Sea and Baltic Sea Area

7

Wolfgang Dormann

Abstract

The salt content of the environment specifically affects the settlement of plants and animals in coastal habitats and the coastal areas of the North Sea and Baltic Sea particularly differ in salt concentrations. The gradient of salt concentration of the North Sea and the Baltic Sea and the seasonal changes of salt content are presented. Although the salt content is low in the Baltic Sea its frequent salt pans showed changing but also high values of salt.

7.1 Sea Water Salinities of the North and Baltic Sea Coastal Water Bodies

The salt content of the environment specifically affects the settlement of plants and animals in coastal habitats (e.g. Remane 1940; Tischler 1993; Begon et al. 1996). Besides the hydrologic differences presented in Chap. 6, the coastal areas of the North Sea and Baltic Sea particularly differ in salt concentrations.

Average surface salinities of the seawater of the German and Danish Coastal Zone were available from various publications (Baudler 2002; Becker 1998; Cairns 1992; Krisch 1999; Lozán et al. 1990; Lozán et al. 1996; Schleswig-Holstein 2004; Mecklenburg-Vorpommern 2004; Schirmer 2004) (Fig. 7.1).

- The great differences in the surface salinities between the North Sea and Baltic Sea, and strong gradients of salinity in some areas are of special interest

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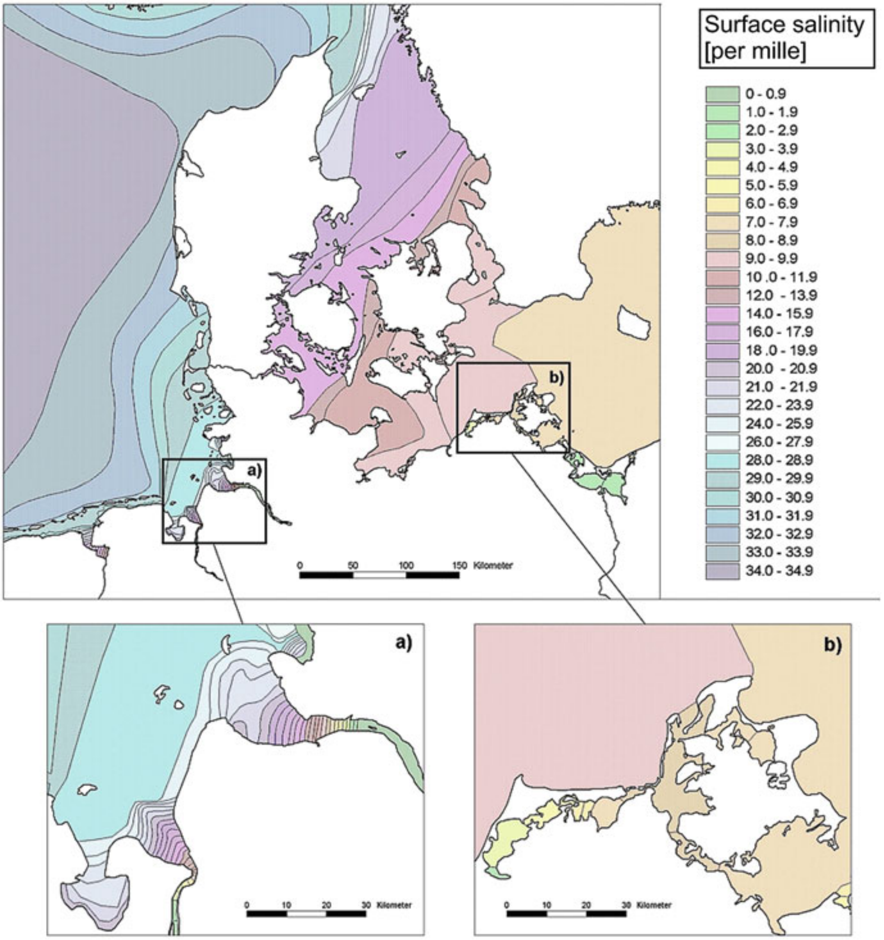

Fig. 7.1 Average surface salinity of sea water at the German and Danish Coast. (**a**) Zoom of the estuaries of the rivers Weser and Elbe (North Sea); (**b**) Zoom of the Pomeranian Bodden Coast (Baltic Sea) (arranged and partially interpolated according to Baudler 2002; Becker 1998; Cairns 1992; Krisch 1999; Lozán et al. 1990; Lozán et al. 1996; Schleswig-Holstein 2004; Mecklenburg-Vorpommern 2004; Schirmer 2004) According to Dormann et al. (2010) (With kind permission of the Bundesamt für Naturschutz (BfN), Bonn)

- The decreasing salinity in the transition zone from the North Sea to the Baltic Sea (Skagerrak and Kattegat)
- The decreasing salinity from the southwest to the northeast in the southern Baltic Sea
- The decreasing salinity in estuarines (in big rivers at the North Sea)
- and the decreasing salinity in coastal bays and in lagoon water bodies

Due to its connection with the Atlantic Ocean, the *North Sea* has had a stable salinity for millennia. The average surface salinity is approximately 34–35%. Greater fluctuations occur merely in coastal areas. The freshwater inflow of the large rivers Elbe, Weser, and Ems is responsible for this effect at the German coast. They reduce the surface salinity in the German Bay to values below 30%. The influence on the salinity of coastal waters depends on the precipitations in their drainage basin and on the thaw periods at the end of the winter. Therefore, high salinity gradients with great dynamics are characteristic in estuarines of the North Sea coast (Fig. 7.1a).

The salinity of the *Baltic* Sea is decisively determined by two primary factors: (1) the saltwater input from the North Sea and (2) the precipitation into the drainage basin of the Baltic Sea. The salinity of the Baltic Sea is regulated by the following factors.

The saltwater input from the North Sea (named Baltic inflows) mainly depends on the power and direction of storms that blow predominantly from western directions.

Additionally, the amount of saltwater inflow is determined by the force and duration of wind and by the height of the Baltic Sea water level. When the water level is lower during west winds, large amounts of salt water flow into the Baltic Sea over the Kattegat. This situation is caused by:

- Strong and steady easterly winds
- A high-pressure area (anticyclone) over the Baltic Sea
- Increased evaporation rates due to high air temperatures in summer before the Baltic inflow season
- Small freshwater inflows by tributary waters due to low rainfall in the catchment area of the Baltic Sea

These differences of the Baltic inflows affect the surface salinity, particularly in the area of the Kattegat and the Belt Sea, and in consequence, the salinity of the coastal habitats. The salinity of the Baltic decreases in phases of prolonged water level stagnation due to an absence of saltwater inflows.

In general, the salinity is reduced by an increased river water supply into the Baltic Sea in periods when the precipitations in the drainage basin of the Baltic Sea are high (Schinke 1996). Therefore, salinity gradients are high in the Baltic Sea between the estuaries of big rivers in the northeast and in the southwestern part of the Kattegat (Fig. 7.1b). Furthermore, precipitations over the mainland lead to regional salinity gradients near the coast, particularly in bays, lagoons, and estuaries (Fig. 7.1).

These processes cause a variation of surface salinity during the year between 0.2–0.8% in the central Baltic Sea and 3–6% in the Belt Sea and the Kattegat. "Major inflows normally occur during winter and spring; they bring relatively cold and oxygen-rich waters to the deep basins. Since 1996, several large inflows have occurred during summer. These inflows have transported high-saline, but warm and low-oxygen water into the deep layers of the Baltic Sea. Overall, a clear trend in salinity cannot be detected" (The BACC II Author Team 2015, p. 9).

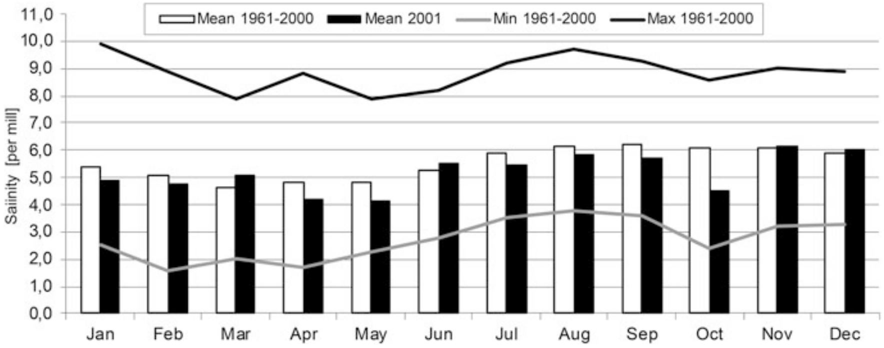

Fig. 7.2 Surface salinity of 'Zingster Strom'. Monthly mean average (m-a), minimum- and maximum-value in the years 1961–2000 as well as monthly mean average values for the year 2001. Data source: University of Rostock, Dr. Baudler

Predictions on the future development of the Baltic inflows and the Baltic salinity under changing climatic conditions have been published by The BACC II Author Team (2015, p. 247/248) with the following results:

Although all studies based on dynamical modeling suggest that in a future climate, Baltic Sea salinity will decrease or remain unchanged compared to the present-day climate (Meier 2006; Meier et al. 2006, 2011, 2012; Neumann 2010); Hansson et al. (2011) claimed that run-off from the total Baltic Sea catchment would decrease if air temperature rises.

Gräwe and Burchard (2011, 2012) and Gräwe et al. (2013) studied local changes in the western Baltic Sea with a high-resolution model. They found no clear tendencies in the projected change in saltwater transport for either medium or major inflow events.

On a locale scale, great differences in the salinity of habitats exist, too. For example, the salinity of the 'Zingster Strom' measured by Baudler and co-workers of the University of Rostock, Laboratory Zingst (written communication) (Fig. 7.2).

On the one hand, the monthly averages and minimum and maximum values of the period 1961–2000 fluctuate enormously. On the other hand, most months show only small deviations from the long-term mean.

The salinity of saltpans, the adjacent Baltic Sea, and the 'Bodden' waters was measured at several points from June 2002 to May 2003. The data are represented for the study areas of 'Großer Werder' and 'Isle of Kirr' (Fig. 7.3).

With only a few exceptions, the salinity of the saltpan waters was considerably higher than that of the adjacent Baltic Sea and the Bodden. Floods of salty seawater during winter and the high evaporation in the following vegetation period cause the high salinity of the saltpan water.

In contrast, on the island of Kirr, lower values were measured in August and November in the saltpan waters, particularly after high precipitations during this period. The saltpans of the larger Gr. Werder showed a different pattern. In this area, precipitations since the beginning of August were too low to reduce the salinity.

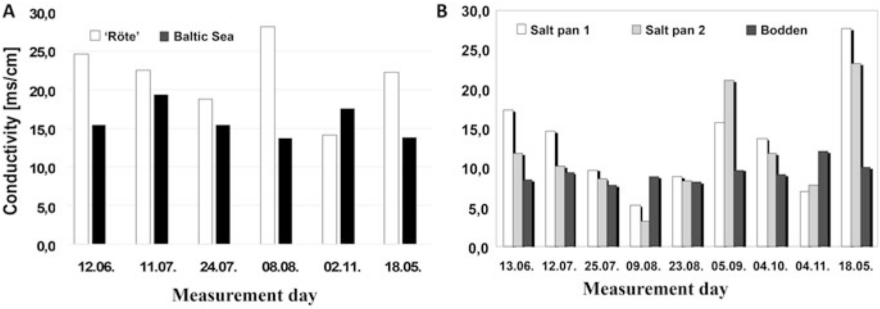

Fig. 7.3 Conductivity of saltpan water compared with that of adjacent areas. (**a**) Großer Werder 'Röte'—Baltic Sea, (**b**) Iles of Kirr salt pans–Bodden. Period: June 2002 to May 2003

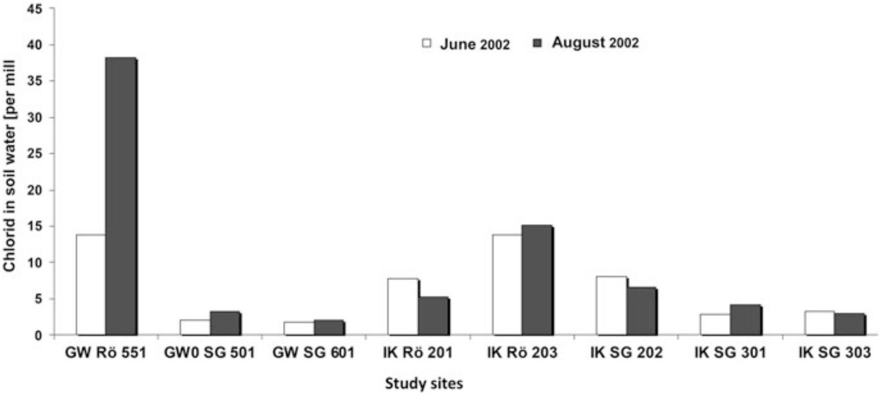

Fig. 7.4 Chloride content in the soil waters of riparian zones of saltpans ('Röten') and salt grassland locations in summer 2002. Study areas 'Großer Werder' (GW) and 'Isle of Kirr' (IK); *Rö* saltpan, *SG* salt grassland; the first two digits of the code indicate the height above MHW, the last one the number of the study site

After the extremely dry February and March 2003, the conductivity increased considerably. Moreover, the period from November until April had substantially lower precipitations than the long-term average. In addition, the conductivity of the saltpan waters was not reduced by high flood events in the winter 2002/2003. Due to the increasing salinity of the saltpan waters, the salinity of soil waters in the riparian zones increases, too (Fig. 7.4).

As can be seen from Fig. 7.4, the 'Röten' soils are characterized by considerably higher chloride contents than the soils of salt grasslands at similar elevations, except on the salt grassland IK SG 202. Due to a depression in the floor, saline water from the Baltic Sea can flow further inland affecting the salt grassland similarly to the saltpans. Therefore, the salt enrichment processes are modified in irregular time intervals. Floods with water of different salt concentrations and the varying salt enrichment process produce a great variety of saline conditions in the habitats. Thus, the semi-terrestrial plants and animals of salt grasslands are exposed to extremely varying salt conditions on a temporal and spatial scale.

Since the frequency and intensity of storms and precipitation are affected by climate change, considerable changes of the salinity of the Baltic Sea are predicted (Schinke 1996).

References

Baudler H (2002) Written communication on surface salinity of the ‘Darß-Zingster Boddenkette’

Becker G (1998) Der Salzgehalt im Wattenmeer. In: Nationalpark Schleswig-Holsteinisches Wattenmeer & Umweltbundesamt (Hrsg) Umweltatlas Wattenmeer, Band 1. Ulmer, Stuttgart, pp 60–61

Begon M, Harper JL, Townsend CR (1996) Ecology–individuals, populations and communities, 3rd edn. Blackwell, London

Cairns WJ (ed) (1992) North Sea oil and the environment. Elsevier Applied Science, London, p 500

Dormann W, Mißkampf R, Kamer N, Mossakowski D (2010) Die Dynamik der Diversität von Tierarten und Zönosen in einer sich wandelnden Umwelt unter besonderer Berücksichtigung von Dispersionsprozessen. In: Schickhoff U, Bodenlandschaft BW, Seiberling S (eds) Entwicklung der Biodiversität in Salzgrasländern der Vorpommerschen Boddenlandschaft, vol 102. Naturschutz und Biologische Vielfalt, Deutschlands, pp 161–226

Gräwe U, Burchard H (2011) Global change and Baltic coastal zones–regionalisation of climate scenarios for the western Baltic Sea. In: Schernewski G, Hofstede J, Neumann T (eds) Global change and Baltic coastal zones. Springer, Dordrecht

Gräwe U, Burchard H (2012) Storm surges in the Western Baltic Sea: the present and a possible future. Clim Dynam 39:165–183

Gräwe U, Friedland R, Burchard H (2013) The future of the western Baltic Sea: two possible scenarios. Ocean Dynam 63:901–921

Hansson D, Eriksson C, Omstedt A, Chen D (2011) Reconstruction of river runoff to the Baltic Sea, AD 1500–1995. Int J Climatol 31:696–703

Krisch H (1999) Written communication on salinity of the Pomeranian Bodden landscape

Lozán JL, Lenz W, Rachor E, Watermann B, von Westernhagen H (1990) Warnsignale aus der Nordsee. Parey, Berlin

Lozán JL, Lampe R, Matthäus W, Rachor E, Rumohr H, von Westernhagen H (1996) Warnsignale aus der Ostsee. Wissenschaftliche Fakten, Parey

Mecklenburg-Vorpommern L (2004). Written communication on surface salinity of the coastal water of Mecklenburg-Western Pomerania

Meier HEM (2006) Baltic Sea climate in the late twenty-first century: a dynamical downscaling approach using two global models and two emission scenarios. Clim Dynam 27:39–68

Meier HEM, Kjellström E, Graham LP (2006) Estimating uncertainties of projected Baltic Sea salinity in the late twenty first century. Geophys Res Lett 33:L15705. https://doi.org/10.1029/2006GL026488

Meier HEM, Andersson HC, Eilola K, Gustafsson BG, Kuznetsov I, Müller-Karulis B, Neumann T, Savchuk OP (2011) Hypoxia in future climates—a model ensemble study for the Baltic Sea. Geophys Res Lett 38:L24608. https://doi.org/10.1029/2011GL049929

Meier HEM, Hordoir R, Andersson HC, Dieterich C, Eilola K, Gustafsson BG, Höglund A, Schimanke S (2012) Modeling the combined impact of changing climate and changing nutrient loads on the Baltic Sea environment in an ensemble of transient simulations for 1961–2099. Clim Dynam 39:2421–2441

Neumann T (2010) Climate-change effects on the Baltic Sea ecosystem: a model study. J Mar Syst 81:213–224

Remane A (1940) Einführung in die zoologische Ökologie der Nord- und Ostsee. In: Grimpe G, Wagler E (eds) Tierwelt der Nord- und Ostsee. Akademische Verlagsgesellschaft, Leipzig

Schinke H (1996) Zu den Ursachen von Salzwassereinbrüchen in die Ostsee. Marine Science Reports No. 12, p 137

Schirmer M (2004) Written communication on surface salinity of the Weser-estuary

Schleswig-Holstein L (2004) Written communication on surface salinity at the Baltic Sea coast of Schleswig-Holstein

The BACC II Author Team (2015) Second assessment of climate change for the Baltic Sea Basin. Springer, Dordrecht, p 515

Tischler W (1993) Einführung in die Ökologie. 4. Aufl., Gustav Fischer, Stuttgart

Soils

8

Hans-Peter Blume

Abstract

The soil units of all project research areas were described. Their functions as part of ecosystems are characterised by the properties of representative profiles. At the coast of the North Sea the soils are predominately classified as Tidalic Fluvisols. The soils of the East Frisian Islands have developed from primarily carbonate-poor sands to loamy sands and are often decalcified. Because of missing tides no Tidalic Fluvisols exist at the Baltic Sea coast. The investigated soils present a broad range of different soil types.

8.1 Introduction

The soil units of all project research areas are described here. Their functions as part of ecosystems are characterised by the properties of representative profiles (for details, see Tables 8.1 and 8.2). The statements are based on soil investigations in summer 1999 during and after a long rainless period. The investigations were carried out under relatively dry soil conditions, completed by simple laboratory tests. Soil texture and structure were described after FAO (2006), and other soil conditions after Schlichting et al. (1995). The soils were classified according to the World Reference Base for Soil Resources (ISSS/ISRIC/FAO 2006), and (in parentheses) according to the German AG Boden (2005) with some additions. Their ecological assessments follow Schlichting et al. (1995) and Blume et al. (2015); see also Blume and Fleige (2015).

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Table 8.1 Representative soils of salt meadows and dunes of the German North Sea coast. (F. Fluvisol; (1−x) = numbers of all described soil profiles)

Profiles/ Horizon	Depth [cm]	Colour Moist	$rb^{1)}$%	Structure	d_B [kg/l]	Moisture	Texture	org. m. %	e.c. stage	pH H_2O	rH stage	Lime stage
1 (1) Gleyi-sali-tidalic F. (Normrohmarsch) of marine sed.; bed, 40 cm MHW, Friedrichskoog												
Ahz	0–10	Bl	30	AB	1.4	M	SL	1	6	8	4	3
Cgz	−28	gb	30	PL/SS		W	SL					3
Crz1	−80	g	4	CO/SS	1.3	VW	SL	2	5	8	3–4	3
Crz2	−100	g	0	CO/SS		VW	SL		5	8	2–3	3
2 (7) Gleyi-hyposali-tidalic F. (Oxidierte Brackrohmarsch) mar. sed.; bed, 80 cm MHW, Friedr-k.												
Ahz	0–9	ddgb	5	GR	1.0	SL	SiL	5	4	8	4	3
Abgz	−42	b	40	GR	1.0	M	SiL	4	4	8	4	3
Czg	100	dg	8	SG/SS		W	LS		4	8	3	3
3 (10) Molli-tidalic F. (Oxidierte Brackrohmarsch) of mar. sed. bed, 140 cm MHW, Friedr.k.												
Ahz1	0–15	dgb	0	GR	1.0	SL	L	6	2	8	2	3
Ahz2	−34	dgb	0	GR	1.3	M	SiL	2				3
AC	−63	lolb	0	SG/SS		M	LS		2	8	5	2
Cgz	−100	gb	50	SG/SS		M	LS		3	8	4	3
4 (113) Stagni-anthropic Regosol (Salzhalt. Pseudogley-Pararendzina) of dike substrate; 180 cm MHW, coast of Wursten												
Ah1	0–6	ddgb	0	GR	1.0	M	LS	9	1	8	4	0
Ah2	−25	dgb	5	VFGR		M	LS					1
C1	−30/40				1.1	M	LS	2	2	8	4	0
C2	−100	lg	5	SG/SS		M	LS		2	8	4	2

5 (65) Protothioni-sali-tidalic F. (Kalkarmes Mischnormwatt) marine sed.; 0 cm MHW; Mellum

Az	0–2	dolg	20	CO	1.4	W	SL	0.9	6	8	3	2
Cgz	−37	g	20	SG/SS	1.5	VW	SiL	0.7				0
Crz1	−40	g	0			VW	LS		6	8	3	0
Crz2	−100	dg	0	SG/SS		VW	LS		6	8	2–3	1

6 (64) Gleyi-sali-tidalic F. (Nasse Normrohmarsch) of marine sed.; 30 cm MHW; Mellum

Agz	0–1	dg	8	CO	1.4	M	SiL	1	5	8	4	0
Cgz	−16	dg	5	SG/SS		W	LS					0
Azb	−25	lyb	5	CO/SS		W	SL					1
Cgz	−60	lyb	5	SG/SS	1.5	VW	LS	0.3	6	7	3	0
Crz	−100	g	0	SG/SS		VW	SiL		6	8	2	2

7 (63) Endogleyi-endosalic Arenosol (Normstrand) of dune/beach sand; 60 cm MHW; Mellum

Azh	0–4	dbg	0	VFGR	1.1	M	LS	3	4	9	4	0
AC	−20	ppb	0	SG		W	FMS					0
Cgz	−78	b	15	SG	1.4	VW	FMS	0.2	6	8	3–4	0
Crz	−100	lolg	0	SG		VW	LS		5	8	2–3	0

8 (27) Sali-gleyi-tidalic F. (Kalkfreie nasse Normrohmarsch) m. s.; 30 cm MHW, Wangerooge

Ahz	0–11	dgrg	4	VFGR	0.3	W	SiL	26	5	7	3	0
Cgz	−26	dg	2	CO/SS		VW	SiL					0
Crz1	−55	dg	0	SG/SS	1.6	VW	FMS	0.7	6	7	2–3	0
Crz2	−100	dgrg	0	SG/SS		VW	FS		6	7	2–3	0

(continued)

Table 8.1 (continued)

Profiles/ Horizon	Depth [cm]	Colour Moist	rb$^{1)}$%	Structure	d_B [kg/l]	Moisture	Texture	org. m. %	e.c. stage	pH H_2O	rH stage	Lime stage
9 (30) Gleyi-sali-tidalic F. (Kalkfreie Normrohmarsch) of mar. sed.; 60 cm MHW; Wangerooge												
Ahz	0–10	ddg	0	VFGR	0.4	M	SiL	23	6	7	5	0
Cgz	–43	lgb	5	SG/SS	1.3	W	LS	1	6	7	4	0
Crz	–100	lgb	3	SG/SS		VW	LS		6	7	3–4	0
10 (34) Endogleyi-endosalic Arenosol (Salzhalt. Gley-Regosol) of dune sand; 180 cm MHW; Wangerooge.												
Ahz	0–8	ddg	0	VFGR	0.3	M	MFS	18	3	7	5	0
AC	–16	lbg	0	SG		M	MFS					0
Cz	–62	lg	0	SG	1.4	M	MFS	0.8	3	7	5	0
Cgz	–90	lg	5	SG		W	FS		4	6	2–3	0
Azb	–100	lbg	0	CO		VW	LS					0
11 (33) Albic Arenosol (Podsol-Regosol) of dune sand; 260 cm MHW: Wangerooge												
AE	0–15	dg	0	VFGR	0.7	M	MFS	6	1	4	4	0
BhC	–71	lb	0	SG	1.4	M	MFS	0.6	1	5	4	0
C	–100	lg	0	SG		M	MFS		1	5	4	0

Explanation see Table 8.2

Table 8.2 Representative soils of salt meadows and dunes of the German Baltic Sea coast

Profile/ Horizon	Depth [cm]	Colourmoist	rb$^{1)}$%	Structure	d_B [kg/l]	Moisture	Texture	org. m %	e.c. stage	pH H_2O	rH stage	Lime stage
1 (13) Gleyi-sali-histic Fluvisol (Salzhalt. Anmoorgley) of mar. sed.; 20 cm a.s.l.; Sehlendorf												
Hz	0–11	ddgb	2	GR	0.5	M	CL	25	5	8	5	1
Ahz	–28	grg	60	GR		M	CL					2
ACrz	–60	ddg	0	CO	0.7	W	LS	10	5	8	2–3	2
Crz	–100	lg	0	CO		VW	MFS		5	8	2	1
2 (15) Endosali-histic Gleysol (Salzhalt. Moorgley) of mar. sed.; 40 cm a.s.l.; Sehlendorf												
Hz	0–7	ddg	5	GR	0.2	M	H4	50	3	6	5	0
Cgz	–24	g	25	CO		M	SiL					0
Crz	–48	lg	5	CO	1.0	M	LS	0.2	4	7	5	0
Ahb	–76	ddgb	0	CO		W	MS/ SiC					0
Crz	–100	bl	0	SG		VW	MFS		3	7	2–3	0
3 (17) Histic Gleysol (Eutropher Normgley) of beach sand; 80 cm a.s.l.; Sehlendorf												
H	0–6	ddg	0	GR	0.4	D	SL	25	1	6	4	0
Cg	–30	dg	20	CO	1.5	SL	SL	2				0
Cr1	–70	ppb	3	SG		M	MFS		0–1	7	3–4	0
Cr2	–100	lbg	0	SG		W	MFS		0–1	7	3–4	0
4 (20) Endogleyic Arenosol (Vergleyter Regosol) of beach sand; 150 cm a.s.l.; Sehlendorf												
OA	0–5	ddgb	0	VFGR	0.5	D	GMS	25	2	5	6	0
C1	–15	pb	0	SG/SS		D	GMS					0
C2	–90	lb	0	SG/SS	1.3	SL	GMS	1	0–1	6	6	0
Cg	–100	rb	10	SG/SS		M	GMS		0	7	4–5	0

(continued)

Table 8.2 (continued)

Profile/ Horizon	Depth [cm]	Colourmoist	rb$^{1)}$%	Structure	d_B [kg/l]	Moisture	Texture	org. m %	e.c. stage	pH H_2O	rH stage	Lime stage
5 (80) Endosali-histic Gleysol (Salzhaltiger Niedermoorgley) of mar. sands; 20 cm a.s.l.; Zingst												
Hz	0–20	ddgb	0	fibric	0.2	W	H3	23	4	6	4	0
ACz	–56	ddg	0	SG/SS	1.5	VW	LS	0.9	4	7	2	0
Hb	–96	ddgb	0	CO		W	H10		4	8	2	0
Cr	–100	lbg	0	SG		W	MS					0
6 (89) Histic Gleysol (Salzarmer Niedermoorgley) of mar. sed.; 60 cm a.s.l.; Zingst												
H/Cz1	0–6	bl	0	VFGR	0.5	M	H3/S	28	2	6	4	0
H/Cz2	–20	ddg	0	VFGR		W	H9/S					0
Cr	–70	lg	0	SG/SS	1.5	VW	LS	1	2	7	3	0
Crz	–100	olg	0	SG/SS		VW	LS		3	7	2–3	0
7 (87) Haplic Fluvisol (arenic, eutric); (Vergleyter Euregosol) beach sed.; 150 cm a.s.l.; Zingst												
Ah	0–8	dgb	0	VFGr	0.5	SL	LS	7	0–1	5	4	0
AC	–55	pg	0	SG/SS	1.1	SL	LS	0.8	0–1	6	4	0
C1	–93	pg	0	SG/SS		M/W	MFS		0–1	6	4	0
C2	–100	b	0	SG		VW	LS					0
8 (69) Endosali-ombri-sapric Histosol (Salzhalt. Norm-Nied.moor) of mar. sed.; 15 cm a.s.l.; Karrendorf												
Hz1	0–5	db	0	GR/fib.	0.5	W	H6/Si	16	5	5	1	0
Hz2	–52	ddgb	0	SB	0.2	VW	H9/Si	50	4	7	3	0
Crz1	–76	g	0	SG		VW	LS					0
Crz2	–100	dg	0	SG		VW	GLS		4	7	2–3	0
9 (74) Histic Gleysol (Salzar. Moorgley) of holo-/pleistocene sed.; 65 cm a.s.l.; Karrendorf												
O	0–2	drb	0	fibric		M	H1					0

H	–28	bl	5	SB	0.4	M	H9	29	1	5	4	0
Cgz1	–55	b	10	CO	1.2	M	LS	2	3	6	4	0
Cgz2	–100	lolb	30	CO		M	L		3	7	3	0

10 (75) Endogleyic Regosol (Salzar. Oxigley) of holo/pleist. sed.; 95 cm a.s.l.; Karrendorf

O	0–4	bl	0	fibric	0.4	M	H5	28	0–1	6	5	0
Ah	–28	gb	0	VFGR	SL	SL	CL					0
Acg	–72	yb	40	SG	1.7	M	LS	0.8	2	6	4	0
Cg	–100	dol	30	CO		M	L		2	7	4	0

11 (79) Humi-anthropic Regosol (Humusreich. Euregosol) of anthro. substr.; 150 cm a.s.l.; Karrendorf

Ah1	0–20	dgb	0	GR	1.0	M	SL	9	0–1	7	5	0
Ah2	–58	dgb	0	VFGR	1.3	M	SL	5	0–1	7	5	0
C1	–95	yb	0	CO		M	CL		0–1	6	5	0
C2	–100	dgb	0	SG		M	LS					0

Explanation of table symbols: *Soil colour* (moist): *b* brown, *ba* black, *bl* blue, g grey, *gr* green, *o* orange, *ol* olive, *pi* pink, *r* red, *w* white, *d* dark, *dd* very dark, *l* light, *p* pale, *pp*. very pale, *y* yellow; $^{1)}$ red brown surface coats of aggregates and channels in %

Structure: SG single grain, *CO* coherent, *GR* granular (*VF* very fine), *PR* prismatic, *AB* angular blocky, *SB* subangular blocky, *PL* platy, *SS* stratified structure

Bulk density: d_B in kg/l; in 0–4 and 30–34 cm depth

Moisture conditions (pF val.): *D* dry (4), *SL* slightly moist (3), *M* moist (2), *W* wet (1), *VW* very wet (0)

Texture: S sand (*FS* fine sand, *MS* medium sand), *LS* loamy sand, *SL* sandy loam, *SCL* sandy clay loam, *SiL* silt loam, *SiCL* silty clay loam, *CL* clay loam, *Si* silt, *SC* sandy clay, *SiC* silty clay, *C* clay; *G* gravel

Organic matter (*org.m.*) in %: 0–4 and 30–34 cm depth. Humification intensity of organic layers (H after von Post): H1 only fibers, H10 no fibres (H1–5 fibric, H6/7 mesic, H8–10 sapric)

Electrical conductivity (e.c. in mS/cm) of saturation extract: e.c. stages: (0) < 0.75, (1) 0.75–2, (2) 2–4, (3) 4–8, (4) 8–15, (5) 15–30, (6) > 30.0–0.75 fresh (limnic), 0.75–15 brackish (−8 oligosaline, −15 mesosaline), >15 saline (polysaline, >30 hypersalic)

pH values: in H_2O (1:2.5); in 5, 40, and 80 cm soil depth; Redox potential (Eh in mV): in 5, 40, and 80 cm soil depth. Transformation to rH values: rH = Eh/29 + 2 pH. rH stages: (1) < 10 (CH_4 formation), (2) 10–13 (SO_4 reduction), (3) 13–19 (Fe^{3+} reduction), (4) 20–29 (Mn^{4+} reduction, no O_2), (5) 29–36 (some O_2, NO_3 reduction), (6) > 36 (many O_2)

Lime (%): measurement in 0–4 and 30–34 cm, valuation in other depths; stages: (0) none, (1) < 0.5%, (2) 0.5–2%, (3) 2–10%, (4) 10–25%

At the coast of the North Sea, soils have developed from silty sands, silt loams, and clay loams with varying contents of carbonates and organic matter and under the influence of strong tides and saline sea water from 11 profiles (Pr.) (Table 8.1). Therefore, the soils are predominately classified as Tidalic Fluvisols. The soils of the East Frisian Islands have developed from primarily carbonate-poor sands to loamy sands and are, therefore, often decalcified (Table 8.1, Pr. 5–11).

The sediments of the mainland coast of Wursten and Dithmarschen were mostly loamy and those of Northern Friesland more clayey, which contained 3–8% carbonate (Table 8.1, Pr. 1–3). Between elevations of −10 to +10 cm MHW, sandy to muddy strand plains developed with Sali-tidalic Fluvisols (Salzwatten [1]), partly with a halophytic plant cover (e.g. Table 8.1, Pr. 5) and reducing conditions near the surface. Almost flooded daily, they are completely wet. At elevations between 20 and 40 cm MHW, Gleyi-tidalic Fluvisols (Normrohmarschen) have developed, which are flooded 50–100 times annually. They are densely covered by halophytes that affect the accumulation of pedogenetic humus. Their epipedon is characterised by an oxidative colour pattern, whereas their subsoil remains strongly reducing. They are hypersalic or polyhaline up to the surface (Table 8.1, Pr. 1, 6, 8). At higher levels, there are Sali-tidalic Fluvisols (Normrohmarschen) of sandy to loamy sediments (Table 8.1, Pr. 9), but their salt contents vary seasonally and very strongly in the topsoil due to influences of rain as well as water evaporation. Finally, Gleyi- and Molli-tidalic Fluvisols (oxidierte Brackrohmarschen) with low salt contents exist (Table 8.1, Pr. 2, 3), which are flooded less than 20 times a year. Gleyi-endosalic Arenosols (Normstrände) (Table 8.1, Pr. 7) have developed from beach and dune sands at elevations between 60 and 100 cm MHW. In higher relief positions, there are *Endogleyi-endosalic* Arenosols (salzhaltige Gley-Regosole; Table 8.1, Pr. 10). Finally, Eutric Arenosols (Euregosol) exist on dunes as well as Albic Arenosols (Podsol-Regosole; Table 8.1, Pr. 11) on older dunes.

Normally, the dikes were built from marine calcareous, sandy to silty sediments, from which Anthropogenic Arenosols and Regosols (Pararendzinen) have developed. Often a stagnic colour pattern is found due to water stagnation because of compaction (Table 8.1, Pr. 4).

From the Baltic Sea, 11 profiles (Pr.) were also investigated. The investigated Bodden areas of the Baltic Sea coast are influenced by saline seawater with minimal tides (not more than 5–10 cm). Therefore, no Tidalic Fluvisols exist. In the lowlands situated at elevations between 10–20 cm above sea level (a.s.l.) and with a high groundwater table, Sali-ombric Histosols (salzhaltige Niedermoore in German; Table 8.2, Pr. 8) and Hyposali-histic Gleysols (salzhaltige Moorgleye; Pr. 2) beside Histic Gleysols (salzarme und freie Moorgleye in German: Pr. 3, 6, 9) have developed. They are characterised by fens. Close to the beach, about 10–20 cm above sea level, the peat horizon is flat and partly destroyed by water erosion and animal tracks (Pr. 1, 5, 8). Higher relief positions are characterised by mineral soils with mainly sandy texture. Endogleyic Regosols (Gleye n German; Pr 10) are found at elevations

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[1] The German term in parentheses.

between 70 and 90 cm above sea level and Fluvisols, Arenosols, and Regosols from 100 to 200 cm above sea level (Regosole in German; Pr. 4, 7, 11).

Drained and intensively grazed fens are strongly humified and earthy (Pr. 9). Influenced by saline seawater up to 50 cm above sea level, the soils are poly- to mesohaline, at higher elevations oligohaline. From 110 cm above sea level, limnic, at least in the subsoil.

8.2 Soils of the Island Borkum (North Sea)

On the island of Borkum, representative soils of three landscape segments were investigated: the southern beach, study area *Ronde* Plate; the south-east slope foot of the Wolde Dunes; and east of the dam in the western tidal area of the Randzell foreshore, study area Grüppenbeete (compare Chap. 4, Fig. 4.3).

In *Ronde* Plate, saline (up to 1.4 m a.s.l.) to brackish/mesohaline Tidalic Fluvisols (Rohmarschen: similar to Table 8.1, Pr. 8, 9) have developed from marine fine sands; the higher situated Arenosols (Gley-Regosole: similar to Table 8.1, Pr. 10) have developed from dune sands. The topsoils of the deeper situated Tidalic Fluvisols are (because of regular flooding and sedimentation) sandy, salic, or polyhaline, and calcareous. The higher elevated soils are decalcified and only oligo- to mesohaline and the Arenosols are nonsaline, at least in the topsoil. The Fluvisols show alkaline reactions and the Arenosols exhibit neutral to weak acid reactions. The marine sediments are enriched with lithogenetic organic matter of sea organisms. The Fluvisols and the Endogleyic Arenosol have only thin (3–6 cm), pedogenetic humus (2–6% org. m.) A-horizons, while a humus layer of 10 cm developed in other Arenosols (as a consequence of a reduced decomposition). The Gleyic Fluvisols are anaerobic, Endogleyic Arenosols are aerobic in the topsoil, and the Eutric Arenosols are completely aerated.

Due to the sandy texture, the nutrient reserves are generally small; the available nutrient contents decrease with increasing relief position. Sites with Eutric Arenosols are dry, those of Endogleyic Arenosols are also dry. The Fluvisols are very wet sites, and higher elevated sites are sometimes moist in the topsoil.

At the foot slope of the *Ronde* Plate, a reed-covered Hyposali-histic Gleysol (salzhaltiger Moorgley) has developed from silty fine sands. A 6 cm thick, strongly humified peat, being carbonate-free and acid at the surface, covers the Hyposali-histic Gleysol. The peat is completely anaerobic, wet, and shows only small nutrient reserves with moderate contents of available nutrients.

Geologically, the investigated salt meadows of the Grüppenbeete are fine sandy tidal sites, covered by 12–47 cm of silt loam. Tidal mud deposits cover only foot slope positions of a sandy beach wall. The beach wall is characterised by an Endosali-endogleyic Arenosol (salzhaltiger Gley-Regosol): similar to that presented in Table 8.1, Pr. 10), otherwise by Gleyi-sali-tidalic Fluvisols (Normrohmarschen). Near a marsh creek, deeply situated Gleyi-sali-tidalic Fluvisols (Nasse Normrohmarschen: similar to Table 8.1, Pr. 1) are calcareous; the other soils are completely decalcified. The soil reactions are neutral to alkaline. The Arenosols and the higher elevated Fluvisols are oligohaline, whereas the other soils are polyhaline. The deep Gleyi-tidalic Fluvisols are completely anaerobic; the remaining soils have oxygen at least at the surface. The Arenosols contain organic matter only in the topsoil (Ah), while the Tidalic Fluvisols are completely humous; the deepest-elevated soils are even humus-rich (up to 20%) near the surface. The Fluvisols have (as a consequence of the loamy texture) high contents of nutrient reserves and available nutrients, while the nutrient reserves of the Arenosols are minimal. The Arenosols are dry to slightly moist, the deeper elevated Fluvisols are normally very wet, and the other Fluvisols wet to moist.

8.3 Soils of the Island Norderney (North Sea)

On the island of Norderney, the soils of the field experiment were investigated, along with the soils of neighbouring dunes of various ages (compare Chap. 4, Fig. 4.4). The field experiment was carried out on redeposited and levelled sands of an elder dune. The soil is a transition between a Protic Arenosol with very low humus contents (humusarmer Lockersyrosem) and a Haplic Arenosol (Normregosol) with a fully developed humous topsoil. Besides a very small humus accumulation, a decalcification of the primarily carbonate-poor dune sands and a moderate acidification has occurred. Neighbouring elder dunes are also characterised by Arenosols with some higher humus contents, while the valley soils among the dunes are gleyed due to high groundwater level. The soils of the younger dunes near the coast have hardly developed: Protic Arenosols with a minimum humus accumulation and an alkaline soil reaction occur. Soils show no saline influence; they are dry, aerated, and contain minimal nutrient reserves and small (N, P) to moderate (Ca, Mg, K) contents of available nutrients.

8.4 Soils of the Island Wangerooge (North Sea)

On the island of Wangerooge, in the area of the Mittelaußengoden (compare Chap. 4, Fig. 4.5), soils of sandy to loamy marine sediments under salt meadows and dune sands under a xerophyte lawn were investigated. The Gleyi-sali-tidalic Fluvisols (Normrohmarschen) of the marine sediments are completely carbonate-free, react alkaline to neutral, loamy in the topsoil, and silty in the subsoil. The upper 7–10 cm are humus-rich (17–29% org. m.). The soils at an elevation of 60 cm MHW are slightly oligohaline; the other soils are completely polyhaline. The soils above 30 cm MHW are moist in the topsoil and enriched with oxygen; the deeper elevated soils are always wet to very wet and are permanently anaerobic. All Gleyi-sali-tidalic Fluvisols have moderate (Ca) to slightly higher nutrient reserves with permanently high contents of available nutrients.

The Arenosols (sandige Regosole) of the dune are decalcified, too. The deeper elevated Endogleyic Arenosols (e.g. Pr. 10) are oligohaline and oxygen poor in the subsoil; the higher elevated soils are salt-free and well-aerated. The highest elevated

Albic (= bleached) Arenosol (Podzol-Regosol: Pr. 11) is strongly acidified (and the process of podzolisation has already begun); the other Arenosols are faintly acid to neutral. The Endogleyic Arenosols have humus-rich topsoil (14–18% org. m.), whereas other Arenosols show normal humus contents (4–6%). The nutrient reserves of all Arenosols are low; the Albic Arenosol shows only low contents of available nutrient reserves, and the other Arenosols display moderate contents.

8.5 Soils of the Island Mellum (North Sea)

On the island of Mellum, sites in the salt meadow areas "Alte Mellum" towards the northwest (Mellum West) and "Hohe Bensiel" northeast of the diked part (Mellum East) were investigated (compare Chap. 4, Fig. 4.7).

In the area Mellum West below MHW, Protothioni-sali-tidalic Fluvisols (Mischnormwatt: Table 8.1, Pr.5) exist; from 10 to 100 cm MHW, Gleyi-sali-tidalic Fluvisols (Normrohmarschen) also occur (Table 8.1, Pr. 6). On higher elevated sites, Arenosols (Lockersyroseme and Regosole) are found. The tidally influenced sites have developed from loamy or silty marine sediments above sandy marine sediments. Arenosols have developed on beach dune ridges.

Sali-tidalic Fluvisols are polyhaline at elevations between 0 and 60 cm MHW, and higher elevated Hyposalic Fluvisols are at least mesohaline. An Areni-sali-tidalic Fluvisol (Normstrand) is polyhaline; Arenosols are oligo- to mesohaline. One Eutric Arenosol (Euregosol) is decalcified but alkaline in the topsoil; the other soils are calcareous and alkaline. The Gleyi-sali-tidalic Fluvisols at MHW are permanently anaerobic, while the others in the upper parts temporarily aerobic: Arenosols are permanently aerated. Protic Arenosols are almost humus-free; the Sali-tidalic Fluvisols at MHW have <1% org. m. Other Fluvisols and Arenosols contain 2–20% org. m. in the upper 4 cm and deeper contents below. Fluvisols at MHW are permanently wet; the other Fluvisols are only moist, at least in the topsoil; the Arenosols are dry. The Fluvisols have moderate to medium nutrient reserves with high contents of available nutrients. The Arenosols have only small nutrient reserves with small to moderate reserves of available nutrients.

In the area of Mellum East, Protothioni-sali-tidalic Fluvisols (Mischnormwatt) exist at 0 cm MHW as well as Gleyi-sali-tidalic Fluvisols (Normrohmarsch) at 30 cm MHW, having developed from sandy calcareous marine sediments (Table 8.1, Pr. 5, 6). Above 50 cm MHW, Endogleyi-hyposalic Arenosols (Normstrände) occur on small beach dune ridges; they are decalcified, at least in the topsoil (Table 8.1, Pr 7). The soil reaction is permanently alkaline. The Fluvisols have only low humus contents; the Gleyic Arenosols show moderately high contents in the topsoil (3%). Fluvisols at MHW are permanently wet and anaerobic (except animal tubes); other Fluvisols are moist and aerated, at least in the topsoil. The Arenosols are moist to slightly moist and aerated, at least in the topsoil. The Fluvisols have moderate nutrient reserves and the Arenosols only small nutrient reserves. The contents of available nutrients are generally moderately high or high in the topsoil.

8.6 Soils of Tidal Areas Wursten at the Outer Estuary of the River Weser

At the coast of the region Wursten, soils of salt meadows West of Arensch, Berensch, of the Oxstedt Creek, and the Oxstedt fallow were investigated (compare Chap. 4, Figs. 4.8 and 4.9).

In the foreshore West of Arensch, Gleyi-sali-tidalic Fluvisols (Normrohmarschen) have developed from calcareous, silty to loamy, and humous marine sediments (similar to Table 8.1, Pr. 1). All investigated soils are permanently polyhaline, calcareous, and react neutral to alkaline. The deeper elevated soils (Nasse Normrohmarschen) are mainly anaerobic, and higher elevated ones (Normale Normrohmarschen) temporarily with moderately aerated topsoils. All soils are almost wet; the higher elevated ones are moist in the topsoil. Soils of loamy sands have moderate nutrient reserves; the others (as a consequence of a loamy texture) have moderately high-to-high nutrient reserves. Generally, the contents of available nutrients are high.

In the foreshore West of Berensch, Gleyi-hypersali-tidalic Fluvisols (Nasse Normrohmarschen) have developed from calcareous and humous, silty marine sediments; at 10 cm above MHW, Gleyi-sali tidalic Fluvisols (Normrohmarschen) have developed at 20–40 cm above MHW from the same sediments. The soils are polyhaline, calcareous, and humous. The lower elevated ones are very wet or wet and un-aerated, whereas the higher situated ones are moist (at least in the topsoil) and aerated. With moderate to slightly higher nutrient reserves, the contents of available nutrients are generally high.

In the meadow at the Oxstedt Creek, Gleyi-hypersali-, Gleyi-sali-, and Gleyi-hyposali- (to endogleyi-) tidalic Fluvisols (nasse, normale, and oxidierte Normrohmarschen) have developed from calcareous, silty to loamy, and humous marine sediments. The soils are poly- to mesohaline, calcareous, silty to loamy, and deeply founded humous (2–9% org. m.). One sand-rich soil is poorer of humus and carbonate as well as faintly acid; the other soils react neutral to alkaline. The lower situated Hypersalic Fluvisols are very wet or wet and normally un-aerated during the whole year; conversely, the Endogleyi-hyposalic Fluvisols are temporarily moist to slightly moist and better aerated, at least in the topsoil. More sandy soils show small nutrient reserves, the other soils have moderate to slightly higher reserves, while the contents of available nutrients are moderately high-to-high.

In the foreshore of the Oxstedt Fallow, polyhaline, Gleyi-hypersali-tidalic Fluvisols in lower elevations (similar to Table. 8.1, Pr. 1), Sali-gleyic ones and oxidised Hyposali-endogleyic ones in higher elevations (similar to Table 8.1, Pr. 3) have developed from calcareous and humous, silty to loamy marine sediments. In the lower slope elevations of a dike, Anthropi-gleyic Regosols (hyposalic) occur. Anthropi-stagnic Regosols (salzhaltige Pseudogley-Pararendzinen) are found at the higher slope elevation.

The soils are permanently alkaline and slightly humous to very humous. The Gleyi-hypersali-tidalic Fluvisols have an alternating wetness and are permanently anaerobic. The Gleyi-salic ones and the Endogleyi-hyposalic ones are moist and aerated in the topsoil. The dike top is strongly compressed and, therefore, perched and only poorly aerated. The contents of available nutrients are generally high, whereas the sandier soils have lower nutrient reserves compared to the loamier ones.

8.7 Soils of the Friedrichskoog Foreshore, Southern Dithmarschen

In the Friedrichskoog, foreshore and formerly pastured soils were investigated (compare Chap. 4, Fig. 4.9). All soils have developed from calcaric and humous, sandy to silty- (loamier near the coast) marine sediments. Therefore, the soils are profoundly calcaric and humous.

In the area of the sheep pastures on beds next to the sea at 20 cm above MHW, sandy to silty Episali-tidalic Fluvisols (Mischnormwatt) have developed under an incomplete *Salicornia* vegetation, while Gleyi-salic ones (Normrohmarschen) exist under a dense vegetation cover at the same elevation: normal ones (nasse and normale Normrohmarschen) at 40 cm above MHW (Table 8.1, Pr. 1), soils with oxidised A horizon (oxidierte Normrohmarschen) at 60 cm MHW, mesohaline Gleyi-hyposali-tidalic Fluvisols (oxidierte Brackrohmarschen) at 80–140 cm above MHW (Pr. 2), and oligohaline Calcari-molli-tidalic Fluvisols at still higher elevations (Pr. 3). Mollic Fluvisols are characterised by a mollic epipedon (= dark coloured Ah horizon with strong humus accumulation, a high base saturation, and a soft granular structure without any layering), due to a strong bioturbation by soil animals.

Soils from 40 to 60 cm above MHW are normally wet, temporarily moist, and slightly aerated in the topsoil. Soils between 80 and 140 cm above MHW are moist to slightly dry and temporarily well-aerated in the topsoil, at least during the summer. The humus contents of the topsoil increase from the polyhaline ones with 2% organic matter to the oligosaline ones with 4–6% organic matter, which is caused by increasing clay contents and humification intensities. Decreasing carbonate-contents by weathering were not found, even in the oligosaline ones. The nutrient reserves are moderate in the lower elevated sites, moderately high in the higher elevated ones (due to higher clay contents), while generally the contents of available nutrients are high.

Two unchanged sites 40–80 cm above MHW are mesohaline Gleyi-hyposali-tidalic Fluvisols (oxidierte Brackrohmarschen) that are already mesohaline and oxidised to a greater depth. A measurable decarbonisation has not been found, and the soil reaction is alkaline. Their topsoils are moderately aerated, wet to moist, and enriched with available nutrients.

8.8 Soils of the Hedwigenkoog Foreshore, Northern Dithmarschen

For more than 10 years, the Hedwigenkoog foreshore has not been grazed (compare Chap. 4, Fig. 4.10). The Episali-tidalic Fluvisol (Übergangs-Mischrohwatt) and a Gleyi-hyposali-tidalic Fluvisol (oxidierte Salzrohmarsch) were investigated. The soils have developed from calcaric and humous, sandy to silty marine sediments. The first site at 0 cm MHW has an incomplete cover of *Salicornia* and *Spartina* vegetation, which is flooded 500 times a year; the second one is elevated 70 cm higher in the upper salt meadow, primarily vegetated with *Festuca* and flooded 70 times a year. The first site is almost permanently wet and anaerobic; the second site is wet to moist, temporarily aerated, and partly oligohaline in the topsoil. The soils show moderate nutrient reserves with moderately high up to high contents of available nutrients.

8.9 Soils at the Sehlendorf Lagoon, Hohwacht Bay

The soils at the Sehlendorf lagoon (comp. Fig. 4.11) have developed from mainly sandy, carbonate-poor marine sediments of the Baltic Sea. The deeper elevated soils (e.g. Table 8.2, Pr. 1 and 2) partly consist of clay loam, the very high-elevated soils of gravel rich sands (Pr. 4). Near to the lagoon and at sites with a high groundwater table, peat formation led to the development of Hyposali-histic Fluvisols (salzhaltige Moorgleye) (e.g. Pr. 2). Directly at the shore at 20 cm above sea level, a Gleyi-sali-histic Fluvisol (salzreicher Anmoorgley: Pr. 1) has developed due to the high salt concentration of the lagoon. At 70–80 cm above sea level, Eutri-histic Gleysols (Normgleye: e.g. Pr. 3) exist without a noticeable influence of saline water. At an elevation higher than 100 cm a.s.l., Eutric Arenosols (sandige eutrophe Regosole) with a narrow (3–5 cm) but strongly humous Ah horizon (5–25% org. matter) have developed. Only the soils situated directly at the shore (Pr.1) are calcaric, and a Calcaric Gleysol (Kalkgley) has developed under a now filled-up former path. The other soils are profoundly decalcified and the Arenosols are moderately acidified.

The Gleyic Fluvisols and Gleysols are wet to very wet sites, with the topsoils aerated only during permanently dry periods. The Arenosols have only small nutrient reserves (due to the high quartz content of the sand) and moderate contents of available nutrients.

8.10 Soils of the Sundic Meadow on the Peninsula Zingst, Western Pomerania

On the peninsula of Zingst, soils along a section of 20–150 cm above sea level (e.g. Table 8.2, Pr. 5–7) were investigated (compare Chap. 4, Fig. 4.12). The soils have mainly developed from marine fine sand to loamy sand. At 20–60 cm a.s.l. (−5 to 54 cm a.s.l. of mineral soil surface), Areni-histic Gleysols (salzarme

Niedermoorgleye: Pr. 6) have developed. Their histic epipedon is eutrophic and sapric (strongly humified). Adjacent to the sea (Pr. 5), the soils are strongly interspersed by sandy sediments, on the one hand, and extremely eroded by wave impact and trampling by cattle on the other. At 1 m a.s.l., Arenosols (sandige Regosole) from sandy marine sediments and dike materials were found above peat, while normal Arenosols (Regosole: Pr. 7) from beach wall sands have developed at 1,5 m a.s.l. These soils (except Pr. 7) are saline: polyhaline near the coast, mesohaline to oligohaline in some distance. All soils are carbonate-free. Their topsoils are moderately to more strongly acidified.

The Histic Gleysols are wet to very wet, and they are aerated in the topsoil only during extended dry periods. The base reserves are low; the contents of available nutrients are moderately high-to-high in the Histic Gleysols, and low to moderate in the Arenosols.

8.11 Soils of the Karrendorf Meadow, Western Pomerania

In the area of the Karrendorf Meadow, soils were investigated between 15 and 150 cm a.s.l. (compare Chap. 4, Fig. 4.13). They have primarily developed from silty to loamy Holocene and Pleistocene sediments (e.g. Table 8.2, Pr. 8–11). At 15 to 65 cm a.s.l. (respectively −5 to +35 cm mineral soil surface), Hyposali-histic Gleysols (salzarme Niedermoorgleye) with a 13 to 28 cm thick peat layer (e.g. Pr. 9) as well as flat Ombri-hyposalic Histosols (salzhaltige Überflutungs- Niedermoore (Pr. 8) with a 40 to 60 cm thick peat layer have developed. At 100 cm above sea level, a Eutri-gleyic Regosol (Oxigley: Pr. 10) and at 150 cm a.s.l. a Humi-anthropic Regosol (humusreicher Regosol) from an anthropogenic deposition have developed. Apart from a non-grazed area, the peat of the Histosols and Histic Gleysols is strongly humified and of an earthy consistence, caused by decades of drainage and grazing (see Sect. 6.3). The upper 1–3 cm are mostly fibric (= rarely humified): they have possibly developed during the last years of seawater flooding after destruction of the former dike. These floodings have led to a strong salinisation (mainly mesohaline). The soils are completely carbonate-free and slightly acidified.

The Histosols and Histic Gleysols are wet to very wet; their topsoil is aerated only during longer lasting dry periods. The Gleyic Regosols are wet to moist, and aerated during the vegetation periods, while the other Regosols are dry and permanently aerated. The soils show moderately high contents of available nutrients.

References

Blume H-P, Brümmer GW, Fleige H, Horn R, Kandeler E, Kögel-Knabner I, Kretzschmar R, Stahr K, Wilke M (2015) Scheffer/Schachtschabel. In: Soil Science. Springer, Berlin

Blume H-P, Fleige H (2015) Watten und Strände–Salzwiesen und Mangrovenwälder. In: Blume HP et al (eds) Handbuch der Bodenkunde. Part 3.3.3.5, ecomed. Wiley-VCH, Landsberg

Boden AG (2005) Bodenkundliche Kartieranleitung, 5th edn. Schweizerbart, Stuttgart
FAO (2006) Guidelines for soil description, 4th edn. FAO, Rome
IUSS/ISRIC/FAO (2006) World reference base for soil resources, 2nd edn World Soil Resource Reports 132. FAO, Rome
Schlichting E, Blume H-P, Stahr K (1995) Bodenkundliches Praktikum, 2nd edn. Blackwell, Berlin

Part II

Historical and Future Changes of the Dune and Salt Marsh Fauna

9 General Aspects of Coastal Vegetation at the North Sea and the Baltic Sea

Detlev Metzing

Abstract

The habitats at the German seacoasts are mainly characterised by different types of beaches, dunes, cliffs, salt marshes, bogs, and water bodies. These often natural or semi-natural habitats have a specific coastal flora and vegetation. Many plant species and communities are closely restricted to the coast. The ecological conditions on the coasts of the North Sea and the Baltic Sea are largely similar but differ in some factors such as the salinity of the seawater and periodicity, number and duration of floods. Many plant species occur on both coasts, others are restricted either to the North Sea or Baltic Sea coast. On the North Sea coast, the highest diversity of vascular plants is found on the islands, due to high habitat diversity, while the mainland coast is largely characterised by salt marshes as well as coastal protection structures and is significantly poorer in species.

9.1 Ecology of Coastal Flora and Vegetation

Coastal habitats are classified into several groups according to their development and characteristics. Incidence, dimension, and characteristics of coastal flora and vegetation are quite different between the North Sea and the Baltic Sea (cf. Duphorn et al. 1995; Heydemann 1997; Kutscher 1995; Pott 1996, see Chap. 3), e.g.:

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- Primary and secondary dunes: white dunes (the term yellow dunes is also often used for this dune type)
- Tertiary dunes: grey dunes, brown dunes, and dune groves
- Dune woods and forests
- Wet and moist dune valleys, dune woods in valleys with high ground-water level
- Brackish and fresh waters in the dune valleys
- Beach plains, drift lines, lower and upper salt marshes, salt meadows
- Coastal mires, marsh mires
- Beach ridges, cliff lines
- Dry grassland and heather on glacial ground (geest, moraine)
- Anthropogenic habitats (dikes, stony groynes, etc.)

The establishment and development of coastal flora and vegetation depend on the specific situation of geomorphology, sea currents, surges, changes of sea level, and tides. The habitats of the North Sea differ mainly in tide dynamics causing a different flooding pattern and the salinity of the vegetation zones from sub-littoral to epi-littoral.

The edaphic conditions of coastal habitats are remarkably more stable and less influenced by human impact than those in inland areas. They are more important than the influence of climate zones and result in azonal vegetation (Richter 2001). Therefore, the spatial distribution of many coastal species is not restricted to special vegetation zones, but ranges over several climate zones. Nevertheless, climate is also a limiting factor for the range limits of many coastal plants (Packham and Willis 1997; Ranwell 1972; Wiedemann and Pickart 2004).

Considering substrate conditions, two pedobiomes are characteristic for coastal habitats (Walter and Breckle 1991):

- Halobiomes (salt marshes, soils with salt content)
- Psammobiomes (dunes and beach habitats, sandy soils)

Periodic flooding by salt water and mud sediments are important factors in salt marshes, wind, and sand in the dunes (Ranwell 1972). Coastal plants exhibit adaptations to these key factors.

Many dune species are adapted to over-sanding, high UV radiation, extreme changes in microclimate, and dryness by morphological or anatomical structures (e.g. thick cuticle, cuticle coating, rolled leaves, water saving tissue, or stolones) (Fischer 1975). Plant species show a decreasing tolerance against salt and an increase in xenomorphic leaf structure and tolerance against over-sanding. Many species associated with dunes and dune valleys need the specific dynamics of the coastal dunes, which are not, or nearly not existent in comparable dunes of the inland (Graebner 1910; Packham and Willis 1997).

Salt marsh halophytes possess different mechanisms to regulate their salt balance (e.g. halo-succulence, salt glands) and are particularly adapted to periodic flooding (e.g. by aerenchymas) (Albert 1982; Chapman 1974; Eber and Strutz-Fischer 1991; Packham and Willis 1997; Schmidtke 1985). In the case of a close adaptation to saline conditions, high metabolic costs arise, which results in a lower growth capacity than in glycophytes under comparable conditions. This is the reason for their restriction to such unfavourable habitats (Albert 1982). Some halophytes occur exclusively at the coast (e.g. *Atriplex portulacoides*, *Blysmus rufus*), whereas other species are restricted to coastal habitats only in a part of their distribution area (e.g. *Alopecurus arundinaceus*, *Oenanthe lachenalii*).

Some species with high genotypic plasticity appear in coastal habitats as different ecotypes, partly also distinguished taxonomically. Red Fescue is present in the dunes with the subspecies *Festuca rubra* subsp. *arenaria*, but in coastal marshes, *Festuca rubra* subsp. *litoralis* occurs (Dierssen 1996; Jäger and Werner 2002).

The low number of species in coastal habitats depends on high demands towards adaptation to these habitats (Gewalt 2003; Haeupler and Schönfelder 1988; Raabe 1981). Furthermore, the geo-morphological and ecological diversity of coastal habitats leads to the development of specific vegetation complexes and syntaxa and, in consequence, to a uniqueness of these ecosystems.

The ecological conditions at the coasts of the North Sea and the Baltic Sea are similar, but differ substantially in the intensity of the factors: salt content, wind force, periodicity, number and duration of flooding. Thus, most plant species occur at both coasts. Only a small part of the halophytes is restricted to subareas of the German coast (Boll 1848; Buchenau 1886; Nöldeke 1873; Schmidtke 1985; Steinhäuser 1934; Weeda and Mennema 1983). The decrease in salt content of the Baltic Sea in an easterly direction is the dispersion barrier for many species of saline habitats (Fukarek 1967).

9.2 Flora and Vegetation of the North Sea Coast

The coasts of the German North Sea belong to the Wadden Sea. Today, their flora can be regarded as completely recorded (cf. Gremmen and Kremers 1971; Prins et al. 1983), with the exception of new immigrating species or neophytes. Distribution maps concerning the vascular plant species of the German North Sea coast were published by Christiansen (1953), Cordes et al. (2007), Dierssen and Mierwald (1987), Garve (1994), Horstmann (1959), Haeupler and Schönfelder (1988), Raabe et al. (1982), Urbschat (1972), and Bettinger et al. (2013).

The number of all taxa (species and infra-specific taxa) in the area of the German North Sea coast is not yet finally determined. Published numbers for partial areas differ depending on the size of the considered area, the scale of the mapping raster, taxonomic classification, consideration of apomictic forms, and separate counting of the species and infra-specific taxa. Van der Maarel and van der Maarel-Versluys (1996) refer to 1068 typical coastal species for Europe, which also include some coastal species s.l. Prins et al. (1983) counted 899 species for the whole Wadden Sea, while Bröring et al. (1993) counted 993 taxa for the Lower Saxon Wadden Sea including established and casual neophytes.

Raabe (1981, cf. van der Ende 1995) mentions 360 indigenous species for the islands and so-called Halligen (small salt marsh islands) of Schleswig-Holstein (an additional 370 archaeophytes and neophytes occur). According to Christiansen (1960), 484 indigenous species exist there, but later he counts 504 indigenous and

159 naturalised species (Christiansen 1961). Buchenau (1901) mentioned 550 species for the East Frisian Islands. Steinhäuser (1934) counted 321 species for the same region without non-native taxa. According to Metzing et al. (2008), 1005 plant taxa, including casual and established neophytes, have been documented over time for the East Frisian Islands, 895 of these after 1980. According to Garve (2004), 1039 species and infra-specific taxa (indigenous species, archaeophytes, and naturalised neophytes) occur in coastal regions of Lower Saxony (including diked sea and river marshes). 152 species are listed in the Red Book of the German North Sea coast (van der Ende 1995).

Ecology and syntaxonomy was described in detail by Dijkema (1983); Doing (1983a, b); Ellenberg (1996); Dahmen et al. (1989); Heykena (1965); Möller (1975); Mühl (1993); Pedersen (1983); Petersen (2000); Pott (1995a, b); Preising et al. (1990, 1997); Raabe (1981); Ringer (1994); Tüxen (1974) and Weber (1999). Dierssen (1988) outlines coastal vegetation intensively in his overview on plant associations in Schleswig-Holstein. Petersen and Pott (2005) published vegetation maps of the 1940s and the 1990s.

The taxa of coastal plants occur in different vegetation complexes, which may be classified in four series: xero-, hygro-, hydro-, and halosere (Hobohm 1993; Pott 1995a, 1996; Westhoff 1947). Plant communities of trampled habitats and ruderal vegetation (on the North Sea islands) were placed in an additional series by Westhoff et al. (1993), the Anthroposeries.

The *halosere* covers vegetation of salt marshes, of the Wadden Sea islands, and the transition zone towards the dunes. A tide dependent zonal sequence of plant associations is the characteristic result of number and duration of floodings, sedimentation rate, and salt content of the substrate. Because the tidal influence depends on the elevation above MHW, the zones run parallel to the coastline (Raabe 1981). Dominant taxa of the pioneer zone (about 400–700 floodings per year, 20–26‰ salt content in the soil) include *Salicornia* spp., *Suaeda maritima*, and the neophytic *Spartina anglica*. The low salt marsh (100–400 floodings per year, 20–26‰ salt content in the soil) is characterised by a dominance of *Puccinellia maritima*; additional species include *Atriplex portulacoides* and *Limonium vulgare*. Floodings are rarer in the high marsh (<100 floodings per year, 5–20‰ salt content in the soil) (Bakker et al. 2005; Raabe 1981). Characteristic species are *Festuca rubra*, *Elymus* spp., *Juncus gerardii*, *Armeria maritima*, *Artemisia maritima*, and *Agrostis stolonifera*. Glycophytes build up the vegetation zone of the dikes and the dunes.

Dependent on topographic structure, soil properties, and agricultural use (grazing intensity, mowing), numerous plant associations develop which are grouped in the following classes: Thero-Salicornietea, Spartinetea maritimae, Juncetea maritimi, and Saginetea maritimae (pro parte) (Pott 1995a, b; Rennwald 2002). Presence and abundance of many species as well as the development of salt marsh associations are strongly influenced by agricultural use. Termination of grazing in large salt marsh areas may result in a dominance of a few species (in particular *Elymus athericus* and *Atriplex portulacoides*) (Bakker et al. 2003).

The *xerosere* covers the vegetation complexes of the beach and the dry, groundwater distant dunes (Pott 1995b; Westhoff 1947). Mainly on the islands and only at a few localities of the mainland (e.g. coast of Eiderstedt), a sequence of plant associations depends on the development, height, and ageing (decalcification, elution of salt and nutrients) of dunes (Ellenberg 1996). The involved plants fix the sand of floodplains, thus starting the development of primary dunes and the accumulation of sand to form white dunes. This process starts with the development of primary dunes initiated by *Elymus farctus*. Drift line species (Cakiletea maritimae), such as *Cakile maritima*, *Salsola kali*, *Atriplex* spp., and *Honckenya peploides,* but also *Glaux maritima,* have no or minor importance for the development of partly ephemeral foredunes (Bernhardt 1992; Heykena 1965). *Puccinellia maritima* and *Elymus athericus* may enhance the development of foredunes under specific circumstances (clayey sand plates, low sand transport) (Heykena 1965; Pott 1995a). *Ammophila arenaria*, × *Calammophila baltica* and—to a minor degree—*Leymus arenarius* effect an additional increase of sand in up to 20 m high secondary dunes (white dunes) shortly after reduction of salt water influence by the development of fresh water lenses. The artificial planting of *Ammophila arenaria* and other species is pushed in many places for coastal protection.

The extreme conditions—in particular the polishing effect of moving sand—are responsible for species poorness of sand plates and secondary dunes. More species (*Oenothera ammophila* (= *O. oakesiana*), *Sonchus arvensis*, *Hieracium umbellatum*, and *Calystegia soldanella*) grow at the lee side of white dunes rather than at the side open to the wind. The plant associations of the primary and secondary dunes form the class Ammophiletea arenariae (Pott 1995a).

The development of grey and brown dunes (tertiary dunes) starts with a colonisation by *Festuca rubra* or *Hippophae rhamnoides* and *Salix repens* (on the East Frisian Islands mainly at the southern slopes) and the development of a soil layer. This vegetation forms the class Koelerio-Corynephoretea (Petersen et al. 2003). Here we find mainly species that are adapted to poor and acidic sandy soils, e.g., *Koeleria arenaria*, *Corynephorus canescens*, *Jasione montana*, and *Viola* spp., which are also found on comparable dry grasslands of the inland. These habitats are relatively species-rich compared with primary and secondary dunes. In recent years, *Carex arenaria*, *Galium mollugo*, and *Holcus lanatus* have dispersed into the grey dunes. Disturbed grey dunes are colonised by *Rubus caesius* (Peters and Pott 1999).

The further development of the stabilised dunes leads to brown podsolic soils from which the dune's name is derived. The vegetation of brown dunes is formed by coastal heaths (with *Empetrum nigrum* and *Calluna vulgaris*, class Calluno-Ulicetea). The exposition of dune slopes causes—in particular in north-south direction—a remarkable differentiation in species dispersion (Gerlach 1995; Heykena 1965; Pott 1995b). On southern slopes, Grey Hair-grass vegetation or Sea Buckthorn shrubs replace the heather. Elder shrubs may settle in dry dune valleys. Other associations of dune shrubs (class Salicetea arenariae) are formed by *Rosa pimpinellifolia*, the neophyte *Rosa rugosa,* and *Salix repens* (Petersen et al. 2003; Weber 1999).

The natural development of the xerosere proceeds to poplar-oak forests if no disturbance by man occurs and a sufficient humus layer is built up (Doing 1983a;

Graebner 1910; Pott 1995b). Shrubs and dune woods accumulated remarkably in the last century because the use of dunes and wood decreased (collection of firewood, pasturing, and sod digging) (Van Dieren 1934). But already in the nineteenth century, some parts of the North Sea islands were forested with pines to fix the dunes (Doing 1983a; Schulze 1910), for instance, on Spiekeroog starting from about 1860 (Meyer-Deepen and Meijering 1979). The question, whether the islands would be treeless without man's impact, is discussed in many cases (Van Dieren 1934).

Nowadays, the growth of trees is interpreted as a final stage of a natural succession in dunes (Pott et al. 1999; Ringer 1994). The tendency for wood growth is lower in the region of the North Frisian Islands than at the southern coast of the North Sea (Heydemann 1997).

The *hygroseries* covers open pioneer associations of lowland and mire vegetation, wet heather, and wooded associations of dune valleys. Petersen (2000) described their ecology and syntaxonomy in detail. The hygrosere is closely interlocked with the hydrosere and is subsumed by some authors to the hydrosere (Pott 1995b; Peters and Pott 1999). The development of this type of vegetation depends on the degree of wetness, and the content of salt and lime. Stocks of low and jaggy pioneer associations grow up (class Isoeto-Littorelletea, containing *Littorella uniflora*, *Samolus valerandi*; class Isoeto-Nanojuncetea with *Centaurium pulchellum*, *Juncus bufonius*, *J. pygmaeus*, and *Radiola linoides*; class Saginetea maritimae with *Centaurium littorale*, *Gentianella uliginosa*, and *Sagina nodosa*).

Increasing dryness, acidification, and coverage by sand cause the development of lowland and mire vegetation (class Scheuchzerio-Caricetea fuscae with *Carex* spp., *Juncus* spp., *Ophioglossum vulgatum*, and *Pedicularis sylvatica*).

Pyrolo-Hippophaetum may be ranked as a transition association to the xerosere. It grows at the borders of older dune valleys with *Salix repens* and *Pyrola rotundifolia.* Wet heaths (class Oxycocco-Sphagnetea with *Erica tetralix* and *Empetrum nigrum*) build up stable and long-lasting stocks if the soil acidification increases and no disturbance occurs. Finally, an invasion of birch trees may lead to birch woodland, in particular, at the lee side of dunes (Peters and Pott 1999; Petersen 2000; Petersen et al. 2003; Pott 1995b; Pott et al. 1999; Rennwald 2002; Ringer 1994).

Associations of the xero- and hygrosere are species-rich and widely restricted to the coastal regions of the North Sea on the dunes of the islands. They only occur at a few localities of dunes of the mainland, e.g., near St. Peter-Ording (Eiderstedt, Schleswig-Holstein) or in a small area near Schillig (Landkreis Wittmund, Lower Saxony).

The *hydrosere* covers associations of water plants, reeds, and tall sedge dominated wetlands, which occur in water bodies of dune valleys and artificial hollows (bomb craters, water hollows, ice ponds, etc.) (Hobohm 1993; Krismann 1992; Niedringhaus and Zander 1998). Specialists of brackish waters, like *Ranunculus peltatus* subsp. *baudotii*, *Ruppia* spp., and *Zannichellia palustris*, are characteristic species in coastal zones. Additionally, many species occur which are also spread in the inland waters such as *Eleocharis* spp., *Hippuris vulgaris*, *Phragmites australis*, and *Potamogeton* spp.

9.3 Flora and Vegetation of the Baltic Sea Coast

Plant distribution maps of the German Baltic Sea coast covering partial geographical or ecological areas were published by Benkert et al. (1996); Bettinger et al. (2013); Christensen and Westdörp (1979); Christiansen (1953); Dierssen and Mierwald (1987); Fukarek (1967); Haeupler and Schönfelder (1988) as well as Raabe et al. (1982).

A specific and current overview on the terrestrial coastal flora of the German Baltic Sea as well as the total number of species has not been published. Benkert et al. (1996) quoted total numbers of taxa, including infra-specific ones, considering all ordinance survey map squares of Mecklenburg-Western Pomerania. These numbers range from 97 to 912 taxa with a mean of 452 for the 81 coastal squares. It must be considered that terrestrial parts in some squares are only very small, causing low numbers, whereas other squares cover large inland areas, including urban areas, which causes high numbers. Therefore, the maximum number (912) is revealed in a square of the city of Rostock. Isermann (1997) counted 243 taxa in the dunes of Western Pomerania. Berg et al. (1996) listed 149 taxa of cormophytes in the Red Data Book of the Baltic Sea coast (including 48 recently not endangered taxa).

Fukarek (1961); Härdtle (1984); Isermann (1997); Kloss (1969); Krisch (1990); and Möller (1975) described ecology and syntaxonomy of partial areas at the German Baltic Sea in detail. Berg et al. (2004) and Dierssen (1988) published phytosociological overviews considering Mecklenburg-Western-Pomerania and Schleswig-Holstein.

The ecological complexes of vegetation may be arranged by succession series in the same manner for the Baltic Sea as for the North Sea coast.

The *halosere* covers salt meadows of the southern and western Baltic Sea coasts where the salt content of the seawater exceeds 5% (Boedeker and Knapp 1996). The salt content of the Baltic Sea displays a horizontal gradient between Kattegat and the Gulf of Finland due to a balance of input of salt-rich water of the North Sea at the Kattegat and the input of fresh water of the rivers from inland areas. The salt content of surface water is 15–25‰ at the Kattegat, 12–14‰ in the Mecklenburg Bay, 8‰ near Rügen, and ca. 1‰ in the Usedom Bodden (Duphorn et al. 1995; Matthäus 1996). The 10‰ isohaline reaches the coast between Warnemünde and Darß (Kloss 1969).

Because of seasonal changes in the amount of fresh water input, seasonal changes of temperature and dynamic processes of the sea, including short-term and year-to-year changes, occur which are diminished in the surface waters (Matthäus 1996). Extreme values ranging from 5.1‰ to 25.2‰ were measured during a period of 8 years in the Wismar Bay (Kloss 1969).

Living conditions at the Baltic Sea coast show a remarkable gradient from a tidal and saline sea to a brackish sea, which is reflected in a floristic gradient (Dierssen 1988; Ellenberg 1996; Schramm 1996). Several halophytes have their southeastern distribution border in the region of the German Baltic Sea coast (e.g. *Atriplex longipes*, *A. portulacoides*, *Cochlearia danica*, and *Limonium vulgare*).

The halosere contains the associations of Thero-Salicornietea (e.g. with *Atriplex pedunculata*, *Bassia hirsuta*, *Salicornia europaea*, and *Suaeda maritima*) growing at muddy coasts, in flat depressions or at the border of beach lagoons (Härdtle 1984; Polte 2004a). *Spartina* does not occur at the Baltic Sea coasts. Reeds and salt meadows of the Baltic Sea coast form the class Juncetea maritimi that are established in the geo-littoral zone depending on the flooding regime, salt content, substrate, and disturbances. Characteristic species are *Artemisia maritima*, *Aster tripolium*, *Glaux maritima*, *Cochlearia danica*, *Juncus gerardii*, *Juncus maritimus*, *Limonium vulgare*, *Plantago maritima*, *Puccinellia* spp., and *Triglochin maritima*. Other species, such as *Potentilla anserina* and *Agrostis stolonifera*, indicate adjacent floodplain grassland (Polte 2004b; Dierssen 1988). Areas with natural or man-made disturbances were settled by salt pioneer grassland (class Saginetea maritimi; in addition to other species *Bupleurum tenuissimum*, *Cochlearia danica*, *Sagina maritima* occur).

Natural salt grassland is only present on small areas at the geo-littoral of the Baltic Sea coast. It occurs as a permanent community at shingle beaches of stable cliff lines or as temporary succession stages on new established land (Jeschke 1987, 1995). Nowadays, anthropogenic plant communities cover the major part of lowland coasts up to 0.5 m above MWL. They develop by the grazing of cattle or horses and replace formerly existing natural salt reeds.

Saline peats are the result of a-periodic flooding, bringing sediments of mud, accumulations of organic material, and compression by the treading of grazing animals. Up to 1 m thick peat layers with high salt content (up to 50‰) form coastal flooding mires. Prior to agricultural use, they were dominated by reed peat; as a consequence of grazing, the mineral content of peat increased (Holz et al. 1996; Jeschke 1987, 1995), proceeding to a brackish reed as climax vegetation. After the end of grazing, they develop in shallow water to a Bolboschoenetum maritimae, above MWL to an Astero-Phragmitetum (Boedeker and Knapp 1996; Krisch 1990; Polte 2004b).

The *xerosere* covers the vegetation complexes of beaches, beach ridges, and dunes. The community of beach ridges of the class Cakiletea maritimae are characterised by *Atriplex* spp., *Cakile maritima*, *Elymus* spp., *Honckenya peploides*, *Lactuca tatarica*, *Rumex crispus*, *Sonchus arvensis*, *Tripleurospermum maritimum*, and *Tussilago farfara.* These species settle on periodically wet drift lines of muddy, sandy, or pebbly substrate. They are partly involved in the development of embryonic or pre-dunes at sandy places, in particular *Honckenya peploides*. According to Isermann (2004), these communities should be excluded from the xerosere, because an obligatory succession towards dunes at the Baltic Sea coast could not be found.

The communities of dunes at the Baltic Sea are typical representatives of the xerosere (class Ammophiletea arenariae with *Ammophila arenaria*, ×*Calammophila baltica*, *Elymus farctus*, *Elymus* hybrids, and *Leymus arenarius*). In contrast to the situation at the North Sea (Benecke and Arnold 1931), the salt sensitive *Ammophila arenaria* is able to settle on the flat beach because of the lower salt content of the Baltic Sea. Therefore, this species takes part in primary dune development.

Sea love grass and marram grass are often planted on artificial dunes as a measure for cost protection. If sand drift decreases, *Festuca rubra* colonises such habitats and Red Fescue dune grassland (Festucetum arenariae; Isermann 2004) will be established. *Carex arenaria* often settles temporarily on sandy areas with sand drift (Dierssen 1996), but this species also colonises all habitats from foredunes up to tertiary dunes (Isermann 1997). Today, grey dunes bear species-rich communities of the class Koelerio-Corynephoretea, but contain no Baltic Sea specific cormophytes—with the exception of *Festuca polesica* in Dune Fescue grassland. In old tertiary dunes, coastal heaths develops (class Calluno-Ulicetea with *Calluna vulgaris*, *Deschampsia flexuosa*, *Empetrum nigrum*, *Erica tetralix*, and *Polypodium vulgare*) (Berg 2004b).

With the settlement of *Betula pendula*, *Quercus robur*, and *Sorbus aucuparia*, the development of shrubs and wood begins. Pines (*Pinus sylvestris*) grow up preferably in a Hieracio-Empetrum community, developing dune pine forests of the class Vaccinio-Piceetea (Isermann 1997; Kutscher 1995). Naturally, pinewoods dominate tertiary dunes (Schickhoff and Seiberling 2003). An endemic Coastal Wintergreen-Pine forest (Empetro nigri-Pinetum sylvestris) exists on alluvial sand undisturbed by wind, on beach ridges, and in old dune valleys of the Baltic Sea coast (Berg 2004c).

The *hygrosere* consists of open pioneer communities, the lowland and mire vegetation, wet heaths and woody associations of the dune valleys and lagoons. They belong to the classes Isoeto-Nano-Juncetea (with *Anagallis minima*, *Carex demissa*, and *Radiola linoides*), Isoeto-Littorelletea (with *Baldellia ranunculoides*, *Littorella uniflora*, and *Samolus valerandi*) and Saginetea maritimae (with *Centaurium littorale*, *Plantago coronopus*, and *Sagina nodosa*). Sedge reeds of the class Scheuchzerio-Caricetea fuscae occur on peaty dune hollows (with *Eleocharis* spp., *Juncus bulbosus*, and *Liparis loeselii*). Wet heaths can be found in dune mires and wet dune valleys (class Oxycooco-Sphagnetea (with *Calluna vulgaris*, *Erica tetralix*, and *Empetrum nigrum*). They exist as a permanent community, but if the groundwater decreases, downy birch woodlands or pinewoods develop (Berg and Bolbrinker 2004; Teppke and Berg 2004; Timmermann 2004).

The *hydrosere* of the sub-littoral at the Baltic Sea coast covers seaweed meadows (class Zosteretea with *Zostera* spp.) and submerse plant communities (class Ruppietea maritimae resp. Potamogetonetea with *Najas marina*, *Potamogeton* spp., *Ruppia maritima*, *Ranunculus peltatus* subsp. *baudotii*, and *Zannichellia palustris*) in brackish beach lagoons, shallow water zones of the Bodden Lagoon, and in small bays (Berg 2004a; Berg et al. 2004; Dierssen 1988; Kloss 1969; Rennwald 2002).

Special features of the Baltic Sea coast are the steep cliffs, which are truncated moraines of the last glaciation period. Ruderal plant communities (class Artemisietea vulgaris with *Cirsium arvense*, *Elymus repens*, *Petasites spurius*, and *Tussilago farfara*) grow there. Slopes without permanent destruction are colonised by the vegetation of the adjacent habitats that partly consist of thermophilic fringes and vegetation of perennial herbs as well as wood associations (Christiansen 1955; Dengler 2004; Drews and Dengler 2004; Heydemann 1997; Kutscher 1995; Pott

1995a). At slopes of lower height, beech wood can grow immediately bordering beach ridges.

9.4 Phytodiversity of the German Coast

The phytodiversity of the coastal area is illustrated in Fig. 9.1, based on the data of BfN (1999) for the 223 selected vascular plant taxa occurring at the coast (the discrepancy to the taxon number in Table 10.1 results from different used classifications). No separation in terms of time has been applied here; all taxa listed as indigenous or naturalised before 1950 and up to after 1980 were treated equally.

High species numbers are characteristic for the East Frisian Islands, the area around Cuxhaven, the North Frisian Islands (particularly Amrum and Föhr), and the coastal area of the town of Rostock. A drop in floristic diversity from the East Frisian Islands towards the mainland coast in Lower Saxony is evident (and similar in Northern Friesland). These differences are the result of unequal habitat diversity. Inevitably, grid cells with very low portions of land mostly have low species numbers. It is not clear if the differences are caused by a different completeness of the floristic census. However, differences caused by possible gaps of floristic recording are equalised by the use of a larger grid scale (Fig. 9.1b).

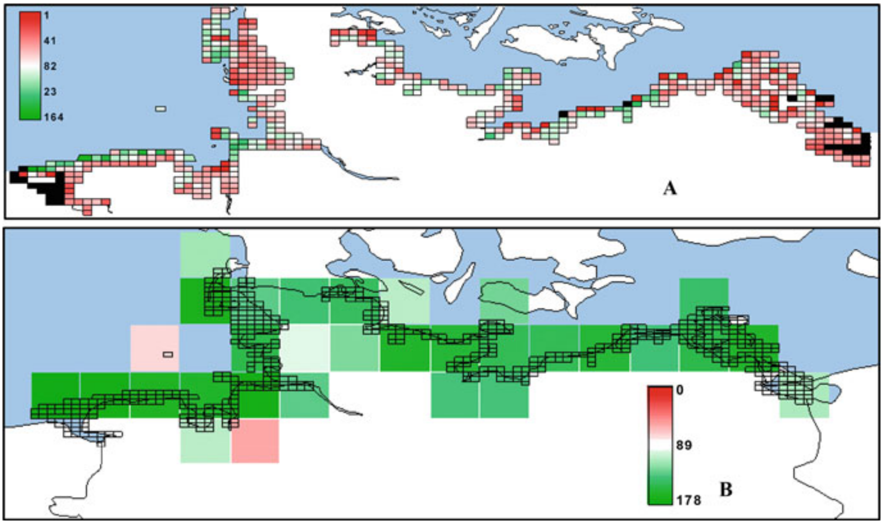

Fig. 9.1 Phytodiversity along the German coast. (**a**) Number of coastal plant species records in grid squares (MTB quadrants) and (**b**) Number of coastal plant species records in grid squares (0.5° × 0.5°), based on a list of 223 selected coastal taxa (FlorKart database: BfN 1999). No records for the black grid cells were available. The two-coloured presentation shows the species-rich areas in green, the species poor areas in red

References

Albert P (1982) Halophyten. In: Kinzel H (ed) Pflanzenökologie und Mineralstoffwechsel. Ulmer, Stuttgart, pp 33–215

Bakker JP, Bos D, Stahl J, De Vries Y, Jensen A (2003) Biodiversität und Landnutzung in Salzwiesen. Nova Acta Leopoldina 87:163–194

Bakker JP, Bunje J, Dijkema K, Frikke J, Hecker N, Kers B, Körber P, Kohlus J, Stock M (2005) Salt marshes. In: Essink K, Dettmann C, Farke H, Laursen K, Lüerssen G, Marencic H, Wiersinga W (eds) Wadden Sea quality status report 2004. Wadden Sea Ecosystem 19:168–179

Benecke W, Arnold A (1931) Zur Biologie der Strand- und Dünenflora, II. Der Salzgehalt der natürlichen Standorte von *Agriopyrum junceum* PB und *Ammophila arenaria* Roth auf dem Sandstrande von Norderney. Berichte der Deutschen Botanischen Gesellschaft 49:363–381

Benkert D, Fukarek F, Korsch H (1996) Verbreitungsatlas der Farn- und Blütenpflanzen Ostdeutschlands. G Fischer, Jena

Berg C (2004a) 3. Klasse: Ruppietea maritimae. In: Berg C, Dengler J, Abdank A, Isermann M (eds) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Weissdorn, Jena, pp 86–92

Berg C (2004b) 20. Klasse: Calluno-Ulicetea. In: Berg C, Dengler J, Abdank A, Isermann M (eds) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Weissdorn, Jena, pp 290–300

Berg C (2004c) 32. Klasse: Vaccinio-Piceetea. In: Berg C, Dengler J, Abdank A, Isermann M (eds) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Weissdorn, Jena, pp 459–468

Berg C, Bolbrinker P (2004) 7. Klasse Isoeto-Nano-Juncetea. In: Berg C, Dengler J, Abdank A, Isermann M (eds) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Weissdorn, Jena, pp 118–124

Berg C, Henker H, Mierwald U (1996) Rote Liste und Artenliste der Gefäßpflanzen des deutschen Küstenbereichs der Ostsee. Schriftenreihe für Landschaftspflege und Naturschutz 48:29–39

Berg C, Dengler J, Abdank A, Isermann M (eds) (2004) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband, Weissdorn, Jena

Bernhardt KG (1992) Besiedlungsstrategien an sandigen Extremstandorten im Tidebereich. Flora 187:271–281

Bettinger A, Buttler KP, Caspari S, Klotz J, May R, Metzing D (eds) (2013) Verbreitungsatlas der Farn- und Blütenpflanzen Deutschlands. Landwirtschaftsverlag, Münster

BfN (1999). www.floraweb.de

Boedeker D, Knapp HD (1996) Ökologie der Salzwiesen, Dünen und Schären. In: Rheinheimer G (ed) Meereskunde der Ostsee, 2nd edn. Springer, Berlin, pp 222–229

Boll E (1848) Die Seestrands- und Salinenflora der deutschen Ostseeländer. Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg 2:67–86

Bröring U, Dahmen R, Haeseler V, von Lemm R, Niedringhaus R, Schultz W (1993) Dokumentation der Daten zur Flora and Fauna terrestrischer Systeme im Niedersächsischen Wattenmeer. Berichte aus der Ökosystemforschung Wattenmeer 2:1–207

Buchenau F (1886) Vergleichung der nordfriesischen Inseln mit den ostfriesischen in floristischer Beziehung. Abhandlungen herausgegeben vom Naturwissenschaftlichen Vereine zu Bremen 9: 361–384

Buchenau F (1901) Flora der Ostfriesischen Inseln (einschliesslich der Insel Wangeroog), 4th edn. Engelmann, Leipzig

Chapman VJ (1974) Salt marshes and salt deserts of the world, 2nd edn. Cramer, Lehre

Christensen E, Westdörp J (1979) Flora von Fehmarn. Mitteilungen der Arbeitsgemeinschaft für Floristik in Schleswig-Holstein und Hamburg 30:1–262

Christiansen W (1953) Neue kritische Flora von Schleswig-Holstein. Möller & Söhne, Rendsburg

Christiansen W (1955) Pflanzenkunde von Schleswig-Holstein, 2nd edn. Wachholtz, Neumünster

Christiansen W (1960) Statistisches über die Flora der Nordfriesischen Inseln. Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein 30:29–33

Christiansen W (1961) Flora der Nordfriesischen Inseln. Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, N F 4:1–127

Cordes H, Feder J, Hellberg F, Metzing D, Wittig B (2007) Atlas der Farn- und Blütenpflanzen des Weser-Elbe-Gebietes. Hauschild, Bremen

Dahmen R, Von Glahn H, von Lemm R, Wolff D (1989) Vegetationssystematische Untersuchungen und großmaßstäbliche Vegetationskartierungen in den Außengroden der niedersächsischen Nordseeküste. Drosera 89:145–168

Dengler J (2004) 25. Klasse: Trifolio-Geranietea sanguinea. In: Berg C, Dengler J, Abdank A, Isermann M (eds) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Weissdorn, Jena, pp 362–379

Dierssen K (1988) Rote Liste der Pflanzengesellschaften Schleswig-Holsteins, vol 6, 2nd edn. Schriftenreihe des Landesamtes für Naturschutz und Landschaftspflege, Schleswig, pp 1–157

Dierssen K (1996) Vegetation Nordeuropas. Ulmer, Stuttgart

Dierssen K, Mierwald U (1987) Atlas der Flora Schleswig-Holsteins und Hamburgs. Wachholtz, Neumünster

Dijkema KS (1983) The salt-marsh vegetation of the mainland coast, estuaries and Halligen. In: Dijkema KS, Wolff WJ (eds) Report 9: Flora and vegetation of the Wadden Sea islands and coastal areas. Balkema, Rotterdam, pp 185–220

Doing H (1983a) The vegetation of the Wadden Sea islands in Niedersachsen and the Netherlands. In: Dijkema KS, Wolff WJ (eds) Report 9: Flora and vegetation of the Wadden Sea islands and coastal areas. Balkema, Rotterdam, pp 165–185

Doing H (1983b) Landscape and island types. In: Dijkema KS, Wolff WJ (eds) Report 9: Flora and vegetation of the Wadden Sea islands and coastal areas. Balkema, Rotterdam, pp 242–267

Drews H, Dengler J (2004) Steilufer an der nordoldenburgischen Küste: Artenausstattung, Vegetation und Pflegekonzept unter besonderer Berücksichtigung der Kalkhalbtrockenrasen und der wärmeliebenden Säume. Kieler Notizen zur Pflanzenkunde in Schleswig-Holstein und Hamburg 32:57–95

Duphorn K, Kliewe H, Niedermeyer R-O, Janke W, Werner F (1995) Die deutsche Ostseeküste. Sammlung geologischer Führer 88, Borntraeger, Stuttgart

Eber W, Strutz-Fischer H (1991) Aerenchyme bei Halophyten. In: Haeseler V, Janiesch P (eds) 3. Oldenburg, Oldenburger Workshop zur Küstenökologie, pp 44–45

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen, 5th edn. Ulmer, Stuttgart

Fischer H (1975) Aufbau, Standortsverhältnisse und Pflanzenverbreitung der ostfriesischen Inseln. Naturwissenschaftliche Rundschau 28:109–115

Fukarek F (1961) Die Vegetation des Darß und ihre Geschichte. Pflanzensoziologie 12:1–321

Fukarek F (ed) (1967) Verbreitungskarten zur Pflanzengeographie Mecklenburgs. 5. Reihe (Küstenpflanzen, 2. Teil). Natur und Naturschutz in Mecklenburg 5:127–213

Garve E (1994) Atlas der gefährdeten Farn- und Blütenpflanzen in Niedersachsen und Bremen. Naturschutz und Landschaftspflege in Niedersachsen 30:1–895

Garve E (2004) Rote Liste und Florenliste der Farn- und Blütenpflanzen in Niedersachsen und Bremen. 5. Fassung, Stand 1.3.2004. Informationsdienst Naturschutz Niedersachsen 24:1–76

Gerlach A (1995) Nachexkursionen Flora und Vegetation der Ostfriesischen Inseln. Teil 1: Spiekeroog. In: Eber W, Homm T, Peppler-Lisbach C (eds) Exkursionsführer zur 45. Jahrestagung der Floristisch-soziologischen Arbeitsgemeinschaft e. V. Oldenburg, pp 67–86

Gewalt M (2003) Vielfalt in der Natur – Phytodiversität. In: Leibniz-Institut für Länderkunde (ed) Nationalatlas Bundesrepublik Deutschland, vol 3. Spektrum Akademischer Verlag, Heidelberg and Berlin, pp. 102–105

Graebner P (1910) Pflanzenleben auf den Dünen. In: Solger F, Graebner P, Thienemann J, Speiser P, Schulze FWO (eds) Dünenbuch. Enke, Stuttgart, pp 183–296

Gremmen NJM, Kremers JWPM (1971) De flora van de nederlandse, duitse en deense waddeneilanden. Katholieke Universiteit, Nijmegen

Haeupler H, Schönfelder P (1988) Atlas der Farn- und Blütenpflanzen der Bundesrepublik Deutschland. Ulmer, Stuttgart

Härdtle W (1984) Vegetationskundliche Untersuchungen in Salzwiesen der ostholsteinischen Ostseeküste. Mitteilungen der Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg 34:1–142

Heydemann B (1997) Neuer biologischer Atlas. Ökologie für Schleswig-Holstein und Hamburg, Wachholtz, Neumünster

Heykena A (1965) Vegetationstypen der Küstendünen und der östlichen und südlichen Nordsee. Mitteilungen der Arbeitsgemeinschaft für Floristik in Schleswig-Holstein und Hamburg 13:1–135

Hobohm C (1993) Die Pflanzengesellschaften von Norderney. Arbeiten aus der Forschungsstelle Küste 12:1–202

Holz R, Herrmann C, Müller-Motzfeld G (1996) Vom Polder zum Ausdeichungsgebiet: Das Projekt Karrendorfer Wiesen und die Zukunft der Küstenüberflutungsgebiete in Mecklenburg-Vorpommern. Natur und Naturschutz in Mecklenburg-Vorpommern 32:3–27

Horstmann H (1959) Flora des Kreises Husum. Mitteilungen der Arbeitsgemeinschaft für Floristik in Schleswig-Holstein und Hamburg 7:1–286

Isermann M (1997) Vegetations- und standortskundliche Untersuchungen in Küstendünen Vorpommerns. Dissertation. Ernst-Moritz-Arndt-Universität Greifswald, Greifswald

Isermann M (2004) 15. Klasse Cakiletea maritimae. In: Berg C, Dengler J, Abdank A, Isermann M (eds) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Weissdorn, Jena, pp 246–256

Jäger EJ, Werner K (eds) (2002) Exkursionsflora von Deutschland 4: Gefäßpflanzen: Kritischer Band, 9th edn. Heidelberg, Berlin

Jeschke L (1987) Vegetationsdynamik des Salzgraslandes im Bereich der Ostseeküste der DDR unter dem Einfluß des Menschen, vol 24. Hercynia, N.F, pp 321–327

Jeschke L (1995) Salzgrasland und Röhrichte an der vorpommerschen Ostseeküste. In: Lamp J (ed) Gemeinsam für die Ostsee. Gesunde Küste – lebendes Meer, vol 9. WWF Tagungsbericht, pp 185–199

Kloss K (1969) Salzvegetation an der Boddenküste Westmecklenburgs (Wismar-Bucht). Natur und Naturschutz in Mecklenburg 7:77–114

Krisch H (1990) Ökologisch-soziologische Artengruppen und Pflanzengesellschaften im Geolitoral der Boddenküste (Ostsee). Phytocoenologia 19:1–28

Krismann A (1992) Bestand an Stillgewässern auf der Insel Föhr im Vergleich mit anderen Regionen Deutschlands. Drosera 92:85–87

Kutscher M (1995) Flora und Fauna an der Ostseeküste von Mecklenburg-Vorpommern. Demmler, Schwerin

Matthäus W (1996) Temperatur, Salzgehalt und Dichte. In: Rheinheimer G (ed) Meereskunde der Ostsee, 2nd edn. Springer, Berlin, pp 75–81

Metzing D, Heine K, Eggers P, Kuhbier H (2008) Die Farn- und Blütenpflanzen der Ostfriesischen Inseln. Schriftenreihe Nationalpark Niedersächsisches Wattenmeer 11:35–60

Meyer-Deepen J, Meijering MPD (1979) Spiekeroog. Naturkunde einer ostfriesischen Insel, Kurverwaltung, Spiekeroog

Möller H (1975) Soziologisch-ökologische Untersuchungen der Sandküstenvegetation an der Schleswig-Holsteinischen Ostsee. Mitteilungen der Arbeitsgemeinschaft für Floristik in Schleswig-Holstein und Hamburg 26:1–166

Mühl M (1993) Zur Synsystematik der Krähenbeerheiden auf den Ostfriesischen Inseln. Drosera 93:11–32

Niedringhaus R, Zander B (1998) Die Kleingewässer der Ostfriesischen Inseln. Schriftenreihe Nationalpark Niedersächsisches Wattenmeer 3:1–270

Nöldeke C (1873) Flora der ostfriesischen Inseln mit Einschluß von Wangeroog. Abhandlungen herausgegeben vom Naturwissenschaftlichen Vereine zu Bremen 3:93–198

Packham JR, Willis AJ (1997) Ecology of dunes, salt marsh and shingle. Chapman and Hall, London

Pedersen A (1983) The vegetation of the Wadden Sea islands in Denmark and Schleswig-Holstein.- In: Dijkema KS, Wolff WJ (eds) Report 9: Flora and vegetation of the Wadden Sea islands and coastal areas. Balkema, Rotterdam, pp 137–165

Peters M, Pott R (1999) Natur und Tourismus auf Norderney. Abhandlungen aus dem Westfälischen Museum für Naturkunde 61:1–174

Petersen J (2000) Die Dünentalvegetation der Wattenmeer-Inseln in der südlichen Nordsee. Husum Druck- und Verlagsgesellschaft, Husum

Petersen J, Pott R (2005) Ostfriesische Inseln. Landschaft und Vegetation in Wandel, Schlütersche, Hannover

Petersen J, Pott R, Janiesch P, Wolff J (eds) (2003) Umweltverträgliche Grundwasserbewirtschaftung in hydrogeologisch und ökologisch sensiblen Bereichen der Nordseeküste. Husum Druck- und Verlagsgesellschaft, Husum

Polte T (2004a) 6. Klasse: Thero-Salicornietea strictae. In: Berg C, Dengler J, Abdank A, Isermann M (eds) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Weissdorn, Jena, pp 114–117

Polte T (2004b) 14. Klasse: Juncetea maritimi. In: Berg C, Dengler J, Abdank A, Isermann M (eds) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Weissdorn, Jena, pp 225–245

Pott R (1995a) Farbatlas Nordseeküste und Nordseeinseln. Ulmer, Stuttgart

Pott R (1995b) Die Pflanzengesellschaften Deutschlands, 2nd edn. Ulmer, Stuttgart

Pott R (1996) Biotoptypen: Schützenswerte Lebensräume Deutschlands und angrenzender Regionen. Ulmer, Stuttgart

Pott R, Fromke A, Peters M, Petersen J, Rieck K (1999) Aktuelle geobotanische Forschung auf den Nordseeinseln. Berichte der Reinhold-Tüxen-Gesellschaft 11:39–108

Preising E, Vahle H-C, Brandes D, Hofmeister H, Tüxen J, Weber HE (1990) Die Pflanzengesellschaften Niedersachsens–Bestandsentwicklung, Gefährdung und Schutzprobleme. Salzpflanzengesellschaften der Meeresküste und des Binnenlandes. Naturschutz und Landschaftspflege in Niedersachsen 20:1–45

Preising E, Vahle H-C, Brandes D, Hofmeister H, Tüxen J, Weber HE (1997) Die Pflanzengesellschaften Niedersachsens–Bestandsentwicklung, Gefährdung und Schutzprobleme. Rasen-, Fels- und Geröllgesellschaften. Naturschutz und Landschaftspflege in Niedersachsen 20:1–146

Prins D, Kuhbier H, Pedersen A, Mennema J, Weeda EJ (1983) Main list with indigenous or naturalized phanerogams and pteridophytes of the Wadden Sea area. In: Dijkema KS, Wolff WJ (eds) Report 9: Flora and vegetation of the Wadden Sea islands and coastal areas. AA Balkema, Rotterdam, pp 323–339

Raabe E-W (1981) Über das Vorland der östlichen Nordsee-Küste. Mitteilungen der Arbeitsgemeinschaft für Floristik in Schleswig-Holstein und Hamburg 31:1–118

Raabe E-W, Brockmann C, Dierssen K (1982) Verbreitungskarten ausgestorbener, verschollener und sehr seltener Gefäßpflanzen in Schleswig-Holstein. Mitteilungen der Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg 32:1–317

Ranwell DS (1972) Ecology of marshes and sand dunes. Chapman and Hall, London

Rennwald E (2002[2000]) Verzeichnis und Rote Liste der Pflanzengesellschaften Deutschlands– mit Datenservice auf CD-ROM. Schriftenreihe für Vegetationskunde 35:1–800

Richter M (2001) Vegetationszonen der Erde. Klett-Perthes, Gotha and Stuttgart

Ringer C (1994) Untersuchungen von Birken-Buschwäldern auf den ostfriesischen Inseln Borkum und Norderney unter vorwiegend synsystematischen und syntaxonomischen Gesichtspunkten. Drosera 94:125–137

Schickhoff U, Seiberling S (2003) Zwischen Land und Meer–Küstenvegetation an Nord- und Ostsee. In: Leibniz-Institut für Länderkunde (ed) Nationalatlas Bundesrepublik Deutschland, 3. Spektrum Akademischer Verlag, Heidelberg and Berlin, pp. 116–117

Schmidtke K-D (1985) Die Küstenvegetation an Nord- und Ostsee. In: Hassenpflug W, Kortum G, Newig J, Pollex W, Schmidtke K-D (eds) An Nord- und Ostsee. Husum Druck- und Verlagsgesellschaft, Husum, Schleswig-Holsteins Küsten, pp 48–78

Schramm W (1996) Pflanzen. In: Rheinheimer G (ed) Meereskunde der Ostsee, 2nd edn. Springer, Berlin, pp 202–204

Schulze FWO (1910) Der Dünenbau. In: Solger F, Graebner P, Thienemann J, Speiser P, Schulze FWO (eds) Dünenbuch. Enke, Stuttgart, pp 377–404

Steinhäuser M (1934) Die floristische Stellung und Herkunft der Pflanzenwelt der ostfriesischen Inseln. Repertorium Europaeum et Mediterraneum 4:65–156

Teppke M, Berg C (2004) 9. Klasse: Littorelletea. In: Berg C, Dengler J, Abdank A, Isermann M (eds) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Weissdorn, Jena, pp 135–142

Timmermann T (2004) 11. Klasse Oxyocco-Sphagnetea. In: Berg C, Dengler J, Abdank A, Isermann M (eds) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung. Textband. Weissdorn, Jena, pp 149–162

Tüxen R (1974) Die Pflanzengesellschaften Nordwestdeutschlands. Liefg. 1., 2nd ed. Cramer

Urbschat J (1972) Flora des Kreises Pinneberg. Mitteilungen der Arbeitsgemeinschaft für Floristik in Schleswig-Holstein und Hamburg 20:1–281

van der Maarel E, van der Maarel-Versluys M (1996) Distribution and conservation status of littoral vascular plant species along the European coasts. J Coast Conserv 2:73–92

Van Dieren JW (1934) Organogene Dünenbildung. Nijhoff, Den Haag

von der Ende M (1995) Rote Liste der Farn- und Blütenpflanzen des deutschen Wattenmeerbereichs und Helgolands. Schriftenreihe für Landschaftspflege und Naturschutz 44:51–61

Walter H, Breckle SW (1991) Ökologie der Erde. 1: Ökologische Grundlagen in globaler Sicht. G. Fischer, Stuttgart

Weber HE (1999) Salicetea arenariae (H2B). Dünenweiden-Gebüsche. In: Dierschke H (ed) Synopsis der Pflanzengesellschaften Deutschlands. Selbstverlag der Floristisch-soziologischen Arbeitsgemeinschaft und der Reinhold-Tüxen-Gesellschaft, vol 6, Göttingen, pp 1–37

Weeda EJ, Mennema J (1983) Phytogeographical aspects. In: Dijkema KS, Wolff WJ (eds) Report 9: Flora and vegetation of the Wadden Sea islands and coastal areas. Balkema, Rotterdam, pp 221–242

Westhoff V (1947) The vegetation of dunes and salt marshes on the Dutch islands of Terschelling. Van der Horst, 's-Gravenhage, Vlieland and Texel

Westhoff V, Hobohm C, Schaminee JHJ (1993) Rote Liste der Pflanzengesellschaften des Naturraumes Wattenmeer unter Berücksichtigung der ungefährdeten Vegetationseinheiten. Tuexenia 13:109–140

Wiedemann AM, Pickart AJ (2004) Temperate zone coastal dunes. In: Martínez ML, Psuty NP (eds) Coastal dunes. Ecological studies, vol 171. Springer, Berlin, pp 53–65

Predicting Plant Distribution Shifts

10

Detlev Metzing and Albrecht Gerlach

Abstract

The effects of climate change on the distribution of vascular plant species characteristic of the marine habitats of German seacoasts were studied. While sea level rise affects plant distribution patterns primarily on a small-scale basis, overall distribution limits are determined mainly by climatic parameters. For several species records from literature and herbaria revealed that their distribution limits shifted within the German coastal area after the end of the nineteenth century. These shifts have been caused primarily by anthropogenic influences (e.g. land use change), but climatic influences must also be considered for some species.

Climatic envelopes were determined based on distribution patterns and climate data. The analysis of distribution patterns and different climatic variables has shown that mean temperatures are the best explanatory factors for the distribution of the species considered. Climate envelopes were used to model potential distribution patterns for recent climate conditions and two climate scenarios. Under a worst-case scenario, the models predict a change in range within the German coastal area for 31% of the species studied ($n = 223$). Depending on the limiting climatic variable (winter or summer temperature), the distribution limits

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for certain species shift either northward or eastward. Climate change will have a significant impact on vascular plant biodiversity in the German coastal area. The projected decline of *Empetrum nigrum*, a keystone species in brown dunes of the islands, will lead to a loss of crowberry heath and a profound change of this dune ecosystem. The possible speed of the migrations depends on the ability of the species to follow the shift in climate boundaries and on whether there is a delay in the response. These effects are not captured by the model and require further research.

A list of indicator species is presented here, which are suitable for detecting a response of plant species to climate change. So far, there are first weak indications (distribution shifts) that can be interpreted as a response of plant species to climate change at the German coast. Monitoring programmes should be established to detect climate change-induced dispersal or decline trends in a timely manner and to achieve a better understanding of climate change impacts on costal biodiversity.

10.1 Introduction

The distribution pattern of the azonal coastal vegetation is mainly formed by edaphic conditions (Sect. 9.1). But climate is also a limiting factor for the distribution of many coastal plants (Packham and Willis 1997; Ranwell 1972; Wiedemann and Pickart 2004). At the coast, distribution boundaries may be more likely correlated with climate than for the inland. Several plant species have a distribution boundary in the German coastal area, e.g. boreal species have their southern boundary here (e.g. *Salix hastata* at Amrum, *Juncus filiformis* at Borkum) and Atlantic and Mediterranean-Atlantic taxa fade away to the north or the northeast (e.g. *Tuberaria guttata* at Norderney, *Alopecurus bulbosus* at the so-called Wurster North Sea coast south of Cuxhaven) (Weeda and Mennema 1983). Because of the relation between climate and plant distribution, the present study concerns the impact of the climate change on the flora and vegetation of the coastal area.

Previous studies about the impact of climate change on the coastal ecosystems focus mainly on the sea level rise, changed flooding events and, therefore, on changes of sedimentation and erosion (Boorman 1992; Dierssen 1993; Dijkema 1992, 1994; Dijkema et al. 1990; Edgerton 1991; Hofstede 1999; Huiskes 1990; Kennedy et al. 2002; McLean and Tsyban 2001; van der Meulen 1990; Neuhaus et al. 1998; Ray et al. 1992; Simas et al. 2001). These indirect effects of climate change affect the distribution patterns of plant species and vegetation on a rather low scale (scale $>10^1$–10^3 m, Metzing 2006). The zonal sequence of species and stands mainly depends on duration and frequency of tidal inundations (Heydemann 1984). Hence, a shift of vegetation zones towards land, in vertical direction to the shoreline, has to be expected. Today, the coasts at the North Sea are largely embanked, and the dikes limit a shift in this direction. This will result in a loss of salt marsh areas (Kennedy et al. 2002; Packham and Willis 1997; Sterr 1996).

Whereas the sea level rise will affect the distribution of the coastal species on a small scale, the climate change caused by the correlation between climate and distribution will shift distribution areas on a large scale (Dahl 1998; Huntley et al. 1995; Jäger 1992; Pearson and Dawson 2003; Woodward 1987) (scale $>10^5$–10^6 m, Metzing 2006). Usually, a northward shift of distribution boundaries is expected due to climate warming (Davis and Zabinski 1992; Gitay et al. 2002; Parmesan 1996). Climate change will have direct consequences by changes of temperature and precipitation. These changes will result in large climatic gradients that affect the species distribution at a supra-regional scale. It may be assumed that despite these effects the main biotope types will remain, although the location patterns will change locally. Hence, these biotopes will maintain as potential habitats of recent flora.

No comprehensive study of the climate change effect on the coastal flora of Germany has been published so far. To study this impact, we have to focus especially on the effects of changing temperatures and precipitation. This contribution concerns the impact of climate change at the distribution areas of vascular plants in coastal habitats. To estimate the impact, we have to answer the following questions:

1. How stable are the distribution boundaries? Are distribution shifts of coastal species evident during the last two centuries?
2. Are climate and distribution patterns correlated?
3. Are observed distribution shifts caused by climate warming?
4. Can we predict changes of the salt marsh and dune flora induced by climate change?
5. Which taxa may serve as indicator species in monitoring programmes?

10.2 Methods

10.2.1 Study Area

The coastal study area considered here includes the salt marshes in the upper parts of the intertidal zone, as well as the beaches and contiguous dune complexes (Fig. 10.1).

10.2.2 Selection of Plant Taxa

223 plant taxa occurring at the German coasts of the North Sea and the Baltic Sea have been chosen (Table 10.1), based on floristic lists for the coast, the Wadden Sea (e.g. Prins et al. 1983), and the Baltic Sea coast (Berg et al. 1996) and other surveys, e.g., Buchenau 1901; Christiansen 1961; Dierssen 1988; Heykena 1965; Kutscher 1995; Pott 1995a, b; Raabe 1981). Taxa restricted to artificial biotopes (e.g. gardens, urban areas) have been excluded. Taxa have been included, if they:

1. are typical species of coastal ecosystems and—at least in Germany—mainly restricted to the coast (e.g. *Atriplex portulacoides*, *Blysmus rufus*, and *Cakile*

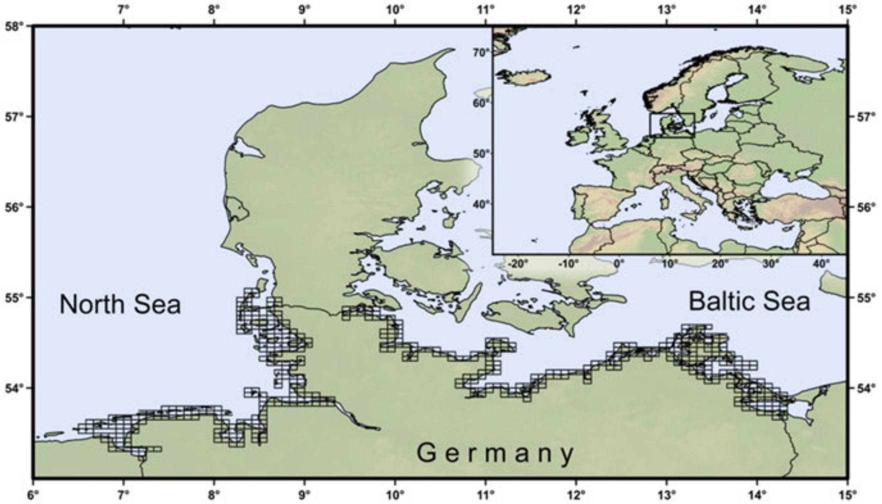

Fig. 10.1 The study area: the coastal area of N-Germany with grid cells of the German ordnance map (MTB) as a spatial basis for the assignment of floristic data

maritima) or occur in some cases in inland salt marshes, too (e.g. *Aster tripolium*, *Salicornia europaea*, *Suaeda maritima*)

2. are not restricted to the coast, but characteristic for maritime plant communities (e.g. *Empetrum nigrum* in the Crowberry heath of the brown dunes, *Corynephorus canescens* in the grassland of grey and brown dunes, *Festuca rubra* in the upper salt marsh)
3. have a distribution limit in the study area or are rare and climatic sensitivity is assumed (e.g. *Bassia hirsuta*, *Rumex longifolius*, *Salix hastata*) (cf. Weeda and Mennema 1983)
4. are important for the morphogenesis of the coastal landscape (e.g. *Ammophila arenaria*, *Festuca rubra*, *Puccinellia maritima*)
5. are neophytes at the coast and have invaded the study area during the last centuries (e.g. *Cotula coronopifolia*, *Senecio vernalis*, *Spartina anglica*)
6. have not or scarcely been reported for the study area, but occur at the coast of adjacent states (e.g. *Crithmum maritimum*, *Beta vulgaris* subsp. *maritima*, *Erica cinerea*).

The number of species was limited to keep the amount of data manageable. The list (Table 10.1) includes not all species occurring in ecosystems of the German seacoasts. However, the selected species are representative for the German coastal flora (cf. Chap. 9).

The historical species distribution patterns have been estimated using more than 400 publications mainly published in the nineteenth century and in the first half of the twentieth century (for full list, see Metzing 2005). Data of herbarium specimens were taken into account for single species as well. As far as possible, the data was

Table 10.1 List of the vascular plant taxa considered for this study, with selected references to occurrences in coastal ecosystems and succession series (according to Metzing 2005, modified)

Taxon	Coastal ecosystems and plant communities	Series
×*Calammophila baltica*	Yellow dunes	Xero
Agrostis stolonifera var. *maritima*	High salt marsh, dune slacks	Halo
Aira caryophyllea	Grey dunes	Xero
Aira praecox	Grey dunes	Xero
Ajuga pyramidalis	Tertiary dunes, dune slacks	Hygro
Allium vineale (*A. kochii*)	Coastal dunes of the Baltic Sea coast	Xero
Alopecurus arundinaceus	Salt marshes, brackish meadows and reeds along the Baltic coast	Halo
Alopecurus bulbosus	High salt marshes of the Weser estuary	Halo
Althaea officinalis	Vegetation of perennial herbs and salt grassland of the Baltic Sea coast	Halo
Ammophila arenaria	Yellow and grey dunes	Xero
Anagallis minima	Dune slacks	Hygro
Anthoxanthum aristatum	Grey dunes	Xero
Anthyllis vulneraria	Coastal dunes, slopes of the Baltic Sea coast	Xero
Apium graveolens	High salt marshes and transition areas between saline and non-saline habitats	Halo
Armeria maritima	High salt marshes	Halo
Arnica montana	Dry heaths and unfertilised grasslands	Xero
Artemisia campestris	Grey dunes, beaches	Xero
Artemisia maritima	High salt marshes	Halo
Aster tripolium	Low to high salt marshes, mud flats	Halo
Atriplex calotheca	Drift lines	Xero
Atriplex glabriuscula	Beaches, sea dunes, and sandy drift lines	Xero
Atriplex laciniata	Beaches and sandy drift lines	Xero
Atriplex littoralis	Low to high salt marsh, drift lines	Xero, Halo
Atriplex longipes	Drift lines	Halo
Atriplex pedunculata	Low to high salt marsh	Halo
Atriplex portulacoides	Low salt marsh	Halo
Atriplex prostrata	Drift lines, low salt marsh	Halo
Bassia hirsuta	Pioneer salt marsh	Halo
Beta vulgaris subsp. *maritima*	Beaches, drift line	Halo, Xero
Betula pubescens	Dune slacks with woods, woodland margins	Hygro
Blysmus rufus	High salt marsh and transition areas to the dunes	Halo
Bolboschoenus maritimus	Salt marshes, brackish swamps	Halo, Hydro
Brassica oleracea	Coastal cliffs, stony beaches	Xero
Bromus thominii	Grey dunes	Xero
Bupleurum tenuissimum	High salt marsh	Halo
Cakile maritima	Beaches, foredunes, and sandy drift lines	Xero

(continued)

Table 10.1 (continued)

Taxon	Coastal ecosystems and plant communities	Series
Calluna vulgaris	Dry heaths of tertiary dunes, unfertilized grasslands, pine woods (Baltic Sea coast)	Hygro, Xero
Calystegia soldanella	Yellow dunes, sandy drift lines	Xero
Carex arenaria	Grey dunes	Xero
Carex distans	High salt marsh	Halo
Carex extensa	Sandy high salt marsh	Halo
Carex flacca	Dune slacks, salt marshes	Hygro
Carex pulicaris	Dune slacks	Hygro
Carex punctata	Sandy high salt marsh	Halo
Carex trinervis	Dune slacks	Hygro
Carum carvi	High salt and brackish marshes	Halo
Centaurium erythraea	Dunes	Xero
Centaurium littorale	Salt marshes, dune slacks	Halo, Hygro
Centaurium pulchellum	Salt marshes, dune slacks	Halo, Hygro
Cerastium diffusum	Grey dunes	Hygro, Xero
Chenopodium foliosum	Grey dunes	Xero
Chenopodium rubrum	Drift lines, salt marshes	Halo, Xero
Cirsium arvense	Highest salt marsh, dunes	Halo, Xero
Cladium mariscus	Reeds	Hydro
Claytonia perfoliata	Dune shrubs	Xero
Cochlearia anglica	Low to high salt marsh	Halo
Cochlearia danica	High salt marsh	Halo
Cochlearia officinalis	High salt marsh	Halo
Corispermum leptopterum	Beaches, dunes	Xero
Coronopus squamatus	High salt marsh	Halo
Corynephorus canescens	Grey and brown dunes	Xero
Cotula coronopifolia	High salt marsh	Halo
Crambe maritima	Beaches, drift lines	Xero
Crithmum maritimum	Drift lines, beaches, cliffs	Xero
Cynodon dactylon	Ruderal dune areas	Xero
Deschampsia flexuosa	Old dunes, dune woods	Xero
Dianthus carthusianorum	Grey dunes	Xero
Dianthus deltoides	Heaths, dry grassland	Xero
Eleocharis parvula	Brackish swamps	Hydro
Eleocharis uniglumis	Salt marshes, brackish swamps	Hygro
Elymus athericus	High salt marshes	Halo, Xero
Elymus farctus	Primary dunes	Xero

(continued)

Table 10.1 (continued)

Taxon	Coastal ecosystems and plant communities	Series
Elymus repens	High salt marsh, grey dunes, beaches	Halo, Xero
Empetrum nigrum	Brown dunes, pine forests	Xero
Epilobium angustifolium	Grey dunes	Xero
Epipactis atrorubens	Dune slacks	Hygro
Epipactis palustris	Dune slacks	Hygro
Erica cinerea	Brown dunes	Xero
Erica tetralix	Dune slacks	Hygro
Erodium ballii	Grey dunes	Xero
Erodium danicum	Dunes (?)	Xero (?)
Erodium lebelii	Grey dunes, dry grassland	Xero
Eryngium maritimum	Beaches, sandy drift lines, yellow dunes	Xero
Euphrasia micrantha	Grey dunes	Xero
Euphrasia stricta	Grey dunes, dune slacks	Hygro, Xero
Festuca polesica	Dunes of the Baltic Sea coast, dry grassland	Xero
Festuca rubra	Yellow to grey dunes, high salt marshes	Halo, Xero
Filago arvensis	Grey dunes, sandy grassland	Xero
Filago minima	Grey dunes, shingles	Xero
Galium mollugo	Grey dunes	Xero
Galium sterneri	Grey dunes	Xero
Galium verum	Grey and brown dunes	Xero
Genista anglica	Dry heaths	Xero
Genista germanica	Dry heaths	Xero
Genista pilosa	Dry heaths	Xero
Genista tinctoria	Dry heaths, dune slacks	Hygro, Xero
Gentianella campestris subsp. *baltica*	Dune heath, dry coastal grassland	Xero
Gentianella campestris. subsp. *campestris*	Dune slacks	Hygro
Gentianella uliginosa	Dune slacks, depressions at shingle beaches of the Baltic Sea coast	Hygro
Glaucium flavum	Beaches and shingles, sandy drift lines	Xero
Glaux maritima	High salt marshes, primary dunes	Halo, Hygro
Hieracium umbellatum	Grey dunes	Xero
Hippophae rhamnoides	Dune shrubs	Xero
Hippuris vulgaris	Brackish waters, dune slacks	Hygro, Hydro
Honckenya peploides	Beaches, sandy drift lines, shingles	Xero
Hordeum marinum	High salt marshes	Halo
Hordeum secalinum	Brackish grassland, pastures	Halo

(continued)

Table 10.1 (continued)

Taxon	Coastal ecosystems and plant communities	Series
Ilex aquifolium	Coastal woods	Xero
Jasione montana	Grey dunes	Xero
Juncus anceps	High salt marshes, dune slacks	Halo, Hygro
Juncus balticus	Dune slacks	Hygro
Juncus bufonius (incl. *J. ranarius*)	Sandy salt marshes, dune slacks	Halo, Hygro
Juncus gerardii	High salt marshes	Halo
Juncus maritimus	High salt marshes, brackish dune slacks	Halo
Juncus pygmaeus	Dune slacks	Hygro
Koeleria arenaria	Grey dunes, dry grassland	Xero
Lactuca tatarica	Beaches, primary and secondary dunes, sandy drift lines	Xero
Lathyrus japonicus	Yellow dunes, young grey dunes	Xero
Leontodon autumnalis	High salt marshes	Halo
Leontodon saxatilis	Grey dunes	Xero
Leymus arenarius	Yellow dunes	Xero
Limonium vulgare	High salt marshes	Halo
Linnaea borealis	Dune slacks, dune woods	Hygro
Linum catharticum	Dune slacks	Hygro
Liparis loeselii	Dune slacks	Hygro
Listera cordata	Dune slacks, dune woods	Hygro
Listera ovata	Brushwood near the coast, wet meadows	
Littorella uniflora	Wet dune slacks	Hygro
Lotus corniculatus	Shingles, grey dunes	Halo, Xero
Lotus tenuis	High salt marshes	Halo
Lycium barbarum	Dune shrubs	Xero
Melilotus dentatus	Brackish grassland, reeds	Halo
Myosotis stricta	Grey dunes	Xero
Myrica gale	Dune slacks	Hygro
Najas marina	Brackish waters	Hydro
Odontites litoralis	High salt marshes	Halo
Oenanthe lachenalii	Reeds, high salt marsh, coastal grassland	Halo
Oenothera ammophila (*O. oakesiana*)	Yellow dunes	Xero
Ononis spinosa	Shingles, high salt marshes	Halo, Xero
Ophioglossum vulgatum	Dune slacks	Hygro
Parapholis strigosa	High salt marshes	Halo
Parnassia palustris	Grey dunes, dune slacks	Hygro
Pedicularis sylvatica	Dune slacks	Hygro
Petasites spurius	Yellow dunes, steep banks	Xero
Phalaris arundinacea	Brackish reeds and swamps	Hydro

(continued)

Table 10.1 (continued)

Taxon	Coastal ecosystems and plant communities	Series
Phleum arenarium	Yellow and grey dunes	Xero
Phragmites australis	High salt marshes, brackish reeds	Halo, Hygro
Pimpinella saxifraga	Shingles, steep banks	Xero
Plantago coronopus	High salt marsh, transition zone to the dunes	Halo
Plantago major subsp. *winteri*	High salt marsh	Halo
Plantago maritima	Low to high salt marsh	Halo
Polygala vulgaris	Grey dunes	Xero
Polygonum oxyspermum. subsp. *oxyspermum*	Shingles, sandy drift lines	Xero
Polygonum oxyspermum subsp. *raii*	Shingles, sandy drift lines	Xero
Polypodium interjectum	Old dunes	Xero?
Polypodium vulgare	Brown dunes, dune pine forests	Xero
Potamogeton filiformis	Brackish waters	Hydro
Potentilla anserina	Drift lines, dune slacks, periodically inundated grassland	Halo
Puccinellia capillaris	High salt marshes	Halo
Puccinellia distans	Disturbed high salt marsh	Halo
Puccinellia maritima	Low salt marsh	Halo
Pyrola minor	Dune slacks, dune woods	Hygro
Pyrola rotundifolia	Dune slacks, dune woods, beech woods of the Baltic Sea coast	Hygro
Radiola linoides	Dune slacks	Hygro
Ranunculus peltatus subsp. *baudotii*	Brackish waters	Hydro
Ranunculus sardous	Brackish pastures	Halo
Rhinanthus angustifolius	Dunes	Xero
Rosa mollis	Shingle shrubs	Xero
Rosa rugosa	Dune shrubs	Xero
Rosa spinosissima	Dune shrubs	Xero
Rubus caesius	Grey dunes	Xero
Rumex crispus	Shingles, sandy drift lines	Xero
Rumex longifolius	Ruderal sites (now extinct at the German coast)	Anthropo
Ruppia cirrhosa	Brackish waters	Hydro
Ruppia maritima	Brackish waters	Hydro
Sagina maritima	Sandy high salt marsh	Halo
Sagina nodosa	Dune slacks	Hygro
Sagina subulata	Dune slacks	Hygro
Salicornia europaea	Pioneer and low salt marsh, depressions in high salt marsh	Halo
Salicornia stricta	Pioneer salt and low marsh	Halo
Salix cinerea	Dune shrubs	Hygro

(continued)

Table 10.1 (continued)

Taxon	Coastal ecosystems and plant communities	Series
Salix daphnoides	Dunes (mostly planted)	Xero
Salix hastata	Dune slacks	Hygro
Salix pentandra	Dune slacks, dune woods	Hygro
Salix repens	Shingle shrubs, dune shrubs	Xero, Hygro
Salsola kali kali	Sandy drift lines, beaches	Xero
Sambucus nigra	Dune shrubs	Xero
Samolus valerandi	Dune slacks	Hygro
Saxifraga tridactylites	Grey dunes, shingles	Xero
Schoenoplectus pungens	Brackish reeds and swamps	Hydro
Schoenoplectus triqueter	Brackish reeds and swamps	Hygro
Schoenus nigricans	Dune slacks	Hygro
Scorzonera humilis	Dry heath, grey dune	Xero
Senecio jacobaea	Yellow and grey dunes, steep banks	Xero
Senecio vernalis	Yellow and grey dunes	Xero
Silene otites	Grey dunes	Xero
Silene viscosa	Yellow and grey dunes	Xero
Sonchus arvensis	High salt marshes, yellow dunes	Halo, Xero
Spartina anglica	Pioneer and low salt marshes	Halo
Spergularia media	Low to high salt marshes	Halo
Spergularia salina	Low to high salt marshes	Halo
Stellaria crassifolia	High salt marshes	Halo
Suaeda maritima	Pioneer and low salt marshes, drift lines, salt pans	Halo
Tetragonolobus maritimus	High salt marshes	Halo
Trifolium campestre	Shingles, grey dunes, steep banks	Xero
Trifolium fragiferum	High salt marshes	Halo, Hygro
Trifolium ornithopodioides	Dike slopes	
Trifolium pratense subsp. *maritimum*	Shingles, dunes, steep banks	Xero
Trifolium repens	High salt marshes	Halo
Triglochin maritima	Low to high salt marshes	Halo
Tripleurospermum maritimum	Drift lines	Halo
Tuberaria guttata	Grey dunes	Xero
Tussilago farfara	Dikes, dune slacks, sandy and loamy steep banks	Hygro, Xero
Ulex europaeus	Grey dunes, steep banks	Xero
Vaccinium uliginosum	Dune slacks	Hygro
Vaccinium vitis-idaea	Dune heath, dune pine forests	Xero
Veronica officinalis	Shingles, grey dunes, dry heath	Xero
Vicia lathyroides	Shingles, grey dunes, dry grassland	Xero
Viola canina	Grey dunes, dune slacks	

(continued)

Table 10.1 (continued)

Taxon	Coastal ecosystems and plant communities	Series
		Hygro, Xero
Viola tricolor var. *maritima*	Grey dunes, yellow dunes	Xero
Zannichellia palustris	Brackish waters	Hydro
Zostera marina	Tidal flats	Halo
Zostera noltii	Tidal flats	Halo

Halo Halosere, *Hydro* Hydrosere, *Hygro* Hygrosere, *Xero* Xerosere; see Sect. 9.2

assigned to corresponding grid squares of the German ordnance maps (the so-called Messtischblätter, MTB) (Fig. 10.1), and to single years (resp. to 30-year periods). Maps were produced from these records documenting the first occurrence at the German coast.

Distribution data for parts of the German coast have been already published by several floristic projects (e.g. Prins et al. 1983: Wadden Sea, Haeupler and Schönfelder 1988: Federal Republic of Germany, Benkert et al. 1996: E-Germany, Garve 1994: Lower Saxony (threatened species), Dierssen and Mierwald 1987: Schleswig-Holstein). The data for Germany has been joined into the FlorKart database by the Federal Agency for Nature Conservation (Bundesamt für Naturschutz, BfN, Bonn). The BfN kindly provided records from this database (as of 1999, cf. www.floraweb.de) for this study. (In the meantime, updated distribution atlases for Lower Saxony (Garve 2007) and Germany (Bettinger et al. 2013) have been published.)

We used the floristic data of all grid cells, which adjoin the coastline (Fig. 10.1). These grid cells may enclose a larger area than the coastal area as defined narrowly by Valentin (1954).

10.2.3 Preparation of Ecograms

Climate and distribution were correlated considering the distribution ranges on a European scale (with adjacent areas; 25° W to 45° E and 30° N to 75° N; Fig. 10.1, inlet). This was assumed to be sufficient for the analysis of climatic factors, which limit the distribution areas.

Distribution data for the selected taxa has been taken from Hulten and Fries (1986); Jalas and Suominen (1986); (Jalas et al. 1999); Meusel et al. (1965); Meusel and Jäger (1978, 1992); and the programme “Atlas Florae Europaeae” (Jalas et al. 1999). Additional data for sub-areas came from Fitter (1978); Fitter et al. (1984); Gibbons and Brough (1998); Mossberg et al. (1992) and many further papers (for a complete list, see Metzing 2005). For a few taxa, only general information about their distribution was available (e.g. from Tutin et al. 1964, 1968, 1972, 1976, 1980), but no distribution maps.

Numerous climatic parameters are available to analyse the relation between climate and distribution ranges: temperature (mean temperature, maximum temperature, minimum temperature, diurnal range, temperature sums, and thermic continentality, a. o.), moisture (precipitation, aridity, and hygric continentality, a. o.), and radiation, wind speed, and vapour pressure. It was evident from previous studies that temperature and precipitation are the major factors to explain the plant distribution patterns on a continental scale (Dahl 1998; Jäger 1992; Jeffree and Jeffree 1994). Thus, it makes sense to reduce the variables to avoid redundancies and minimise the amount of data in the analysis.

Based on the digital climate and distribution maps, we scrutinised the relevance of temperature and moisture indices in a correspondence analysis (DCCA). In this direct gradient, analyses of the single taxa were arranged according to their biogeographic similarity along the climatic gradients. Gradients closely correlated with the first and second axis are most significant (ter Braak and Šmilauer 1998).

Climate data was obtained from the IPCC-Data Distribution Centre (IPCC-DDC 1999, for dataset construction, see New et al. 1999) for the period 1961–1990 with a spatial resolution of 0.5° (an area of about 32 × 55 km in the study area). Continentality, aridity, annual mean values, a. o. were calculated from the original data. The relevance of climatic factors was tested by a DCCA with the programme CANOCO 4 (ter Braak and Šmilauer 1998).

Two scenarios are used to predict the dislocation of distribution areas, which are based on the global model ECHAM4/OPYC3, and have been regionalised by statistical downscaling for the German coasts by von Storch et al. (1998) (cf. Chap. 2).

The distribution areas (for the area 25° W to 45° E and 30° N to 75° N) of the selected taxa were digitised and transferred to a geographic information system (software: IDRISI, Clark Labs, Worcester, USA) to analyse the relation to climatic data.

10.2.4 Preparation of Climate Envelope Models

Current and future distribution areas of selected species have been modelled on the base of the climate envelopes calculated from climate data and present distribution ranges (see Sect. 10.2.4). The data has been transferred from distribution maps made in a GIS (IDRISI, Clark Labs) using present climate data and the climate scenarios.

The values of relative and absolute frequency usually show a non-normal distribution with skewness or a bimodal distribution (cf. Fig. 10.13). Several influences, e.g., distribution history, competition, interaction of different factors, and less precise floristic data, are reasons for this non-normal distribution. Hence, models have to be calibrated for each taxon individually, after the first runs with specific statistic values as minima, maxima, or quartiles. Besides calculation of the Kappa index (Sachs 2004), a visual verification was used to check and optimise the quality of the modelled ranges for the single taxa (comparison of real and modelled distribution patterns). For this procedure, the spatial overlay of distinct climatic ranges has been plotted.

The different relevancies of the three used temperature parameters at the range boundaries of *Ilex aquifolium* are shown in Fig. 10.2. The areas, which fit the realised

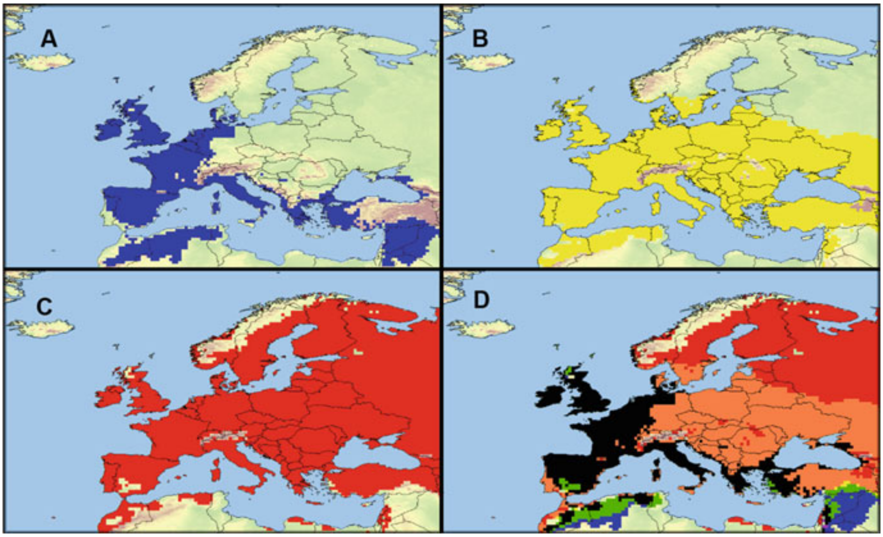

Fig. 10.2 Spatial overlay of climatic niche dimensions for Holly, *Ilex aquifolium*. The overlay of T_{Jan} (blue, (**a**)), T_{Jul} (red, (**c**)), and T_{Year} (yellow, (**b**)) results in the potential species area (= climate envelope, black, (**d**)). For further explanations, see text

climatic niche dimensions of the species for T_{Jan}, $T_{Jul,}$ and T_{Year}, are drawn in black. Blue areas only equal the species niche dimension of the January temperature, blue areas that of the July temperature, and yellow areas that of the annual temperature. In green, violet, or orange areas, two of the three thermic parameters are in concordance with the species niche. It is obvious that the distribution range of *Ilex aquifolium* is mainly limited by the winter temperature (the climate envelope is highly correlated to the mean temperature of January).

The recent and modelled distribution ranges of *Ilex aquifolium*, based on the climatic envelope for three thermic parameters (mean temperature for January, July, and year), are shown in Fig. 10.3. In Fig. 10.4, the factor precipitation (left column: precipitation in July; right column: annual precipitation) is additionally included. The differences of the modelled distribution areas with or without included precipitation turned out to be negligible for the Central European area. From other species ranges, similar results have been gained. As the number of parameters in the model should be as low as possible, only the three temperature variables have been used in the further study. Inland areas have been excluded in the model output for species strictly limited to coastal habitats.

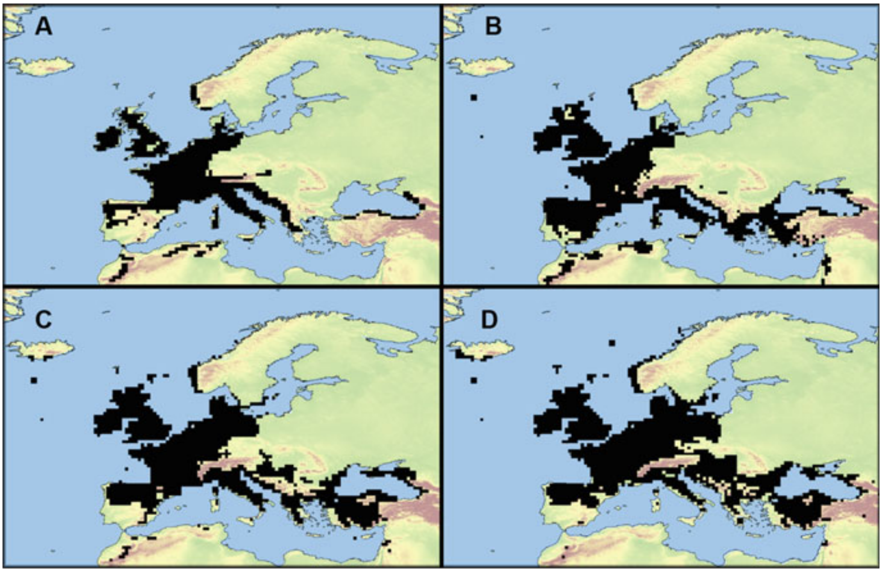

Fig. 10.3 (**a**) Distribution range of *Ilex aquifolium* in Europe, (**b**) modelled species range (climatic envelope shape for T_{Jan}, $T_{Jul,}$ and T_{Year}) for different scenarios: present climate, (**c**) best-case scenario, and (**d**) worst-case scenario

10.3 Historical Changes in Plant Distribution

As the number of plant species in the coastal ecosystems is high, the historical distribution process is illustrated exemplarily only for the three species *Calystegia soldanella* (Figs. 10.5 and 10.6), *Empetrum nigrum* (Fig. 10.7), and *Hippophae rhamnoides* (Fig. 10.8).

The occurrence of *Calystegia soldanella* in Germany is restricted to the North Sea coast (Fig. 10.5). The species has been found within the last two centuries on all East Frisian Islands and on Northern Friesland islands with a Pleistocene core. At the west coast of Schleswig-Holstein, it was firstly recorded from the early twentieth century (cf. Tables 10.2 and 10.3). But in some cases, the species was present only for a short time. However, for the scope of this study the expansion of the distribution area at certain times is more important than the lasting time of occurrence. This is evident for this species, which dispersed to the north in the last century.

Interpretation of the data suffers under a spatial fuzziness of the results, caused by the used fine grid size. In many cases, the spatial information cannot be assigned to a particular grid cell, but to a geographic region only. In best cases, records are assigned to distinct entities, i.e., islands. In worst cases, they only noted “coast” or a particular study area. Elimination of this data would cause a loss of information, whereas the inclusion would result in a more general pattern. The latter case may

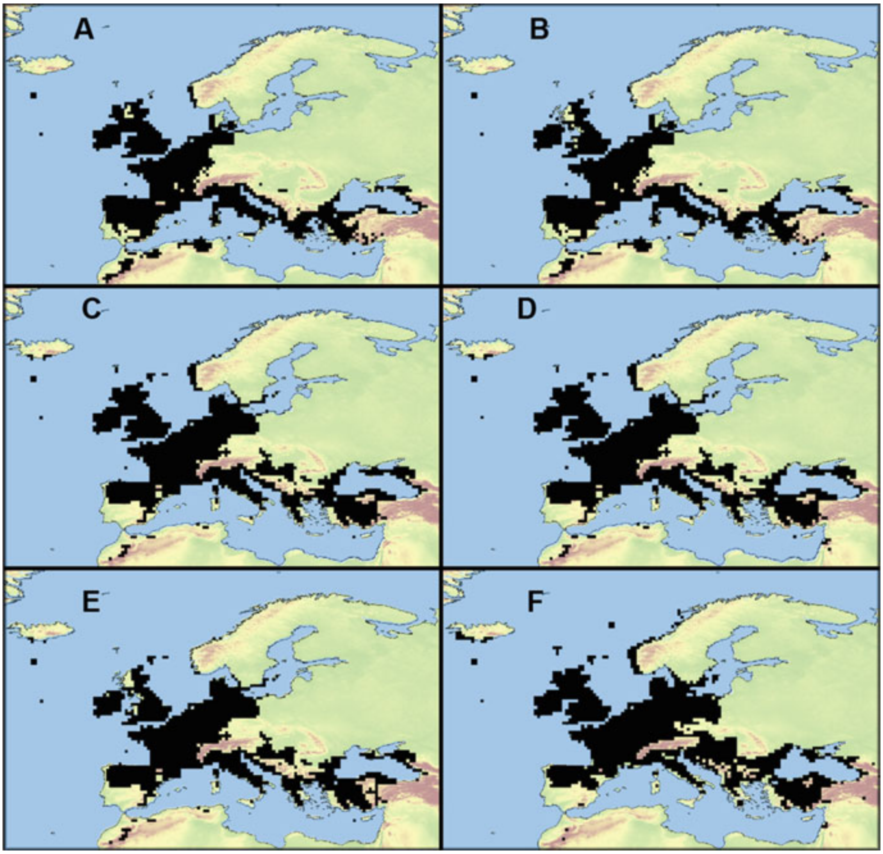

Fig. 10.4 Modelled species range of *Ilex aquifolium* in Europe with precipitation. (**a, c, e**) climatic envelope shape for T_{Jan}, T_{Jul}, T_{Year}, and P_{Jul}, (**b, d, f**) climatic envelope shape for T_{Jan}, T_{Jul}, T_{Year}, and P_{Year} for different scenarios: present climate (**a, b**), best-case scenario (**c, d**), and worst-case scenario (**e, f**)

imply that a species is generally present in a large area, e.g., *Empetrum nigrum* (Fig. 10.6). For the Baltic Sea coast, the data of this species is based mainly on data of Christiansen (1953), who used a coarser grid size than used in the present study. The transfer to the more detailed grid simulates occurrences where the species was not present, which becomes evident if they are compared with the data of the BfN (Fig. 10.8). The greater part of the entries for the coast of Mecklenburg-Vorpommern originates from findings after 1950 by Benkert et al. (1996). It is assumed that the species were present in many grid cells before 1950, which, however, cannot be verified by the data found in literature or herbarium data. In the case of *Hippophae rhamnoides,* the problem of imprecise data becomes even more obvious (Fig. 10.7). The map for *Hippophae rhamnoides* gives the impression that the species is generally distributed along the Baltic Sea coast. This

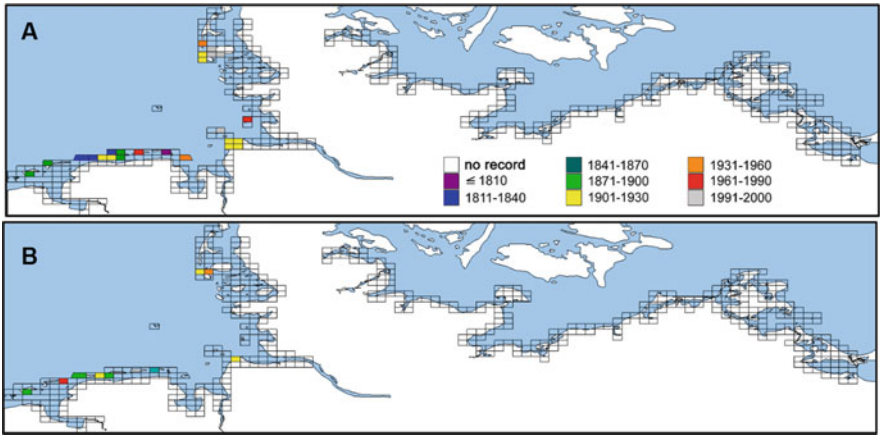

Fig. 10.5 First records of *Calystegia soldanella* according to (**a**) literature and (**b**) herbarium samples

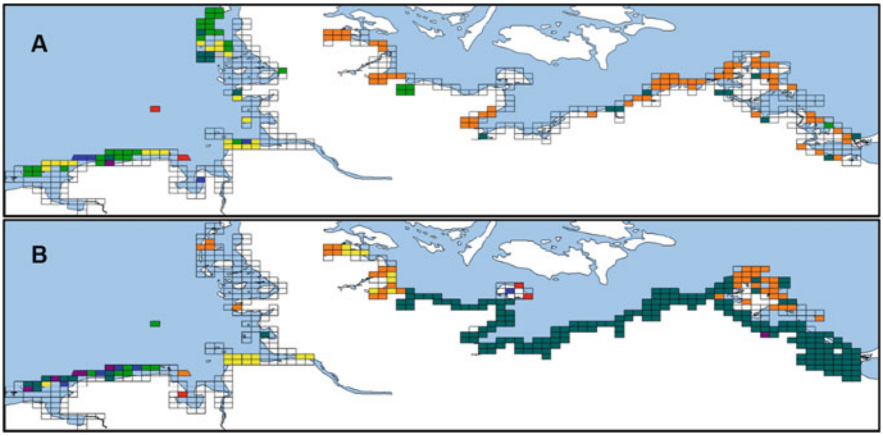

Fig. 10.6 First records of (**a**) *Empetrum nigrum* and (**b**) *Hippophae rhamnoides* according to the literature. For colours, see Fig. 10.5

is caused using the quite general information according to Boll (1848), who stated that the species could be found between the Kieler Förde (Bay of Kiel) and Breitling "auf lehmhaltigeren Stellen des Strandes [at more loamy sites of the beach]". Although the species is not rare in this part of the coast, the map simulates a higher frequency than can be derived from the distribution of loamy grounds in the same part (Fig. 10.9).

For the purpose of this study, it is sufficient to subsume the findings for larger geographical areas (Fig. 10.8) and time periods to detect regressive or progressive shifts of particular species. But it has to be stressed that the maps do not reflect

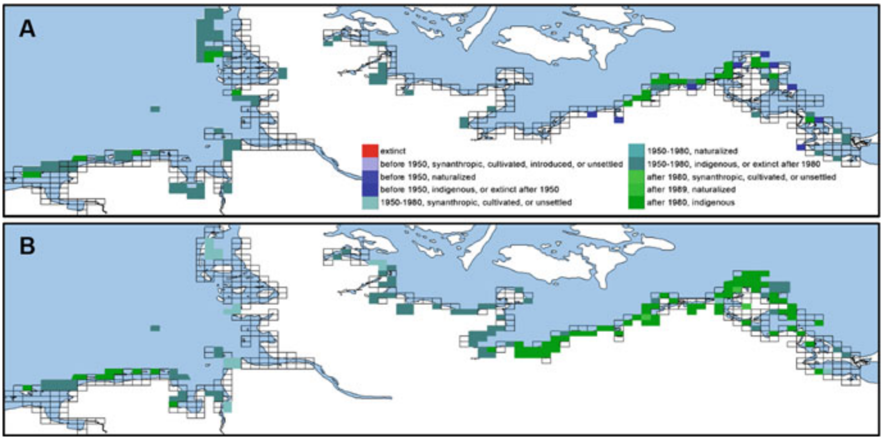

Fig. 10.7 Distribution of (**a**) *Empetrum nigrum* and (**b**) *Hippophae rhamnoides* at the German coast (database: BfN 1999)

Fig. 10.8 Areas considered for the graphic illustration of first records. *Am* Amrum, *Ba* Baltrum, *Bo* Borkum, *Fe* Fehmarn, *Fö* Föhr, *H* Helgoland, *Ju* Juist, *La* Langeoog, *Ls* Langeneß, *Me* Mellum, *Mv* Mecklenburg-Vorpommern (coastal area), *Nd* Nordstrand, *NL* The Netherlands, *No* Norderney, *Ns* Lower Saxony (coastal area), *Nw* Neuwerk, *Pe* Pellworm, *Rü* Rügen, *So* Schleswig-Holstein (east coast), *Sp* Spiekeroog, *Sw* Schleswig-Holstein (west coast), *Sy* Sylt, *Tr* Trischen, *Us* Usedom, *Wa* Wangerooge

the same accuracy as dot maps made by recent and standardised mapping projects. The difference between the grid maps and the subsumed maps is demonstrated for the examples given in Figs. 10.6, 10.7, and 10.9.

Plant taxa with an enlarged distribution range within the German coastal area found by the compilation of published records are listed in Table 10.3.

Table 10.2 First records of *Calystegia soldanella* at the coast of Northwest Germany

Locality	First record	Reference	First herbarium specimen
Borkum	1879	Häpke (1880)	Wolde-dunes, L. Häpke, 1879 (BREM)
Juist	1881	Buchenau (1881)	NW of airfield, H. Kuhbier, 1987 (BREM)
Norderney	1824	Meyer (1824)	s. l., R. Bielefeld, 1898 (BREM)
Baltrum	1908	Leege (1908)	s. l., Behrends and Schatteburg, 1912 (BREM)
Langeoog	1890	Buchenau (1891)	Westende, Kossenhaschen, 1890 (BREM)
Spiekeroog	1986	Garve (1994)	
Wangerooge	1737	Meyer (1824)	s. l., Kellner, 1842 (BREM)
Mellum	1948	Tabken (1960)	
Scharhörn	2000	Hellwig and Kuhbier (2000)	
Neuwerk	1982?	Mang (1982) [at Neuwerk/Scharhörn only as "extinct"]	
Cuxhaven	1905	Junge (1913)	Between Duhnen and Arensch, J. Schmidt, 1905 (HBG)
Amrum	1905	Junge (1913) [according to Christiansen (1949) already found in 1904]	Norddorf, P. Junge, 1902 (HBG)
Sylt	1949	Christiansen (1953)	

10.4 Climate and Plant Distribution: Ecograms

10.4.1 Climate Key Variables

The graphs (Figs. 10.10, 10.11, and 10.12) show the ordination of distribution areas for 115 plant taxa and 43 climatic variables (Detrended Canonical Correspondence Analysis, DCCA). The variables of temperature are orientated along a convex line, positively related to the first axis, which indicates a good explanation of the distribution patterns. The mean temperatures of January and July are orientated opposite to the first axis, caused by the low correlation between winter and summer temperatures (in summer the main temperature gradient in Europe runs from north to the south, whereas in winter it is orientated from east to west, Metzing and Gerlach 2001). The coldness variables (number of frost days) are orientated contrary to the temperatures: the higher the mean temperature of a specific area, the lower the number of frost days.

The variables of precipitation are arranged along an oval (Fig. 10.11). The variables for the precipitation of summer and winter are orientated in opposition to

Table 10.3 List of taxa that have been mainly found at parts of the German coast after the end of the nineteenth century

Taxon	Comment
Alopecurus bulbosus	Weser estuary: documented since 1898 (Plettke 1903); neglected previously?
Artemisia campestris	North Sea coast: after 1931, but disappeared mostly afterwards (von der Ende 1995; Garve 1994)
Atriplex calotheca	West coast of Schleswig-Holstein: after 1900, but according to Garve (1982), the taxon has been misinterpreted here
Atriplex longipes	East Frisian Islands: after 1949, but perhaps overlooked previously (Garve 1982)
Calystegia soldanella	West coast of Schleswig-Holstein: since 1904 (Christiansen 1949), but only sporadic present
Corispermum leptopterum	Coast of the North Sea and the Baltic Sea: after 1910 (Köck 1986; Lohmeyer and Sukopp 1992), neophyte
Crithmum maritimum	Helgoland: 1935 (Kremer and Wagner 2001; Panknin 1937), since 2000 persistent population
Cynodon dactylon	East Frisian Islands (Spiekeroog): after 1980 documented and persistent (Lienenbecker 2004)
Dianthus deltoides	Islands of the Wadden Sea: after 1949 (Weeda and Mennema 1983)
Euphrasia micrantha	North Frisian Islands: after 1906 (Christiansen 1961), misjudged or overlooked previously (Dierssen and Mierwald 1987)?
Galium sterneri	North Frisian Islands (Sylt): the species has been described firstly in 1960 (cf. Wisskirchen and Haeupler 1998)
Glaucium flavum	North Sea coast: more frequent since the 1980s (Borcherding 1999)
Ilex aquifolium	East Frisian Islands: after 1933, occasionally planted (Leege 1937)
Juncus anceps	Baltic Sea coast (N Stralsund) (Hobohm 1995)
Juncus maritimus	West coast of Schleswig-Holstein: after 1935 (Hobohm 1986; Metzing and Gerlach 2001; Raabe 1970)
Lactuca tatarica	Baltic Sea coast: since 1902; North Sea coast: after 1947 (Knapp and Jage 1978), neophyte (Lohmeyer and Sukopp 1992)
Linnaea borealis	East Frisian Islands: after 1930; North Frisian Islands: only temporary; probably introduced with material for afforestations (cf. Bielefeld 1900; Türk 1994)?
Oenothera ammophila (*O. oakesiana*)	North Sea coast: after 1905, firstly described as species in 1905. Probably confused with *Oenothera* taxa previously (van Dieren 1934)
Polygonum oxyspermum subsp. *oxyspermum*	East coast of Schleswig-Holstein: since 1971 (Eigner 1972), according to Dierssen and Mierwald (1987) rare there, but native
Polygonum oxyspermum subsp. *raii*	North Sea coast: since 1960 (Christiansen 1961), according to Dierssen and Mierwald (1987) rare there, but native
Puccinellia capillaris	North Frisian Islands: since 1951, probably present there previously but interpreted as *Puccinellia distans* or *P. retroflexa* (Christiansen 1961; Dierssen and Mierwald 1987)

(continued)

Table 10.3 (continued)

Taxon	Comment
Salicornia spp.	North Sea coast: the spread of some *Salicornia* taxa is certainly delusive, caused by taxonomic problems and changed interpretations.Baltic Sea coast (Greifswald): *Salicornia stricta* 1999 (Blümel et al. 1999) singular occurrence?
Salix daphnoides	North Sea coast: after 1900 probably only synanthropic (planted) (Haeupler and Muer 2000)
Senecio vernalis	North Sea coast: since 1930, neophyte (Lohmeyer and Sukopp 1992)
Spartina anglica	North Sea coast: since 1927, introduced and planted for coastal defence purposes (König 1948; Reise 1994; Tabken 1951)

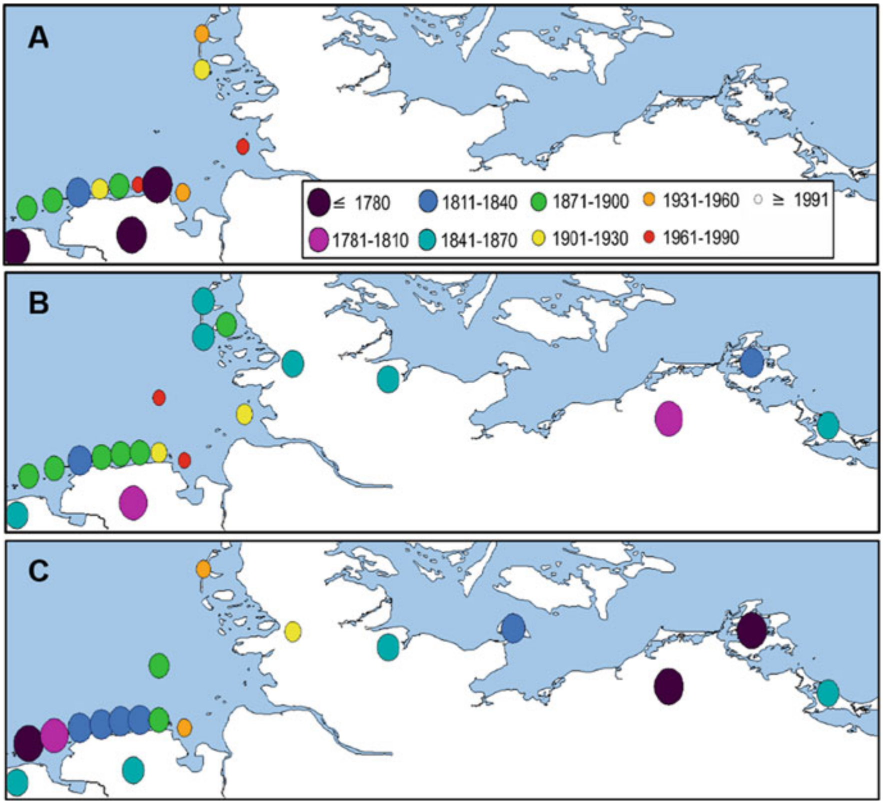

Fig. 10.9 First records of (**a**) *Calystegia soldanella*, (**b**) *Empetrum nigrum*, and (**c**) *Hippophae rhamnoides* according to data from literature

the central variable of annual mean precipitation. The precipitation pattern is not homogeneous for Europe; in both the north and Mediterranean regions, rainfall is highest in summer and winter, respectively: the higher the mean annual temperature, the higher the maximum of winter precipitation.

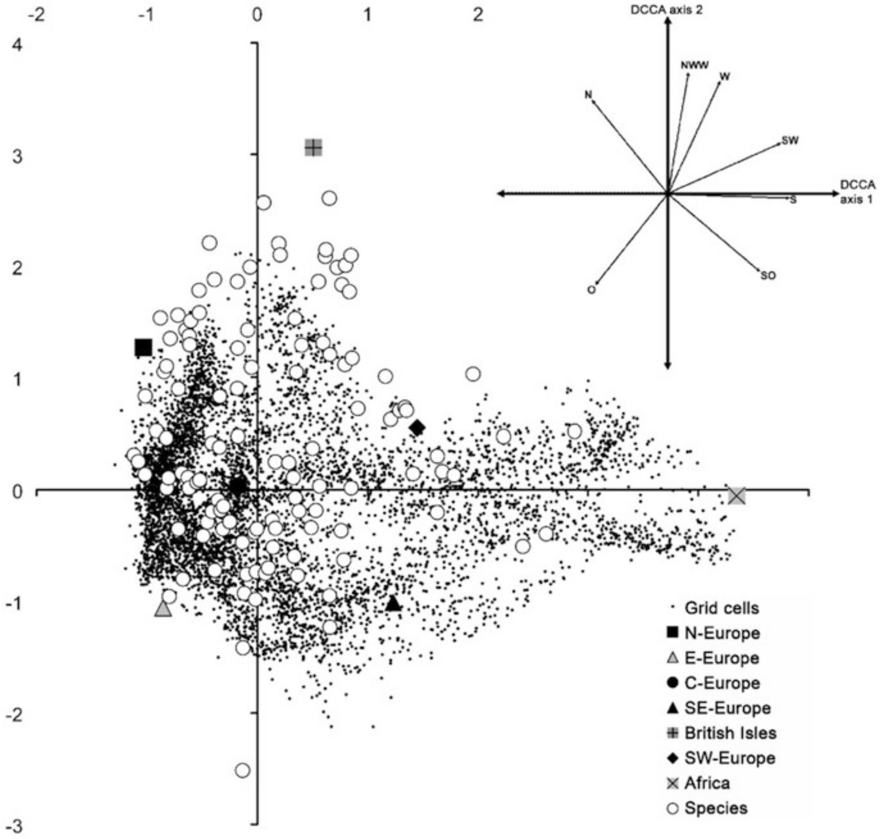

Fig. 10.10 Ordination diagram of a Detrended Canonical Correspondence analysis (DCCA) for distribution areas of 115 plant taxa and 43 climatic variables. The ordination of geographic grid cells (small points) and geographic areas is plotted. The inlay (top right) illustrates the extrapolated geographic orientation

The variables of the diurnal range of temperature form a separate group with a vague correlation to the mean summer temperatures. The variables for continentality, represented by the annual temperature range and the indices according to Conrad (1946, thermic sentimentality) and Henze (1929, hygric continentality), are orientated in eastward direction (Fig. 10.10 top right), opposite to precipitation maxima in winter.

The correspondence analysis supports the high correlation of temperatures and distribution patterns, which is less distinct for precipitation. Therefore, we choose the temperature variables T_{Jan}, T_{Jul}, T_{Year} (mean temperatures for January, July, year and P_{Year} (mean annual precipitation) for further analyses (ecograms, models).

These variables often have been used for climatic characterisation in other studies (e.g. Hoffmann 2000; Jackson and Overpeck 2000; Jeffree and Jeffree 1994, 1996).

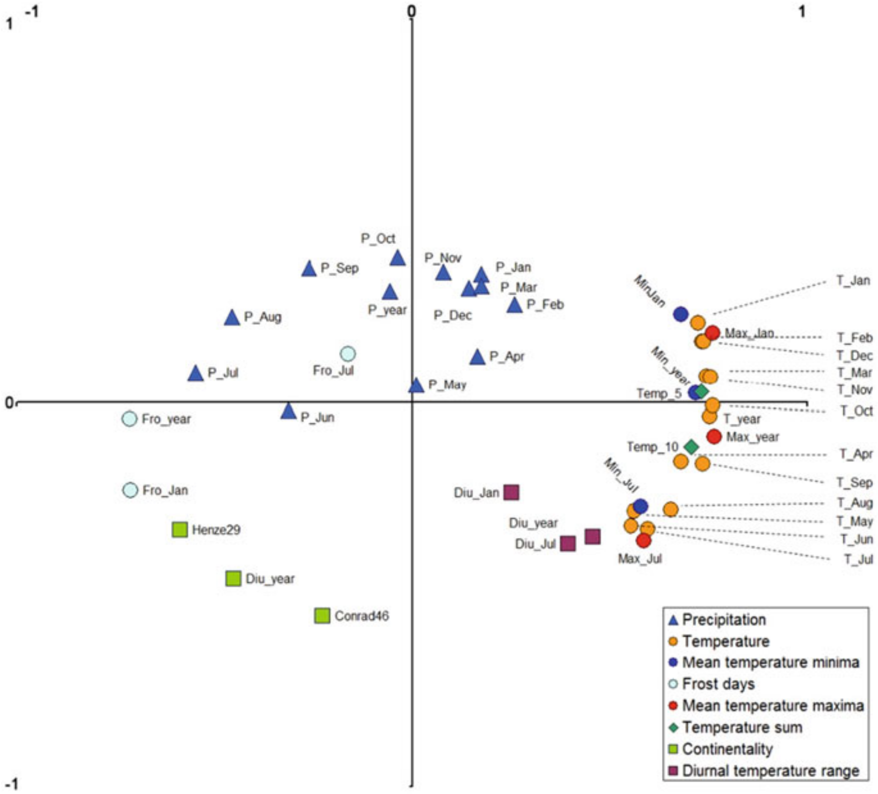

Fig. 10.11 Results of the Detrended Canonical Correspondence Analysis (DCCA) for distribution areas of 115 plant taxa and 43 climatic variables (cf. Fig. 10.10). The climate variables for the ordination of geographic grid cells (small points) and geographic areas are plotted. The trend arrows of the gradients have been omitted for clearness of the graph

At the same time, these temperature variables represent the annual temperature regime. The combination of January and July temperatures includes the factor thermic continentality, defined by a high annual temperature range.

If other climatic variables are included in the analysis, the results did not change or revealed high accuracy (Table 10.4 and Fig. 10.4).

The correlations between arranged plant taxa and climate variables for the European area show the preferences of single taxa. Continentally distributed species are, e.g., *Lactuca tatarica*, *Petasites spurius*, and *Melilotus dentatus*. Atlantic species, such as *Erica cinerea*, *Myrica gale,* and *Ulex europaeus*, are arranged to the top of the DCCA graph, in direction of higher precipitation. Thermophilic taxa, occurring in the Mediterranean area, e.g., *Juncus maritimus*, *Glaucium flavum*, and *Crithmum maritimum*, are arranged towards higher temperatures and a longer

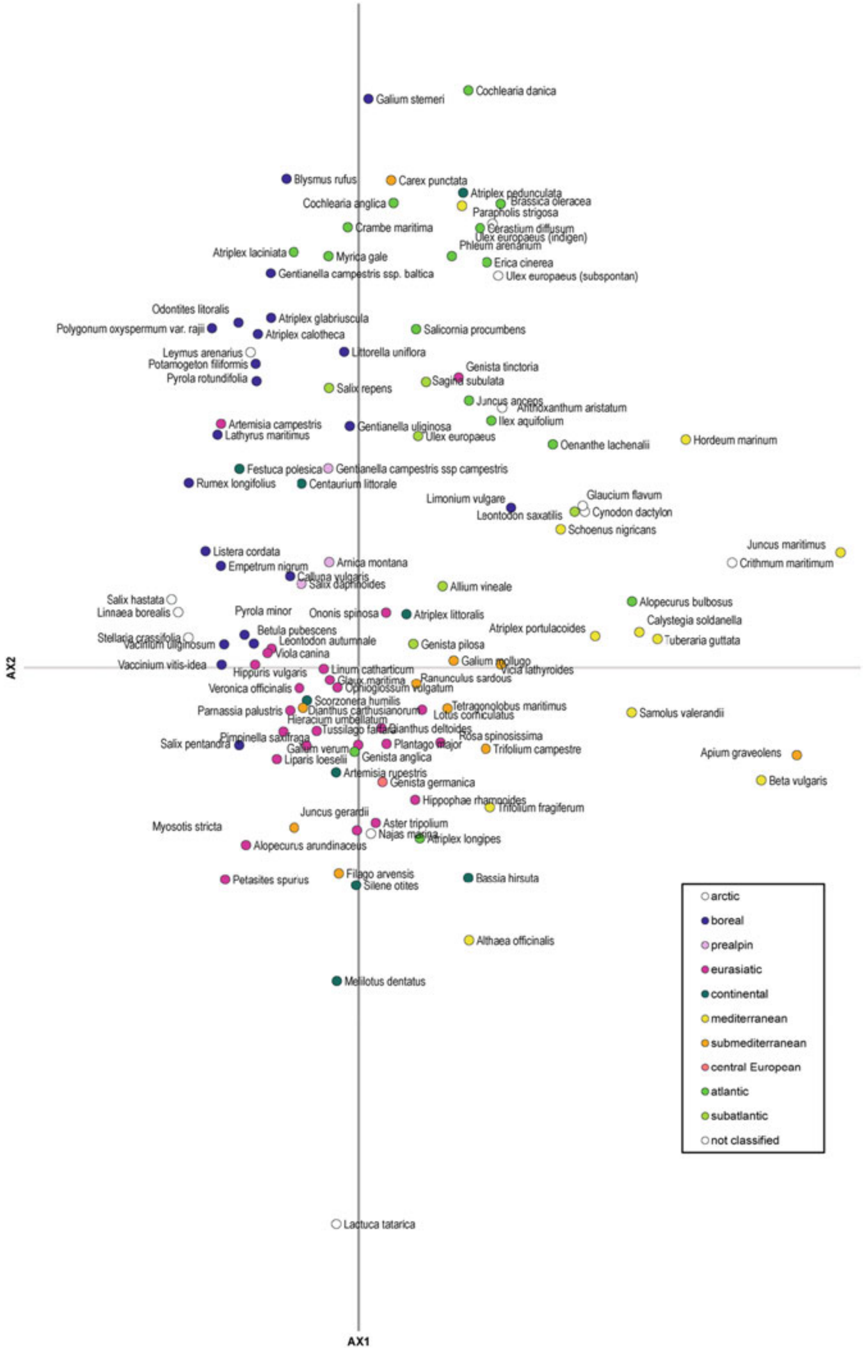

Fig. 10.12 Results of the Detrended Canonical Correspondence Analysis (DCCA) for distribution areas of 115 plant taxa and 43 climatic variables (cf. Figs. 10.10 and 10.11), but stretched in vertical direction to avoid overlaps of the species markings

Table 10.4 Climatic variables used for the models and ecograms and their correlation to other variables

T$_{\text{Year}}$	R	T$_{\text{Jan}}$	r	T$_{\text{Jul}}$	r	P$_{\text{Year}}$	r
T$_{\text{Oct}}$	1.00	T$_{\text{Feb}}$	1.00	T$_{\text{Aug}}$	0.99	P$_{\text{Nov}}$	0.93
Max$_{\text{Year}}$	0.99	T$_{\text{Dec}}$	0.99	Respirat	0.99	P$_{\text{Oct}}$	0.92
Min$_{\text{Year}}$	0.99	Max$_{\text{Jan}}$	0.99	Max$_{\text{Jul}}$	0.99	6$_{\text{coldest}}$	0.90
T$_{\text{Sep}}$	0.99	Min$_{\text{Jan}}$	0.99	Tsum$_{05\text{–}07}$	0.99	6$_{\text{warmest}}$	0.90
T$_{\text{Nov}}$	0.99	T$_{\text{Nov}}$	0.97	T$_{\text{Jun}}$	0.99	P$_{\text{Sep}}$	0.90
T$_{\text{Mar}}$	0.99	T$_{\text{Mar}}$	0.97	Min$_{\text{Jul}}$	0.98	Walt$_{\text{Jan}}$	0.90
T$_{\text{Apr}}$	0.98	Min$_{\text{Year}}$	0.95	T$_{\text{Sep}}$	0.96	P$_{\text{Mar}}$	0.90
T$_{\text{Dec}}$	0.96	T$_{\text{Oct}}$	0.94	T$_{\text{May}}$	0.96	P$_{\text{Dez}}$	0.90
Respirat	0.95	T$_{\text{Year}}$	0.93	lnResp	0.94	P$_{\text{Apr}}$	0.84
T$_{\text{Feb}}$	0.95	Temp$_5$	0.92	Max$_{\text{Year}}$	0.93	P$_{\text{Jan}}$	0.84
Temp$_5$	0.95	Max$_{\text{Year}}$	0.91	T$_{\text{Apr}}$	0.93	P$_{\text{Feb}}$	0.80
T$_{\text{Aug}}$	0.95	T$_{\text{Apr}}$	0.87	T$_{\text{Year}}$	0.92		
Temp$_1$0	0.95	T$_{\text{Sep}}$	0.87	Temp$_{10}$	0.91		
T$_{\text{May}}$	0.94	Temp$_{10}$	0.86	T$_{\text{Oct}}$	0.91		
Max$_{\text{Jan}}$	0.94	Rad$_{\text{Jan}}$	0.84	Min$_{\text{Year}}$	0.88		
Tsum$_{05\text{–}07}$	0.93	Respirat	0.80	Rad$_{\text{Jan}}$	0.87		
T$_{\text{Jan}}$	0.93	Fro$_{\text{Tag}}$	−0.95	Temp$_5$	0.85		
Min$_{\text{Jul}}$	0.92	Fro$_{\text{Dur}}$	−0.95	T$_{\text{Nov}}$	0.85		
T$_{\text{Jun}}$	0.92	Fro$_{\text{Jan}}$	−0.94	T$_{\text{Mar}}$	0.85		
T$_{\text{Jul}}$	0.92	Jalas_50	−0.82	Rad$_{\text{Jul}}$	0.83		
Min$_{\text{Jan}}$	0.91			Walt$_{\text{Jul}}$	−0.83		
Rad$_{\text{Jan}}$	0.90			Cloud$_{\text{Jul}}$	−0.83		
Max$_{\text{Jul}}$	0.89			Fro$_{\text{Dur}}$	−0.83		
lnResp	0.89			Fro$_{\text{Day}}$	−0.83		
Fro$_{\text{Day}}$	−0.96			Moist$_{\text{Year}}$	−0.82		
Fro$_{\text{Dur}}$	−0.96			Moist$_{\text{Jul}}$	−0.82		
Fro$_{\text{Jan}}$	−0.87			Cloud$^{\text{Year}}$	−0.81		
Moist$_{\text{Jul}}$	−0.81						
Moist$_{\text{Year}}$	−0.80						

Only climate variables with $-0.8 > r > 0.8$ (r = correlation coefficient) are shown here. For abbreviations, see Table 10.7 in appendix.

vegetation period. Nordic species are arranged opposite to the Mediterranean species, e.g. *Linnaea borealis*, *Listera cordata*, and *Pyrola rotundifolia* (Fig. 10.12).

10.4.2 Ecograms (Climate Envelopes)

The climatic potentials of the plant taxa, depending on environmental factors, are visualised here in ecograms. This method allows the presentation of the climatic amplitude covered by species areas. It equals the *climate envelope* (CE; realised niche, Guisan and Zimmermann 2000), which is defined by the climatic space that

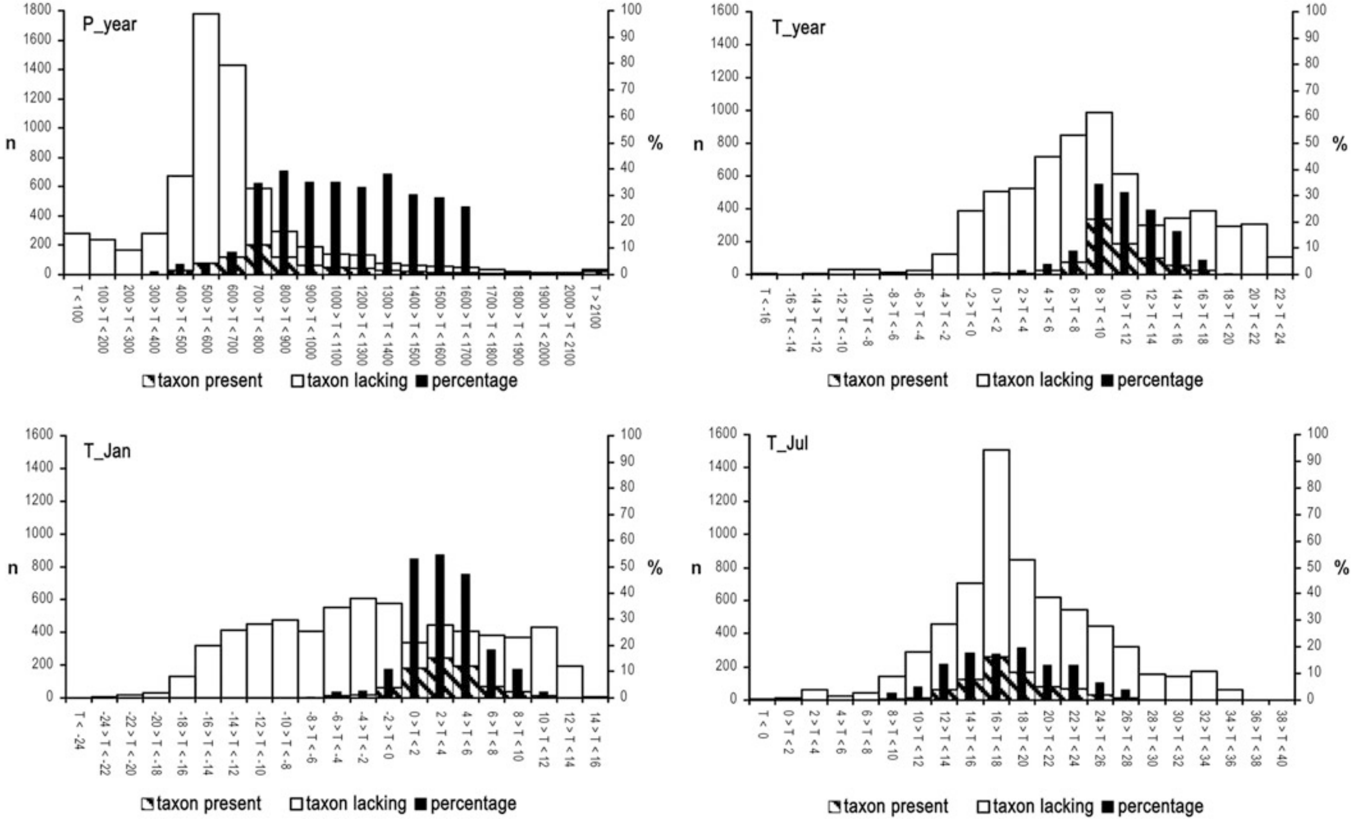

Fig. 10.13 Frequency diagram for *Ilex aquifolium*. Mean annual precipitation (P_{year}), mean annual temperature (T_{year}), mean January temperature (T_{Jan}), and mean July temperature (T_{Jul}). The x-axes show classes of precipitation or temperature, left y-axes the number of grid cells, and right y-axes the percentage of grid cells inhabited by the plant species

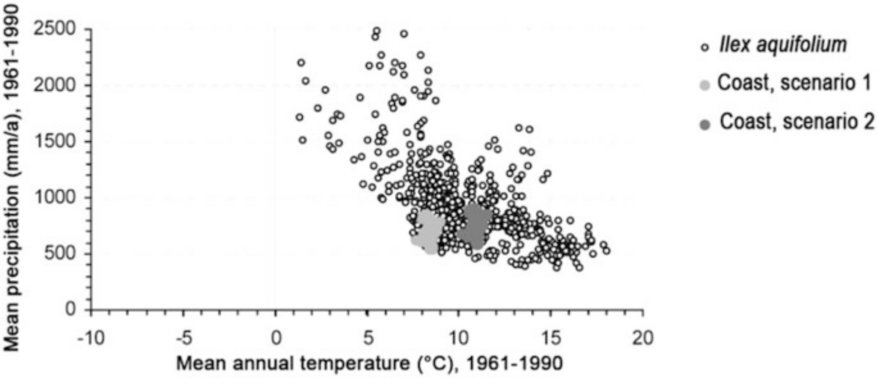

Fig. 10.14 Ecogram of the climatic envelope for *Ilex aquifolium*. Each point represents climate values of a grid rectangle with a geographical extension of 0.5°× 0.5° in which the species were recorded. The present climatic space (time period 1961–1990) of the German coastal area is indicated by light grey spots. The dark grey spots reflect the climate, which will prevail at the German coast in 2050 according to the worst-case scenario: a 2.5° increase in annual temperature and 15% more precipitation in winter

corresponds to the geographic boundaries within which a plant taxon is considered to grow and reproduce under natural conditions (Box et al. 1993, 1999).

Diagrams of frequency can also visualise the CE, showing the amount or percentage of grid cells with occurrence of specific taxa, the distribution of the taxa along ecological gradients, and comparisons of the different taxa (Hoffmann 2000; Hoffmann et al. 2002). The diagrams in Fig. 10.13 reveal the number of grid cells for climate data classes, the number of grid cells where a taxon (here *Ilex aquifolium*) is present, and the percentage of the inhabited grid cells for all climate data classes. They may serve for the interpretation of the importance of a climatic variable for the presence or absence of a taxon.

Ecograms visualise the combination of two ecological factors and their relevance (derived from correlation) for a plant taxon better than frequency diagrams. In ecograms, the climatic spaces of distribution areas are emphasised (Figs. 10.14 and 10.15), combined with the climate amplitude of present and future specific geographic areas (cf. Figs. 10.15 and 10.17). It has to be considered that the climate values of the single grid cells represent a large area (0.5° latitude and longitude, ca. 1760 km^2). In areas with a high elevation gradient (e.g. the coast of Norway where mountains with cold climate and coastal strips with a more moderate climate are close together), the average climatic values may differ from a specific local climate. Taking this partly haziness into account, the ecograms are a valuable tool to interpret distribution boundaries and their climatic limitations.

The climatic space of the German coast at the margin of the holly's climate envelope indicates the eastern distribution margin of the species in Mecklenburg-Western Pomerania (Fig. 10.14). Under the predicted warming, the climate of the German coasts shifts more towards the centre of holly CE. Regarding this shift, an eastward expansion of the distribution area has to be expected (which has been

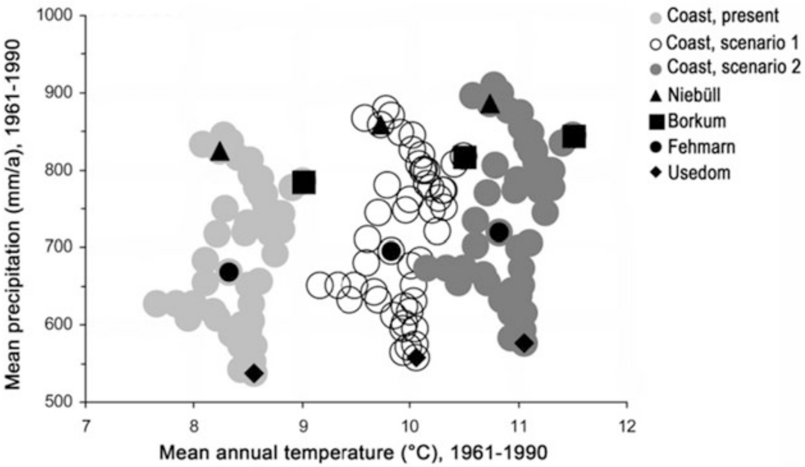

Fig. 10.15 Ecogram of the German coastal area for recent and predicted climate regimes (mean values for annual temperature and precipitation). Light grey spots: recent climatic space of the German coast (reference period: 1961–90), circles respective dark grey spots: climatic space of the German coast under the predicted best-case respective worst-case scenarios. The position of four localities is marked for Borkum (East Friesland), Niebüll (North Friesland), Fehmarn (Holstein) and Usedom (Western Pomerania)

confirmed by Walther et al. 2005). Figure 10.16 illustrates the ecogram for winter and summer temperatures (represented by annual mean temperatures for January and July).

The ecograms reveal that precipitation is less decisive for the distribution patterns than temperature (this would be different for areas with warmer climates and higher aridity, e.g., in the subtropics!). Concerning ecograms, distribution shifts are not expected from changed (increasing) precipitation. Even in the distribution models, precipitation plays no important role in determining the distribution ranges (cf. Fig. 10.4).

For interpretation and comparison of species ecograms, the climatic spaces of geographical regions are of interest, as shown in Fig. 10.17 for temperatures (T_{Jan} und T_{Jul}). Mountain areas with lower mean temperatures cause the conspicuous tails of some point cluster patterns (Figs. 10.18 and 10.19).

The point cluster patterns indicate the geographical position of species' ranges roughly (with respect to the German coast). Figure 10.20 shows the ecogram of *Aster tripolium*, which is largely confined to the coast. The point clusters at the left top of the ecogram illustrate the continental distribution area north of the Black Sea. Species with an eastern distribution centre (areas with low winter but similar summer temperatures) are arranged more at the left side, Nordic species left below. The diagonal running from top left towards right below equals the gradient of continentality. Figure 10.21 shows this arrangement for four species: *Linnaea borealis* (Arctic-Nordic), *Lactuca tatarica* (continental, native area), *Crithmum maritimum* (Mediterranean-west Oceanic), and *Ulex europaeus* (oceanic).

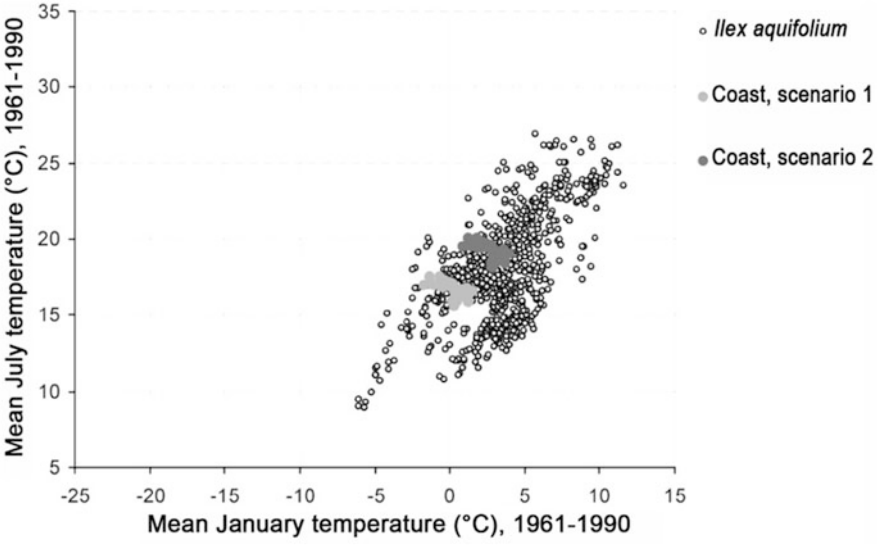

Fig. 10.16 Ecogram of the climatic envelope for *Ilex aquifolium*. Each point represents climate values of a grid rectangle with a geographical extension of 0.5° × 0.5° and with a record of the species (more explanations, see Fig. 10.14)

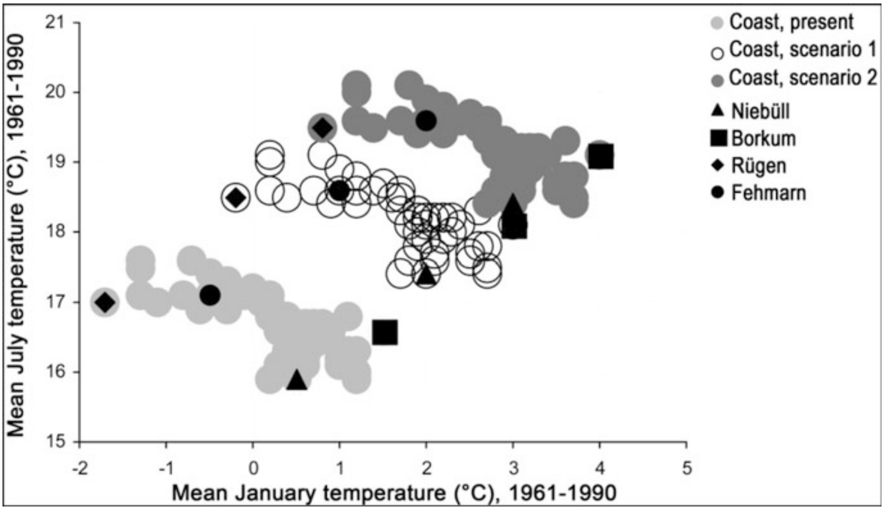

Fig. 10.17 Ecogram of the German coastal area for recent and predicted climate regimes (mean values for January and July temperature) (more explanations, see Fig. 10.15)

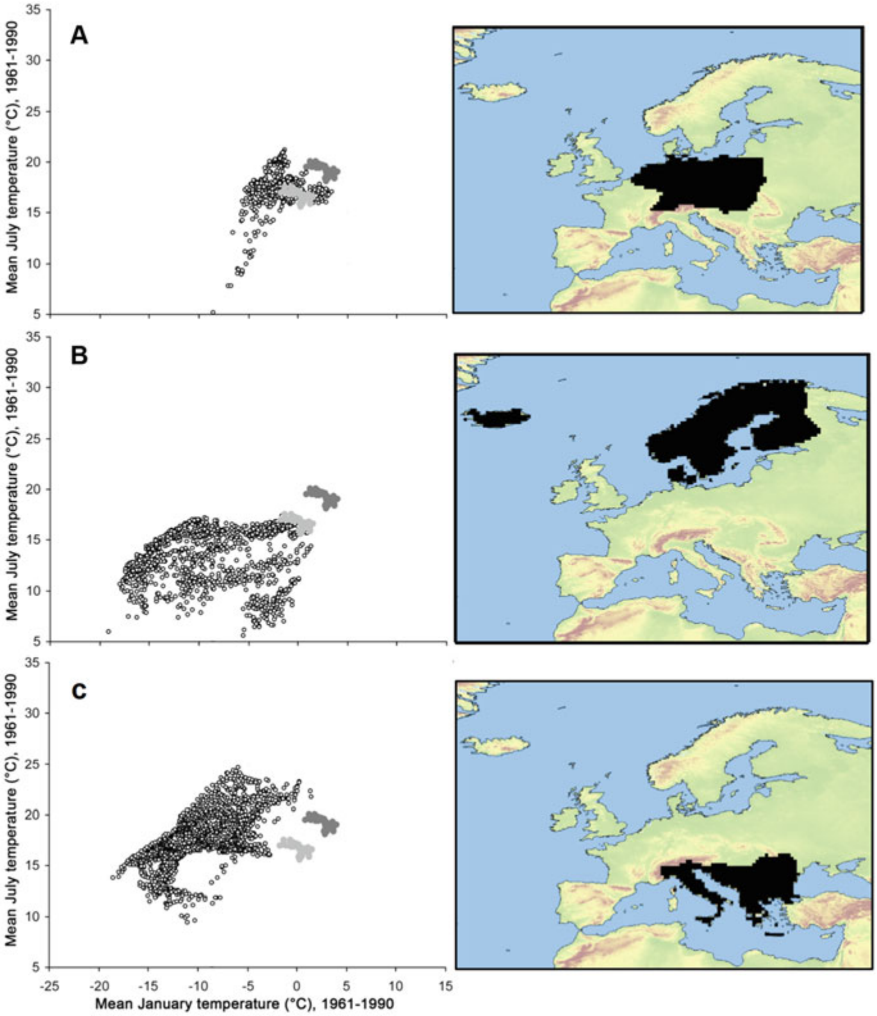

Fig. 10.18 Climatic space for (**a**) Central Europe, (**b**) North Europe (without the British Isles), and (**c**) Southeast Europe. The graph shows the temperature range for the central part of Europe (black circles) as well as for the German coast (*present* light grey; predicted worst-case scenario: dark grey)

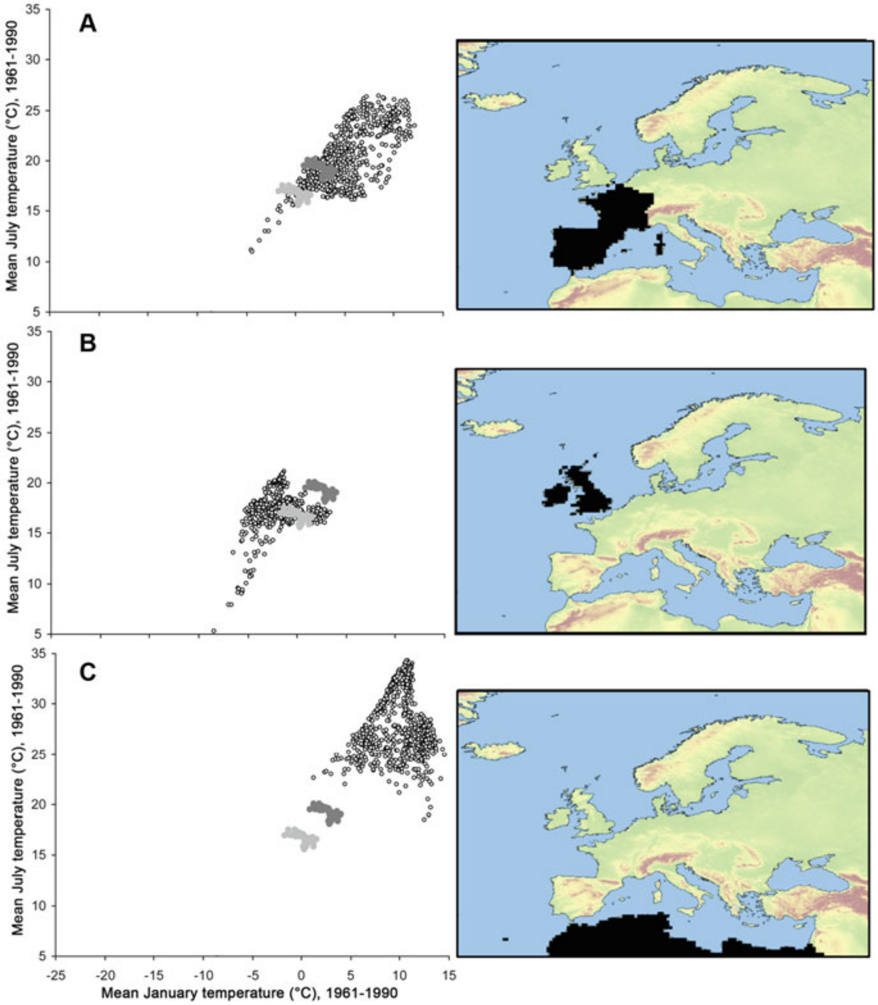

Fig. 10.19 Climatic space for (**a**) Southwest Europe, (**b**) the British Isles, and (**c**) North Africa (north of 30° N); The graph shows the temperature range for the southwestern part of Europe (black circles) as well as for the German coast (present: light grey; predicted worst-case scenario: dark grey)

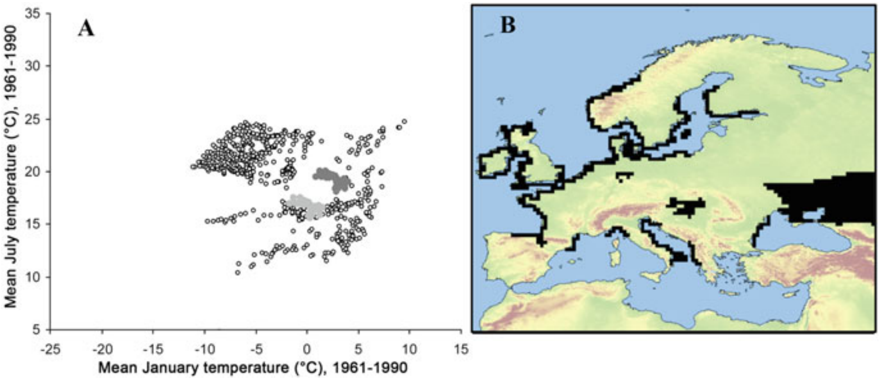

Fig. 10.20 Ecogram (**a**) and distribution area (**b**) for *Aster tripolium*. For further explanations, see Fig. 10.16 and text

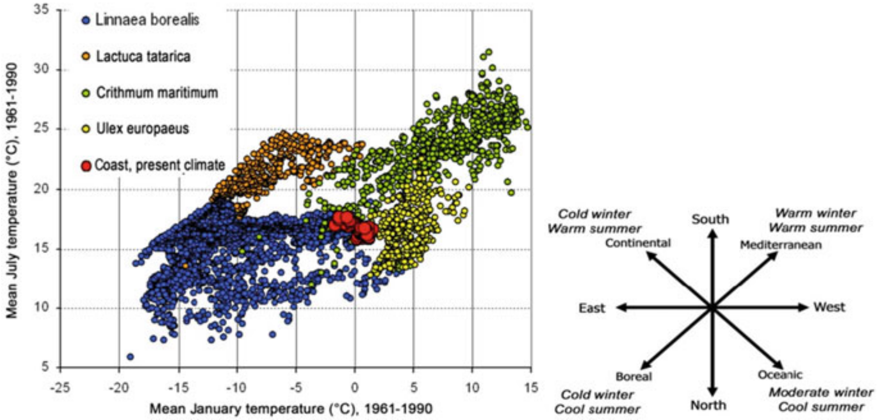

Fig. 10.21 Relations of thermic gradients, continentality, and geographic orientation, exemplarily illustrated for four plant species. Red points: German coast

10.5 Modelling of Prospective Plant Distribution Data

10.5.1 Climatic Sensibility of Single Taxa

There are several techniques available to model distribution ranges in response to changing environmental conditions (Segurado and Araújo 2004). Here we use a climate envelope model to predict future distribution shifts based on the given climate scenarios.

The impact of climate change on the single species distribution areas can be estimated from the ecograms and the models.

No climatic envelopes have been calculated here for taxa, which have no distribution boundaries in Germany, or which have wide distribution ranges, extending to areas with a warmer climate than expected for the German coast. It has to be assumed that the predicted climate change will not affect the presence of these taxa within the German coastal area (these taxa are marked in Table 10.1).

Examples of potential range shifts within the German coastal area are presented here for four species based on the scenarios provided by von Storch et al. (1998). The predictions concerning range shifts are, therefore, valid only for this region (and adjacent areas), as the changes of climate will not be uniform for all of Europe.

10.5.1.1 *Atriplex longipes* Drej., Amaranthaceae (Chenopodiaceae)

Distribution: *Atriplex longipes* is confined to coastal habitats, in particular, salt marshes. At the German coast only the subspecies *Atriplex longipes* subsp. *longipes* occurs. Its distribution area ranges from Britain to Scandinavia (Fig. 10.24). According to Jalas et al. (1999), the species reaches its southern distribution boundary at the German coast including The Netherlands (van der Meijden 1996; Weeda et al. 1985) and the British coasts (Preston et al. 2002) (Fig. 10.23). Certainly, the species has been neglected for a long time and was recently stated as extinct in Britain (Blamey and Grey-Wilson 1989; Garve 1982, 1994; Krisch 1991). Concerning the records documented since 1949 for the East Frisian Islands, the species was disregarded for a long time, although it has not immigrated into this region. A first record for the Weser estuary dates from 1849 (Garve 1982). The species is also distributed along the southern Baltic Sea coast. Marsson (1869) reported it for Zingst and Usedom and Krisch (2002) most recently for the region of Rügen (Figs. 10.22 and 10.23).

Climatic impact: Fig. 10.23 (B) is based on the data in Jalas et al. (1999) and shows the potential occurrence of the taxon even at the Dutch coast, although the real southern distribution limit lies more in the south (Fig. 10.23). In Fig. 10.25, the occurrence in South England (Preston et al. 2002) is included. Climatic warming will result in a shift of the climate envelope in a northern direction, as the species obviously is sensitive to higher summer temperatures (Figs. 10.23, 10.24, and 10.25).

Atriplex longipes is already endangered by use and destruction of its habitats, mainly for touristic purposes (von der Ende 1995). The predicted climate change will stress the population of the German coast additionally and future disappearance of the species here must be expected.

10.5.1.2 *Atriplex portulacoides* L. Amaranthaceae (Chenopodiaceae)

Distribution: The Sea Purslane is distributed along the European coasts, in the north up to 56° N. In Germany, *Atriplex portulacoides* is confined to the Wadden Sea area (Fig. 10.26). Old records from the Baltic Sea coast, "1791 bei Warnemünde" as published by Timm (Boll 1860) were doubted by Fukarek and Henker (1983). Boll (1848) listed the species for the Baltic area in general; Baumgardt (1848) mentioned it for the island of Usedom. The species, characteristic for the "*Halimione portulacoides* salt-marsh community" (Halimionetum portulacoides, Pott 1995b),

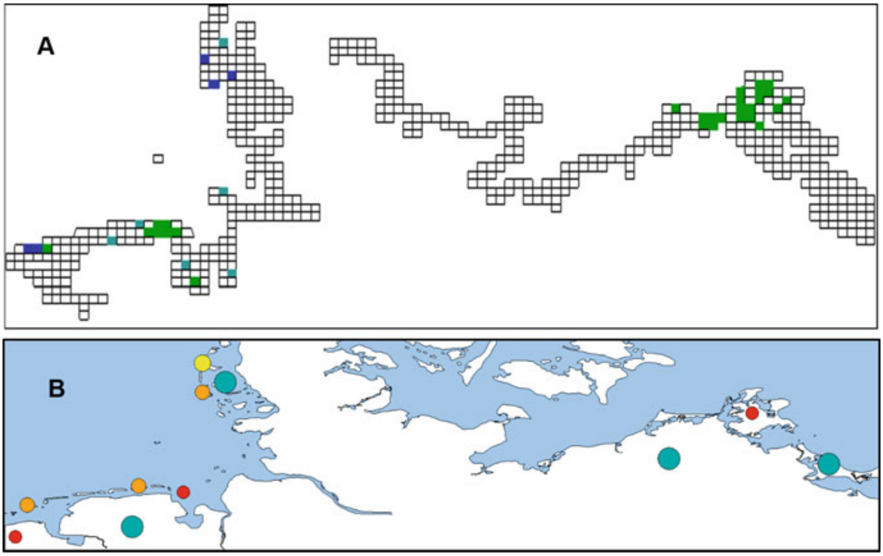

Fig. 10.22 Distribution of *Atriplex longipes* at the German coast (**a**) and first records according to literature (**b**). Data: BfN 1999. Modified according to Krisch 2002. For an explanation of colours, see Figs. 10.7 and 10.9

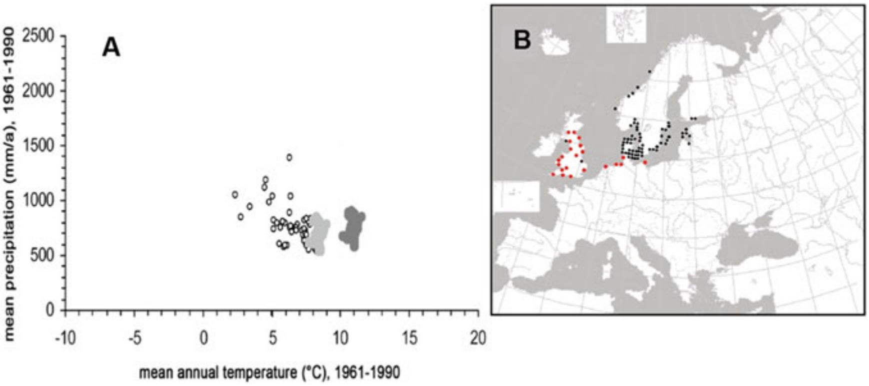

Fig. 10.23 (**a**) Ecogram of *Atriplex longipes* subsp. *longipes*. For explanations, see Fig. 10.14, (**b**) Distribution of *Atriplex longipes* subsp. *longipes* in Europe (●). (Graphic from Jalas et al. (1999), modified, completed after Weeda et al. (1985); Krisch (2002); and Preston et al. (2002) (●))

is sensitive to grazing and hence becomes dominant only in non-grazed areas. The species favours a well-drained aerobic soil environment and good nutrient supply (Rodwell 2000).

Climatic impact: It is evident from the ecograms that increasing temperatures are favourable for the species in the northern part of Europe (Fig. 10.27). An expansion

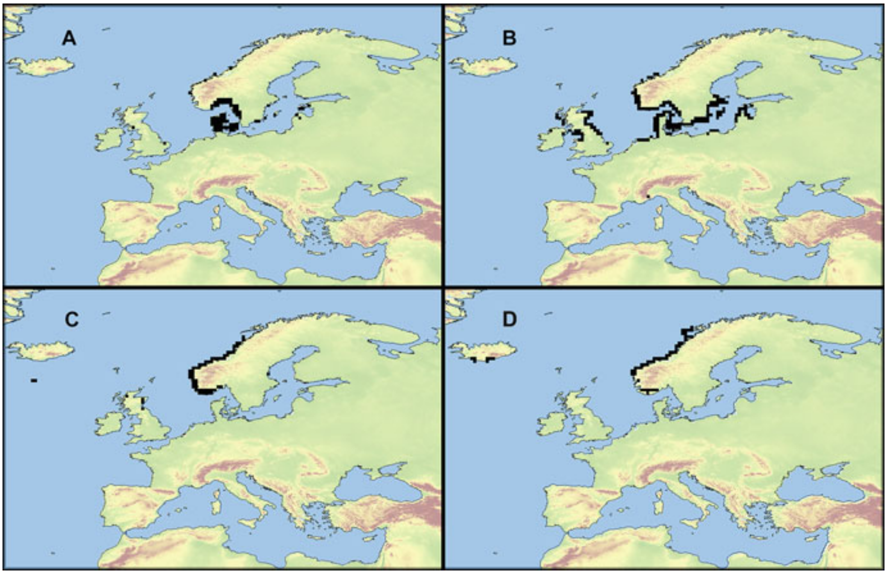

Fig. 10.24 Distribution of *Atriplex longipes* subsp. *longipes* in Europe (**a**) according to Jalas et al. (1999); modelled distribution range (climatic envelope) along the coast for various scenarios: recent climate (**b**), scenario 1 (**c**), scenario 2 (**d**)

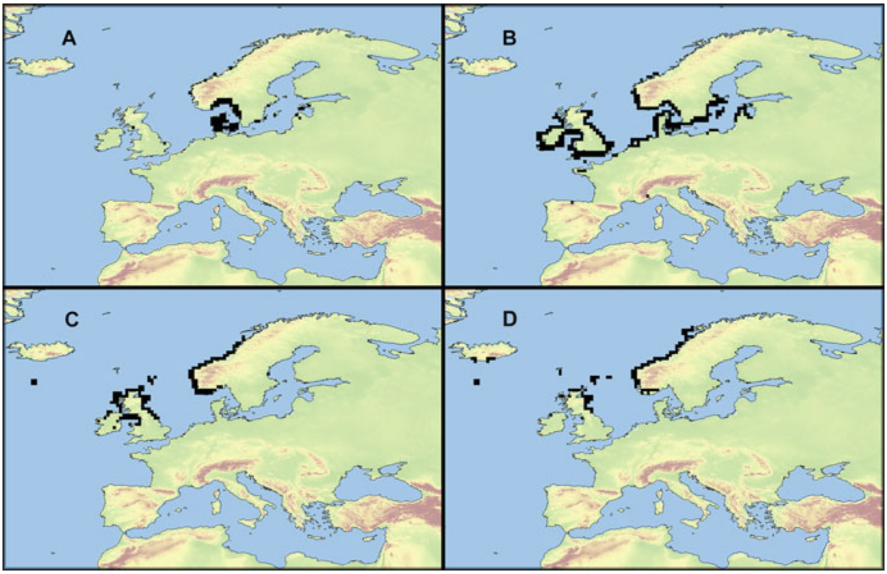

Fig. 10.25 Distribution of *Atriplex longipes* subsp. *longipes* in Europe (**a**) according to Jalas et al. (1999); Weeda et al. (1985); Krisch (2002); Preston et al. (2002), modelled distribution range (climatic envelope) along the coast for various scenarios: recent climate (**b**), scenario 1 (**c**), scenario 2 (**d**)

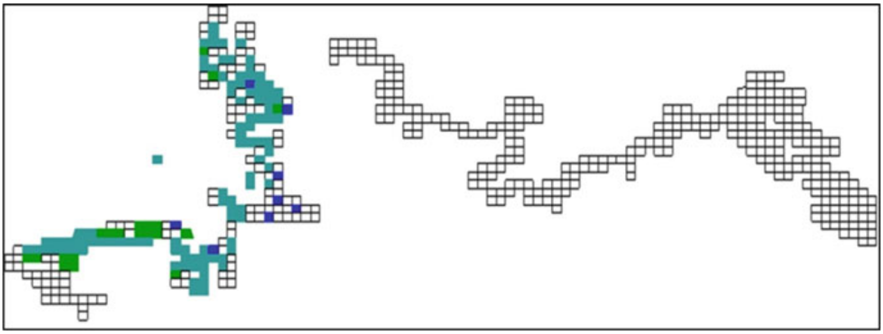

Fig. 10.26 Distribution of *Atriplex portulacoides* at the German coasts. Data: BfN 1999. For explanation of colours, see Fig. 10.7

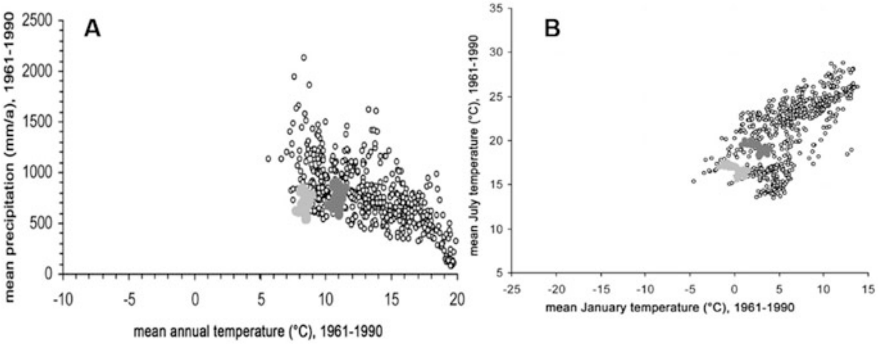

Fig. 10.27 Ecograms of the climatic envelope for *Atriplex portulacoides* for (**a**) mean annual precipitation and mean annual temperature, (**b**) mean July temperature and mean January temperature. Points represent climate values of a grid rectangle with a geographical extension of 0.5° × 0.5° where the species is present; light grey spots: present climatic space (time period 1961–1990); dark grey spots: prevalence at the German coast in 2050 according to the worst-case scenario: 2.5° increase in annual temperature and 15% more precipitation in winter

of the distribution range towards the north is probable according to the model (Fig. 10.28). Chapman (1950) published the northern distribution limit at the 16° C-July-isotherm. However, the species already recently occurs in areas with much lower July temperatures, e.g., in England and Ireland (cf. Fig. 10.28). The ecogram indicates that low winter temperatures limit the northern distribution (Fig. 10.27). This has been confirmed by observations of plant damages after strong frosts (Beeftink et al. 1978; De Leeuw 1992). Iversen (1954, cited after Ranwell 1972) described the range expansion at the peninsula of Skallingen (Denmark) between 1931 and 1954 by more moderate temperatures.

The expansion of the species in eastern direction, as predicted by the model, depends not only on the climate but also on environmental site conditions as well. Recurrent (tidal) inundations and a saline habitat are necessary for the establishment

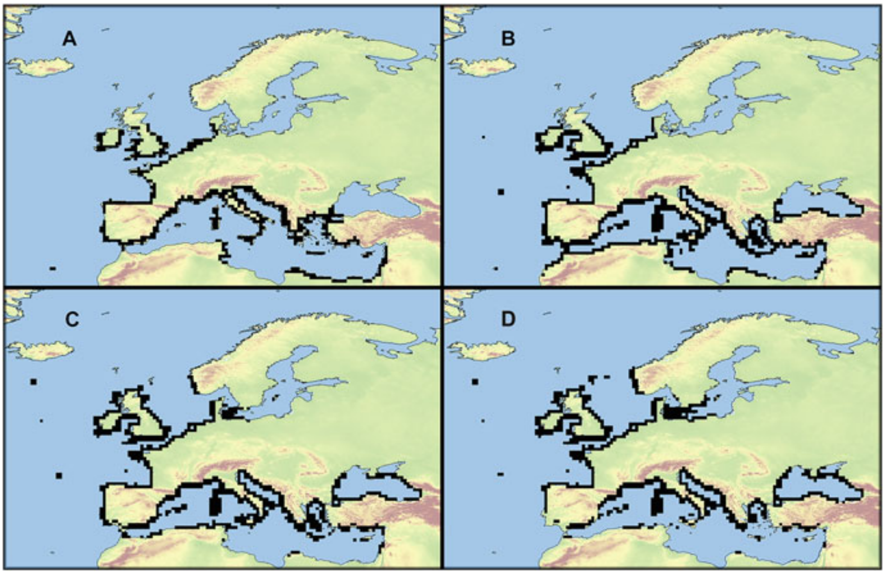

Fig. 10.28 *Atriplex portulacoides* in Europe. Distribution (**a**), modelled distribution range (climatic envelope) along the coast for various scenarios: recent climate (**b**), scenario 1 (**c**), scenario 2 (**d**)

of the eu-halophytic species (Chapman 1950). On the one hand, this may be in contradiction to an expansion to the Baltic Sea coast, although it may be possible according to the climate conditions. On the other hand, Sea Purslane occurs in the Mediterranean area on shingle, dunes, in salines and lagoons with saline soils that have insignificant tidal sea level fluctuations (Chapman 1974). The model predicts an expansion towards the north but this will not concern the German coast, as the species is already distributed up to Denmark. In Schleswig-Holstein, the species is endangered by habitat disturbances, such as destructions by tourism, agriculture, and amelioration (von der Ende 1995); the climate apparently has no relevance here (Fig. 10.29).

10.5.1.3 *Crithmum maritimum* L. Apiaceae

Distribution: *Crithmum maritimum* did not belong to the German flora according to Wisskirchen and Haeupler (1998). But in 2000, the species was found at the island of Helgoland and was published as “new for Germany” (Kremer and Wagner 2001; cf. Christiansen and Kohn 1958, where the species has not been listed). These authors neglected the record on Helgoland in 1935 by Panknin (1937); Metzing (2005). However, no herbarium specimens of these findings have been preserved up to today [the specimens of Panknin in the Berlin herbarium (B) were probably destroyed in 1943]. The new population on Helgoland expanded in the following years (Kremer, in litt.) and the species is still present there (Fig. 10.30). The nearest occurrences of the species were reported from the West Frisian Islands Texel and Ameland (van Oostroom and Mennema 1969; van Oostroom and Reichgelt 1965).

Fig. 10.29 Areas in Europe with mean temperature in July <16 °C. Dark grey: reference period 1961–1990

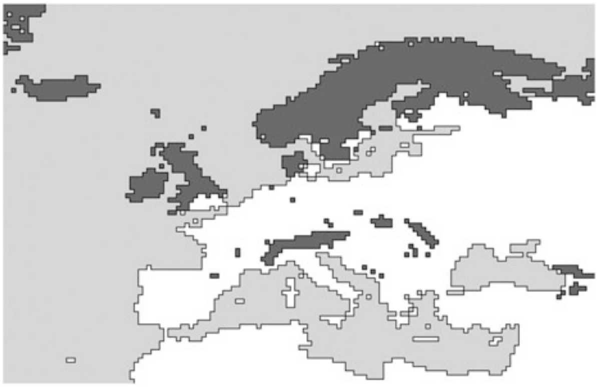

Fig. 10.30 First records of *Crithmum maritimum* according to literature. For an explanation of the colours, see Fig. 10.9

Boll mentioned the species for the Netherlands already in 1848, whereas according to Weeda et al. (1987) the species was found there for the first time at the turn of the century (nineteenth/twentieth century).

Climatic impact: The models show an increasing overlap of the climatic envelope and the future climate range at the German coast (Fig. 10.31). In Great Britain, *Crithmum maritimum* is found southwest of the 4.6 °C-January isotherm (Crawford and Palin 1981), although the species can tolerate even colder temperatures in winter; the model (Fig. 10.32) is based on a minimum mean temperature in January of 1.5 °C (Fig. 10.32).

As a consequence of climate warming, an expansion of the distribution area into the study area has to be assumed (Fig. 10.32). Originally, the species was distributed in spray-drenched rock crevices, ledges on sea-cliffs, coastal rocks, and on stabilised shingle. It also grows in maritime grasslands, on harbour walls, and stone sea defences (Weeda et al. 1987; Wiggington in Preston et al. 2002). Similar habitats are also present at the German coast. So immigration there seems to be possible. The recent findings in Germany may be considered as a first indication of a recent range expansion (Metzing and Gerlach 2001). Efficient long-distance seed dispersal of *Crithmum maritimum* by sea-surface currents has also been proven by genetic studies (Latron et al. 2020). Most recently, the species has been found on the island of Pellworm (west coast of Schleswig-Holstein), too (Eigner 2014).

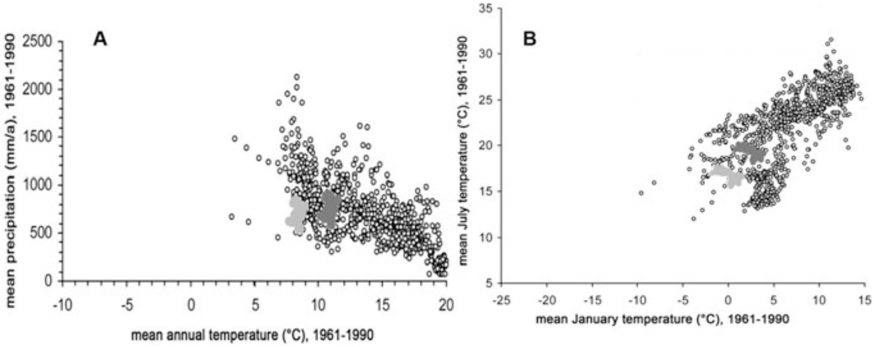

Fig. 10.31 Ecograms of the climatic envelope for *Crithmum maritimum* for (**a**) mean annual precipitation and mean annual temperature, and (**b**) mean July temperature and mean January temperature. Points represent climate values of a grid rectangle with a geographical extension of 0.5° × 0.5° where the species is present; light grey spots: present climatic space (time period 1961–1990); dark grey spots: prevalence at the German coast in 2050 according to the worst-case scenario: 2.5° increase in annual temperature and 15% more precipitation in winter

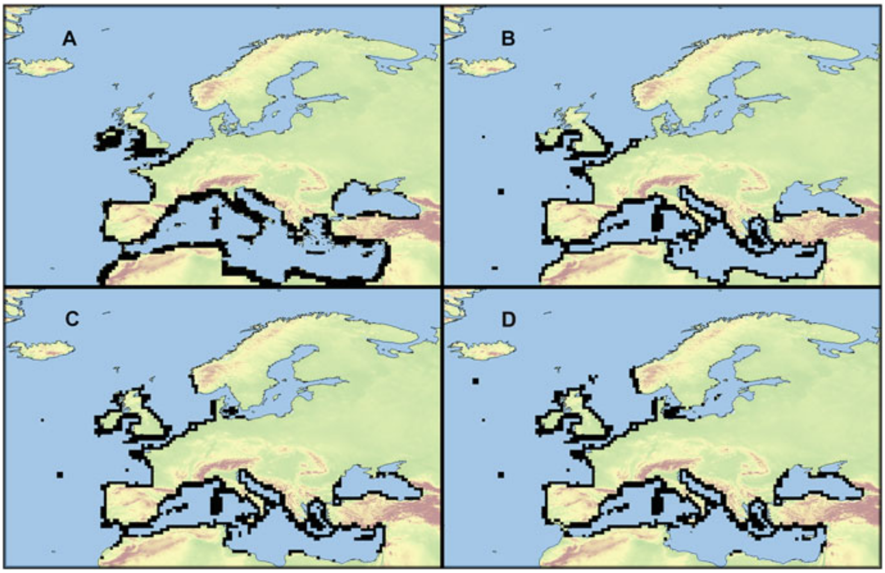

Fig. 10.32 *Crithmum maritimum* in Europe. Distribution (**a**), modelled distribution range (climatic envelope) along the coast for various scenarios: recent climate (**b**), scenario 1 (**c**), and scenario 2 (**d**)

10.5.1.4 *Ulex europaeus* L. Fabaceae

Distribution: The native distribution area of the Gorse is confined to the Atlantic parts of Europe (Meusel et al. 1965). Considering sub-spontaneous occurrences, the species is deemed as a temperate Atlantic geo-element (Walter and Straka 1970). At

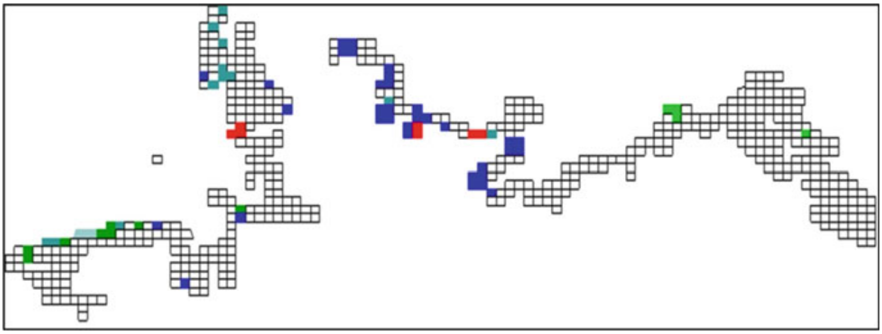

Fig. 10.33 Distribution of *Ulex europaeus* at the German coasts. Data: BfN (1999). For an explanation of colours, see Fig. 10.7

the German coast, the species originally was not native; it has been cultivated for different purposes (Litterski and Berg 2000; Meyer 1824; Meusel et al. 1965) (Figs. 4.2, 4.3, 4.4, 4.5, 4.6, 4.7, 4.8) and is considered to be feral at some places now (Buchenau 1901; Dierssen and Mierwald 1987; Garve 1994; Jaap 1898; Knuth 1895; Meyer 1849; Schreitling 1971). It is not sure, whether the species reproduce by seed at the German coast or by creeping roots and re-sprouts from stumps (Hoshovsky 2004) (Fig. 10.33).

Climate impact: The species is sensitive to very cold winters, although adult plants can stand fairly severe frosts. During severe winters, a great part of gorse bushes can be killed; thus, a succession of very cold winters may have a disastrous effect on the distribution of *Ulex europaeus*. In Great Britain, it rarely occurs above 150 m and then only at south-facing slopes (Savidge 1970). The species grows well in the moderate climate on the island of Sylt, whereas it can freeze at the mainland of Schleswig-Holstein during severe winters (Heydemann 1997). Limiting factors are inhibited germination at low temperatures and sensitivity of the symbiotic nitrogen-fixing bacteria to severe cold temperatures. Moreover, adult plants are sensitive to cold winds (Zabkiewicz 1976). This explains the good growth of planted specimens and the lacking natural reproduction by seeds at the German coast. The ecograms (Fig. 10.34) show that the predicted future climate of the German coast comes closer to the climate envelope of the native populations of the gorse, whereas the degree of continentality is decisive (Fig. 10.35). Therefore, an eastward expansion has to be assumed due to the changing gradient of winter temperatures (Fig. 10.36). Day length also affects the latitudinal distribution of the species, as short-day conditions inhibit maturation and prevent thorn formation and flowering (Zabkiewicz 1976). This may limit the northward expansion (to Scandinavia), but it is less relevant for the German coast, because the species flowers freely on Sylt (Heydemann 1997; 131). The species generally establish slowly in new areas (Zabkiewicz 1976).

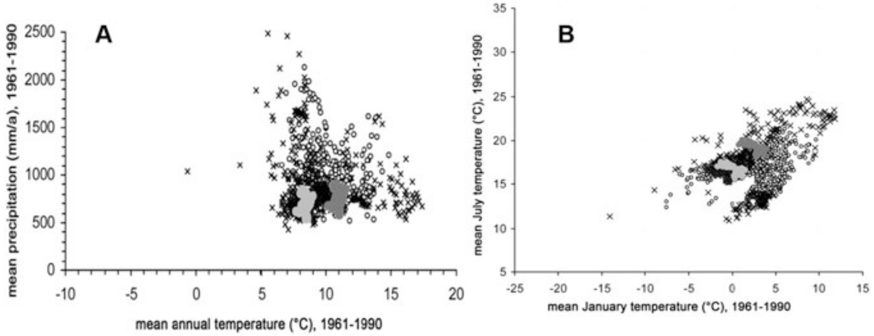

Fig. 10.34 Ecograms of the climatic envelope for *Ulex europaeus* for (**a**) mean annual precipitation and mean annual temperature, and (**b**) mean July temperature and mean January temperature. Points represent climate values of a grid rectangle with a geographical extension of 0.5° × 0.5° where the species is present; light grey spots: present climatic space (time period 1961–1990); dark grey spots: prevalence at the German coast in 2050 according to the worst-case scenario: 2.5° increase in annual temperature and 15% more precipitation in winter

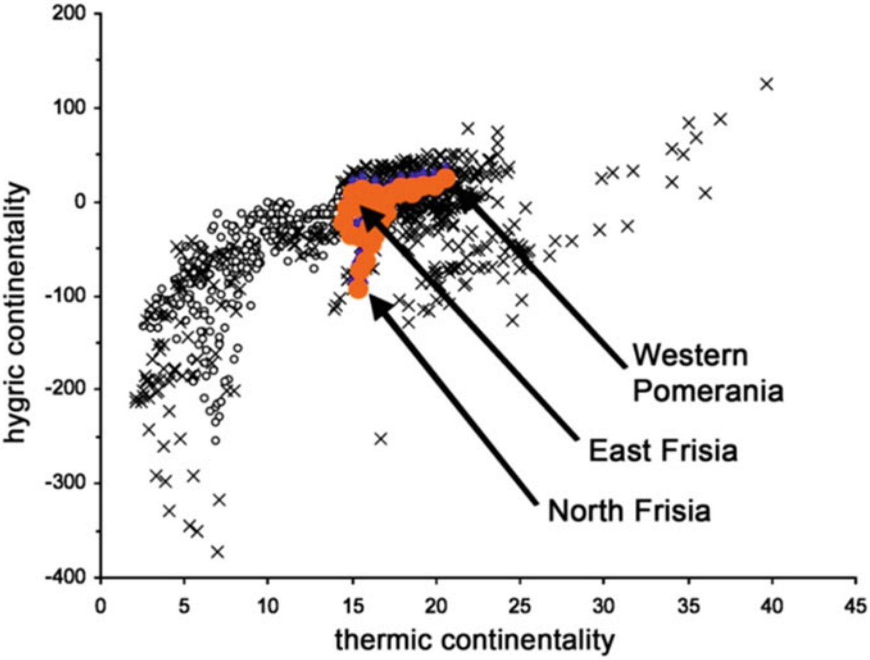

Fig. 10.35 Ecogram for *Ulex europaeus.* Climate range of grid cells where *Ulex europaeus* occurs (○ indigenous, x sub-spontaneous) (in Europe and adjacent areas) with regard to continentality according to Conrad (1946; thermic continentality) and Henze (1929; hygric continentality). ▲ = recent climatic range at the German coast, ● = predicted future climatic range at the German coast (scenario 2)

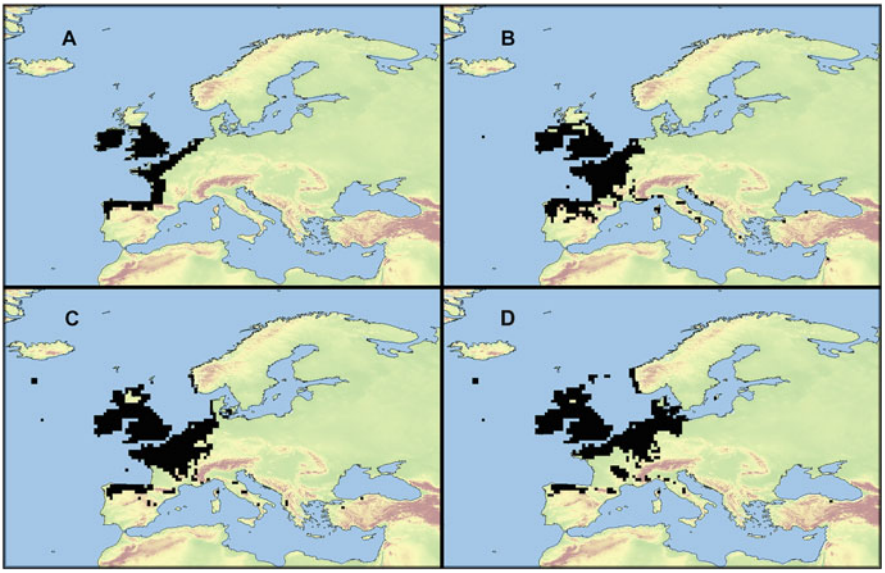

Fig. 10.36 *Ulex europaeus* in Europe. Distribution (**a**) (native area according to Meusel et al. 1965), modelled distribution range (climatic envelope) along the coast for various scenarios: recent climate (**b**), scenario 1 (**c**), and scenario 2 (**d**)

10.5.2 The Potential Change of the Coastal Flora under Climate Change

The predictions derived from the ecograms and models are summarised for the German coasts and both scenarios in Table 10.5. The table provides information about the potential increase or decrease of the plant taxa considered in this study. Already known decreases or retreats are also indicated also by the Red List status.

Based on the ecograms and models, a shift of the climate envelope within the German coastal area has to be expected for 70 (31%) of all (223) taxa (worst-case scenario). A retreat is probable for 39 taxa (17%), for two more taxa this trend is not clear (1%). The climate envelope of 21 taxa (9%) will expand within the study area, for 8 taxa (4%) this is also possible, but not sure. No prediction can be given for 8 taxa (4%) due to insufficient knowledge of the distribution area or taxonomic uncertainties. The climate change will probably not affect the presence of 145 taxa (65%) at the German coasts (Fig. 10.37, Table 10.5).

The number of declining taxa only slightly differs between the North Sea and the Baltic Sea coast (28 resp. 33 versus 27 resp. 35). The number of taxa that probably will expand their distribution ranges at the North Sea coast is smaller than for the Baltic Sea coast (21 resp. 22 versus 25 resp. 26). This can be explained by the predominant shifts of the climate envelopes to the northeast. Species currently only present at the North Sea coast can potentially spread to the Baltic Sea coast. The

Table 10.5 List of the taxa included in this study with specifications of potentially progressive (↑) or regressive (↓) distribution shifts within the coastal area of Germany and the degree of threat; uncertain predictions are signified by a question mark (from: Metzing 2005). For those taxa with a distinct congruence or real and modelled area (Kappa index $\kappa \geq 0.4$), the name is printed in bold. # = No calculation of the climate envelope as even the distribution pattern does not indicate a change of presence under the predicted scenarios for the study area

Taxon	NS SC1	BS SC1	NS SC2	BS SC2	RL NS	RL WW	RL NW	RL WB	RL SB	RL D
Agrostis stolonifera var. *maritima*					*					*
Aira caryophyllea **#**										V
Aira praecox **#**					*					V
Ajuga pyramidalis **#**					0	–	0			*
Allium vineale [*A. kochii*]	[–]		[–]		* [–]			[–]	[1]	*
Alopecurus arundinaceus	–	↓	–	↓↓	–			–	1	2
Alopecurus bulbosus	↑	↑↑	↑	↑↑	2	2	–			2
Althaea officinalis	↑↑	↑	↑↑	↑	1			2	3	3
Ammophila arenaria **#**					*					*
Anagallis minima **#**					3	2	1			2
Anthoxanthum aristatum		↑?		↑?	*					N
Anthyllis vulneraria subsp. *maritima* **#**					3	3	–	3	3	3
Apium graveolens **#**					2	2	1	1	2	3
Armeria maritima **#**					*			3	3	V
Arnica montana	↓		↓	↓	2	0	2			3
Artemisia campestris			(↓)?			0	P			*
Artemisia maritima **#**					*			*	3	*
Aster tripolium **#**					*			3	3	*
Atriplex calotheca	(↓)	↓	(↓)	↓	–			0	1	2
Atriplex glabriuscula	↓?	↓	↓	↓	R	P	1	2	1	2
Atriplex laciniata	↑?	↑?	↑?	↑?	R	0	1			1
Atriplex littoralis **#**					*					*
Atriplex longipes	↓	↓	↓	↓	*	*	1	–	P	*

Atriplex pedunculata					3	2	1	1	1	3
Atriplex portulacoides		↑↑?		↑↑?	*	*	2			*
Atriplex prostrata **#**					*					*
Bassia hirsuta	?	?	?	?	–	–	1	1	0	2
Beta vulgaris subsp. *maritima*	↑	↑ (?)	↑	↑ (?)	R	–	–			*
Betula pubescens **#**					*					*
Blysmus rufus	↓	↓	↓	↓	2	2	1	1	1	2
Bolboschoenus maritimus **#**					*					*
Brassica oleracea	↑	–	↑	↑	–	–	–			R
Bromus thominii **#**					*					*
Bupleurum tenuissimum **#**					0	1	1	1	1	2
Cakile maritima **#**					*			*	3	*
×*Calammophila baltica*	↓		↓	↓	*					*
Calluna vulgaris **#**					*					*
Calystegia soldanella		↑↑	(↑)	↑↑	1	1	1			1
Carex arenaria **#**					*					*
Carex distans **#**						3	2	3	3	3
Carex extensa **#**					*	P	2	2	2	V
Carex flacca **#**					*	3	*			*
Carex pulicaris **#**					1	0	0			2
Carex punctata **#**		–		–	2	1	–			1
Carex trinervis	↑	↑↑	↑	↑↑	2	2	0			2
Carum carvi **#**					3	3	*			*
Centaurium erythraea **#**								3	3	*
Centaurium littorale **#**					*			2	2	*
Centaurium pulchellum **#**					*			2	2	V
Cerastium diffusum	↑↑?			↑↑?	3	p	P			3

(continued)

Table 10.5 (continued)

Taxon	NS SC1	BS SC1	NS SC2	BS SC2	RL NS	RL WW	RL NW	RL WB	RL SB	RL D
Chenopodium foliosum **#**					*					N
Chenopodium rubrum **#**					*					*
Cirsium arvense **#**					*					*
Cladium mariscus **#**					2					3
Claytonia perfoliata **#**					*					N
Cochlearia anglica **#**						*	3	3	2	V
Cochlearia danica			↓?	↓?	*			3	*	*
Cochlearia officinalis **#**					1	1	1	3	1	2
Corispermum leptopterum	(↑)?	(↑)?	(↑)?	(↑)?	*					N
Coronopus squamatus **#**					3					3
Corynephorus canescens **#**					*					*
Cotula coronopifolia **#**					3	2	2	P	–	N
Crambe maritima	↓	↓	↓	↓	R	0	–	2	1	3
Crithmum maritimum	↑	↑↑	↑	↑↑	n. i.					R
Cynodon dactylon	↑	↑	↑	↑	u					N
Deschampsia flexuosa **#**					*					*
Dianthus carthusianorum	↑?		↑?		u	P	P			V
Dianthus deltoides					3	–	1			V
Eleocharis parvula **#**					–			1	0	2
Eleocharis uniglumis **#**					*			*	3	V
Elymus athericus **#**		–		–	*					*
Elymus farctus **#**					*			*	3	*
Elymus repens **#**					*					*
Empetrum nigrum	↓	↓	↓	↓	*					V
Epilobium angustifolium **#**					*					*

Epipactis atrorubens **#**					–			–	3	V
Epipactis palustris **#**					2	2	1			3
Erica cinerea	↑↑	↑↑	↑↑	↑↑	–					2
Erica tetralix **#**										V
Erodium ballii	?	?	?	?	*			P	*	*
Erodium danicum	?	?	?	?	–			P	–	–
Erodium lebelii	?	–	?	–	*					*
Eryngium maritimum **#**					3	2	3	2	1	2
Euphrasia micrantha		↓		↓	–	2	1			2
Euphrasia stricta **#**					*	3	3			*
Festuca polesica	–	↓	–	↓	–			–	P	3
Festuca rubra **#**					*					*
Filago arvensis **#**					*					*
Filago minima **#**					*					*
***Galium mollugo* s. str.**	↑	↑	↑	↑	–					D
Galium sterneri	↓		↓		–	–	1			R
Galium verum **#**										*
Genista anglica		↑		↑	0					3
Genista germanica	↓?	↓?	↓	↓	–	–	0			3
Genista pilosa **#**					–					V
Genista tinctoria **#**					1					V
Gentianella campestris* subsp. *baltica					0	1	0			
Gentianella campestris subsp. *campestris*	↓	–	↓	–	–					3
Gentianella uliginosa	↓	↓	↓	↓	0	1	–			1
Glaucium flavum	↑	↑↑	↑	↑↑	R					R
Glaux maritima **#**					*					*
Hieracium umbellatum **#**					*					*

(continued)

Table 10.5 (continued)

Taxon	NS SC1	BS SC1	NS SC2	BS SC2	RL NS	RL WW	RL NW	RL WB	RL SB	RL D
Hippophae rhamnoides **#**					*					*
Hippuris vulgaris **#**					2			2	1	V
Honckenya peploides **#**					*					*
Hordeum marinum	↑	↑↑	↑	↑↑	0	0	0			0
Hordeum secalinum **#**						3	*			3
Ilex aquifolium	↑?	↑	↑?	↑	*			–	1	*
Jasione montana **#**					*					*
Juncus anceps		↑		↑	*	*	2			*
Juncus balticus	↓	↓	↓	↓	0	1	–	0	1	1
Juncus bufonius (incl. *J. ranarius*) **#**					*					*
Juncus gerardii **#**					*			3	3	*
Juncus maritimus	↑		↑		*	*	P	P	*	*
Juncus pygmaeus		↑↑		↑↑	–	–	1			1
Koeleria arenaria	↑?	↑↑?	↑?	↑↑?		3	–			3
Lactuca tatarica					*			P	*	N
Lathyrus japonicus	↓	↓	↓	↓	R	2	*	3	3	3
Leontodon autumnalis **#**					*					*
Leontodon saxatilis **#**					*			2	2	*
Leymus arenarius		↓	↓	↓	*					*
Limonium vulgare		↑?		↑?		2	*	3	2	*
Linnaea borealis	↓	↓	↓	↓	1					1
Linum catharticum **#**					*	3	3			*
Liparis loeselii	↓		↓	↓	2	1	–			2
Listera cordata	↓	↓	↓	↓	–	–	0			3
Listera ovata **#**					3					*

Littorella uniflora **#**					2	2	1			2
Lotus corniculatus **#**					*					*
Lotus tenuis **#**						3	–	3	3	V
Lycium barbarum **#**					*					N
Melilotus dentatus	↓	↓		↓	0			1	2	3
Myosotis stricta			↓							*
Myrica gale					3					3
Najas marina					–			–	2	*
Odontites litoralis	↓	↓	↓	↓	1	1	*	3	2	2
Oenanthe lachenalii	↑?		↑?		3	2	1	2	2	3
Oenothera ammophila (*O. oakesiana*)		??		??	*					N
Ononis spinosa **#**					*			3	3	*
Ophioglossum vulgatum **#**					3	2	2	2	2	3
Parapholis strigosa	V				*	3	3	2	1	3
Parnassia palustris **#**					2	1	–			3
Pedicularis sylvatica **#**					2	0	3			3
Petasites spurius	–	↓	–	↓	1			P	*	3
Phalaris arundinacea **#**					*					*
Phleum arenarium					*	3	–	2	2	3
Phragmites australis **#**					*					*
Pimpinella saxifraga **#**										*
Plantago coronopus **#**					*			3	2	*
Plantago major subsp. *winteri*					G			?	3	3
Plantago maritima **#**					*			*	3	*
Polygala vulgaris **#**					3	3	*			V
Polygonum oxyspermum subsp. *oxyspermum*	–	↓	–	↓	–			1	0	R
Polygonum oxyspermum subsp. *raii*	↓	–	↓	–	–	–	1			R

(continued)

Table 10.5 (continued)

Taxon	NS SC1	BS SC1	NS SC2	BS SC2	RL NS	RL WW	RL NW	RL WB	RL SB	RL D
Polypodium interjectum	–		–		–					*
Polypodium vulgare **#**					*					*
Potamogeton filiformis	–	↓	–	↓	0					2
Potentilla anserina **#**					*					*
Puccinellia capillaris	↓	↓	↓	↓	R	P	*	?	P	3
Puccinellia distans **#**					*					*
Puccinellia maritima **#**					*			3	3	*
Pyrola minor			↓	↓	3	3	3			3
***Pyrola rotundifolia* [subsp. *maritima*]**	(↓)		↓(↓)		R [3]	2	1			R
Radiola linoides **#**					3	2	2			2
Ranunculus peltatus subsp. *baudotii* **#**					3	2	3	2	3	3
Ranunculus sardous **#**					3			2	2	3
Rhinanthus angustifolius **#**						3	3	–	1	3
Rosa mollis **#**					–			P	P	R
Rosa rugosa **#**					*					N
Rosa spinosissima **#**					3	2	3			3
Rubus caesius **#**					*					*
Rumex crispus **#**					*					*
Rumex longifolius	↓	↓	↓	↓	–					N
Ruppia cirrhosa **#**					2	P	1	3	*	3
Ruppia maritima **#**					2	2	1	2	*	2
Sagina maritima **#**					*	2	1	2	2	V
Sagina nodosa **#**					3	2	3	2	2	2
Sagina subulata					–	–	1			1
Salicornia europaea					*			3	3	*

Salicornia stricta					*					*
Salix cinerea **#**					*					*
Salix daphnoides	↓		↓	↓	U			–	P	2
Salix hastata	↓	–	↓	–	–	–	P			R
Salix pentandra	↓	↓	↓	↓	3					*
Salix repens subsp. *argentea* **#**					*			3	3	*
Salsola kali subsp. *kali* **#**					*			3	3	*
Sambucus nigra **#**					*					*
Samolus valerandi **#**					2	2	–	2	2	2
Saxifraga tridactylites					*					*
Schoenoplectus pungens **#**					1	1	0			1
Schoenoplectus triqueter	?	?	?	?	3	2	1			2
Schoenus nigricans					3					2
Scorzonera humilis **#**					–	–	2			3
Senecio jacobaea **#**					*					*
Senecio vernalis					*					N
Silene otites **#**					3	3	1			3
Silene viscosa	–	–	–	–	–			P	0	1
Sonchus arvensis **#**					*					*
Spartina anglica		–		–	*					N
Spergularia media **#**					*					*
Spergularia salina **#**					*					*
Stellaria crassifolia	–	↓	–	↓	–					0
Suaeda maritima **#**					*			3	3	*
Tetragonolobus maritimus	–		–		u			–	1	3
Trifolium campestre **#**					*					*
Trifolium fragiferum **#**					*			3	3	V

(continued)

Table 10.5 (continued)

Taxon	NS SC1	BS SC1	NS SC2	BS SC2	RL NS	RL WW	RL NW	RL WB	RL SB	RL D
Trifolium ornithopodioides					–	–	P			1
Trifolium pratense (subsp. *maritimum*)					*					D
Trifolium repens **#**					*					*
Triglochin maritima **#**					*			3	3	V
Tripleurospermum maritimum **#**					D					*
Tuberaria guttata	↑	↑	↑↑	↑↑	R	1	–			1
Tussilago farfara **#**					*					*
Ulex europaeus	↑	↑	↑	↑	3	2	2			N
Vaccinium uliginosum	↓	↓	↓	↓	3					V
Vaccinium vitis-idaea	↓		↓	↓	2	*	1			*
Veronica officinalis **#**					*					*
Vicia lathyroides **#**					3					V
Viola canina **#**										V
Viola tricolor var. *maritima*					*	*	3	?	*	*
Zannichellia palustris **#**										*
Zostera marina **#**					3	2	3			3
Zostera noltii **#**					3	2	3	1	1	3
Potential decrease	28	27	33	35						
Potential increase	21	25	22	26						

SC1 scenario 1 (best case), *SC2* scenario 2 (worst case), *NS* German North Sea coast, *BS* German Baltic Sea coast; *RL* Red List of: *NS* Lower Saxony coastal region (Garve 2004), *WW* Wadden Sea area of Lower Saxony (von der Ende 1995), *NW* Wadden Sea area of Schleswig-Holstein and Hamburg (von der Ende 1995), *WB* Baltic Sea coast of Schleswig-Holstein (Berg et al. 1996), *SB* Baltic Sea coast of Mecklenburg-Western Pomerania (Berg et al. 1996), *D* Germany (Metzing et al. 2018), ↑↑ predicted immigration, * not threatened,– not present, *0* extinct or missing, *1* threat of extinction, *2* strongly endangered, *3* endangered, *D* no sufficient data, *G* possibly in peril, *N* neophyte, *n. i.* no information, *P* potentially endangered, *R* extremely rare, *u* unsteady occurrence, *V* near threatened,? [in the columns of the Red Lists] present, but status not known

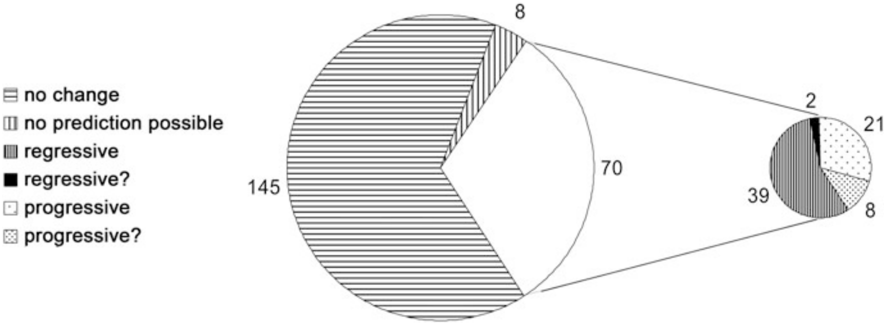

Fig. 10.37 Number of plant taxa for which a shift of the climate envelope will affect the flora of the German coasts (worst-case scenario)

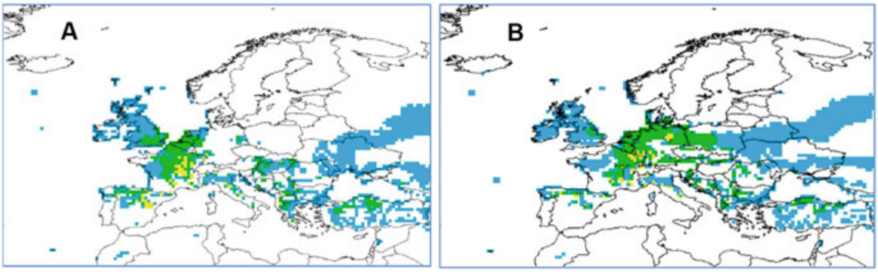

Fig. 10.38 Areas with recent climate similar to the predicted climate for the German coast (best-case scenario: (**a**), worst-case scenario: (**b**)), considering three temperature variables (mean annual yearly temperature, January, and July). The highest congruence exists in the yellow grid cells. In green areas, only two temperature variables (and in blue grid cells only one) recently match the future climate at the German coast (Calculation based on data provided by: IPCC-DDC 1999, reference period 1961–1990)

number of taxa with regressive distribution areas is higher than those with progressive ranges. According to this simplified interpretation, we expect a decrease of the total species number. Hence, a lower phytodiversity (in the sense of species diversity, Hobohm 2000) will be more notable at the North Sea than at the Baltic Sea.

However, for the balance between immigration and emigration one should also consider the immigration of taxa that occur actually outside the German coasts. Thus, the question must be answered from where taxa may immigrate to the German coast. At coasts of Central and Western Europe, the same annual temperature ranges and the same temperatures for January and July as predicted for the German coast are only partly realised, e.g., in The Netherlands up to N-France and SE-England (Fig. 10.38). It has to be assumed that coastal taxa will predominantly spread along the coastline to the German coast. The immigration of species from the Mediterranean area or the Black Sea coast would require long-distance dispersal across the European continent, which is not impossible but unlikely. However, the intentional or unintentional introduction of diaspores by humans and the transport over long distances may happen and facilitate the establishment of alien plants. Plant species may invade even from inland areas of East and Central France. Nevertheless, the successful establishment of non-coastal plants in maritime habitats is less probable.

Several coastal plant taxa have a distribution boundary in the area of the Dutch, Belgian, and French coasts (cf. David 2002; van Dieren 1934; Dijkema 1984; Gibbons and Brough 1998; Mayer 1936; van der Meijden 1996; Weeda and Mennema 1983). Underlined taxa have their easternmost boundary in the Netherlands, at least currently, and are possible candidates for climate change-induced range expansion into the German coastal zone:

Arthrocnemum perenne (Mill.) Fourc. (Amaranthaceae)
Asparagus prostratus Dum. (Liliaceae)
Astragalus arenarius L. (Fabaceae)
Catapodium marinum (L.) C. E. Hubb. (Poaceae)
Crithmum maritimum L. (Apiaceae), but recently found at the German coast (see Sect. 10.5.1)
Dianthus gallicus Pers. (Caryophyllaceae)
Erica cinerea L. (Ericaceae)
Erodium maritimum Sm. (Geraniaceae)
Euphorbia paralias L. (Euphorbiaceae), but recently found at the west coast of Schleswig-Holstein (Haacks et al. 2016)
Euphorbia portlandica L. (Euphorbiaceae)
Frankenia laevis L. (Frankeniaceae)
Inula crithmoides L. (Asteraceae)
Lagurus ovatus L. (Poaceae)
Limonium binervosum agg. (Plumbaginaceae), but recently found at Helgoland (Garve and Kuhbier 2016)
Limonium dodartii (Girard) Kuntze (Plumbaginaceae)
Matthiola sinuata R. Br. (Brassicaceae)
Medicago marina L. (Fabaceae)
Polygonum maritimum L. (Polygonaceae)
Salicornia fragilis P. W. Ball and Tutin (Amaranthaceae)
Salicornia pusilla Woods (Amaranthaceae)
Spergularia rupicola Lebel (Caryophyllaceae)
Suaeda vera J. F. Gmelin (Amaranthaceae), but recently found in Schleswig-Holstein (Graeber and Hebbel 2022)

10.6 Discussion

10.6.1 Methodology

The ecograms are an appropriate tool for a preliminary estimation whether the climate in an area may be sufficient for a species even under climate change conditions. Using these data, potentially threatened species can be ascertained under the predicted climate changes in an area. However, the ecograms only roughly reflect the direction of dislocations for distribution boundaries. A more detailed idea can be given by modelling the distribution areas, based on the predicted climate change and the climate envelope ("climate envelope model").

Due to the heterogeneous spatial and temporary resolution, historical data does not have the high precision that can be obtained from recent and standardised floristic inventories, which has to be considered for their interpretation and evaluation. Usually, complete distribution patterns are available only for a few, mostly rare or botanical attractive species (cf. Kloss and Succow 1966).

The quality of floristic data also depends on the attractiveness or rarity of the respective taxa. As botanists often have a special interest in extraordinary species (e.g. orchids or rare species such as *Calystegia soldanella*), records of these species are more detailed than for common plants and they are represented in herbaria to a higher degree (Metzing 2005). Similarly, the islands with their fascinating landscapes and nature as well as distinct geographic entities have been investigated to a higher extent than the mainland coasts.

A first record gives no information whether the species is established in a specific area or not. This can only be verified by further published information. Moreover, the documentation of a particular locality or grid cell does not provide information about the frequency of species. *Progressive shifts* (expansion of a distribution area) are more easily detected from first records than *regressive shifts* (reduction of a distribution area) from verification of absences. The accurate time of extinction has been recorded only in very few cases. However, the regression of particular species has been noticed and published by botanists in many cases subsequently. For more recent time periods, the interpretation of published distribution maps and Red Lists give a good estimation about declining species ranges.

Analysing historical data, confusion may also derive from taxonomic classification and nomenclature. The less drastic problem of repeated name changes during the last centuries can be solved by consideration of older synonyms. The diverging interpretation about the circumscription of particular taxa is a more serious problem. This process of taxonomic changes has not yet ended. An example is the still confusing taxonomy and nomenclature of *Salicornia,* because the three species accepted were not distinguished in the old literature. Infra-specific taxa typical for maritime habitats, e.g., *Agrostis stolonifera* var. *maritima*, *Plantago major* subsp. *winteri*, or *Trifolium pratense* subsp. *maritimum,* are rarely mentioned in old literature, although it has to be assumed that these taxa were present at the coast during earlier times.

Wrong or at least doubtful records are another possible source of confusion, which has already been pointed out by Ascherson (1888) with regard to the publication of Knuth (1887).

10.6.2 Direction and Rates of Distribution Shifts

Generally, it is assumed that distribution shifts induced by the predicted climate change will occur in polar direction (Gitay et al. 2002). This can be confirmed by our study for most distribution areas. However, some species (in particular Atlantic taxa) with a distribution limit in Germany and adjacent regions are highly correlated with winter temperatures, which enable us to predict an eastward shift.

The models show the direction, distances, and rates of potential distribution shifts, which are needed to be in equilibrium with the climate conditions. But, the inherent character of ecological systems causes a delayed response to changing environmental conditions (IPCC 2002). The real change of distribution patterns will differ among taxa. They will show individual reactions and different migration rates (Franklin et al. 1992; Huntley 1991; Webb III 1992).

Progressive (immigration) and regressive (extinction, emigration) migration have to be distinguished. Whereas immigration is limited by the potential dispersal rate and the establishment ability, growing and completing entire life cycles on new sites depend on delayed mortality and extirpation caused by hardiness and long-lasting life cycles (Jackson and Overpeck 2000; Kirilenko and Solomon 1998) (Table 10.6).

Perennial species may persist a long time under less favourable conditions and even under critical temperatures for germination or establishment. Hence, regressive distribution boundaries will be relocated more slowly than expected from the change of climate patterns. This is especially true for tree species (Franklin et al. 1992), which, however, play only a marginal role in most coastal habitats. But most salt marsh species are perennial. Hence, a delayed reaction has to be assumed here (Adam 2002).

Table 10.6 Attributes of plant species affecting persistence and migration rates

Persistence	High	Low
Genetic variability	High	Low
Life span	Long	Short
Sensitivity to temperature	Only during germination or establishment	During the whole life cycle
Reproduction	Vegetative	Only sexual
Seed bank	Long lasting	Lacking
Migration rate	**Fast**	**Slow**
Reproduction rates	High	Low
Begin of reproductive stage	Early	Late
Diaspores	Mobile (e.g. anemochorous, ornithochorous, hydrochorous)	Largely immobile (autochorous)
Ecological amplitude	Euryoecious	Stenoecious
Dormancy	High variability of duration	Low variability of duration

At the progressive distribution boundaries, the realised migration rate determines the equilibrium between the distribution of plant species and climate change in future. Species with broad ecological amplitude (euryoecious species), high reproduction rates, and mobile diaspores have an advantage compared to stenoecious species (Nathan 2001) (Table 10.6). Species with a long life cycle will show a delayed response (Iverson et al. 2004; Malcolm et al. 2002; Webb III 1992). Plant species dispersed by wind (e.g. most members of the daisy family, orchids, and ferns) or by birds may reach new habitats faster than species with heavy disseminules and without special dispersal strategies (Bonn and Poschlod 1998). Generally, the colonisation of new areas is a long-lasting process. Hence, a delayed response to climate change has to be assumed for most species (Jackson and Overpeck 2000). The chance for successful establishment is at least as important as dispersal (Melillo et al. 1996). The dispersal of fruits, multi-germ seed balls, or vegetative propagules by floating in seawater is an appropriate strategy of many coastal plant species to reach new isolated areas (Packham and Willis 1997).

Even the type of distribution boundary affects the speed of distribution shifts. Range boundary shifts are faster when they are physiologically determined and slower when they are caused by competitive processes.

High migration rates may favour persistence, because the extinction of marginal populations, e.g., caused by a severe winter, may be quickly compensated by the establishment of new marginal populations during years with mild winters.

The shift of distribution ranges is only one effect of the changing environmental conditions. According to the modelled distribution areas, position and size of distribution areas may also change. Migration (M) and persistence (P) result in a "rubber band effect": If the shift of climatic gradients (S) is compensated ($P + M > S$), the distribution range may increase. If persistence and migration rates are low ($P + M < S$), the area size will shrink. Species with low persistence and potential migration rates are particularly endangered by climate change (Berry et al. 2003). Theoretical changes of size range at the regressive and progressive distribution boundaries that also consider a delayed species response to climate change are shown in Fig. 10.39. The real size of bio-climatically appropriate areas (affected by the spatial heterogeneous ratio of sea and land) is omitted in this theoretical model, but would result in an additional change of the potential distribution ranges.

Persistence and migration rates are usually neglected by climate envelope models. Therefore, some authors (e.g. Davis et al. 1998, for a discussion, see Pearson and Dawson 2003) questioned the validity of these models. However, migration rates models are fraught with many uncertainties and often fail to reflect realised migration rates (Higgins et al. 2003; Pitelka 1997). This is due to insufficient knowledge, e.g., about autecology and physiological limits, potential resistance, and migration rates as well as about the sensitivity of the different life cycle stages for most species. There is still an enormous demand for further research (Kappelle et al. 1999).

Nevertheless, it has to be discussed whether species are able to shift their distribution ranges according to the climate change. Depending on the various limiting temperature parameters (winter or summer temperature), the spatial density of isotherms, and the climate change scenarios used here, the migration range shifts

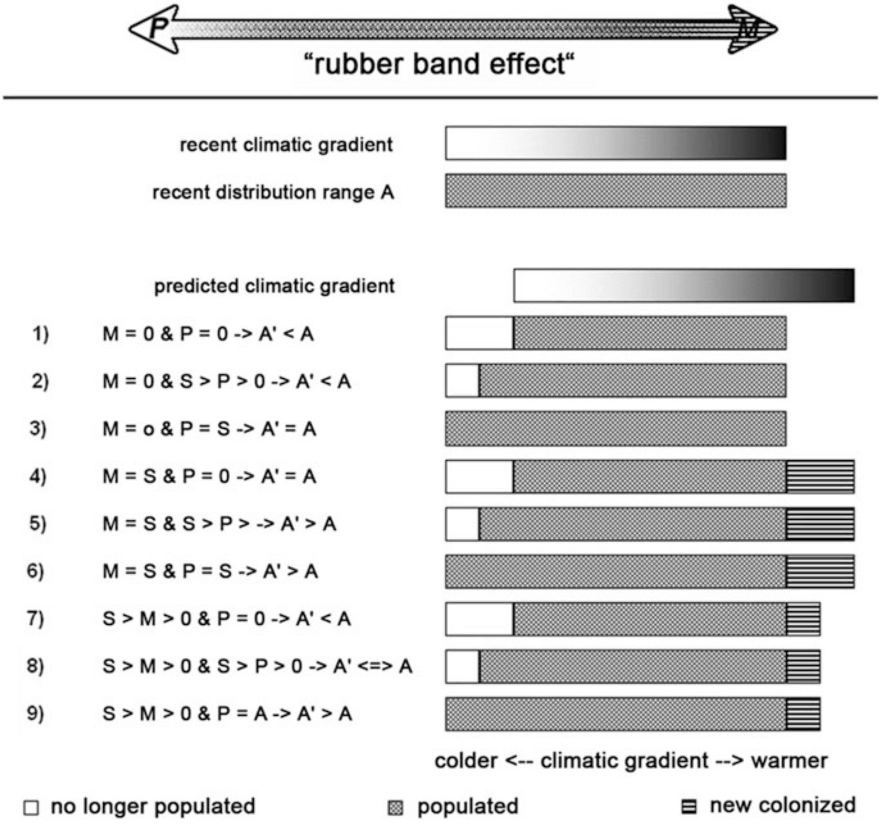

Fig. 10.39 Theoretical model for the effects of migration rates (M) and persistence (R) on the size of distribution areas by climate change ("rubber band effect"). A size of recent distribution range, A' size of the future distribution range, S shift of the climate gradient

between at least 400 km and 1000 km distance according to the models. This means that species ranges have to move with a speed of about 8–20 km year^{-1} (the lower value of 8 km year^{-1} corresponds to the best-case scenario with a warming of 1.5 K).

Calculations of migration rates usually tend to underestimate the realised migration rates (Higgins and Richardson 1999; Higgins et al. 2003). For a few plant species, migration ranges can be derived from palaeo-record studies or more recent observations. The natural reforestation after the last glacial period in Central Europe took a long time, e.g. the migration of *Fagus sylvatica* from the Alpine foothills to Northern Germany lasted about 2500–3000 years and is still ongoing in England and Scandinavia (Lang 1994; Pott 1997). The realised migration rate was calculated for both beech and other tree species with 150–300 m year^{-1} and 40–2000 m year^{-1}, respectively (Huntley 1991; Lang 1994; Nathan 2001). The Spring Groundsel (*Senecio vernalis*), originating in East Europe and invading Central Europe from the beginning of the nineteenth century, covered a distance of 700 km within

100 years, hence about 7 km year^{-1} (cf. Beger in Wagenitz 1981). Migration rates of 6–50 km year^{-1} were recorded for other invasive plant species (Malcolm et al. 2002). For the functional plant types of grasses and herbs, mean migration rates of 10 km year^{-1} were supposed (Kirilenko and Solomon 1998). For *Cakile maritima*, migration rates of 50 km year^{-1} were observed in California (Barbour and Rodman 1970; Sauer 1988). These values indicate that the observed migration rates fall within the middle and upper range of the modelled distribution shifts—particularly for the worst-case scenario.

Coastal habitats provide more favourable conditions for dispersal compared with habitats of other regions, such as cultivated landscapes, settlement areas, or high mountains. High fragmentation of suitable habitats is an important factor that limits a fast dispersion (Davis 1989; Iverson and Prasad 2002; Thomas 2003). Scattered small suitable and isolated habitats prevent shifts of progressive distribution boundaries and the colonisation of habitats. At the coast, most habitats are low fragmented along great distances and arranged in linear order. Therefore, no significant dispersal barriers for migration exist along coasts. This is particularly true for the habitats of the drift lines and salt marshes (Beeftink 1977), but less distinct for dune habitats or salt grasslands of the Baltic Sea coast. Only the land barrier of Schleswig-Holstein has to be passed (or bypassed via Jutland) for a potential migration from the Wadden Sea to the Baltic Sea coast. The decreasing salt concentration in the Baltic Sea towards the east was not taken into account in the models, but may act as distribution barrier for some halophytic species.

Disseminules of many coastal plant species, mainly those of the salt marshes, drift lines, and fore- and yellow dunes, are well adapted to dispersal by seawater and may float over long time periods and distances (Chang 2006; Hensen 1998; Huiskes et al. 1995; Koutstaal et al. 1987; Leege 1913; Packham and Willis 1997). In drift line material as well as in floating water, diaspores of many species can be found (Gerlach 1999; Persicke et al. 1999; Wolters et al. 2004, 2005). The predominant western wind direction as well as the main tidal currents running parallel to the coastline of the Wadden Sea favours the dispersion for species immigrating from western or southwestern regions. Moreover, the predominant wind direction and the stronger winds at the coast are advantageous for long-distance dispersion of anemochorous species from (south) west to (north) east. The bird-mediated dispersion of seeds and diaspores along the coast is of high importance (Figuerola and Green 2002a, b; Figuerola et al. 2002; Leege 1937; Reinke 1909; Vivian-Smith and Stiles 1994). The strict demand of coastal habitat conditions may be a disadvantage, because plants cannot evade to inland habitats with similar environmental conditions (here: climate). In general, the conditions for progressive distribution shifts are rather favourable at the coast.

The response of individual species will result in new species compositions with changed biotic interactions. As distribution boundaries depend only partly on physiological limits but additionally on biotic factors and competition among species (Bullock et al. 2000; Guisan and Zimmermann 2000), the model predictions may fail in some cases (Davis et al. 1998). The potential migration rates are limited by the slowest partner, if interdependences among species are very confined or taxon-specific (pollinator plant or phytophage plant). The different climate sensitivities may change the biotic interactions and result in modified competition and ecological ranges, which are predicted by the models (Davis and Zabinski 1992). However, the great number of observed responses to climate change, which correspond with the model predictions, shows that equilibrium models are appropriate tools to predict future distribution shifts caused by climate change (Parmesan and Yohe 2003; Parmesan 2004).

Disturbance variables (agriculture, coastal defence, habitat destruction, a. o.), which already affect coastal plant species, may be amplified or extenuated by the climate change. The number of presently threatened plant species is higher for salt marshes than for dunes (Metzing et al. 2018). According to our study, climate change will result in an inverse effect, so that 30 species of dunes and dune slacks, but only eight species of salt marshes will suffer under a reduced distribution range at the German coast (Metzing 2005). The distribution shifts predicted in this study represent only a part of potential plant species responses to changing climate. Climate change and effects of other environmental factors are combined in a complex framework with presently unknown and only partially quantified consequences (Gitay et al. 2001).

Of particular interest from a human perspective are the effects of climate change on key species that characterise coastal ecosystems or those that are important for coastal protection. Such species with a predicted retreat in the Wadden Sea are, e.g., *Leymus arenarius* and ×*Calammophila baltica*. Both species are planted for coastal defence purposes in yellow dunes. *Empetrum nigrum* is another species, for which the model predicts a loss in the Wadden Sea under the worst-case scenario. On islands of the German coast, the Crowberry predominantly colonises the cooler northern slopes of dunes, where drought stress is less likely. Already now, long summer dry periods lead to a partial dieback of the stands (Mühl 1993). Here, the combination of temperature and humidity determines the southern distribution limit (Metzing 2005; Hein et al. 2021). A loss of this species will change the appearance and function of brown dunes at the islands conspicuously (Metzing 2010).

10.6.3 Climate Change and Biodiversity

The species number of the German coastal area was never a stable variable. Most changes of species numbers in the past two centuries can be explained by anthropogenic effects such as the introduction and dispersion of neophytes, the destruction of habitats, agriculture, land use change, a. o. (cf. Berg et al. 1996; Bröring and Niedringhaus 1989; van der Ende 1995; Korneck et al. 1996; Lohmeyer and Sukopp 1992; Raabe 1973). In view of the predicted climate change, climate will gain a higher relevance on future plant distributions compared with other causes of declining or enlarging distribution ranges. The results of this study enable us to interpret and discriminate the potential causes of flora changes in the future. The potential effect of climate change on biodiversity in the coastal area is evident. For nearly a third of the studied plant taxa, an effect of climate change on their distribution along the German coasts can be expected with a half of them that may disappear from this area or at least from parts of it. The balance of immigration and local extinction will determine a loss or gain of biodiversity.

Potential immigration is more difficult to estimate than emigration, because potential invaders may come not only from coastal regions, but also from the inland, which was omitted in this study for methodological reasons. The generally higher species diversity in southern regions is no basis to predict an increasing plant species number at the German coasts. Maps of phytodiversity (e.g. Barthlott et al. 1996; Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo 2001) reveal no significant difference between the species number at the German coasts and the channel coast (N-France, S-England).

Climate change is no reason to assume a retarded species loss because many studies prove the opposite process (Gitay et al. 2002). Thomas et al. (2004) analysed the extinction risk of endemic plant and animal species and ascertained 15–37% (depending on the scenario and different ecosystem complexes). Leuschner and Schipka (2004) mentioned a species loss of 5–30% in Central Europe, based on a review of published studies (flora and fauna). According to Bakkenes et al. (2002), an average of 32% of the plant species will disappear in Europe (at 44% of the total geographical area size). In The Netherlands, a loss of 64 species caused by anthropogenic and climate effects has been countervailed by the immigration of 84 species (neophytes) during the last decades (Kappelle et al. 1999). In this study, we predict a shrinkage of distribution ranges within the area of the German coasts for 17% of the studied taxa, whereas the definite percentage depends on size and position of the geographical area regarded. This may be countervailed by immigration of alien species, at least partly (Metzing 2005).

10.7 Conclusion

Whereas prior studies about the consequences of climate change for coastal habitats mainly deal with sea level rise effects, this study focuses on the effect of a warming climate on the flora of salt marshes and dunes of the North Sea and Baltic Sea coasts. However, the modelling and prediction of future distribution shifts are only one step towards an understanding of flora changes caused by climate change (Leuschner and Schipka 2004). The enhancement of the used models, further approaches, and adjustments with results from monitoring projects (to be established!) as well as ecophysiological experiments for key species will increase our knowledge about probable effects of climate change on the coastal flora and its consequences for nature conservation, coastal defence and the interaction with other variables (Metzing 2005, 2006).

Appendix

Table 10.7 Abbreviations, Origin and Calculation of Climate Data and Derived Variables

Abbreviation	Climatic parameter (1961–1990)	Calculation	Source of data
Temp.	*Mean temperature*		
T_{year}	Mean temperature of the year	$(T_{Jan} + T_{Feb} + \ldots + T_{Dec})/ 12$	
$T_{Jan;}$ $T_{Feb, \ldots\ldots}$ T_{Dec}	Mean temperature in January, February……December		IPCC-DDC 1999
Temp. Max.	*Maximum temperature*		
Max_{year}	Mean maximum temperature of the year	$(Max_{Jan} + Max_{Feb} + \ldots + Max_{Dec})/ 12$	
$Max_{Jan;}$ Max_{Jul}	Mean maximum temperature in January; July		IPCC-DDC 1999
Temp. Min.	*Minimum temperature*		
Min_{year}	Mean minimum temperature of the year	$(Min_{Jan} + Min_{Feb} + \ldots + Min_{Dec})/ 12$	
$Min_{Jan;}$ Min_{Ju}	Mean minimum temperature in January; July		IPCC-DDC 1999
Frost	*Ground frost frequency*		
Fro_{year}	Mean number of frost days in the year	$(Fro_{Jan} + Fro_{Feb} + \ldots + Fro_{Dec})/ 12$	
$Fro_{Jan;}$ Fro_{Jul}	Mean number of frost days in January; July		IPCC-DDC 1999
Psum	*Precipitation sum*		
$6_{coldest}$	Sum of mean precipitation November to April	$P_{Nov} + P_{Dec\ +\ \ldots\ +}\ P_{Apr}$	
$6_{warmest}$	Sum of mean precipitation May to October	$P_{Mai} + P_{Jun\ +\ \ldots\ +}\ P_{Okt}$	
P_{SUMJA}	Sum of mean precipitation June to august	$P_{Jun} + P_{Jul\ +}\ P_{Aug}$	
Tsum	*Temperature sum*		
$Tsum_{05–07}$	Sum of mean temperature May to July	$T_{May} + T_{Jun\ +}\ T_{Jul}$	
$Temp_5$	Months with mean temperature > 5 °C	$n_{T\ >\ 5°C}$	

$Temp_{10}$	Months with mean temperature > 10 °C	$n_{T > 10°C}$	
Ampl.	*Temperature ranges*		
Diu_{Year}	Mean diurnal range of the year	$(Diu_{Jan} + Diu_{Feb} + \ldots + Diu_{Dec})/ 12$	
Diu_{Jan}	Mean diurnal range in January		IPCC-DDC 1999
Diu_{Jul}	Mean diurnal range in July		IPCC-DDC 1999
$Ampl_{Year}$	Difference between coldest and warmest mean monthly temperature	Maximum (T_{Jul} /T_{Aug})–minimum (T_{Jan} / T_{Feb})	
Cont.	*Continentality*		
Conrad46	Thermic continentality after Conrad (1946)	$\frac{1,7\ AmplJ}{\sin(\varnothing + 10°)} - 14$	
Jalas50	Hygric continentality after Jalas (1950)*	$\frac{P_{Jun}+P_{Jul}+P_{Aug}}{(P_{Jan}+P_{Feb}+\ldots+P_{Dec})} 100$	
Henze29	Hygric continentality after Henze (1929)	$(P_{May} + P_{Jun} + P_{Jul})–(P_{Aug} + P_{Sep} + P_{Oct})$	
Angot06	Hygric continentality after Angot (1906)*	$6_{warmest}/6_{coldest}$	
P	*Precipitation*		
P_{Year}	Mean precipitation (mm) of the year	$(P_{Jan} + P_{Feb} + \ldots + P_{Dec})$	
$P_{Jan;}\ P_{Feb.\ldots\ldots}\ P_{Dec}$	Mean precip. (mm) in January, February. . ...December		IPCC-DDC 1999
Moist.	*n. of wet days (P > 0,1 mm)*		
$Moist_{Year}$	Mean number of wet days in the year	$(Moist_{Jan} + Moist_{Feb} + \ldots + Moist_{Dec})/12$	
$Moist_{Jan;}\ Moist_{Jul}$	Mean number of wet days in January; July		IPCC-DDC 1999
Cloud.	*Cloud cover (%)*		
$Cloud_{Year}$	Mean cloud cover in the year	$(Cloud_{Jan} + Cloud_{Feb} + \ldots + Cloud_{Dec})/12$	
$Cloud_{Jan,}\ Cloud_{Jul}$	Mean cloud cover in January; July		IPCC-DDC 1999

(continued)

Table 10.7 (continued)

Abbreviation	Climatic parameter (1961–1990)	Calculation	Source of data
Hygr.	*Hygric indices (aridity indices)*		
Lau_{Mean}	Rel. Aridity after Lauer, year	$(12\ P_{\text{Year}})/(T_{\text{Year}} + 10)$	
Lau_{Jul}	Rel. Aridity after Lauer, July	$(12\ P_{\text{Jul}})/(T_{\text{Jul}} + 10)$	
$\text{Walt}_{\text{Mean}}$	Rel. Aridity after Walter, year	$P_{\text{Year}} - 2T_{\text{Year}}$	
$\text{Walt}_{\text{Jul;}}\ \text{Walt}_{\text{Jan}}$	Rel. Aridity after Walter, July; January	$P_{\text{Jul}}-2T_{\text{Jul;}}\ P_{\text{Jan}}-2T_{\text{Jan}}$	
Resp.	*Respiration*		
Respirat	Respiration after Skre (1979)	$\text{Re} = 0{,}575\ T_{\text{Jul}} + 0{,}101\ T_{\text{Jan}}-2{,}77$	
lnResp	Respiration, logarithmic	$\ln_{\text{Re}}$	
Rad.	*Radiation (W/m^2)*		
$\text{Rad}_{\text{Jul;}}\ \text{Rad}_{\text{jan}}$	Mean radiation in July; January		IPCC-DDC 1999
Wind	*Wind speed (m/sec)*		
$\text{Wind}_{\text{Year}}$	Mean wind speed in the year	$(\text{Wind}_{\text{Jan}} + \text{Wind}_{\text{Feb}} + \ldots + \text{Wind}_{\text{Dec}})/12$	
$\text{Wind}_{\text{Jan;}}\ \text{Wind}_{\text{Jul}}$	Mean wind speed in January; July		IPCC-DDC 1999
* Cited according to Tuhkanen 1980			

References

Adam P (2002) Salt marshes in a time of change. Environ Conserv 29:39–61

Ascherson P (1888) Ueber Knuths Flora von Schleswig-Holstein. Abhandlungen des Botanischen Vereins der Provinz Brandenburg 29:132–166

Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Glob Chang Biol 8:390–407

Barbour MG, Rodman JE (1970) Saga of the west Coast Sea-rockets: *Cakile edentula* ssp. *californica* and *C. maritima*. Rhodora 72:370–386

Barthlott W, Lauer W, Placke A (1996) Global distribution of species diversity in vascular plants: towards a global world map of phytodiversity. Erdkunde 50:317–327

Baumgardt E (1848) Flora von Pommern und Rügen, 2nd edn. F. Müller, Stettin

Beeftink WG (1977) The coastal salt marshes of western and northern Europe: an ecological and phytosociological approach. In: Chapman VJ (ed) Ecosystems of the world 1: wet coastal ecosystems. Elsevier, Amsterdam, pp 109–155

Beeftink WG, Daane MC, de Munck W, Nieuwenhuize J (1978) Aspects of population dynamics in *Halimione portulacoides* communities. Vegetatio 36:31–43

Benkert D, Fukarek F, Korsch H (1996) Verbreitungsatlas der Farn- und Blütenpflanzen Ostdeutschlands. G. Fischer, Jena

Berg C, Henker H, Mierwald U (1996) Rote Liste und Artenliste der Gefäßpflanzen des deutschen Küstenbereichs der Ostsee. Schriftenreihe für Landschaftspflege und Naturschutz 48:29–39

Berry PM, Dawson TP, Harrsion PA, Pearson RG, Butt N (2003) The sensitivity and vulnerability of terrestrial habitats and species in Britain and Ireland to climate change. J Nat Conserv 11:15–23

Bettinger A, Buttler KP, Caspari S, Klotz J, May R, Metzing D (eds) (2013) Verbreitungsatlas der Farn- und Blütenpflanzen Deutschlands. Landwirtschaftsverlag, Münster

BfN (1999) FloraWeb. Accessed March 1 1999 from www.floraweb.de

Bielefeld R (1900) Flora der ostfriesischen Halbinsel und ihrer Gestade-Inseln. D. Soltau, Norden

Blamey M, Grey-Wilson C (1989) The illustrated flora of Britain and northern Europe. Hodder and Stoughton, London

Blümel C, Kiphuth S, Brozio K (1999) Floristische Mitteilungen aus Greifswald und Umgebung I. Botanischer Rundbrief für Mecklenburg-Vorpommern 33:71–80

Boll E (1848) Die Seestrands- und Salinenflora der deutschen Ostseeländer. Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg 2:67–86

Boll E (1860) Flora von Mecklenburg. Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg 14:1–404

Bonn S, Poschlod P (1998) Ausbreitungsbiologie der Pflanzen Mitteleuropas. Quelle & Meyer, Wiesbaden

Boorman LA (1992) The environmental consequences of climatic change on British salt marsh vegetation. Wetl Ecol Manag 2:11–21

Borcherding R (1999) Raritätenkabinett: Der Gelbe Hornmohn (*Glaucium flavum*). Wattenmeer International 17:27

Box EO, Crumpacker DW, Hardin ED (1993) A climatic model for location of plant species in Florida, U.S.A. J Biogeogr 20:629–644

Box EO, Crumpacker DW, Hardin ED (1999) Predicted effects of climatic change on distribution of ecologically important native tree and shrub species in Florida. Clim Chang 41:213–248

Bröring U, Niedringhaus R (1989) Veränderungen der Wanzen- und Zikadenfauna innerhalb von 50 Jahren auf der ostfriesischen Insel Borkum (Hemiptera: Heteroptera, Geocorisae; Auchenorrhyncha). Oldenburger Jahrbuch 89:337–356

Buchenau F (1881) Flora der Ostfriesischen Inseln. Braams, Norden [a. o.]

Buchenau F (1891) Flora der Ostfriesischen Inseln, 2nd edn. H. Braams, Norden

Buchenau F (1901) Flora der Ostfriesischen Inseln (einschliesslich der Insel Wangeroog), 4th edn. W Engelmann, Leipzig

Bullock JM, Edwards RJ, Carey PD, Rose RJ (2000) Geographical separation of two *Ulex* species at three spatial scales: does competition limit species' ranges? Ecography 23:257–271

Chang ER (2006) The role of dispersal constraints in the assembly of salt marsh communities. PhD thesis, University of Groningen

Chapman VJ (1950) Biological flora of the British Isles: *Halimione portulacoides* (L.) Aell. J Ecol 38:214–222

Chapman VJ (1974) Salt marshes and salt deserts of the world, 2nd edn. J. Cramer, Lehre

Christiansen W (1949) Verzeichnis der Pflanzen-Standorte in Schleswig-Holstein. In: Bücher der Heimat, vol 2. Die Heimat, Kiel

Christiansen W (1953) Neue kritische Flora von Schleswig-Holstein. H. Möller & Söhne, Rendsburg

Christiansen W (1961) Flora der Nordfriesischen Inseln. Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg N. F 4:1–127

Christiansen W, Kohn H-L (1958) Flora von Helgoland. Abhandlungen herausgeben vom Naturwissenschaftlichen Verein zu Bremen 35:209–227

Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo (2001) Number of species. Accessed April 12, 2003, from http://www.fmnh.helsinki.fi/english/botany/afe/publishing/nrspecie.gif

Conrad V (1946) Usual formula of continentality and their limits of validity. Trans Am Geophys Union 27:663–664

Crawford RMM, Palin MA (1981) Root respiration and temperature limits to the north-south distribution of four perennial maritime plants. Flora 171:338–354

Dahl E (1998) The phytogeography of northern Europe. Cambridge University Press, Cambridge

David J (2002) Les plantes du bord de mer. Editions Jean-Paul Gisserot, Luçon

Davis MB (1989) Lags in vegetation response to greenhouse warming. Clim Chang 15:75–82

Davis MB, Zabinski C (1992) Changes in geographical range resulting from greenhouse warming: effects on biodiversity in forests. In: Peters RL, Lovejoy TE (eds) Global warming and biological biodiversity. Yale University Press, New Haven, pp 297–308

Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S (1998) Making mistakes when predicting shifts species range in response to global warming. Nature 391:783–786

de Leeuw J (1992) Dynamics of salt marsh vegetation. Proefschrift, Rijksuniversiteit, Groningen

Dierssen K (1988) Rote Liste der Pflanzengesellschaften Schleswig-Holsteins. Schriftenreihe des Landesamtes für Naturschutz und Landschaftspflege Schleswig-Holstein 6:1–157

Dierssen K (1993) Mögliche Auswirkungen von Klimaänderungen auf die Vegetationsentwicklung in Küsten-Salzrasen. In: Schellnhuber H-J, Sterr H (eds) Klimaänderung und Küste. Einblick ins Treibhaus, Springer, Berlin and Heidelberg, pp 189–195

Dierssen K, Mierwald U (1987) Atlas der Flora Schleswig-Holsteins und Hamburgs. K. Wachholtz, Neumünster

Dijkema KS (1984) Nature and environment series, no. 30. In: Salt marshes in Europe. European Committee for the Conservation of Nature and Natural Sources, Strasbourg

Dijkema KS (1992) Sea level rise and management of salt marshes. Wadden Sea Newsletter 2:7–10

Dijkema KS (1994) Auswirkungen des Meeresspiegelanstiegs auf die Salzwiesen. In: Lozán JL, Rachor E, Reise K, von Westernhagen H, Lenz W (eds) Warnsignale aus dem Wattenmeer. Blackwell Wissenschaftsverlag, Berlin, pp 196–200

Dijkema KS, Bossinade JH, Bouwsema P, Glopper RJD (1990) Salt marshes in the Netherlands Wadden Sea: rising high tide levels and accretion enhancement. In: Beukema JJ, Wolff WJ, Brouns JJWM (eds) Expected effects of climatic change on marine coastal ecosystems. Kluver, Dordrecht, pp 173–188

Edgerton LT (1991) The rising tide. Global warming and world sea levels. Island Press, Washington

Eigner J (1972) Polygonum oxyspermum Meyer et Bunge neu für Schleswig-Holstein. Kieler Notizen zur Pflanzenkunde in Schleswig-Holstein 4:21–25

Eigner J (2014) Der Meerfenchel (*Crithmum maritimum*) auf Pellworm. Kieler Notizen zur Pflanzenkunde 40:53–55

Figuerola J, Green AJ (2002a) How frequent is external transport of seeds and invertebrate eggs by waterbirds? A study in Doñana, SW Spain. Arch Hydrobiol 155:557–565

Figuerola J, Green AJ (2002b) Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshw Biol 47:483–494

Figuerola J, Green AJ, Santamaría L (2002) Comparative dispersal effectiveness of wigeongrass seeds by waterfowl wintering in south-West Spain: quantitative and qualitative aspects. J Ecol 90:989–1001

Fitter A (1978) An atlas of wild flowers of Britain and northern Europe. Collins, London

Fitter R, Fitter A, Farrer A (1984) Grasses, sedges, rushes and ferns of Britain and northern Europe. Collins, London

Franklin JF, Swanson FJ, Harmon ME, Perry DA, Spies TA, Dale VH, McKee A, Ferrell WK, Means JE, Gregory SV, Lattin JD, Schowalter TD, Larsen D (1992) Effects of global climatic change on forests in northwestern North America. In: Peters RL, Lovejoy TE (eds) Global warming and biological diversity. Yale University Press, New Haven, pp 244–257

Fukarek F, Henker H (1983) Neue kritische Flora von Mecklenburg (1. Teil). Archiv der Freunde der Naturgeschichte in Mecklenburg 23:28–133

Garve E (1982) Die *Atriplex*-Arten (Chenopodiaceae) der deutschen Nordseeküste. Tuexenia 2: 287–333

Garve E (1994) Atlas der gefährdeten Farn- und Blütenpflanzen in Niedersachsen und Bremen. Naturschutz und Landschaftspflege in Niedersachsen 30:1–895

Garve E (2004) Rote Liste und Florenliste der Farn- und Blütenpflanzen in Niedersachsen und Bremen. 5. Fassung, Stand 1.3.2004. Informationsdienst Naturschutz Niedersachsen 24:1–76

Garve E (2007) Verbreitungsatlas der Farn- und Blütenpflanzen in Niedersachsen und Bremen. Naturschutz und Landschaftspflege in Niedersachsen 43:1–507

Garve E, Kuhbier H (2016) Floristische Überraschungen auf Helgoland. Floristische Rundbriefe 50:72–83

Gerlach A (1999) Winter driftline debris on the Wadden island of Mellum, Germany; distribution, quantity and decomposition. Abhandlungen herausgegeben vom Naturwissenschaftlichen Verein zu Bremen 44:707–724

Gibbons B, Brough P (1998) Der grosse Kosmos-Naturführer Blütenpflanzen, 2nd edn. Franckh-Kosmos, Stuttgart

Gitay H, Brown S, Easterling W, Jallow B (2001) Ecosystems and their goods and services. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskel K, Johnson CA (eds) Climate change 2001: the scientific basis. Cambridge University Press, Cambridge, pp 235–342

Gitay H, Suárez A, Watson RT, Dokken DJ (eds) (2002) Climate change and biodiversity. IPCC Technical Paper V. Intergovernmental Panel on Climate Change, Geneva

Graeber U, Hebbel J (2022) Die Strauchige Sode (*Suaeda vera*) – eine mediterrane Küstenpflanze neu im Schleswig-Holsteinischen Wattenmeer. Kieler Notizen zur Pflanzenkunde 46:27–36

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186

Haacks M, Janinhoff N, Petersen J, Stock M, Dauck H-P, Bertram G (2016) Floristische Besonderheiten der Nordseeküstendünen Schleswig-Holsteins 2012–2014. Kieler Notizen zur Pflanzenkunde 41:105–123

Haeupler H, Muer T (2000) Bildatlas der Farn- und Blütenpflanzen Deutschlands. E. Ulmer, Stuttgart

Haeupler H, Schönfelder P (1988) Atlas der Farn- und Blütenpflanzen der Bundesrepublik Deutschland. E. Ulmer, Stuttgart

Häpke L (1880) Notizen über die Flora von Borkum. Abhandlungen herausgegeben vom Naturwissenschaftlichen Vereine zu Bremen 6:507–509

Hein N, Merkelbach J, Zech K, Weijers S (2021) Drought sensitivity of *Empetrum nigrum* shrub growth at the species' southern lowland distribution range margin. Plant Ecol 222:305–321

Hellwig U, Kuhbier H (2000) Flora der Farn- und Blütenpflanzen von Scharhörn und Nigehörn. Seevögel 21:19–25

Hensen I (1998) Life strategies in salt marsh communities of the east Frisian North Sea coast (North-Western Germany). Fragmenta Floristica et Geobotanica 43:237–256

Henze H (1929) Ozeanität und Kontinentalität bei den sommerlichen Niederschlägen Norddeutschlands. Meteorologische Zeitung 46:129–137

Heydemann B (1984) Das Ökosystem "Küsten-Salzwiese"– ein Überblick. Faunistisch-Ökologische Mitteilungen 5:249–279

Heydemann B (1997) Neuer biologischer Atlas. Ökologie für Schleswig-Holstein und Hamburg. Wachholtz, Neumünster

Heykena A (1965) Vegetationstypen der Küstendünen an der östlichen und südlichen Nordsee. Mitteilungen der Arbeitsgemeinschaft für Floristik in Schleswig-Holstein und Hamburg 13:1–135

Higgins SI, Richardson DM (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. Am Nat 153:464–475

Higgins SI, Nathan R, Cain ML (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84:1945–1956

Hobohm C (1986) Die Salzwiesen von Sylt. Kieler Notizen zur Pflanzenkunde in Schleswig-Holstein und Hamburg 18:57–99

Hobohm C (1995) Gibt es *Juncus anceps* an der Ostseeküste? Floristische Rundbriefe 29:144–150

Hobohm C (2000) Biodiversität. Quelle & Meyer, Wiebelsheim

Hoffmann MH (2000) Biogeography and climatic differentiation of two annual species of Teesdalia R Br. (Brassicaceae). J Biogeogr 27:989–999

Hoffmann MH, Welk E, Zapp M (2002) Climatic mean diagrams: a technique for assessing the climatic differentiation of species. Plant Syst Evol 231:191–202

Hofstede JLA (1999) Mögliche Auswirkungen eines Klimawandels im Wattenmeer. Petermanns Geogr Mitt 143:305–314

Hoshovsky M (2004) Element stewardship abstract for *Ulex europaeus*. Nature Conservancy, Arlington

Huiskes AHL (1990) Possible effects of sea level changes on salt-marsh vegetation. In: Beukema JJ, Wolff WJ, Brouns JJWM (eds) Expected effects of climatic change on marine coastal ecosystems. Kluver, Dordrecht, pp 167–172

Huiskes AHL, Koutstaal BP, Herman PMJ, Beeftink WG, Markusse MM, de Munck W (1995) Seed dispersal of halophytes in tidal salt marshes. J Ecol 83:559–567

Hulten E, Fries M (1986) Atlas of north European vascular plants: north of the tropic of cancer, vol 3. Koeltz, Königstein

Huntley B (1991) How plants respond to climate change: migration rates, individualism and the consequences for plant communities. Ann Bot 67:15–22

Huntley B, Berry PM, Cramer W, McDonald AP (1995) Modelling present and potential future ranges of some European higher plants using climate response surfaces. J Biogeogr 22:967–1001

IPCC (1999) Data Distribution Centre Providing climate change and related scenarios for impacts assessments. CD-ROM, Version 1.0. IPCC DDC, Norwich

IPCC (2002) Klimaänderung 2001: Synthesebericht. Deutsche IPCC Koordinierungsstelle des BMBF und BMU, Bonn

Iverson LR, Prasad AM (2002) Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. For Ecol Manag 155:205–222

Iverson LR, Schwartz MW, Prasad AM (2004) How fast and far might tree species migrate in the eastern United States due to climate change. Glob Ecol Biogeogr 13:209–219

Jaap O (1898) Zur Gefässpflanzen-Flora der Insel Sylt. Allgemeine Botanische Zeitschrift für Systematik, Floristik, Pflanzengeographie etc 4(5–6):19–20

Jackson ST, Overpeck JT (2000) Responses of plant populations and communities to environmental changes of the late quaternary. Paleobiology 26:194–220

Jäger EJ (1992) Kausale Phytochorologie und Arealdynamik. Habilitation thesis. Martin-Luther-Universität, Halle-Wittenberg

Jalas J, Suominen J (1986) Atlas Florae Europaeae: Caryophyllaceae (Silenoideae), vol 7. Committee for mapping the flora of europe and societas biologica fennica, Vanamo

Jalas J, Suominen J, Suominen R (1999) Atlas Florae Europaeae 1999. PC program, free evaluation copy. Botanical Museum, Finnish Museum of Natural History, Helsinki

Jeffree EP, Jeffree CE (1994) Temperature and the biogeographical distributions of species. Funct Ecol 8:640–650

Jeffree CE, Jeffree EP (1996) Redistribution of the potential geographical ranges of mistletoe and Colorado beetle in Europe in response to the temperature component of climate change. Funct Ecol 10:562–577

Junge P (1913) Über *Atriplex laciniatum* L. und *Convolvulus soldanella* im deutschen Nordseegebiet. Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein 15: 321–327

Kappelle M, van Vuuren MMI, Baas P (1999) Effects of climate change on biodiversity: a review and identification of key research issues. Biodivers Conserv 8:1383–1397

Kennedy VS, Twilley RR, Kleypas JA, Cowan H Jr, Hare SR (eds) (2002) Coastal and marine ecosystems and global climate change. Potential effects on U. S. resources. Pew Center on Global Climate Change, Arlington

Kirilenko AP, Solomon AM (1998) Modelling dynamic vegetation response to rapid climate change using bioclimatic classification. Clim Chang 38:15–49

Kloss K, Succow M (1966) Karten zur Pflanzengeographie Mecklenburgs. Dritte Reihe. Salz- und Strandpflanzen (1. Teil). Wissenschaftliche Zeitschrift der Ernst-Moritz-Arndt-Universität Greifswald 15:9–40

Knapp HG, Jage H (1978) Zur Ausbreitungsgeschichte von *Lactuca tatarica* (L.) CA Meyer in Mitteleuropa. Feddes Repertorium 89:453–474

Knuth P (1887) Flora der Provinz Schleswig-Holstein, des Fürstentums Lübeck, sowie des Gebietes der freien Städte Hamburg und Lübeck, vol 1. O Lenz, Leipzig

Knuth P (1895) Flora der Nordfriesischen Inseln. Lipsius & Tischer, Kiel

Köck U-V (1986) Verbreitung, Ausbreitungsgeschichte, Soziologie und Ökologie von *Corispermum leptopterum* (Aschers.) Iljin in der DDR. I. Verbreitung und Ausbreitungsgeschichte. Gleditschia 14:305–325

König D (1948) Spartina townsendii an der Westküste von Schleswig-Holstein. Planta 36:34–70

Korneck D, Schnittler M, Vollmer I (1996) Rote Liste der Farn- und Blütenpflanzen (Pteridophyta et Spermatophyta) Deutschlands. Schriftenreihe für Vegetationskunde 28:21–187

Koutstaal BP, Markusse MM, de Munck W (1987) Aspects of seed dispersal by tidal movements. In: Huiskes AHL, Blom CWPM, Rozema J (eds) Vegetation between land and sea. Dr W Junk Publ, Dordrecht, pp 226–233

Kremer BP, Wagner A (2001) Crithmum maritimum L. neu für Deutschland. Floristische Rundbriefe 34:1–8

Krisch H (1991) Atriplex longipes Drejer auch an der deutschen Ostseeküste. Botanischer Rundbrief für Mecklenburg-Vorpommern 23:41–43

Krisch H (2002) Über *Atriplex longipes* und die Nachweise derselben in Vorpommern. Floristische Rundbriefe 35:73–84

Kutscher M (1995) Flora und Fauna an der Ostseeküste von Mecklenburg-Vorpommern. Schwerin, Demmler

Lang G (1994) Quartäre Vegetationsgeschichte Europas. G. Fischer, Jena [a. o]

Latron M, Arnaud J-F, Ferla H, Gode C, Duputie A (2020) Effects of contemporary shifts of range margins on patterns of genetic structure and mating system in two coastal plant species. Heredity 124:336–350

Leege O (1908) Ein Beitrag zur Flora der ostfriesischen Inseln. Abhandlungen herausgegeben vom Naturwissenschaftlichen Verein zu Bremen 19:313–322

Leege O (1913) Der Memmert. Eine entstehende Insel und ihre Besiedlung durch Pflanzenwuchs. Abhandlungen herausgegeben vom Naturwissenschaftlichen Verein zu Bremen 21:283–327

Leege O (1937) Endozoische Samen-Verbreitung von Pflanzen mit fleischigen Früchten durch Vögel auf den Nordseeinseln. Abhandlungen herausgegeben vom Naturwissenschaftlichen Verein zu Bremen 30:262–284

Leuschner C, Schipka (2004) Vorstudie Klimawandel und Naturschutz in Deutschland. BfN-Skripten 115:1–33

Lienenbecker H (2004) Ein Vorkommen des Hundszahngrases (*Cynodon dactylon* (L.) Pers.) auf Spiekerog/Ostfriesland. Floristische Rundbriefe 37:75–76

Litterski B, Berg C (2000) Naturräumliche Bindung und Einbürgerung von Neophyten in Mecklenburg-Vorpommern. Gleditschia 28:47–63

Lohmeyer W, Sukopp H (1992) Agriophyten in der Vegetation Mitteleuropas. Schriftenreihe für Vegetationskunde 25:1–185

Malcolm JR, Markham A, Neilson RP, Garaci M (2002) Estimated migration rates under scenarios of global climate change. J Biogeogr 29:835–849

Mang FWC (1982) Alphabetisches Verzeichnis der wildwachsenden Farn- und Blütenpflanzen von Neuwerk und Scharhörn. Hamburger Küstenforschung 41:43–95

Marsson TF (1869) Flora von Neu-Vorpommern und der Inseln Rügen und Usedom. W. Engelmann, Leipzig

Mayer E (1936) Beiträge zur Pflanzengeographie der europäischen Sandstrand- und Küstendünengebiete. Inaugral-Dissertation. Westfälische Wilhelms-Universität, Münster

McLean RF, Tsyban A (2001) Coastal zones and marine ecosystems. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskel K, Johnson CA (eds) Climate change 2001: the scientific basis. Contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 343–370

Melillo JM, Prentice IC, Farquhar GD, Schulze E-D, Sala OE (1996) Terrestrial biotic responses to environmental change and feedbacks to climate. In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) Climate change 1995. Cambridge University Press, Cambridge, The science of climate change, pp 447–481

Metzing D (2005) Küstenflora und Klimawandel der Einfluss der globalen Erwärmung auf die Gefäßpflanzenflora des deutschen Küstengebietes von Nord- und Ostsee. Dissertation. Carl von Ossietzky Universität, Oldenburg. http://oops.uni-oldenburg.de/138/2/metkue05.pdf

Metzing D (2006) Natur im Einfluss des Klimawandels wie verändern sich Flora und Fauna? Bremer Beiträge für Naturkunde und Naturschutz 8:31–49

Metzing D (2010) Global warming changes the terrestrial flora of the Wadden Sea. Wadden Sea Ecosystem 26:211–215

Metzing D, Gerlach A (2001) Climate change and coastal flora. In: Walther G-R, Burga CA, Edwards PJ (eds) "Fingerprints" of climate change: adapted behaviour and shifting species ranges. Kluwer Academic/Plenum Publ, New York, pp 185–201

Metzing D, Garve E, Matzke-Hajek G, Adler J, Bleeker W, Breunig T, Caspari S, Dunkel F, Fritsch R, Gottschlich G, Gregor T, Hand R, Hauck M, Korsch H, Meierott L, Meyer N, Renker C, Romahn K, Schulz D, Zimmermann F (2018) Rote Liste und Gesamtartenliste der Farn- und Blütenpflanzen (Trachaeophyta) Deutschlands. Naturschutz und Biologische Vielfalt 70(7):13–358

Meusel H, Jäger EJ (1978) Vergleichende Chorologie der zentraleuropäischen Flora, vol 2 (Text- und Kartenteil). G. Fischer, Jena

Meusel H, Jäger EJ (1992) Vergleichende Chorologie der zentraleuropäischen Flora, vol 3 (Text- und Kartenteil). G. Fischer: Jena

Meusel H, Jäger EJ, Weinert E (1965) Vergleichende Chorologie der zentraleuropäischen Flora, vol 1 (Text- und Kartenteil). G. Fischer, Jena

Meyer GFW (1824) Ueber die Vegetation der Ostfriesischen Inseln. Zweiter Abschnitt: Betrachtung der Vegetation, Hannoversches Magazin, pp 145–198

Meyer GFW (1849) Flora Hanoverana excursoria enthaltend die Beschreibungen der phanerogamischen Gewächse Norddeutschlands in den Flussgebieten der Ems, Weser und Unterelbe geordnet nach natürlichen Familien. Vandenhoeck & Ruprecht, Göttingen

Mossberg B, Stenberg L, Ericsson S (1992) Den nordiska floran. Wahlström & Widstrand, Stockholm

Mühl M (1993) Zur Synsystematik der Krähenbeerheiden auf den Ostfriesischen Inseln. Drosera 93:11–32

Nathan R (2001) Dispersal biogeography. In: Levin SA (ed) Encyclopedia of biodiversity, vol 2. Academic Press, San Diego [a. o.], pp 127–152

Neuhaus R, Dijkema KS, Reinke H-D (1998) Die Gefährdung der Flora und Fauna an Küsten durch den Meeresspiegelanstieg. In: Lozán JL, Grassl H, Hupfer P (eds) Warnsignal Klima. Wissenschaftliche Auswertungen, Hamburg, pp 313–317

New M, Hulme M, Jones P (1999) Representing twentieth-century space-time climate variability. Part I: development of a 1961–90 mean monthly terrestrial climatology. J Clim 12:829–856

Packham JR, Willis AJ (1997) Ecology of dunes, salt marsh and shingle. Chapman and Hall, London

Panknin W (1937) Ein vereinzelter Fund von *Crithmum maritimum* L. auf der Helgoländer Düne. Feddes Repertorium Specierum Novarum Regni Vegetabilis 41:191

Parmesan C (1996) Climate and species' range. Nature 382:765–766

Parmesan C, Galbraith H (2004) Observed impacts of global climate change in the U.S. Pew Center of Global Climate Change, Arlington (USA)

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pearson RG, Dawson TP (2003) Predicting the species of climate change on the distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr 12:361–371

Persicke U, Gerlach A, Heiber W (1999) Zur botanischen Zusammensetzung von Treibsel der niedersächsischen Deichvorländer und Deichabschnitte. Drosera 99:23–34

Pitelka LF (1997) Plant migration and climate change. Am Sci 85:464–473

Plettke F (1903) Alopecurus bulbosus Gouan, eine für Deutschland neue Phanerogame, einheimisch bei Geestemünde. Jahrbuch des Vereins für Naturkunde an der Unterweser 1901/02:42–44

Pott R (1995a) Farbatlas Nordseeküste und Nordseeinseln. E. Ulmer, Stuttgart

Pott R (1995b) Die Pflanzengesellschaften Deutschlands, 2nd edn. E. Ulmer, Stuttgart

Pott R (1997) Von der Urlandschaft zur Kulturlandschaft–Entwicklung und Gestaltung mitteleuropäischer Kulturlandschaften durch den Menschen. Verhandlungen der Gesellschaft für Ökologie 27:5–26

Preston CD, Pearman DA, Dines TD (eds) (2002) New atlas of the British flora. Oxford University Press, Oxford

Prins D, Kuhbier H, Pedersen A, Mennema J, Weeda EJ (1983) Main list with indigenous or naturalized phanerogams and pteridophytes of the Wadden Sea area. In: Dijkema KS, Wolff WJ (eds) Report 9: Flora and vegetation of the Wadden Sea islands and coastal areas. A. A. Balkema, Rotterdam, pp 323–339

Raabe E-W (1970) Die Wanderung von *Juncus maritimus* an der jütischen Westküste. Kieler Notizen zur Pflanzenkunde in Schleswig-Holstein 2:8–9

Raabe E-W (1973) Über die Belastung des Badestrandes am Bottsand. Kieler Notizen zur Pflanzenkunde in Schleswig-Holstein 5:49–67

Raabe E-W (1981) Über das Vorland der östlichen Nordsee-Küste. Mitteilungen der Arbeitsgemeinschaft für Floristik in Schleswig-Holstein und Hamburg 31:1–118

Ranwell DS (1972) Ecology of marshes and sand dunes. Chapman and Hall, London

Ray GC, Hayden BP, Bulger AJ Jr, McCormick-Ray MG (1992) Effects of global warming on the biodiversity of coastal-marine zones. In: Peters RL, Lovejoy TE (eds) Global warming and biological diversity. Yale University Press, New Haven, pp 91–104

Reinke J (1909) Die ostfriesischen Inseln. Studien über Küstenbildung und Küstenzerstörung. Wissenschaftliche Meeresuntersuchungen N F 10:1–79

Reise K (1994) Das Schlickgras *Spartina anglica*: die Invasion einer neuen Art. In: Lozán JL, Rachor E, Reise K, von Westernhagen H, Lenz W (eds) Warnsignale aus dem Wattenmmeer. Blackwell, Berlin, pp 211–214

Rodwell JS (ed) (2000) British plant communities. Vol. 5: Maritime communities and vegetation of open habitats. University Press, Cambridge

Sachs L (2004) Angewandte Statistik: Anwendung statistischer Methoden, 11th edn. Springer, Berlin

Sauer JD (1988) Plant migration: the dynamics of geographic patterning in seed plant species. University of California Press, Berkeley

Savidge JP (1970) Changes in plant distribution following changes in local climate. In: Perring F (ed) The flora of a changing Britain. EW Classey, Hampton, pp 25–31

Schreitling K-T (1971) Otto Leege: der Botaniker. In: Nitzschke H (ed) Otto Leege. Der Vater des Memmert, Erforscher Ostfrieslands und seiner Inseln. Ostfriesische Landschaft, Aurich, pp 31–42

Segurado P, Araújo MB (2004) An evaluation of methods for modelling species distributions. J Biogeogr 31:1555–1568

Simas T, Nunes JP, Ferreira JG (2001) Effects of global climate change on coastal salt marshes. Ecol Model 139:1–15

Sterr H (1996) Klimawandel und mögliche Auswirkungen auf die deutsche Nordseeküste. Schriftenreihe der Schutzgemeinschaft Deutsche Nordseeküste 9:9–30

ter Braak CJF, Šmilauer P (1998) CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca

Tabken H (1951) Spartina townsendii an der oldenburgischen Küste. Oldenburger Jahrbuch 51:240

Tabken H (1960) Die Flora der Insel Mellum. Oldenburger Jahrbuch 59:132–139

Thomas C (2003) Climate change and habitat fragmentation. In: Green RE, Harley M, Miles L, Scharlemann J, Watkinson A, Watts O (eds) Global climate change and biodiversity. RSPB, Bedfordshire, pp 22–23

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Ferreira de Siqueira M, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427:145–148

Tuhkanen S (1980) Climatic parameters and indices in plant geography. Acta Phytogeographica Suecica 67:1–105

Türk W (1994) Flora und Vegetation der Insel Amrum Bestand, Wandel und Gefährdung. Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein 64:17–89

Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (1964) Flora Europaea. In: Lycopodiaceae to Platanaceae, vol 1. University Press, Cambridge

Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (1968) Flora Europaea. In: Rosaceae to Umbelliferae, vol 2. University Press, Cambridge

Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (1972) Flora Europaea. In: Diapensiaceae to Myoporaceae, vol 3. University Press, Cambridge

Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (1976) Flora Europaea. In: Plantaginaceae to Compositae (and Rubiaceae), vol 4. University Press, Cambridge

Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (1980) Flora Europaea. In: Alismataceae to Orchidaceae (Monocotyledones), vol 5. University Press, Cambridge

Valentin H (1954) Die Küsten der Erde, 2nd edn. Gotha, Berlin

van der Meijden R (1996) Heukel's flora van Nederland, 22nd edn. Wolters-Noordhoff, Groningen

van der Meulen F (1990) European dunes: consequences of climate change and sealevel rise in Dunes of the European coasts. Geomorphology–hydrologysoils. In: Bakker TW, Jungerius PD, Klijn JA (eds) Catena Supplement. Catena, Cremlingen-Destedt, pp 209–223

van Dieren JW (1934) Organogene Dünenbildung. Nijhoff, Den Haag

van Oostroom SJ, Mennema J (1969) Nieuwe vondsten van zeldzame planten in Nederland, hoofzakelijk in 1969. Gorteria 4:167–177

van Oostroom SJ, Reichgelt TJ (1965) Nieuwe vondsten van zeldzame planten in Nederland, hoofzakelijk in 1964. Gorteria 2:109–120

Vivian-Smith G, Stiles EW (1994) Dispersal of salt marsh seed on the feet and feathers of waterfowl. Wetlands 14:316–319

von der Ende M (1995) Rote Liste der Farn- und Blütenpflanzen des deutschen Wattenmeerbereichs und Helgolands. Schriftenreihe für Landschaftspflege und Naturschutz 44:51–61

von Storch H, Schnur R, Zorita E (1998) Szenarien und Beratung. Anwenderorientierte Szenarien für den norddeutschen Küstenbereich. Final report of the BMBF project, FKZ 01 LK 9510/0

Wagenitz G (1981) In: Conert HJ, Hamann U, Schultze-Motel W, Wagenitz G, Parey P (eds) Pteridophyta, Spermatophyta Illustrierte Flora von Mitteleuropa. Bd. 3(2): Angiospermae, Dicotyledones 1 Teil 1. Hamburg, Berlin

Walter H, Straka H (1970) Arealkunde. Floristisch-historische Geobotanik. E, Ulmer

Walther G-R, Berger S, Sykes MT (2005) An ecological 'footprint' of climate change. Proc R Soc B 272:1427–1432

Webb T III (1992) Past changes in vegetation and climate: lessons for the future. In: Peters RL, Lovejoy TE (eds) Global warming and biological diversity. Yale University Press, New Haven, pp 59–75

Weeda EJ, Mennema J (1983) Phytogeographical aspects. In: Dijkema KS, Wolff WJ (eds) Report 9: Flora and vegetation of the Wadden Sea islands and coastal areas. AA Balkema, Rotterdam, pp 221–242

Weeda EJ, Westra R, Westra C, Westra T (1985) Nederlandsche oecologische Flora. In: Wilde planten en hun relaties 1. IVN, Amsterdam

Weeda EJ, Westra R, Westra C, Westra TT (1987) Nederlandsche oecologische Flora. In: Wilde planten en hun relaties 2. IVN, Amsterdam

Wiedemann AM, Pickart AJ (2004) Temperate zone coastal dunes. In: Martínez ML, Psuty NP (eds) Coastal dunes, Ecological Studies, vol 171. Springer, Heidelberg, pp 53–65

Wisskirchen R, Haeupler H (1998) Standardliste der Farn- und Blütenpflanzen Deutschlands. Ulmer, Stuttgart

Wolters M, Geertsma J, Chang ER, Veeneklass RM, Carey PD, Bakker JP (2004) Astroturf seed traps for studying hydrochory. Funct Ecol 18:141–147

Wolters M, Garbutt A, Bakker JP (2005) Plant colonization after managed realignment: the relative importance of diaspore dispersal. J Appl Ecol 42:770–777

Woodward FI (1987) Climate and plant distribution. Cambridge University Press, Cambridge

Zabkiewicz JA (1976) The ecology of gorse and its relevance to New Zealand forestry. In: CGR C (ed) The use of herbicides in forestry in New Zealand. FRI symposium: proceedings of a meeting arranged by the Forest research institute / New Zealand Forest Service. New Zealand Forest Service, Forest Research Institute, Rotorua, pp 63–70

General Aspects of Coastal Carabid Beetle and Spider Fauna at the North Sea and the Baltic Sea

11

Dietrich Mossakowski and Ulrich Irmler

Abstract

This chapter reviews the knowledge hitherto available for coastal arthropod groups under study: Many species of the epigaeic ground beetles (Carabidae) and spiders (Araneae) are well-known as indicators for natural and man-made changes of environmental factors and habitats. Basic aspects were geographical distribution, the sequences of zones in the salt marshes, ecological key factors as salt content, number of floods and soil type as well agricultural use. Salt marshes are endangered habitats and many of the species living there are threatened. Only few data exist on climate change impact on carabids and spiders, none could be found on those of coastal habitats.

11.1 Introduction

The border between the sea and land holds a zone of habitats where terrestrial and marine animals, such as arthropods, exist under extreme conditions (Knülle 1953; Heydemann 1967a). Conditions in this zone are determined by flooding and a more or less high content of salt in the water. For spiders and ground beetles, as studied in this project, soil type is also important.

The high number of animal species makes it necessary to focus the research studies on a few taxa. Up to 1990, more than 7000 animal species are known from

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the East Frisian Islands, a part of the study area (Bröring et al. 1993; Niedrighaus et al. 2008, 7432 recorded species). Many species of the epigaeic ground beetles (Carabidae) and spiders (Araneae) are well-known as indicators for natural and man-made changes in environmental factors and habitats (Thiele 1977; Hänggi et al. 1995; Reinke and Irmler 1994; Irmler and Gürlich 2004).

Comprehensive data on spiders and carabid beetles have been published on the salt marshes from other regions, e.g., the Mont St. Michel Bay of Northern France (Pétillon et al. 2008), which differ strongly from the Central European fauna. In particular, the size of the French salt marshes is unique in Europe. The study sites are more or less plane with only small differences in elevation for over more than 1 km (pers. comm. Julien Pétillon). Mean tides range from 10 to 11 m, but the sites are only flooded during spring tides and characterised by the invasion of the grass *Elymus athericus* (Pétillon et al. 2005). Therefore, they are not included in our discussion.

Studies on carabid beetles and spiders which were performed on de-embankment sites are found in Chap. 22.

11.2 Geographical Distribution and Sequence of Zones

11.2.1 Geographical Distribution

To predict changes in distribution areas, it is necessary to evaluate the available data on the geographical distribution of the species considered. This seems to be simple at first glance. But different problems arise when detailed maps of a large number of species must be prepared: (1) after the first comprehensive work with point maps for carabid beetles of Fenno-Scandia (Lindroth 1945b), maps were published for many countries, but for a long time no maps were available for all of Germany until Bleich et al. (2013) started their electronic atlas with the grid of the topographic map at 1: 25,000 and Trautner et al. (2014) published a printed atlas using a 10x10 km grid, (2) the data are published for periods of occurrence but the classification of periods differs among authors, (3) actively flying species may occur at remote places where they may not be able to build up permanent populations (Bangsholt 1983), and (4) contradictory data exists in the literature, etc.

Distribution maps for spiders exist since 1996 (*Nachweiskarten der Spinnen, Arachnologische Gesellschaft* 2021) and are available electronically. They offer accurate data at least with the grid of the topographic map at 1:25,000 and function with temporal tracking of the chronological order of occurrence. An overview of spider distribution is available in Nentwig et al. (2018).

The hitherto known data for relevant species is compiled in Table 11.1 for spiders and in Table 11.2 for ground beetles (for the data of our project cf. Chaps. 14 and 27).

The individual species of saline habitats display characteristic patterns as may be extracted from the maps in Turin et al. (1977) and Turin (2000). A high number of these species occurs only in coastal habitats of Atlantic (*Cillenus litoralis*),

Table 11.1 Spider (Araneae) species in salt marshes and dunes with salt influence ordered according to their habitat preferences. Species highlighted in bold were found in our project

	Hey	HSN	S & F ‘94		R & I	Hab. pref.		NL	D	DK	D	PL	D
Araneae	‘60	‘95	N	B	‘94	flood	salt	N	N	N, B	B	B	In
***Robertus heydemanni*[1]**	hb*		L		ht	1	3		+	+			
Praestigia duffeyi	hb	hb	L		hp	4	3	+	+	+			
***Ozyptila westringi*[2]**			L	?L		1	3	+	+				
Silometopus ambiguus		(hp)	TT		hp	1	3	+	+	+	+		
Silometopus incurvatus			?L	?L	ht		3	+	+	+	+	+[co]	
Pardosa purbeckensis	hp	hb-hp	T	T	ht	2	3	+	+	+	+		-[d]
Enoplognatha mordax		hb	TT		ht	2	2	+	+	+	+	+	Ina
Argenna patula		hp	L	L	ht	1	2°	+	+	+	+[b]	+	Ina
Erigone arctica maritima	hb	hp	T		ht	1	2	+	+	+	+	+[e]	In
Erigone longipalpis	hb	hp	TT	TT	htf	1	2	+	+	+	+	+	In
Erigone dentigera							2	+[g]		+[h]		-[mo]	In
Erigone psychrophila							2						
Allomengea scopigera	hp?		L	L	ht	1	1°	+	+	+	+	+	In
Ceratinopsis stativa					(ht)	1	1°	+[n]	+	+[n]	+	+[n]	In
Oedothorax retusus		(hp)	T	T	ht	2	1°	+	+	+	+	+	In
Walckenaeria vigilax			L	TT	ht	2	1°	+	+	+	+	+	In
Porrhomma microphthalmus		hp	TT		ht	1	1°	+	+	+	+	+	In
Silometopus reussi	hb*	(hp)	T		ht	1	1°	+	+	+	+	+	In
Agyneta decora			L		ht	1	1	+	+	+	+	+[n]	In
Arctosa leopardus			TT	TT		2	1	+	+	+	+	+	In
undefined Ceratinella brevipes				L		1	1	+	+	+	+	+	In
Clubiona stagnatilis		(hp)	T	T	ht	1	1	+	+	+	+	+	In
Hypomma bituberculatum			T	T	ht	1	1	+	+	+	+	+	In
Tenuiphantes tenuis		(hp)	T	T	ht	1	1	+	+	+	+	+	In

(continued)

Table 11.1 (continued)

	Hey	HSN	S & F '94		R & I	Hab. pref.		NL	D	DK	D	PL	D
Araneae	'60	'95	N	B	'94	flood	salt	N	N	N, B	B	B	In
Leptorhoptrum robustum	hb*?	hp	T		ht	1	1	+	+	+		+	In
Oedothorax apicatus	hp	(hp)	T		ht	1	1	+	+	+	+	+	In
Oedothorax fuscus	hp	(hp)	T	T	ht	1	1	+	+	+	+	+	In
Pirata piraticus			T	L	ht	2	1	+	+	+	+	+	In
Pocadicnemis juncea			TT		ht	1	1	+	+	+	+	+	In
Silometopus elegans				?L	ht	1	1	+		+	+	$+^{n}$	In
Troxochrus scabriculus			T		ht	0	1	+	+	+	+	+	In
Walckenaeria kochi		hp	L		ht	2	1	+	+	+	+	+	In
Silometopus curtus[+]	hp						?						
Hypselistes jacksoni				L			1°	+		+	+	+	In
Satilatlas britteni				?			1°	+		+		$+^{n}$	In
Prinerigone vagans	hb*		T				1	+	+	$+^{h}$			In

References: Hey: Heydemann (1960); HSN: deduced from Hänggi et al. (1995); S & F: Schultz and Finch (1994); R & I: Reinke and Irmler (1994); preferences according to Chap. 27; ° deviating from Chap. 27; distribution at the coasts of the North Sea and the Baltic Sea

hb halobiontic (3), *hp* halophilic (2), *ht* halo tolerant (1), *L* characteristic species, *TT* very typical and *T* typical species (with respect to the degree of presence in comparable habitats of coastal regions). *Hab*, pref habitat preference (high values indicate high preference for the respective factor, for more details, see Chap. 8); flood sensitivity against flood; salt degree of preference for salt habitats; + occurrence documented; *shaded* species of the expert system (Chap. 28) which occurred in the studied areas

* Details concerning only German regions

[1]: Separated from *R. arundinacea* (Wiehle 1965)

[**2**]: Removed from synonymy with *O. trux* (Wunderlich and Schultz 1995), *DK* Denmark, *PL* Poland, *N* North Sea, *B*: Baltic Sea;

[a] Some records from inland (indigenous?)

[b] One old record

[c] Fiszer (1988): second record in Poland

[d] *P. purbeckensis*; one inland record (map in Staudt 2006)

[e] *E. arctica mar.* Poland; Fauna Europaea (2006) (FE) + and Blick et al. (2004) +; Murphy (2006) no

[f] *E. longipalpis* R & I: "significantly most abundant habitat is salt marsh", thus: 2 = hp.

Table 11.1 (continued)

[g] *E. dentigera* NL; FE no and Murphy (2006) no; Staudt (2006) yes, Blick et al. (2004) yes!
[h] *E. dentigera* and *Prinerigone vagans* DK: all no; Scharff and Gudik-Sørensen (2006) +
[m] Murphy (2006) +
[n] Murphy (2006) no
[o] Starega (2004): species needs confirmation or re-examination
[x] Deviating from the data in (FE) and Murphy (2006), *S. ambiguus* occurs in northern and western Europe, *S. curtus* in the Mediterranean region. Blick (2014) written comm., following Denis (1963) and Locket (1964), who emphasised the status of two separate species; see Blick (2014); Nomenclature follows Platnick (2006), updated by World Spider Catalog (2015)

Table 11.2 Ground beetle (Carabidae) species in salt marshes and dunes with salt influence. Species of sandy beaches were included if they were classified as halobiontic or halophilic in the references. Species highlighted in bold were included in our expert system

	Len	Loh	Hor	Hey	MM	Hab. pref.		NL	D	DK	DK	D	PL	D
Carabidae	‘29	‘54	‘59	‘62	07	Flood	Salt	North Sea			Baltic Sea			In
Bembidion iricolor	hb	hb	hb	hb	hb	1	3[1]	+	+	+	.	+[a]	.	.
Pogonus luridipennis	hb	hb	hb	hb	hb	1	3[1]	+	+	+	.	.	In	In
Bembidion normannum	hb	hb	hb	hb	hb	4	3[1]	+	+	+	+	+[b]	.	.
Pogonus chalceus	hb	hb[*]	hb	hb	hb	4	3	+	+	+	+	-[c]	.	In
Dicheirotrichus gustavii	hb	hb	hb	hb	hb	4	3[1]	+	+	+	+	+	+	In
Bembidion aeneum	hb	hb	hb	hb	hb	2	3[1]	+	+	+	+	+	+	In[e]
Dyschirius salinus	hb	hb	hb	hb	hb	1	3	+	+	+	+	+	+	In
Dyschirius chalceus	hb	hb	hb	.	hb	1	3[1]	+	+	+	+	+	+	In
Anisodactylus poeciloides	hb	hb	hb	.	hb	1	3	+			+	+	+	In
Bembidion pallidipenne	hp	hb	hp	.	hp	3	3	+	+	+	+	+	+	.
Cicindela maritima	hp	.	hb	.	hp	1	3	+	+	+	+	+	+	.
Bembidion ephippium	hb	hb	hb	hb	hb	4	3	+	+	+	.	.	.	.
Acupalpus elegans	hb	.	hb	.	hb	0	3	+	+[f]	.	.	.	+	In
Bembidion tenellum	.	hp	hp	.	hb	1	3	+	-[g]	.	+	+	+	In
Agonum monachum	.	.	hb	.	hb	3	3	.	.	.	.	+	.	In[h]
Amara strandi	.	.	hb	.	hb	0	3	.	.	.	.	.	+	In
Bembidion aspericolle	hb	hb[*]	hb	.	hb	0	3	.	.	.	.	.	.	In
Dicheirotrichus obsoletus	hb	.	hb	.	hb	4	3	+	.	.	.	.	.	In
Dyschirius extensus	hb	.	hb	.	hb	1	3	.	.	.	.	.	.	In
Pogonus iridipennis	hb	.	hb	.	hb	?	3	.	.	.	.	.	.	In
Tachys scutellaris	hb	.	hb	.	hb	0	3	+	.	.	.	.	.	In
Pogonus litoralis	hb	.	.	.	.	?	3	+	.	.	.	.	.	.
Cylindera trisignata	.	.	.	.	.	1	3	+	.	.	.	.	.	.
Cillenus lateralis	hb	.	hp	hb	hb	4	2[4]	+	+	+	+	.	.	Est

Table 11.2 (continued)

Bembidion minimum	.	hp*	hp	hp	hp	2	2	+	+	+	+	+	+	In
Amara convexiuscula	hp	.	hp	hp	ht	1	2	+	+	+	+	+	+	In
Dyschirius obscurus	hp	hp*	hp	.	hp	2	2	+	+	+	+	+	+	In
Dyschirius impunctipennis	hb	hp*	hp	.	hp	1	2[3]	+	+	+	+	+	+	.[i]
Bembidion fumigatum	hb	hb	hp	.	hp	2	2	+	+	+	+	+	+	In
B. cruciatum polonicum	.	.	.	.	ht	2	2	.	.[k]	+	+	+	+	.
Bembidion saxatile	hp	.	.	.	ht	2	2	.	.[l]	+	+	+	+	In
Harpalus cephalotes	.	.	.	.	hp	?	2	.	.	.	.	.	.	In
Pterostichus cursor	.	.	hp	.	hb	0	2[4]	.	.	.	.	.	.	In
Blemus discus	.	.	.	.	.	1	1	+	+	+	+	+	+	In
Dyschirius globosus	.	.	.	.	.	1	1	+	+	+	+	+	+	In
Dyschirius thoracicus	.	.	.	.	ht	2	1	+	+	+	+	+	+	In
Masoreus wetterhallii	.	.	.	.	.	0	1	+	+	+	+	+	+	In
Omophron limbatum	.	.	.	.	.	2	1	+	+	.	+	+	+	In
Stenolophus mixtus	.	.	.	.	.	2	1	+	+	+	+	+	+	In
Bembidion transparens	.	.	.	.	ht	2	1[4]	.	.	.	+	+	+	In
	.	.	.	.	.	1	1	+	+	.	.	+	+	In
Carabus clathratus	.	.	.	.	no	2	1	+	+	+	+	+	+	In
Amara majuscula	.	.	.	.	.	0	0	+	.	+	+	+	+	In
Amara ingenua	.	.	hp	hp	hp	0	1[2]	.	.	+	+	+	+	In
Amara strenua	.	.	.	.	hp	0	1	+	+[m]	+[n]	.	.	+	In
Bembidion maritimum	hb	.	hp	.	hp	4	1[3,4]	+	+	+	.	.	.	Est
Amara quenseli silvicola	ht	.	.	.	ht	0	1	+	+	+	+	+	+	In
Harpalus melancholicus	.	.	.	.	ht	0	1	+	.	.	+	+	+	In
Bradycellus distinctus	.	.	.	.	hp	?	1	+	.	.	.	.	.	.
Harpalus modestus	.	.	.	.	ht	0	0	In	.	.	.	.	+	In
Bembidion varium	.	ht*	.	hp?	no	.	0[3]	+	+	+	+	+	+	In

(continued)

Table 11.2 (continued)

	Len	Loh	Hor	Hey	MM	Hab. pref.		NL	D	DK	DK	D	PL	D
Carabidae	‘29	‘54	‘59	‘62	07	Flood	Salt	North Sea			Baltic Sea			In
Bembidion lunatum	.	ht*	.	hp	.	.	0^3	+	+	+	+	+	+	In
Carabus granulatus [o]	.	.	.	(hp)	.	.	0^3	+	+	+	+	+	+	In
Dyschirius nitidus [p]	.	hb*	.	.	no	.	0^3	+	+	.	.	.	+	In
Nebria livida	.	ht*	.	.	ht	.	0^4	+	+	+	+	+	+	In
Nebria Salina	.	ht*	.	.	no	.	0^4	+	+	+	+	+	.	In
Ophonus diffinis	.	.	.	.	hb	.	0^4	.	.	.	.	.	+	In
Amara concinna	.	.	.	.	no	.	0	.	.	.	.	.	In	In

Species ordered according to their salt preferences: 0: haloxen; 1: halotolerant; 2: halophil; 3: halobiont (see also Chap. 28). Len: Von (1929); Loh: Lohse (1954); Hor: Horion (1959); Hey: Heydemann (1962); MM: Müller-Motzfeld (2007); preferences according to Chap. 8; distribution at the German North Sea, the Baltic Sea and adjacent countries’ coasts

Est coast and estuaries, *in*, inland occurrence (additional: Gersdorf and Kuntze 1957; Trost 2007), *hb* halobiontic, *hp* halophilic, *ht*, halo tolerant, *Hab. pref* habitat preference (0: no, from 1 low to 4 high; for more details, see Chap. 26)

Numbers in column salt preference indicate specifications ([1]) in the expert system (Chap. 26) or an increased value by 1 in ([2]) the expert system, in ([3]) Irmler and Gürlich (2004), and in ([4]) Dormann (2015); flood: sensitive against flood; salt: in salt habitats; +: occurrence; occurrence in the study areas; NL: The Netherlands (Turin 2000); D Germany, DK Denmark (Bangsholt 1983), division at Skagen; PL Poland (Burakowski et al. 1973, 1974; Stachowiak 2008)

* (Loh) Classification was not noted by the author, but deduced from the text

[a] Gürlich and Tolasch 2006: Glücksburg

[b] stable population at Fehmarn and Heiligenhafen (Gürlich and Tolasch 2006; own obs. 13.7.2002 (15 ex.)); not in Poland (Stachowiak 2008), not in Lithuania (Tamutis et al. 2011)

[c] up to 30 km inland to Baltic Sea coast (Eider-Treene-Sorge area)

[e] coastal inlands

[f] Gürlich and Tolasch 2006: Sylt, Hallig Hooge

[g] old records, questionable

[h] old records Kyffhäuser Mountain, Thuringia (Schmidt 2004)

[i] old records Brandenburg, Thuringia? (Horion 1959)

[k] records, questionable

[l] old records, questionable

[m] one record: St. Peter-Ording (Gürlich and Tolasch 2006)

Table 11.2 (continued)

[n] one record: Fehmarn (Gürlich and Tolasch 2006)

[o] haloxen species; Heydemann (1962): occurrence below 5‰ salt content; but p 881: halophilic

[p] Gürlich (1999): hb

[x] Müller-Motzfeld (2007): without salt preference although stated by other authors; Nomenclature follows Müller-Motzfeld (2004)

Atlanto-Mediterranean (*Pogonus litoralis*), and some other Atlanto-Baltic regions (*Bembidion aeneum*). A second group of species occurs at salty localities in the inland, many of them also in coastal habitats (*Pogonus chalceus*), but some do not reach the coasts in our region (*Bembidion aspericolle*). It is characteristic that some of the latter species also occur in the Pontic and Caspian regions.

In our study region, the variation of coastal habitats differs distinctly between the North Sea and the Baltic Sea. Salt marshes developed at both coasts in leeward situations, beaches, and dunes mostly at sites open to the sea. Thus, beaches at the North Sea coast suffer under heavy wave and wind impact and are sparsely covered by vegetation and inhabited by animals. At the Baltic Sea, wave and wind has a lower impact on beaches, which are, therefore, more densely covered by vegetation and inhabited by animals (Seer et al. 2015; Schierding et al. 2014). Additionally, cliff coasts are rare at the North Sea, but frequent at the Baltic Sea. Many coastal carabid and spider species are found exclusively at the Baltic Sea coast, because less harsh ecological conditions on the beaches and cliffs are found there more frequently. According to Vahder and Irmler (2010), a high number of spider species live on beaches that are absent on salt marshes, e.g. *Arctosa cinerea* and *Pardosa agricola*. Beaches differ in the sand and shingle composition: *A. cinerea* is typical for sandy beaches with few stones, *P. agricola* prefers shingle beaches. Similar observations are made for carabid species living at cliffs (Schierding et al. 2014). The composition of silt and clay is responsible for the occurrence of some species, e.g. *Nebria livida*, *Bembidion stephensi*, and *Asaphidion pallipes*.

The data (Table 11.1) displays many differences, considers geographical distribution, and assesses habitat preferences. In particular, the assessment of saline habitat preference differs among many species. This may be due to spider's high dispersal power by ballooning. Another reason may be associated with the restricted areas of most studies.

The compilation of the data on carabid beetles resulted in many differences depending on the source. This is obvious, if habitat preferences are evaluated (Table 11.2). But they also exist in simple distribution data. This phenomenon may be due to false determinations in some species. *Pogonus chalceus* is a helpful example: the distribution area of this species is restricted in our region to the North Sea coast and inland habitats. But many references recorded this species for the Baltic Sea coast of Germany, Poland, and the Baltic States. Moreover, specific species are found for the eastern Baltic Sea coast in the comprehensive study of Schliemann (2010), e.g., *Bembidion fumigatum* and *B. transparens*. The catch of single specimens reveals an incorrect impression of a stable population while it is migrating and unable to establish a new population under the local conditions (Bangsholt 1983). In consequence, some records are marked as questionable in Table 11.2 or need validation (noted as? in Stachowiak 2008) and must be omitted for further evaluation.

Irmler and Gürlich (2004) assigned salt marsh species according to the electric conductivity (EC) of their habitats in Schleswig-Holstein using statistical analyses. They found an EC value of higher than 5 meaning polyhaline environmental conditions only for *Dicheirotrichus gustavii* and *Pogonus chalceus*, which coincides with values equal to—or higher than 3 in Table 11.2. Other species with values between 2 and 3 listed in Table 11.2, e.g., *Bembidion minimum*, prefer mesohaline conditions. Several species might reflect uncertain salt values, e.g., *Pogonus chalceus*, which should be represented by a higher salt value, whereas *Bembidion aeneum* might be estimated too high because only an EC value of 2.2 was calculated by Irmler and Gürlich (2004). This species is also recorded from brackish habitats in the inland of Schleswig-Holstein and Lower Saxony. Thus, the assignment to haline conditions at the coast was actually uncertain.

11.2.2 Sequence of Zones

In particular at the North Sea coast, the arthropod fauna of salt marshes displays a series of characteristic assemblages caused by a gradient of decreasing intensity of flooding events. These series of zones start from the seaside with the *Salicornia* zone, via the lower and higher salt marshes to more or less brackish or limnic zones in front of dikes.

This sequence of zones is obvious in the vegetation. The zonation of salt marsh animals, in particular in arthropods, was often studied using the vegetation zones as a basis. In these studies, the zonation of animal and vegetation communities reveals identical patterns. Heydemann (1960: Araneae; 1962: Carabidae) intensively studied the distribution and ecology of spiders and ground beetles along these zones under tidal influence at the German North Sea coast. He reviewed (1983, 1984) the fauna of the lower, Schaefer (1983) that of the higher salt marshes. Zonation of Staphylinidae as well reflect exactly the zonation of the vegetation (Irmler and Heller 2002).

Later, zonation of animals was analysed independent of the vegetational zonation, e.g., by Irmler and Heydemann (1986) and Andresen et al. (1990). Främbs et al. (2002), too, published a detailed investigation on zone specific differentiation in salt marsh habitats after regeneration measures (compare also Olbrich (1994) and Kinder et al. (2003)). The results (Chap. 14) provide characteristic examples for a pattern in which the demands of animals coincide with that of plants.

Meanwhile, partial data on the fauna of the present study was published: Finch et al. (2007) published data on an elevation gradient of island salt marshes at Borkum and Wangerooge. Reinke et al. (2000) discuss the zonation of spiders and carabid beetles in salt marshes along an inundation gradient. Irmler et al. (2002) performed an un-weighted average cluster analysis on the basis of species dominances, which resulted in two groups for carabids as well as for spiders in the salt marshes at the North Sea coast (foreland Friedrichskoog), but three groups at the Baltic Sea coast (Bay of Howacht). Dormann et al. (2008) analysed the material of the coastal gradient including natural salt marshes without any human impact. They found four zones for carabid beetles due to the existence of a natural transition from salt marsh to the Wadden Sea.

Using material of the present study and own data on raised bogs, Mossakowski (2007) tested the thesis that in habitats with extreme environmental conditions (as can be stated for the lower salt marshes of the North Sea coast) only few species live in high abundance. While carabids display the same behaviour in raised bogs and lower salt marshes, spiders show low numbers of species only in the lowest salt marsh zone but high numbers in raised bogs. Thus, general statements are not useful. Differentiations according to habitats, taxon, and regions are necessary.

11.3 Ecological Key Factors

Prior to a discussion of impact factors that are responsible for the occurrence of carabid and spider species in salt marshes, the theory of the ecological niche has to be discussed which was not sufficiently reflected in many old ecological studies. According to Hutchinson (1959), the ecological niche is the hyperdimensional space of a species habitat. It is divided into a realised niche, which means the space in which the species lives under natural conditions, including chemical and physical site factors, the competition with species living in the same habitat, and the fundamental niche which considers the total physiological flexibility of the species without competition. A species can rarely use the fundamental niche because in the field interspecific competition is always realised. Therefore, a species living only in salt marshes at the Northern German coast may live in non-saline habitats under changed competition conditions. The restriction of a species to salt marshes can either be related to a need for salt, a tolerance to salt, a tolerance to flooding or less competition compared to other habitats. In most cases, we have no idea why individual species are restricted to or prefer salt marshes. Deriving ecological demands from field studies may be erroneous, because it cannot be distinguished why the species lives under the specific environmental conditions. The description of the realised niche fits usually only for a specific geographical region with similar competition. Therefore, in this study the terms halobiontic or halophilic should be understood as an expression for the realised niche at the Northern German coast of the North Sea and the Baltic Sea. Halobiontic means that it is restricted to habitats with high salt content, halophilic means that it also occurs in lower numbers in low-saline or non-saline habitats.

Discussions in the past about halophilic or halotopophilic species are not helpful (Heydemann 1962). Furthermore, the realised and the fundamental niches were considered for the definition in only few cases.

11.3.1 Flooding

Marked differences exist in the flood regimes of the North Sea and the Baltic Sea (Chap. 6). Animals of the lower salt marshes at the North Sea coast are flooded regularly. Higher elevated sites are flooded irregularly. Additionally, higher floods, such as storm surges, occur mainly in the winter season. Flooding events at the Baltic Sea coast happen irregularly depending on the power and direction of the wind and on independent oscillations of the water level (seiches).

Differences in the distribution and the abundance of salt marsh species between the North Sea and Baltic Sea are described, e.g. *Dicheirotrichus gustavii* is found most abundantly in the salt marshes of the North Sea coast but in lower numbers at the Baltic Sea coast and becomes extinct eastwards with a decreasing salt content of the water (Lohse 1954; Heydemann 1962; Bangsholt 1983). Soils of the salt marshes differ between the North Sea and the Baltic Sea: they normally are clayey or sandy, but also peaty in a few places at the North Sea coast, whereas they are mainly peaty at the Baltic Sea coast.

Studies in the past controversially interpreted the dependency of terrestrial arthropods of salt marshes on flooding or salinity. Heydemann (1968) stated that no species relies on flooding essentially. In contrast, Lohse (1987) cited some species, which he categorised as dependent on tidal flooding (e.g. *Cillenus lateralis, Bembidion maritimum*; cf. Fig 11.1). But both authors have not differentiated between realised and fundamental niches.

We understand Lohse's graphs as stimulating contributions to the discussion. But his interpretations have to be critically scrutinised to distinguish the realised and fundamental niches because data varies according to the different climates of coastal and inland saline habitats, different competition conditions, the dispersal potentials of the species, and historical conditions.

In the salt marshes, only a few species are adapted to terrestrial as well as to marine conditions (Hildebrandt 1997). Species react to an increasing water level, heavier storm floods, and other catastrophic impacts. Damage by drifting is avoided by some species within soil tubes or holes visited just before the flooding events (Evans et al. 1971; Heydemann 1983). A small part of tested specimens of *Cillenus lateralis* was able to recover after submergence of 1 or 2 h (Elliot et al. 1983).

Some spider and carabid species are able to climb on plants and to rest some days under submersion conditions (Palmén 1949; Heydemann 1967a). Some arthropods of salt marshes are able to survive in soil-crevices to avoid high-energy consumption when flooded (Foster and Treherne 1979). In flooding experiments, the spider *Erigone longipalpis* survived saline water submersion for 4 days (Bethge 1973). Other strategies to escape floodings are flight (macropterous Carabidae), climbing up to higher strata, and evasion to higher elevated terrestrial sites (Treherne and Foster 1977; Irmler and Heydemann 1985).

According to Doyen (1976), carabid beetles living in intertidal habitats are partially or totally wingless which is interpreted as an adaptation to this zone with frequent inundations (Luff and Eyre 2000). In the population of *Pogonus chalceus*, the proportions of specimens with developed wings depend on the age of the salt marsh (Desender 1985). These beetles only fly under warm and calm weather conditions (Meyer 1997). Under experimental high tide conditions, Irmler et al. (2002) described an increasing activity and avoidance of flooding by running into higher parts (Chap. 20). However, long-distance migrations corresponding to the tidal rhythms were never observed (on hydrochore drift, see Chap. 21). However, shifts of the total population within the flooding gradient were observed for the spider *Erigone longipalpis* depending on changed MHW values in different years (Irmler and Heydemann 1985).

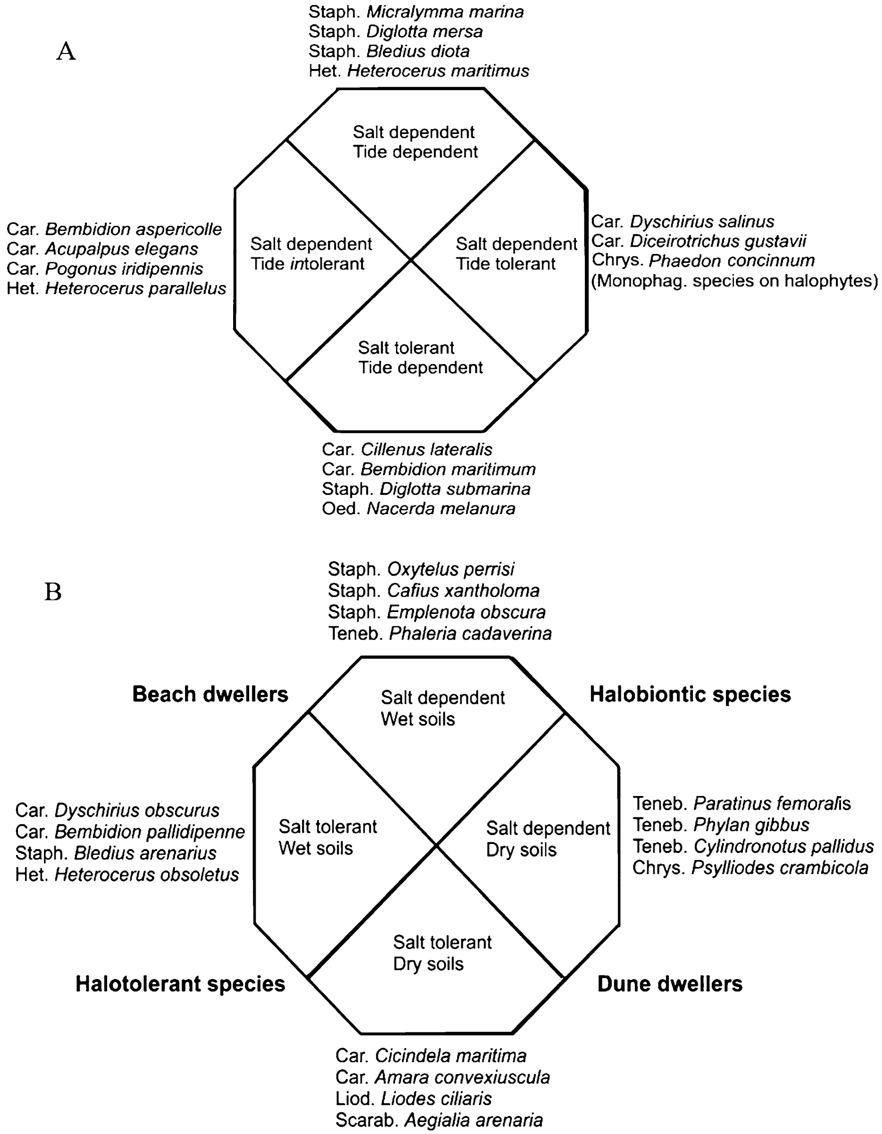

Fig. 11.1 Phenomenological analysis of ecological factors controlling the dispersion of beetles in coastal and inland habitats under influence of (**a**) salt and tide or (**b**) salt and humidity. Beach species were included in this analysis but omitted in the present study of dunes and salt marshes. Changed according to Lohse (1987). *Staph.* Staphylinidae, *Car.* Carabidae, *Oed.* Oedemeridae, *Het.* Heteroceridae, *Chrys.* Chrysomelidae, *Curc.* Curculionidae, *Teneb.* Tenebrionidae, *Liod.* Liodidae, *Scarab* Scarabaeidae

Treherne and Foster (1977) found a circadian rhythm in *Dicheirotrichus gustavii.* In laboratory experiments, no indication was found for a synchronisation with the tides, because the field study at two sites that differed in the high tide phase by 6 h displayed the identical diurnal rhythm in the two populations (Foster 1983).

Heydemann (1962) deduced from his comparative studies on foreland and poldered salt marshes that flooding or storm surges destroyed 90% of the specimens of terrestrial salt marsh animals. Främbs (1997) found a direct influence of storm surges on salt marsh carabid species at the Wursten coast foreland as well as in the summer polder on the foots of the Berensch dunes in March after two extreme storm surges at the end of January. Carabid beetles are normally in their hibernating habitats in this period. As a consequence of the storms, waves, and currents, they must have washed out from their hibernation habitats which was never observed in winter seasons without such extreme storm surges.

11.3.2 Salt

Among terrestrial insects, only some species, e.g., dipteran (Remmert 1955) and collembolan species (Witteveen and Joosse 1987) directly depend on salt. But for spiders and beetles, such relationships were never found. The spider *Erigone arctica* was characterised as halobiontic in Northern Germany corresponding to its realised niche here, but the fundamental niche shows no dependence on salt (Heydemann 1967a).

The origin of many salt marsh carabid species was characterised as Pannonic-Asiatic, a region where these species also occur in non-coastal and fresh habitats (Horion 1959). Some carabid species only occur in saline habitats in the inland, e.g. *Bembidion aspericolle.* This species shows a continental distribution and lives at the Mediterranean and Atlantic coasts up to Southwestern France. Therefore, Müller-Motzfeld (written comm.; Müller-Motzfeld 2007) interpreted its absence at the North Sea coast as a result of the climate conditions.

The discussion of a preference for saline habitats must also consider the importance of salt concentrations in the soil, e.g. for *Dicheirotrichus gustavii* as eu- to mesohalobiontic and *Amara convexiuscula* as oligohalobiontic (Heydemann 1962).

Schmidt (2002) studied a number of habitats and sites at the Mecklenburg coast. His assessments of salt preference are listed in Table 11.3.

In salt gradient experiments, both Lindroth (1949) and Heydemann (1967a) found a preference for saline conditions in *Bembidion minimum*, *Bembidion aeneum,* and *Dicheirotrichus gustavii*. Dutt (2004) described the same results for *Bembidion pallidipenne, B. minimum, Dyschirius salinus,* and *Anisodactylus poeciloides*. The choice of substrate differed between males and females of *B. pallidipenne* and *Dyschirius salinus*, which was interpreted as an advantage for the salt demanding larvae living in the ground. A direct osmotic influence of the salt on the haemolymph of the two species was supposed to be unlikely. The mean haemolymph osmolarity in the halobiontic *Anisodactylus poeciloides* and in *Cicindela maritima* did not depend significantly on the salt content of the substrate (Dutt 2004).

Table 11.3 Salt preference of coastal carabid beetles at the Mecklenburg coast (MV) selected from Schmidt (2002)

Species	Salt preference	Selected remarks
Agonum monachum	oligo-steno-halobiontic	brackish reeds
Amara convexiuscula	? oligo-eury-halobiontic	
Amara ingenua	? halobiontic (oligohalin)	pioneer habitats
Amara quenseli	low halo tolerance	
Anisodactylus poeciloides	meso-steno-halobiontic	
Bembidion aeneum	oligo-steno-halobiontic	
Bemb. cruciatum polonicum	halo tolerant	stenotop.: coastal cliffs; climate?
Bembidion fumigatum	oligo-steno-halobiontic	
Bembidion lunatum	halophilic	
Bembidion minimum	oligo-meso-euryhalobiontic	
Bembidion pallidipenne	oligo-steno-halobiontic	
Bembidion saxatile	?	MV stenotopic: coastal cliffs
Bembidion stephensi	?	cliffs (coast + inland)
Bembidion transparens	halo tolerant	coast + inland
Bembidion tenellum	oligo-meso-euryhalobiontic	
Cicindela maritima	oligo-steno-halobiontic	
Harpalus melancholicus	halophilic (oligo-meso-halobiontic?)	Psammobiontic
Dicheirotrichus gustavii	halobiontic	
Dyschirius chalceus	meso-(eury)-halobiontic	
Dyschirius obscurus	halophilic	climate?
Dyschirius salinus	oligo-meso-(eury) halobiontic	
Harpalus neglectus	low halo tolerance	Psammobiontic
Nebria livida	–	cliffs (coast + inland)

Irmler and Gürlich (2004) calculated indicator values based on extensive material from diverse habitats and localities in Schleswig-Holstein. This species index is the weighted mean for the environmental factor. Out of a total of 182 species, 15 species were classified as oligo-, meso-, or polyhaline. *Amara convexiuscula* and *Bembidion aeneum* were classified as oligohaline, similar to the rating of our expert system (Chap. 27). 10 species were ranked as mesohaline. Seven of them are characterised to have no preference for saline habitats or to be at least halo-tolerant (e.g. *Bembidion assimile, B. bipunctatum, B. bruxellense*). This interpretation is in agreement with the expert system as well as the characterisation of the remaining three species, which prefer saline habitats. Three species showed a preference for polyhaline habitats, i.e. *Dicheirotrichus gustavii* and *Pogonus chalceus*. *Bembidion varium* was characterised as halo-tolerant and the index as a first tool for the evaluation of species assemblages.

In saline water, *Dicheirotrichus gustavii* keeps its osmotic pressure constant for 1 day, which is interpreted as an important prerequisite for a colonisation of saline habitats (Heydemann 1968). Heydemann (1967b) found that larvae of

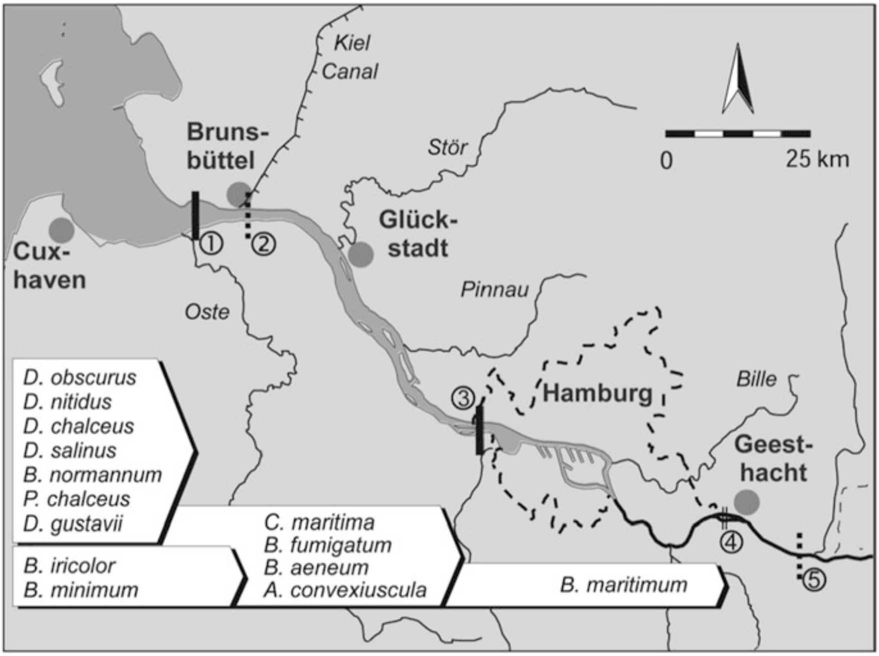

Fig. 11.2 Distribution of halobiontic and halophilic carabid beetles along the river Elbe. #1–5: Distribution limits of beetles due to salinity and flooding. High salt content (>5‰) extend up to the Oste mouth (#1). Salt-water influence ranges up to Wedel (#3) in summer, but only up to the river Stör mouth near Glückstadt in winter. Natural tides reached Lauenburg (#5). This will happen only during very high tides after construction of the Geestacht weir (according to Gürlich 1999)

Dicheirotrichus gustavii survived flooding by marine water twice as long as adults: 50% survived 20 days with permanent flooding by water of 32% salt content.

The impact of salt for the distribution of salt preferring species is displayed in estuaries such as the Elbe estuary near Hamburg. Gürlich (1999) studied the distribution from the salt water of the North Sea to fresh water near Geesthacht (Fig. 11.2). In Fig. 11.1, the 5% border representing brackish water conditions is located at line 1, upper brackish water border in winter is at line 2, the referring line in summer is at line 3, and pure fresh water border is at line 4. The four border lines are indicated by distribution borders of species. Euhalobiontic to mesohalobiontic species find their limit at line 1, oligohalobiontic species at line 4.

11.3.3 Soil

Soil type strongly influences the distribution of arthropods. In his fundamental work on carabid beetles, Lindroth (1945a, 1949) was one of the first who comprehensively emphasised the ecological importance of soil type and structure. Later, Müller-

Motzfeld (1989) and Irmler and Gürlich (2004) stressed the importance of soil types for the occurrence of carabid species. The ground beetle *Carabus clathratus*, for example, is a characteristic species of swamps and raised bogs in Northern Germany where it also occurs in peaty depressions of dunes on the Frisian Islands. In the salt marshes of the North Sea coast, it is rarely distributed on locally developed peaty soils. At the Baltic Sea coast, it occurs frequently and in high abundances because peaty soils are widespread in salt marshes (Schliemann 2010).

Specific salt marsh dwelling carabid species prefer heavy soils like clay (*Bembidion minimum, Dicheirotrichus gustavii, Dyschirius chalceus, Pogonus chalceus,* etc.). For the German North Sea coast, Meyer et al. (1997) listed 11 spider species which prefer salt marshes on clay (e.g. *Praestigia duffi, Pardosa purbeckensis*, *Leptorhoptrum robustum, Walckenaeria kochi, Oedothorax retusus*).

Species of carabids and spiders on beaches of the North Sea and the Baltic Sea coasts differ depending on the sand-shingle mixture (Schierding et al. 2014; Vahder and Irmler 2010). Characteristic species among carabids that are found on both sandy and shingle beaches include *Bembidion pallidipenne, Cicindela maritima* (however, extremely rare), and *Bembidion saxatile*, respectively. Among spiders, both *Arctosa cinerea* and *Pardosa agricula* prefer sandy and shingle beaches, respectively. *Masoreus wetterhallii, Harpalus modestus*, and *Amara fulva* are common dune dwellers among carabids (Lohse 1954; Schierding et al. 2014), while among spiders, *Arctosa perita* and *Xysticus kochi* prefer dunes (Vahder and Irmler 2010). *Masoreus wetterhallii* is not restricted to dunes in eastern regions, e.g. in Mecklenburg-Western Pomerania (Müller-Motzfeld 1989) and Saxony-Anhalt (Hoffmann 2000).

11.3.4 Agricultural Use

Most salt marshes were or are under agricultural use. Stock et al. (1997) mentioned that only 4% of the salt marshes of the North Sea coast in Schleswig-Holstein had been ungrazed for a long time (current status in 1993).

The influence of grazing on the arthropod fauna of salt marshes was studied at the North Sea coast by Irmler and Heydemann (1986); Irmler et al. (1987); Rahmann et al. (1987); Andresen et al. (1990); Grell (1992); Meyer and Reinke (1995, 1996), Meyer et al. (1995, 1997) and at the Baltic Sea coast by Müller-Motzfeld et al. (1996) and Schliemann (2003).

Irmler and Heydemann (1986) and Rahmann et al. (1987) published quantitative data on various taxa including spiders and beetles. Rahmann et al. (1987) only referred to numbers of higher taxa. Many results found by pitfall trapping revealed, however, erroneous results because data gained by pitfall traps for single species are in contradiction to density results regarding the effect of grazing (Irmler and Heydemann 1986).

Grazing provokes a very complex chain of effects which changes depending on the ecological demands of the species. Irmler et al. (1987) described the effects for the spider *Erigone longipalpis*. On the one hand, physical effects due to lower vegetation change the insolation: the increasing evaporation and the decreasing air moisture influence the population density. On the other hand, the decreasing density of Collembola, the preferred prey of the spider, and the damage of webs by the cattle constrains the spider to a running predatory behaviour that is reflected by a higher activity with a higher energy demand under grazed conditions. Both effects finally lead to a decreasing population density with increasing grazing intensity.

From their studies at the Wursten Coast, Främbs et al. (2002) suggest that there is also a direct impact by agricultural use: many carabid beetles are more protected against drifting by waves in high growing vegetation than in short grazed pastures.

Grazing also has an effect on the salt content of the soil because it leads to increased dryness of the soil, causing higher salinity (Irmler and Heydemann 1986).

Agricultural use, in particular grazing of coastal salt marshes, influences the development, composition, and zonation of vegetation and invertebrates (Irmler and Heydemann 1986; Dierssen et al. 1994). Under grazing conditions, faunal assemblages were found in lower elevations than under ungrazed conditions (Andresen et al. 1990). This was explained with the higher net sedimentation under ungrazed conditions. The implications of extensive and intensive grazing by sheep or cattle were well studied at the North Sea coast which resulted in specific recommendations for grazing management (Andresen et al. 1990; Stock et al. 1997).

The effect of grazing on the vegetation development of salt marshes differs between the North Sea and the Baltic Sea coasts. Therefore, a differentiated assessment is required, e.g. habitat preference of specific species may be different between these areas. For example, the lycosid spider *Pardosa purbeckensis* prefers ungrazed salt marshes at the North Sea coast, while it nearly exclusively occurs in extensively grazed salt marshes at the Baltic coast. The same phenomenon was found for other species such as *Dicheirotrichus gustavii*, *Erigone longipalpis*, and *Walckenaeria kochi*.

In spite of the influence of both the grazing intensity and the regeneration of salt grassland at the North Sea coast (Meyer and Reinke 1996) and the Baltic Sea coast (Schultz 1997), respectively, many species are known as indicators of specific vertical zones. At the Baltic Sea, brackish reed vegetation developed under ungrazed conditions with the endangered species *Bembidion fumigatum* and *B. transparens*, whereas under grazed conditions the common *B. minimum* occurs (Schliemann 2010).

11.3.5 Endangered Species and Nature Conservation

Coastal habitats, salt marshes, and many of their inhabiting species are threatened by human activities. At the North Sea coast, large areas are part of the Wadden Sea National Park. At the Baltic Sea coast, they are under nature protection. Their specialised flora and fauna are of high value for nature conservation and have been the reason to include salt marshes in the ecological network NATURA 2000 of the European habitat directive and further international conservation agreements (e.g. Hofstede 2003).

Table 11.4 Salt marsh spiders and their specifications in a Red List. Selected from Reinke et al. (1998). Column S-H identical to Lemke et al. (2013)

Araneae	Habitat	Red List		
		DE	S-H	MVP
Argenna patula	Salt marsh, waterside, grassland wet & dry	U	3	2
Praestigia duffeyi	Salt marsh	R	.	.
Ceratinopsis stative	Salt marsh, dry, waterside, dunes	3	2	1
Erigone dentigera	Salt marsh	R	3	3
Erigone longipalpis	Salt marsh	.	.	4
Hypselistes jacksoni	Salt marsh, moorland, waterside, dry, dunes	2	3	4*
Leptorhoptrum robustum	Salt marsh, grassland wet & dry	.	.	3
Prinerigone vagans	Salt marsh, field	.	3	.
Saltilatlas britteni	Salt marsh	1	G	0
Silometopus ambiguus	Salt marsh	R	.	4*
Silometopus elegans	Salt marsh, waterside	3	3	4
Silometopus incurvatus	Salt marsh, waterside	R	3	4*
Walckenaeria kochi	Salt marsh, moorland, grassland wet	3	3	3
Pardosa purbeckensis	Salt marsh	3	.	4
Enoplognatha mordax	Salt marsh, dunes, waterside	2	3	3
Robertus heydemanni	Salt marsh	R	3	.
Ozyptila simplex	Salt marsh	.	2	.
Ozyptila westringi	Salt marsh, waterside	R	2	.

DE Germany, *S-H* Schleswig-Holstein, *MVP* Mecklenburg-Western Pomerania
0: Extinct; 1: Critically endangered; 2: Endangered; 3: Vulnerable endangered; 4: Potentially endangered; 4*: Only single records, potentially heavily endangered; *U* Unknown status; *R* Geographical restriction; *G* Assumed endangerment

Based on his comprehensive material and his extensive knowledge, Heydemann (1973, 1980) described the habitats of salt marshes in the Wadden Sea, the high number of their species, and the threats by anthropogenic impacts. Wachlin et al. (1990) and Müller-Motzfeld (1997) accentuated the importance of coastal habitats of the Baltic Sea for nature protection and species conservation and analysed the risk of assessment in Mecklenburg-Vorpommern. Impact factors and endangerment of carabids (Schierding et al. 2014) and spiders (Vahder and Irmler 2010) were also studied for the Baltic Sea coasts of Schleswig-Holstein. Besides threatened habitats, Red Lists denominate endangered species, in our case, of salt marshes and dunes (spiders: Table 11.4, carabid beetles: Table 11.5).

Müller-Motzfeld (2007) listed 22 halobiontic and 13 halophilic carabid species. 91% of the halobiontic species are recorded in the Red List of Germany (Trautner et al. 1997). Because of their restricted geographic distribution, Germany has a high responsibility for conservation of the following species of salt and coastal habitats: *Dyschirius extensus*, *Bembidion pallidipenne*, *Agonum monachum*, *Amara quenseli silvicola, Amara strenua*, and on a lower level for *Bembidion aeneum*, *B. aspericolle*, *B. cruciatum polonicum*, *B. maritimum*, and *Dicheirotrichus gustavii* (Müller-Motzfeld 2007).

Table 11.5 Salt marsh and coastal carabid species among selected Red List species and salt preference (Salt) selected from Müller-Motzfeld (2007; Tables 1 and 2) and Red List characterisation for Germany and the northern Federal States. D: Germany (Trautner et al. 1997); M: Mecklenburg-Western Pomerania (Müller-Motzfeld and Schmidt 2008); A: Lower Saxony (Assmann et al. 2003); and G: Schleswig-Holstein (Gürlich et al. 2011)

Species	Salt	D	M	A	G	Species	Salt	D	M	A	G
Acupalpus elegans	hbiont	3	–	1	1	*Dicheirotrichus gustavii*	hbiont	V	2	*	*
Acupalpus exiguus	htol	3	*	V	*	*Dicheirotrichus obsoletus*	hbiont	1	–	1	–
Acupalpus interstitialis	hphil	R	–	–	–	*Dyschirius chalceus*	hbiont	1	1	1	2
Acupalpus maculatus	htol	3	–	–	–	*Dyschirius extensus*	hbiont	1	–	0	–
Agonum monachum	hbiont	1	1	–	–	*Dyschirius impunctipennis*	hphil	2	1	2	2
Amara quenseli silvicola	htol	2	3	2	2	*Dyschirius laeviusculus*	htol	2	1	1	0
Amara strandi	hbiont	1	–	–	–	*Dyschirius nitidus*	htol	2	?	1	2
Amara strenua	hphil	2	–	2	R	*Dyschirius salinus*	hbiont	V	3	*	*
Anisodactylus poeciloides	hbiont	2	2	2	1	*Harpalus cephalotes*	hphil	0	–	–	–
Bembidion aspericolle	hbiont	2	–	2	–	*Harpalus melancholicus*	htol	2	1	–	–
Bembidion ephippium	hbiont	1	–	0	1	*Harpalus neglectus*	htol	2	3	2	2
Bembidion fumigatum	hphil	3	*	3	*	*Nebria livida*	htol	3	3	2	3
Bembidion iricolor	hbiont	2	–	2	3	*Ophonus diffinis*	hbiont	1	–	–	–
Bembidion maritimum	hphil	2	–	3	2	*Ophonus puncticollis*	htol	V	?	2	–
Bembidion pallidipenne	hphil	2	2	2	2	*Ophonus subsinuatus*	hphil	1	–	–	–
Bembidion saxatile	htol	V	*	–	V	*Pogonus chalceus*	hbiont	V	–	*	*
Bembidion tenellum	hbiont	1	V	1	2	*Pogonus iridipennis*	hbiont	1	–	1	–
Bembidion transparens	htol	3	*	–	–	*Pogonus luridipennis*	hbiont	2	–	1	2
Carabus clathratus	htol	2	3	2	1	*Pterostichus cursor*	hbiont	0	–	–	–
Cicindela maritima	htol	2	1	1	1	*Pterostichus taksonyis*	htol	0	–	–	–
Cillenus lateralis	hbiont	2	–	2	1	*Tachys scutellaris*	hbiont	1	–	0	–

11.4 Previous Main Research Topics and Open Questions

The most comprehensive studies of the German and Dutch coastal habitats were performed in order to study the consequences of diking on vegetation and animals. Salt marshes depend on floods. Therefore, diking offers the possibility to analyse the ecological processes combined with the impact of floods on salt marsh biocenoses (Heydemann 1960, 1962: Schleswig-Holstein; Haeck 1971: Ijsselmeer-Polder; Meijer 1980: Lauwerszee-Polder).

Later, the main topic of zoo-ecological salt marsh studies changed. The influence of grazing and questions of management (Irmler and Heydemann 1986; Rahmann et al. 1987; Andresen et al. 1990; Dierssen et al. 1994; Olbrich 1994; Burkhardt 1995; Meyer and Reinke 1996; Meyer et al. 1997) and the consequences of re-embankment on flora and fauna (Müller-Motzfeld et al. 1996; Müller-Motzfeld and Holz 1996; Främbs et al. 2002) were the focus of research.

Along the elevation gradient from the Wadden Sea to dunes, soil types strongly change corresponding to the intensity and dynamics of floods and salt content. Experimental studies in the field and in the lab were performed by Heydemann (1968), who found many adaptations in salt marsh species to overcome flooding, e.g., 50% of experimental individuals of *Dicheirotrichus gustavii* survived 5 days of submersion and 56 days on the surface of water (both: 6–8 °C, 32‰), whereas the salt marsh spiders *Erigone arctica* and *Leptorhoptrum robustum* are able to spin nets under water during submergence (Heydemann 1979).

Some species, such as *Cillenus lateralis*, *Bledius spectabilis* (Staphylinidae), and *Heterocerus fenestratus* (Heteroceridae), are known to construct burrow systems in the soil (Bro Larsen 1936). This behaviour largely prevents direct exposure of the beetles to seawater during submergence twice a day (Evans et al. 1971). *Dicheirotrichus gustavii* hides in cracks without digging burrows (Bro Larsen 1951). This species reduces its oxygen consumption drastically when covered experimentally by seawater. A large increase of the oxygen consumption rate indicated anoxic conditions during submergence. Beetles, removed from their burrows after a tidal submersion, were mobile or had a very short recovery time indicating that they had access to air supply during the tidal submersion (Evans et al. 1971).

Lohse (1987) deduced the factors relevant for the habitat preference of beetles by a comparative analysis of diverse habitats, which differed in the combination of the influence of salt, tides, soil type, and humidity. He stated, for instance, that the tides and not the content of salt are the key factor for the occurrence of *Cillenus lateralis* (Fig. 11.1).

The influence of tides and salt content on the dispersion of salt marsh species may be differentiated when the situations in estuaries and at the lower course of streams are compared. Unfortunately, the respective studies give an inhomogeneous picture and they differ from the results of Lohse (1987). According to Hildebrandt (1990, River Weser estuary), *Cillenus lateralis* depends on salt habitats. Assmann and Terlutter (1999) also characterised the species as an exclusive salt-dependent species. Terlutter (1999, River Ems) found *Bembidion maritimum* only at river shores which were under salt influence. In contrast, Assmann and Terlutter (1999, River Ems) noted localities without any salt. Gürlich (1999, River Elbe) evaluated *B. maritimum* as halophilic. Desender and Maelfait (1999) found the species as well as the spider *Praestigia duffeyi* only in brackish habitats of the Schelde River.

Many questions are open—as normal in science, e.g. the elevation gradient has only been roughly described (see above) or we have insufficient knowledge of the differences in dispersion along a coastal gradient and of the ecology of salt marsh species, etc. Additionally, the central question is nearly unresolved for most species: how does salt influence the terrestrial arthropods?

11.5 The Problem of Missing Knowledge on the Biology of Coastal Species

Bro Larsen (1936) published her classical and fundamental paper on the tunnel-digging beetles. She found that salt marsh species of the carabid genus *Dyschirius* hunt the staphylinid beetles of the genus *Bledius* in their tubes. But in many cases, only poor knowledge on biology and ecology of salt marsh species exists to predict future changes in behaviour and dispersion and, therefore, to assess the reaction of the assemblages in general.

Interesting biological data is published on staphylinid beetles of salt marshes. Some *Bledius* species are able to store food (Bro Larsen 1952) and *Bledius spectabilis* discriminates food with a low salt content under laboratory conditions. Beetles of the latter species showed an insignificant increase of Na^+ concentration in their haemolymph, but a high increase in their rectal fluid when feeding on food with a salt content of 4.0% (Bro Larsen 1953).

Only few studies analysed circadian rhythms in salt marsh arthropods. Foster (1983) showed by a comparison of field data that the activity of *Dicheirotrichus gustavii* follows a circadian rhythm. After a first flooding, this species will rest in the soil during the next tide. Moreover, laboratory experiments under constant darkness revealed a free-running circadian locomotor activity rhythm (Treherne and Foster 1977).

Evans (1976) studied *Thalassotrechus barbarae* (Horn) from the rocky intertidal zone at the Pacific coast of California. In the field, locomotor activity was performed during night and the low tide. In laboratory experiments, a stable circadian rhythm was found and a circatidal rhythm of locomotor activity persisted 3 days but subordinated to the dominant circadian rhythm.

Spring and autumn breeders were distinguished in carabid beetles (Larsson 1939), which are both present in salt marsh habitats. Paarmann (1976) established a special subgroup of seasonal propagation, the summer breeder, for the salt marsh species *Pogonus chalceus*. This species produces one generation per year in our region, but one generation after the other due to the temperature conditions alone without influence of day length. He suggested that other species of this habitat might belong to the same type; a hypothesis, which only can be falsified by further laboratory studies.

Detailed experiences are available on the ability of salt species to colonise new habitats. Some spiders are able to disperse by ballooning (Duffey 1956) and halobiontic and halophilic carabid beetles are in general able to fly, but some of them only with low flight activity. The relations between wing dimorphism, reproduction, and evolution in the specific salt marsh beetle *Pogonus chalceus* was studied by Desender (1985, 1989). Studies on light-ships (Heydemann 1967b) and on newly built islands (Topp 1988: Gr. Knechtsand; Plaisier and Schultz 1991: Lütje Hörn) showed that such habitats can be colonised by many arthropods without problems.

The regulating factors of abundance and occurrence differ between spiders and carabid beetles. In general, the vegetation structure plays an important role for the dispersion of spiders in salt marshes (Schaefer 1983; Burkhardt 1995).

It is difficult to evaluate the reaction of animals on climate change without comprehensive knowledge of their ecological demands. For woods, the dependence of climate impacts on carabids is studied using *Carabus intricatus*. The frequency of the species decreased in the northern and western lowlands of Germany since the beginning of the twentieth Century (Gries et al. 1973). The decrease of frequency of this southerly distributed species was correlated with the change from Continental climate conditions with warm summers and cold winters to a more Atlantic character of climate with low temperatures in summer and relatively high temperatures in winter. This process started already before the beginning of the twentieth century. An increase of temperature seems to favour the re-colonisation of northern regions if we assume that the temperature conditions in summer are responsible for the process. However, Malausa (1977) found in experiments that the species needs low temperatures during its winter diapause (<5 °C) of over 5 months for egg ripening. Therefore, *C. intricatus* will not benefit from the general temperature increase at its northern border, because the temperatures in winter will be not as low and last long enough as needed for the development of this species (Mossakowski 1996).

Most visible impacts of climate change are changes of species distribution. Such a recent influence was also described—as for other taxa—for spiders and carabid beetles. A striking example seems to be *Argiope bruennichi,* an araneid spider with a Mediterranean distribution centre that was found only at a few locations in Central Europe up to the 1950s, now distributed here area-wide (Sacher 2001; Arages 2021). Other species with southern distribution areas, such as *Kryptonesticus eremita* (Jäger 1998), *Oecobius maculatus* (Hänggi 2003), and *Zoropsis spinimana* (Hänggi and Bolzern 2006), were discussed to benefit from climate change, but no coastal species are included.

The impact of climate change on carabid beetles was studied more intensively in mountainous forests (Müller-Kroehling et al. 2014) and in the alpine hypogean and epigean fauna (e.g. Brandmayr and Pizzolotto 2016; Gobbi 2020). Only few coastal carabid species are known which might have an advantage due to climate change: The Atlantic-Mediterranean salt marsh species *Pogonus littoralis* was found in Belgium (Desender et al. 2008) and might be a candidate to colonise The

Netherlands and the German coasts in the future. *Dyschirus rivularis* was found recently in The Netherlands, far from the next known location (Turin 2000).

In his review considering salt marsh insects and spiders, Foster (2000) stated "However, we know next to nothing about most of these animals: particularly neglected are certain abundant and diverse insect groups such as Diptera and Lepidoptera".

References

Andresen H, Bakker JP, Bronges M, Heydemann B, Irmler U (1990) Long-term changes of salt marsh communities by cattle grazing. Vegetation 89:137–148

arages (2021) (Arachnologische Gesellschaft). https://arages.de/arachnologie-vernetzt/atlas-der-spinnentiere

Assmann T, Terlutter H (1999) Die längszonale Gliederung der Laufkäferfauna der Ems. Laufkäfer in Auen. Angewandte Carabidologie 1:33–40

Assmann T, Dormann W, Främbs H, Gürlich S, Handke K, Huk T, Sprick P, Terlutter H (2003) Rote Liste der in Niedersachsen und Bremen gefährdeten Sandlaufkäfer und Laufkäfer (Coleoptera: Cicindelidae et Carabidae) mit Gesamtartenverzeichnis. Informationsdienst Naturschutz Niedersachsen 23:70–95

Bangsholt F (1983) Sandspringernes og løbebillernes udbredelse og forekomst i Danmark ca. 1830-1981. Dansk Faunistik Bibliothek 4:1–271

Bethge W (1973) Ökologisch-physiologische Untersuchungen über die Bindung von *Erigone longipalpis* (Araneae, Micryphantidae) an das Litoral. Faunistisch-ökologische Mitteilungen 4:223–240

Bleich O, Gürlich S, Köhler F (2013 /start). Verzeichnis und verbreitungsatlas der käfer deutschlands. www.coleokat.de

Blick T (2014) The long-lasting story of the wrong naming of *Silometopus ambiguus* as *S. curtus* (Araneae: Linyphiidae). Arachnologische Mitteilungen 47:45–48

Blick T, Bosmans R, Buchar J, Gajdoš P, Hänggi A, Van Hesldingen P, Ružicka V, Starega W, Thaler K (2004) Checkliste der spinnen mitteleuropas. checklist of the spiders of central Europe. (Arachnida: Araneae). http://www.arages.de/checklist.html#2004_Araneae. Accessed 1 Dec 2004

Brandmayr P, Pizzolotto R (2016) Climate change and its impact on epigean and hypogean carabid beetles. Period Biol 118:147–162. https://doi.org/10.18054/pb.2016.118.3.4062

Bro Larsen E (1936) Biologische Studien über die tunnelgrabenden Käfer auf Skallingen. Videnskabelige meddelelser fra Dansk naturhistorisk forening, Kobenhavn 100:1–231

Bro Larsen E (1951) Studies on the soil fauna of Skallingen. Oikos 1:166–192

Bro Larsen E (1952) On subsocial beetles from salt marsh, their care of progeny and adaption to salt and tide. Transactions of the 9 International Congress of Entomology, Amsterdam 1:502–506

Bro Larsen E (1953) Successionsstudier i et havendigsområde, Skomargersletten, Skallingen. Geografisk Tidskrift 52:182–200

Bröring U, Dahmen R, Haeseler V, von Lehm R, Niedrighaus R, Schultz W (1993) Dokumentation der Daten zur Flora und Fauna terrestrischer Systene im niedersächsischen Wattenmeer. Berichte aus der Ökosystemforschung Wattenmeer 2(2):1–119

Burakowski B, Mroczkowski M, Stefanska J (1973 1974), Katalog fauny polski, Coleoptera-Carabidae, part 1 and 2. Panstwowe Wydawnictwo Naukowe, Warszawa

Burkhardt P (1995) Vegetationsstruktur und Überflutung als Faktoren für die Verteilung der Spinnen (Araneae) in den Salzwiesen der Wurster Küste. Diplomarbeit, Universität Bremen

Denis J (1963) Notes sur les érigonides. XXV. A propos de deux espèces de Camargue. Bull Soc zool France 88:392–398

Desender K (1985) Wing dimorphism and reproductive biology in the halobiont carabid beetle *Pogonus chalceus* Marsham (Coleoptera, Carabidae). Biol Jaarboek Dodonaea 53:89–100

Desender K (1989) Heritability of wing development and body size in a carabid beetle, *Pogonus chalceus* Marsham, and its evolutionary significance. Oecologia 78:513–520

Desender K, Maelfait JP (1999) Diversity and conservation of the arthropods in tidal marshes along the river Schelde. Biol Conserv 87:221–229

Desender K, Dekoninck W, Maes D, Crevecoer L, Dufrene M, Jacobs M, Lambrechts J, Pollet M, Stassen E, Thys N (2008) Een nieuve verspreidingsatlas van den loopkevers en zandloopkevers (Carabidae) in Belgie. Rapporten van het Instituut voor Natuur- en Bosonderzoek, Brussel

Dierssen K, Eischeid I, Fock H, Gettner S, Hamann U, Haase A, Kiehl K, Mieth A, Reinke HD, Tischler T, Tulowitzki I, Walter J (1994) Ökosystemforschung Wattenmeer Schleswig-Holstein, Teilvorhaben A 5.2 (Pflanzen) und A 5.3 (Tiere). In: Bioindikation im Supralitoral. kiel

Dormann W (2015) Die biotopspezischen laufkäferarten der küsten und binnenlandsalzstellen deutschlands unter besonderer berücksichtigung einer globalen klimaänderung (coloeptera, carabidae). Diploma thesis, University Bremen, pp. 235

Dormann W, Metzing D, Mossakowski D (2008) Klimafolgen und Küsten: Auswirkungen auf die Verteilung und Verbreitung von Laufkäfern der Salzwiesen (Carabidae). Insecta 11:51–62

Doyen JT (1976) Marine beetles (except Staphylinidae). In: Cheng L (ed) Marine insects. North Holland, Amsterdam, pp 497–519

Duffey E (1956) Aerial dispersal in a known spider population. J Anim Ecol 25:85–111

Dutt E (2004) Autökologische untersuchungen an ausgewählten salzcarabiden im hinblick auf ihre natürlichen lebensbedingungen. Diplomarbeit Universität Greifswald:1–81

Elliot P, King PE, Fordy MR (1983) Observations on *Cillenus lateralis* samouelle, an intertidal Carabid (Col.). The entomological monthly Magazine 119:85–89

Fauna Europaea (2006). http://www.faunaeur.org/distribution.php

Evans WG (1976) Circadian and circatidal locomotory rhythms in the intertidal beetle *Thalassotrechus barbarae* (horn): Carabidae. J Exp Mar Biol Ecol 22:79–90

Evans PD, Ruscoe CNE, Treherne JE (1971) Observations on the biology and submergence behaviour of some littoral beetles. Journal of the Marine Biolog 51:375–386

Finch OD, Krummen H, Plaisier F, Schultz W (2007) Zonation of spiders (Araneae) and carabid beetles (Coleoptera: Carabidae) in island salt marshes at the North Sea coast. Wetl Ecol Manag 15:207–228. https://doi.org/10.1007/s11273-006-9024-4

Fiszer J (1988) The second locality of a rare spider *Silometopus incurvatus* (O. P. Cambridge) (Aranei, Erigonidae) in Poland. Przegla Zool 32:529–533

Foster WA (1983) Activity rhythms and the tide in a salt marsh beetle *Dicheirotrichus gustavii*. Oecologia 60:111–113

Foster WA (2000) Coping with the tides: adaptations of insects and arachnids from British saltmarshes. In: Sherwood BR, Gardiner BG, Harris T (eds) British saltmarshes. Linnean Society, London, pp 203–222

Foster WA, Treherne JE (1979) Adaptive strategies of airbreathing arthropods from marine salt marshes. In: Jeffries RL, Davy AJ (eds) Ecological processes in coastal environments. Blackwell Scientific Publications, Oxford, pp 165–175

Främbs H (1997) Auswirkungen von Sturmfluten auf die Laufkäfer (Col. Carabidae) der Nordseeküste. Arbeitsberichte Landschaftsökologie Münster 18:47–61

Främbs H, Kinder M, Hielen B, Böhme B, Günther CP, Rachor E, Cordes H, Mossakowski D (2002) Renaturierung salzbeeinflußter Lebensräume der Nordseeküste, vol 68. BfN-Skripten, p 325

Gersdorf E, Kuntze K (1957) Zur Faunistik der Carabiden Niedersachsens. Berichte der Naturhistorischen Gesellschaft zu Hannover 103:101–136

Gobbi M (2020) Global warming challenges, threats and opportunities for ground beetles 8 (coleoptera, Carabidae) in high altitude habitats. Acta Zool Acad Sci Hung 66(Suppl):5–20. https://doi.org/10.17109/AZH.66.Suppl.5.2020

Grell O (1992) Einfluss der beweidung auf brackwasser-röhricht und insel-salzwiese. Faunistisch-ökologische Mitteilungen, Suppl. 13:21–43

Gries B, Mossakowski D, Weber F (1973) Coleoptera Westfalica: Familia Carabidae, genera *Cychrus*, *Carabus* und *Calosoma*. Abhandlungen des Landesmuseums für Naturkunde, Münster 35:1–80

Gürlich S (1999) Die Laufkäfer der tideelbe. Laufkäfer in auen. Angewandte Carabidologie, Suppl. 1:3–32

Gürlich S, Tolasch T (2006). www.entomologie.de/hamburg/karten/

Gürlich S, Suikat R, Ziegler W (2011) Die käfer schleswig-holsteins–rote liste. Band 1. http://www.schleswig-holstein.de/UmweltLandwirtschaft/DE/NaturschutzForstJagd/_DL/rl_kaefer_band1__blob=publicationFile.pdf

Haeck J (1971) The immigration and settlement of carabid beetles in the new Ijsselmeer-polders. Miscellaneous papers, Landbouwhogeschool, Wageningen 8:33–51

Hänggi A (2003) Nachträge zum "Katalog der schweizerischen spinnen"–3. Neunachweise von 1999 bis 2002 und nachweise synanthroper spinne. Arachnol Mitt 26:36–54

Hänggi A, Bolzern A (2006) *Zoropsis spinimana* (Araneae: Zoropsidae) neu für Deutschland. Arachnologische Mitteilungen 32:8–10

Hänggi A, Stöckli E, Nentwig W (1995) Lebensräume mitteleuropäischer Spinnen. Charakterisierung der Lebensräume der häufigsten Spinnenarten Mitteleuropas und der mit diesen vergesellschafteten Arten. Centre Swisse de cartographie de la faune, Neuchatel

Heydemann B (1960) Die biozönotische Entwicklung vom Vorland zum Koog. Vergleichend-ökologische Untersuchungen an der Nordseeküste. 1. Spinnen (Araneae). Abhandlungen der math.-nat. Klasse der Akademie der Wissenschaften und Literatur Mainz 11:745–913

Heydemann B (1962) Die biozönotische Entwicklung vom Vorland zum Koog. Vergleichend-ökologische Untersuchungen an der Nordseeküste. 2. Käfer (Coleoptera). Abhandlungen der math-nat Klasse der Akademie der Wissenschaften und Literatur Mainz 11:765–964

Heydemann B (1967a) Die biologische Grenze Land–Meer im Bereich der Salzwiesen. Franz Steiner, Wiesbaden, p 200

Heydemann B (1967b) Der Überflug von Insekten über Nord- und Ostsee nach Untersuchungen auf Feuerschiffen. Deutsche Entomologische Zeitschrift NF 14:185–215

Heydemann B (1968) Das Freiland- und Laborexperiment zur Ökologie der Grenze Land-Meer. Zool AnzSuppl 31:256–309

Heydemann B (1973) Zum Aufbau semiterrestrischer Ökosysteme im Bereich der Salzwiesen der Nordseeküste. Faunistisch-ökologische Mitteilungen 4:155–168

Heydemann B (1979) Responses of animals to spatial and temporal environmental heterogeneity within salt marshes. In: Jeffries RL, Davy AJ (eds) Ecological processes in coastal environments. Blackwell Scientific Publications, Oxford, pp 145–163

Heydemann B (1980) Die ökologische Gefährdung des Wattenmeeres und Grundlagen zu seinem Schutz. Natur und Landschaft 55:240–249

Heydemann B (1983) Ecology of the arthropods of the lower salt marsh. In: Smit CJ, den Hollander J, van Wingerden WKRE, Wolff WJ (eds) Terrestrial and freshwater fauna of the Wadden Sea area. (report 10 of the Wadden Sea working group). Stichting Veth, Leiden, pp 145–163

Heydemann B (1984) Das Ökosystem "Küsten-Salzwiese"–ein Überblick. Faunistisch-ökologische Mitteilungen 5:249–279

Hildebrandt J (1990) Terrestrische Tiergemeinschaften der Salzwiesen im Ästuarbereich. Dissertation Universität Bremen

Hildebrandt J (1997) Wie sind terrestrische Wirbellose an Überflutungen angepaßt? Arbeitsber. Landschaftsökologie Münster 18:15–28

Hoffmann E (2000) Zönotische und populationsökologische Untersuchungen an Laufkäfern (Coleoptera, Carabidae) zur Bedeutung von Habitatqualität und Habitatfragmentierung. Dissertation Universität Bremen, p 167

Hofstede JLA (2003) Integrated management of artificially created salt marshes in the Wadden Sea of Schleswig-Holstein, Germany. Wetland Ecology Management 11:183–194

Horion A (1959) Die halobionten und halophilen Carabiden der deutschen Fauna. Wissenschaftliche Zeitschrift der Martin-Luther-Universität Halle-Wittenberg 8:549–556

Hutchinson GE (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? Am Nat 93:145–159

Irmler U, Gürlich S (2004) Die ökologische Einordnung der Laufkäfer (Coleoptera: Carabidae) in Schleswig-Holstein. Faunistisch-ökologische Mitteilungen, Supplement 32:1–117

Irmler U, Heller K (2002) Zonierung der Staphylinidae in einem Salzgrünland der schleswig-holsteinischen Nordseeküste. Faunistisch-ökologische Mitteilungen 8:219–229

Irmler U, Heydemann B (1985) Populationsdynamik und Produktion von *Erigone longipalpis* (Araneae, Micryphantidae) auf einer Salzwiese Nordwestdeutschlands. Faunistisch-Ökologische Mitt 5:443–454

Irmler U, Heydemann B (1986) Die ökologische Problematik der Beweidung von Salzwiesen an der Niedersächsischen Küste–am Beispiel der Leybucht. Beihefte zu Naturschutz und Landschaftspflege in Niedersachsen 15:1–115

Irmler U, Heydemann B, Wrage HA (1987) Veränderungen der Wirbellosenfauna in Salzwiesen durch Beweidung. In: Kempf N., Lamp NJ, Prokosch P (Hrsg) Salzwiesen: Geformt von Küstenschutz, Landwirtschaft oder Natur? WWF-Tagungsbericht 1:243–254

Irmler U, Heller K, Meyer H, Reinke HD (2002) Zonation of ground beetles (Coleoptera: Carabidae) and spiders (Araneida) in salt marshes at the north and the Baltic Sea and the impact of the predicted sea level increase. Biodivers Conserv 11:1129–1147

Jäger P (1998) Weitere Funde von *Nesticus eremita* (Araneae: Nesticidae) in Süddeutschland mit Angaben zur Taxonomie im Vergleich zu N. cellulanus. Arachnologische Mitteilungen 15:13–20

Kinder M, Främbs H, Hielen B, Mossakowski D (2003) Regenration von Salzwiesen in einem Sommergroden an der Nordseeküste: EF-Vorhaben "Salzwiesenprojekt Wurster Küste". Natur und Landschaft 78:343–353

Knülle W (1953) Zur Ökologie der Spinnen an Ufern und Küsten. Z Morph Ökol 42:117–158

Larsson SG (1939) Entwicklungstypen und Entwicklungszeiten dänischer Carabiden. Entomologiske Meddelelser, Kobenhavn 20:277–560

Lemke M, Reinke HD, Vahder S, Irmler U (2013) Die Spinnen Schleswig-Holsteins, Rote Liste. Ministerium für Energiewende, Landwirtschaft. In: Umwelt und ländliche Räume des Landes Schleswig-Holstein, keil. www.umweltdaten.landsh.de/nuis/upool/gesamt/spinnen/rl_spinnen_2013.pdf

Lindroth CH (1945a) Die fennoskandischen Carabidae. I. (Spezieller Teil). Göteborgs Kungl. Vetenskaps och Vitterhets-Samhälles Handlingar. Se 4:Göteborg

Lindroth CH (1945b) Die fennoskandischen Carabidae. II. (Karten). Göteborgs Kungl. Vetenskaps och Vitterhets-Samhälles Handlingar. Se 4:Göteborg

Lindroth CH (1949) Die fennoskandischen Carabidae. III. (allemeiner teil). göteborgs kungl. vetenskaps och vitterhets-samhälles handlingar, vol 4, Göteborg

Locket GH (1964) Type material of British spiders in the O. Pickard-Cambridge collection at Oxford. Ann Mag Nat Hist 7:257–278

Lohse GA (1954) Die Laufkäfer des Niederelbegebietes und Schleswig-Holsteins. Verhandlungen des Vereins für naturwissenschaftliche Heimatforschung Hamburg 31:1–39

Lohse GA (1987) Ökologische Faktoren, die das Vorkommen von Küstenkäfern bestimmen. Mitteilungen der deutschen Gesellschaft für allgemeine und angewandte Entomologie 5:66–68

Luff M, Eyre MD (2000) Factors effecting the ground beetles (Coleoptera:Carabidae) of some British coastal marshes. In: Sherwood BR, Gardiner BG, Harris T (eds) British saltmarshes. Linnean Society, London, pp 235–245

Malausa JC (1977) Étude écophysiologique de la diapause hivernale chez les adultes de *Chaetocarabus intricatus* L. (Coleoptera, Carabidae). Ann Zool Ecol Animal 9:637–647

Meijer J (1980) The development of some elements of the arthropod fauna of a new polder. Oecologia 45:220–235

Meyer T (1997) Reaktionen von *Pogonus chalceus* (Marsham) und *Dicheirotrichus gustavii* Crotch (Coleoptera, Carabidae) auf Überflutungen in den Salzwiesen der Wurster Küste. Diplomarbeit, Universität Bremen

Meyer H, Reinke HD (1995) Spezialisierung und räumlich-zeitliche Einnischung der Wirbellosenfauna in Salzwiesen. Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 10:485–490

Meyer H, Reinke HD (1996) Veränderungen der biozönotischen Struktur der Wirbellosenfauna von Salzwiesen durch unterschiedliche Beweidungsintensitäten mit Schafen. Faunistisch-ökologische Mitteilungen 7:109–151

Meyer H, Fock H, Haase A, Reinke HD, Tulowitzki I (1995) Structure of the invertebrate fauna in salt marshes of the Wadden Sea coast of Schleswig-Holstein influenced by sheep-grazing. Helgoländer Meeresuntersuchungen 49:563–589

Meyer H, Reinke HD, Irmler U (1997) Die Wirbellosenfauna unterschiedlicher Salzwiesen an der Nordseeküste in Schleswig-Holstein und Niedersachsen. Faunistisch-ökologische Mitteilungen 7:267–284

Mossakowski D (1996) Auswirkungen von Klimaänderungen auf Salzwiesen und ihre Fauna. SDN-Kolloquium Klimaänderung und Küste. Schriftenreihe der Schutzgemeinschaft Deutsche Nordseeküste 1:46–60

Mossakowski D (2007) Salzwiesen und Hochmoore: Extremstandorte? Angewandte Carabidologie 8:9–16

Müller-Kroehling S, Jantsch M, Fischer HS, Fischer A (2014) Modelling the effects of global warming on the ground beetle (Coleoptera: Carabidae) fauna of beech forests in Bavaria, Germany. Eur J Entomol 111:35–49

Müller-Motzfeld G (1989) Laufkäfer (Coleoptera: Carabidae) als pedobiologische Indikatoren. Pedobiologia 33:145–153

Müller-Motzfeld G (1997) Küstenlebensräume des deutschen Ostseeraumes und deren Bedeutung für den Biotop- und Artenschutz. Schriftenreihe für Landschaftspflege und Naturschutz 52:25–36

Müller-Motzfeld G (2004) Adephaga 1: Carabidae (Laufkäfer). In: Freude H, Harde KW, Lohse GA, Klausnitzer B (eds) Die Käfer Mitteleuropas, vol 2, 2nd edn. Spektrum-Verlag, Heidelberg, Berlin, p 521

Müller-Motzfeld G (2007) Die Salz- und Küstenlaufkäfer Deutschlands–Verbreitung und Gefährdung. Angewandte Carabidologie 8:17–27

Müller-Motzfeld G, Holz R (1996) Die Karrendorfer Wiesen 1994. Bisherige Ergebnisse der wissenschaftlich-begleitenden Untersuchungen im Überblick. Natur und Naturschutz in Mecklenburg-Vorpommern 32:141–146

Müller-Motzfeld G, Schmidt J (2008) Rote Liste der Laufkäfer Mecklenburg-Vorpommerns. Ministerium für Landwirtschaft, Umwelt und Verbraucherschutz Mecklenburg-Vorpommern, p 34. http://www.lung.mv-regierung.de/dateien/rote_liste_laufkaefer.pdf

Müller-Motzfeld G, Schultz R, Pössel KU (1996) Die Laufkäferfauna der Karrendorfer Wiesen als Indikator für die Sukzession der epedaphischen Arthropodenfauna nach dem Deichrückbau. Natur und Naturschutz in Mecklenburg-Vorpommern 32:112–129

Murphy J (2006) British Arachnological society. World distribution atlas. http://www.britishspiders.org.uk/html/bas.php?page=world

Nentwig W, Blick T, Bosmans R, Gloor D, Hänggi A, Kropf C (2018) Spinnen Europas. Version 4.2018. https://www.araneae.nmbe.ch

Niedrighaus R, Haeseler V, Janiesch P (2008) Die flora und fauna der ostfriesischen inseln–artenverzeichnis und auswertungen zur biodiversität. In: Schriftenreihe Nationalpark Niedersächsiches Wattenmeer, vol 11, pp 1–470

Olbrich B (1994) Überflutung, salzgehalt und beweidung als faktoren für carabiden im gradienten des vorlandes der wurster küste. Diploma thesis, University of Bremen. pp. 80

Paarmann W (1976) The annual periodicity of the polyvoltine ground beetle *Pogonus chalceus* marsh. (Col. Carabidae) and its control by environmental factors. Zool Anz 196:150–160

Palmén E (1949) Felduntersuchungen und Experimente zur Kenntnis der Überwinterung einiger Uferarthropoden. Annales entomologici Fennica, Suppl 14:169–179

Pétillon J, Ysnel F, Canard A, Lefeuvre JC (2005) Impact of an invasive plant (*Elymus athericus*) on the conservation value of tidal salt marshes in western France and implications for management: responses of spider populations. Biol Conserv 126:103–117

Pétillon J, Georges A, Canard A, Lefeuvre JC, Bakker JP, Ysnela F (2008) Influence of abiotic factors on spider and ground beetle communities in different salt-marsh systems. Basic and Applied Ecology 9:743–751

Plaisier F, Schultz W (1991) Kolonisationserfolg von Spinnen (Araneae) und Laufkäfern (Carabidae, Coleoptera) auf der Nordseeinsel Lütje Hörn. Drosera 91:7–20

Platnick NI (2006) In: Merrett P, Cameron HD (eds) The world spider Catalog, version 7.0. http://research.amnh.org/entomology/spiders/catalog/index.html

Rahmann M, Rahmann H, Kempf N, Hoffmann B, Gloger H (1987) Auswirkungen unterschiedlicher landwirtschaftlicher Nutzung auf die Flora und Fauna der Salzwiesen an der ostfrisieschen Wattenmeerküste. Senckenberg Marit 19:163–193

Reinke HD, Irmler U (1994) Die Spinnenfauna (Araneae) Schleswig-Holsteins am Boden und in der bodennahen Vegetation. Faunistisch-ökologische Mitteilungen, Suppl 17:1–147

Reinke HD, Irmler U, Klieber A (1998) Die Spinnen Schleswig-Holsteins, Rote Liste Landesamt für Natur und Umwelt des Landes Schleswig-Holstein.. www.schleswig-holstein.de/UmweltLandwirtschaft/DE/NaturschutzForstJagd/_DL/RL_Spinnen_pdf__blob=publicationFile.pdf

Reinke HD, Heller K, Irmler U (2000) Zonierung der Spinnen und Laufkäfer (Araneida, Coleoptera: Carabidae) im Überflutungsgradienten der Salzwiesen an Nord- und Ostsees. Entomologia Basiliensia 22:115–120

Remmert H (1955) Substratbeschaffenheit und Salzgehalt als ökologische Faktoren für Dipteren. Zoologische Jahrbücher, Systematik 83:453–474

Sacher P (2001) Zur Arealerweiterung von Argiope bruennichi (Araneae: Araneidae) in Deutschland–wie genau sind unsere frühen Daten? Arachnologische Mitteilungen 22:29–36

Schaefer M (1983) The arthropod fauna of high salt marshes. In: Smit CJ, den Hollander J, van Wingerden WKRE, Wolff WJ (eds) Terrestrial and freshwater fauna of the Wadden Sea area, (report 10 of the Wadden Sea working group). Stichting Veth, Leiden, pp 57–67

Scharff N, Gudik-Sørensen O (2006) Checklist of Danish spiders (Araneae). Version 02-12-2006. www.zmuc.dk/entoweb/arachnology/dkchecklist.htm

Schierding M, Seer F, Irmler U (2014) Ground beetles of the Baltic Sea coast in Schleswig-Holstein (northern Germany)–impacts of environmental parameters and spatial use. Angew Carabid 10: 23–34

Schliemann S (2003) Zum einfluss der beweidung auf laufkäfergesellschaften (coleoptera: carabidae) in küstenüberflutungs-gebieten. Diplomarbeit Universität Greifswald:100

Schliemann S (2010) Zum Einfluss der Beweidung auf Laufkäfergesellschaften (Coleoptera, Carabidae) in den Küstenüberflutungsmooren der südlichen Ostseeküste. Universität Greifswald, Dissertation, p 151

Schmidt J (2002) Habitatpräferenzen küstentypischer Laufkäfer der Mecklenburgischen Ausgleichsküste (Insecta: Coleoptera: Carabidae). University Rostock, Diploma thesis

Schmidt J (2004) Platynini. In: Müller-Motzfeld G (ed) Feude-Harde-Lohse-Klausnitzer 2. Adephaga Vol 1: Carabidae (Laufkäfer). München, Spektrum, pp 253–282

Schultz R (1997) Die Laufkäfer (Coleoptera: Carabidae) als Indikatoren der Renaturierung des Salzgrünlandes im Ostseebereich Vorpommerns. Cuvillier, Göttingen, p 232

Schultz W, Finch OD (1994) Biotoptypenbezogene Verteilung der Spinnenfauna der nordwestdeutschen Küstenregion. Cuvillier, Göttingen, Charakterarten, Typische Arten und Gefährdung

Seer FK, Irmler U, Schrautzer J (2015) Effects of trampling on beach plants at the Baltic Sea. Folia Geobot 50:303–315

Stachowiak M (2008) Przegląd systematyczny biegaczowatych Polski (*Coleopteras*, Carabidae). Wersja skrócona. entomo.pl/coleoptera/carabidae/index.php

Starega W (2004) Check-list of polish spiders (Araneae, except Salticidae). www.arachnologia.edu.pl/wykazpaj.html

Staudt A (Coord) (2006) Nachweiskarten der spinnentiere deutschlands. Arachnologische gesellschaft. http://www.spiderling.de/arages/

Stock M, Kiehl K, Reinke HD (1997) Salzwiesenschutz im Schleswig-Holsteinischen Wattenmeer. Schriftenreihe des Nationalparks Schleswig-Holsteinisches Wattenmeer 7:1–46

Tamutis V, Tamutė B, Ferenca R (2011) A catalogue of Lithuanian beetles (Insecta, Coleoptera). ZooKeys 121:1–494. https://doi.org/10.3897/zookeys.121.732

Terlutter H (1999) Die Carabidenfauna der unteren Ems zwischen Hebrum und Emden. Laufkäfer in Auen. Angewandte Carabidologie, Suppl 1:41–53

Thiele HU (1977) Carabid beetles in their environment. Springer, Berlin, Heidelberg, New York

Topp W (1988) Besiedlung einer neu entstandenen Insel durch Laufkäfer (Col., Carabidae). Zool Jb Syst 115:329–361

Trautner J, Müller-Motzfeld G, Räunicke MB (1997) Rote Liste der Sandlaufkäfer und Laufkäfer Deutschlands (Coleoptera: Cicindelidae et Carabidae), 2. Fassung, Stand Dezember 1996. Naturschutz und Landschaftsplanung 29:261–273

Trautner J, Fritze M, Hanning K, Kaiser M (eds) (2014) Distribution atlas of ground beetles in Germany. BoD–Books on Demand, Norderstedt

Treherne JE, Foster WA (1977) Diel activity of an intertidal beetle, Dicheirotrichus gustavi crotch. J Anim Ecol 46:127–138

Trost M (2007) Laufkäfer der Salzstellen Sachsen-Anhalts–eine Übersicht. Angewandte Carabidologie 8:35–49

Turin H (2000) De Nederlandse loopkevers. Verspreiding en ecologie (Coleoptera: Carabidae). In: Nederlands Fauna 3. Utrecht, Leiden

Turin H, Haeck J, Hengeveld R (1977) Atlas of the carabid beetles of the, Netherlands. Amsterdam, New York

Vahder S, Irmler U (2010) The spider fauna of Baltic Sea coast habitats. Faunistisch-Ökologische Mitteilungen 9:131–148

Von LH (1929) Die Salzkäfer der Nord- und Ostseeküste mit Berücksichtigung der angrenzenden Meere sowie des Mittelmeeres, des Schwarzen und des Kaspischen Meeres. Akademische Verlagsgesellschaft, Leipzig, p 162

Wachlin V, Müller-Motzfeld G, Jacobs HJ (1990) Konsequenzen für den Arten- und Biotopschutz an der Küste. Natur und Umwelt (Rostock) 15:87–90

Wiehle H (1965) Beiträge zur Kenntnis der deutschen Spinnenfauna IV. Mitteilungen aus dem zoologischen Museum Berlin 41:11–57

Witteveen J, Joosse ENG (1987) Growth, reproduction and mortality in marine littoral Collembola at different salinities. Ecological Entomology 12:459–469

World Spider Catalog (2015) World spider catalog. Natural history museum Bern, version 16. http://wsc.nmbe.ch. Accessed 26 Apr 2015

Wunderlich J, Schultz W (1995) *Ozyptila westringi* (Thorell 19873), eine in Deutschland seltene Krabbenspinnenart (Arachnida: Araneae: Thomisidae). Beiträge zur Arachnologie 4:329–333

Changes of the Fauna of Digger Wasps and Bees (Hymenoptera, Aculeata) of the North Frisian Island of Sylt: Effects of Climate Change?

12

Volker Haeseler

Abstract

The range of digger wasps and bee species was recorded on the North Frisian Island of Sylt from 1997 to 1999. There was no striking increase of thermophilic species. For the social species and their cuckoo species (bumblebees and cuckoo bumblebees) however, there was an obvious decrease regarding the indigenous species on the North Frisian Island. This cannot be explained by climatic causes.

12.1 Introduction

Among the Hymenoptera, many digger wasps and bees are arenicolous and xerothermophilic. Due to the cool and wet climate, some species have their distribution boundary on the northern German mainland. But they benefit from the warmer climate on the North Sea islands, where they find suitable habitats in the small-scale pattern of different landscape elements such as dunes, moraine 'Geest' with cliff-like breaking edges, and heathland. In particular, these landscape elements are found on the North Frisian Island of Sylt, where the studies presented here were conducted. Since extensive records of digger wasp species and bee species of the East and the North Frisian Islands are available from the past 20–30 years and also from previous time periods, changes in the range of these species should become evident here. Here, only a rough overview is introduced. A more detailed version, finished in 2003, has been published by Haeseler (2020).

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12.2 Time Period, Area of Investigation, Materials and Methods

The records obtained for the coastal region from 1997 to 1999 originated from the North Frisian Island of Sylt. During 8 one-week excursions, the digger wasp and bee species were recorded in all relevant habitats in order to obtain a most representative overview, which is needed for comparisons with previous data (1968–1981) collected on the neighbouring island of Amrum (Haeseler 1981) as well as with surveys on the East Frisian Islands carried out from 1975 to 1996.

The records were obtained using insect nets. In order to protect nature and species, automatic traps (e.g. coloured traps, malaise traps, window traps, etc.) were not employed. Particular emphasis was given to an intensive application of this method and, hence, to a frequent presence in the field. Based on a critical examination of previous, own field studies on aculeate Hymenoptera (cf. Haeseler 1972, 1990; Haeseler and Ritzau 1998), it is assumed that the sampling intensity for the present study has yielded a representative record of digger wasps and bees on the island of Sylt.

The nomenclature of digger wasps corresponds to that of Bitsch and Leclercq (1993), Bitsch et al. (1997, 2001). Nomenclature of bees corresponds to that of Schwarz et al. (1996) and Schwarz and Gusenleitner (1997). A special permit to catch bees was obtained.

12.3 Results and Discussion

12.3.1 Present Status for the North Frisian Island of Sylt

In total, 68 digger wasp species, 107 solitary bee species and their cuckoo bees, as well as 16 bumblebee and cuckoo bumblebee species were recorded on Sylt from 1997 to 1999.

Solitary species and their cuckoo species: Except for two species, *Andrena labialis* (Kirby 1802) and *Melecta luctuosa* (Scopoli 1770), all species published from the period before 1997 and already known to the author as occurring on Sylt were also recorded during the present study. However, it has to be taken into account that the island of Sylt was insufficiently investigated prior to the present study, because only 14 records of digger wasp species and 27 records of bee species were known so far. Therefore, it is not surprising that a total of 54 digger wasp and 80 bee species have now been recorded for the island of Sylt for the first time.

Social species (bumblebees) and cuckoo bumblebees: With bumblebee species and their cuckoo species, the recording situation differs completely from the above-mentioned groups. Two cuckoo species were recorded on Sylt for the first time. The occurrence of 14 species was confirmed, but 11 (= 44%) additional species (out of 25 bumblebees and cuckoo bumblebees known for the island of Sylt so far) were not confirmed. This is particularly striking, because, in general, due to their size and numerous worker bees, social bee species are relatively easy to record.

A comparison of the bumblebee and cuckoo bumblebee populations at the end of the first half of the twentieth century (1934–1938 and around 1948, cf. Zimmermann 1935; Krüger 1939, 1949) with the end of the second half of the twentieth century reveals that the unconfirmed species were not at all rare in the first half. In contrast, some of these species were extremely numerous or even common species at those times.

For the digger wasps and bees studied in the present paper, an indigenous distribution of the individual species can usually be inferred from the records. Conspicuous dispersion phenomena are relatively seldom in solitary species (cf. Johnson 1969; Haeseler 1974; Mikkola 1978, 1986). Social species, however, change their sites before and after hibernation. In particular during spring and autumn, drifts are observed, especially after mating, when queens are always found in migrations parallel to the coast (Mikkola 1978).

Due to phenomena related with dispersion biology, the solitary species and accompanying cuckoo species should be studied separately from the social species and their cuckoo species, in order to assess changes in the composition of species ranges (e.g. appearance and disappearance of species).

12.3.2 Solitary Species and their Cuckoo Species

From 1997 to 1999, nearly all published records of species known from the North Frisian Island of Sylt were confirmed. For species found on Amrum or Föhr, but not on Sylt, the absence of these species on Sylt remains to be verified in the future. In most cases, lacking confirmations may not indicate extinction but merely recording deficits (cf. Haeseler and Ritzau 1998).

The new records of 134 species on the island of Sylt are explained as follows: (1) An intensive recording has never been performed on Sylt before and (2) a comparatively large number of species characteristic for the ‘Geest’ was found in accordance with the regional variety of the landscape. From the time prior to and after 1950, the geest-species are also known from the mainland of the county of Schleswig (Haeseler 1972; Emeis 1960, 1968; Wagner 1938; van der Smissen 1998, etc.).

Among the species recorded on Sylt from 1997 to 1999, and almost unknown for Denmark according to Lomholdt (1984) and Jørgensen (1921), four digger wasp species and 10 bee species had been found in the county of Holstein before 1950. In the county of Schleswig, these species were found only after 1950. An unexpected dispersal to the north was observed for the following species:

- For the conspicuous mining bee *Andrena cineraria* (Linnaeus 1758) recorded on a North Frisian Island for the first time (Morsum, 29.6.1997), dispersal to the northwest had already been documented earlier (Haeseler 1973). Hence, it is not surprising that, having been recorded by Jørgensen (1921) at only one site in Denmark, this species in the meantime has become indigenous (again?) also on Sylt and farther to the north in Denmark. In the past 34 years, the species passed a distance of 220 km from the area of Lübeck/Ratzeburg to List on Sylt, which corresponds to a dispersal speed of 6.5 km per year, on average.

- Together with *A. cineraria*, the conspicuous cuckoo species *Nomada lathburiana* (Kirby 1802) is also represented on the island of Sylt. According to Wagner (1938), *N. lathburiana* was also merely known for the southeast of Schleswig-Holstein. For Denmark, this species was known for eastern regions only (Copenhagen and Lolland) (Jørgensen 1921).
- The biggest surprise was the presence of the conspicuous digger wasp *Astata boops* (Schrank 1781) on the island of Sylt (first records: 29.6.1997 near Morsum, 4.7.1997 List near AWI). This thermophilic species, unknown for Denmark according to Lomholdt (1984), had already been documented, however, in the nineteenth century for Schleswig-Holstein in the Kiel and Ratzeburg areas (Wüstnei 1886, Lomholdt, in litt.). Thereafter, until approximately 1990, recordings were exclusively noted for the area of Lauenburg.

The following example documents that false estimates regarding assumed areal expansion are very likely:

- The solitary bee *Anthophora retusa* (L. 1758) is another striking recording for Sylt. In Schleswig-Holstein, this species has been found only in the Lauenburg area so far (Wagner 1938; van der Smissen 1998; own records). Based on the records for Sylt, it seems very likely that the species has colonised Sylt in the course of its dispersal to the northwest during the past 20–40 years. However, there are no records of this species for the rest of Schleswig-Holstein. This is in contradiction to the hypothesis of a recent successive dispersal to the northwest. Within the scope of a parallel revision of historical data, the inspection of the Emeis-Collection (Natural History Museum Flensburg) revealed that this species was already found on Sylt near Keitum on May 20, 1948. Thus, *A. retusa* has inhabited the island of Sylt for at least more than half a century. Its presence there is certainly explained by a considerably earlier dispersal process. This is supported by records of the cuckoo of *Anthophora retusa*, *Melecta luctuosa*, that was already observed on Sylt in 1946 (van der Smissen 2001).

12.3.3 Bumblebee and Cuckoo Bumblebee Species

In contrast to the findings for solitary species, findings for social species did not correspond with the presently presumed decrease of social bee species. In general, it is supposed that the decrease of bumblebees in Central Europe is caused by a large-scale cleaning out of the countryside and an intensified agriculture (cf. von Hagen and Wolf 1993, 2002). However, the rural landscape has not been cleaned out in all areas, e.g. agriculture has not been intensified on the Frisian Islands since the end of World War II. In contrast, agricultural land-use has distinctly decreased there. It is especially striking that, nevertheless, 44% of the bumblebee species recorded on the island of Sylt before 1950 were not found in the period from 1997 to 1999.

In spite of the secular climatic changes with very different effects responsible for the general decrease of bumblebees, their drop-off seems only explainable by their different behaviour as compared to solitary bee species. As mentioned above, bumblebees and cuckoo bumblebees tend to spread before and after hibernation. Thus, within the range of the North Frisian Islands with comparatively favourable development conditions, part of the population is constantly emigrating. On the one hand, a compensation by immigration from the mainland is not possible because various species have been missing there for a long time. On the other hand, the missing compensation might depend on a general worsening of living conditions that makes reproduction rates on the mainland too low to compensate the losses on the island.

Overall, considering the distribution patterns of digger wasps and bees analysed in the present study, only a few species can be assumed to have expanded their areas, most of them being representatives of very different faunal elements. While *Andrena angustior* (Kirby 1802) and *A. synadelpha* Perkins 1914, for example, can be assigned to the Atlantic species, *Megachile lapponica* Thomson 1872 is a rather boreal species, which has immigrated into the region from the northeast. Most of the other species are rather south-oriented species.

Future studies will reveal, whether these territorial shifts should be interpreted as climate change effects or merely secular fluctuations at the margins of distribution areas. With the data collected within the scope of the present research and the data obtained since 1975 for the groups studied in the coastal region of the German North Sea area, favourable prerequisites are provided to both determine changes in population sizes and scrutinise the possible causes.

12.4 Conclusions

Investigations on the presence of digger wasps and bees have been continuously performed in the coastal region of the southern North Sea for about 30 years. The present range of digger wasp and bee species was recorded on the North Frisian Island of Sylt from 1997 to 1999. Obviously, only few species of the digger wasps and solitary bees as well as their cuckoo species migrated to this island during the past 20–50 years, among them the mining bee *Andrena cineraria* (Linnaeus 1758), the cuckoo bee *Nomada lathburiana* (Kirby 1802), and the digger wasp *Astata boops* (Schrank 1781). The increase and decrease of the species numbers of this group, characterised as thermophilic, are balanced at present. For the social species and their cuckoo species (bumblebees and cuckoo bumblebees), however, an obvious decrease was found regarding the indigenous species on the North Frisian Islands. This can neither be explained by direct anthropogenic changes of the landscape on the Frisian Islands nor by climatic changes. The reason may be found in the continuous deterioration of living conditions for this species group on the mainland during the past century. However, such negative changes have not occurred on the islands. The number of bumblebee females leaving the island before and after hibernation is obviously not compensated adequately by immigration from the mainland.

References

Bitsch J, Leclercq J (1993) Hyménoptères Sphecidae d'Europe occidentale 1. Faune de France 79: 1–325

Bitsch J, Barbier Y, Gayubo SF, Schmidt K, Ohl M (1997) Hyménoptères Sphecidae d'Europe occidentale 2. Faune de France 82:1–429

Bitsch J, Dollfuss H, Bouček Z, Schmidt K, Schmid-Egger C, Gayubo SF, Antropov AV, Barbier Y (2001) Hyménoptères Sphecidae d'Europe occidentale 3. Faune de France 86:1–459

Emeis W (1960) Übersicht über die gegenwärtige Zusammensetzung der Wildbienenfauna Schleswig-Holsteins. Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein 31:66–74

Emeis W (1968) Die Bienenwelt der schleswigschen Geest. Jahrbuch für die Schleswiger Geest 1968:84–103

Haeseler V (1972) Anthropogene Biotope (Kahlschlag, Kiesgrube, Stadtgärten) als Refugien für Insekten, untersucht am Beispiel der Hymenoptera Aculeata. Zoologische Jahrbücher, Abt für Systematik, Ökologie und Geografie der Tiere 99:133–212

Haeseler V (1973) Zur Kenntnis der Aculeaten- und Chrysididenfauna Schleswig-Holsteins und angrenzender Gebiete (Hymenoptera), 2. Beitrag. Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein 43:51–60

Haeseler V (1974) Aculeate Hymenopteren über Nord- und Ostsee nach Untersuchungen auf Feuerschiffen. Entomologica Scandinavica 5:123–136

Haeseler V (1981) Über weitere Hymenoptera Aculeata von der Nordfriesischen Insel Amrum. Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein 51:37–58

Haeseler V (1990) Wildbienen der Ostfriesischen Insel Norderney. Faunistisch-Ökologische Mitteilungen 6:125–146

Haeseler V (2020) Veränderung der Grabwespen- und Bienenfauna (Hymenoptera, Aculeata) der Nordfriesischen Insel Sylt – Auswirkungen einer Klimaänderung. Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen 47:745–767

Haeseler V, Ritzau C (1998) Zur Aussagekraft wirbelloser Tiere in Umwelt- und Naturschutzgutachten – was wird tatsächlich erfaßt? Zeitschrift für Ökologie und Naturschutz 7:45–66

Johnson CG (1969) Migration and dispersal of insects by flight. Methuen, London

Jørgensen L (1921) Bier. Danmarks Fauna 25:1–265

Krüger E (1939) Die Hummeln und Schmarotzerhummeln von Sylt und dem benachbarten Festland. Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein 23:28–123

Krüger E (1949) Hummelbeobachtungen von der Insel Sylt. Bombus 1:247–248

Lomholdt O (1984) The Sphecidae (Hymenoptera) of Fennoscandia and Denmark. Fauna Entomol Scand 4:1–452

Mikkola K (1978) Spring migration of wasps and bees on the southern coast of Finland. Annales Entomologici Fennica 44:10–26

Mikkola K (1986) Direction of insect migrations in relation to the wind. In: Danthanaryana W (ed) Insect flight – dispersal and migration. Springer, Berlin, pp 152–171

Schwarz M, Gusenleitner F (1997) Neue und ausgewählte Bienenarten für Österreich – Vorstudie zu einer Gesamtbearbeitung der Bienen Österreichs (Hymenoptera, Apidae). Entomofauna 18:301–372

Schwarz M, Gusenleitner F, Westrich P, Dathe HH (1996) Katalog der Bienen Österreichs, Deutschlands und der Schweiz (Hymenoptera, Apidae). Entomofauna, Supplement 8:1–398

Van der Smissen J (1998) Beitrag zur Stechimmenfauna des mittleren und südlichen Schleswig-Holstein und angrenzender Gebiete in Mecklenburg und Niedersachsen (Hymenoptera Aculeata: Apidae, Chrysididae, "Scolioidea", Vespidae, Pompilidae, Sphecidae). Mitteilungen der Arbeitsgemeinschaft Ostwestfälisch-lippischer Entomologen 14(Beiheft 4):1–76

Van der Smissen J (2001) Die Wildbienen und Wespen Schleswig-Holsteins – Rote Liste. Landesamt für Natur und Umwelt des Landes Schleswig-Holstein, Flintbek

Von Hagen H-H, Wolf H (1993) Höchste Zeit zur Rettung der Hummeln der Offenlandschaften. Natur und Landschaftskunde 29:7–9

Von Hagen H-H, Wolf H (2002) Droht uns eine Bestäubungskrise? Informationsdienst Naturschutz Niedersachsen 22:161–165

Wagner ACW (1938) Die Stechimmen (Aculeaten) und Goldwespen (Chrysididen s.l.) des westlichen Norddeutschland. Verhandlungen des Vereins für Naturwissenschaftliche Heimatforschung zu Hamburg 26:94–153

Wüstnei W (1886) Beiträge zur Insektenfauna Schleswig-Holsteins, 2. Stück. Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein 6:27–45

Zimmermann K (1935) Zur Fauna von Sylt. Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein 21:274–286

Historical Changes in the Carabid Beetle Fauna of Mecklenburg-Western Pomerania

13

Gerd Müller-Motzfeld

Abstract

Four types of faunal change were presented which differ in spatial dimension, the form of processes and their time scale. Based on the carabid database of Mecklenburg-Western Pomerania quantified faunal changes for selected periods of the last decades were shown. Four periods were distinguished, the data of which led to a group of species with increasing and another with decreasing numbers. The current status of exclusive salt and coastal carabid species of Mecklenburg-Western Pomerania was described for the same periods. Four phases of faunal changes by analysing the Central European carabid fauna were reported. If all species are regarded, climate dependent changes are responsible for increased immigrations of Atlantic species in the west, while continental species immigrated in the east.

13.1 Faunal Change

The term ‘faunal change’ refers to different processes which all lead to a distinct alteration of the composition of the animal community in a selected area. In contrast to botanists, who distinguish between ‘flora’ as the species-inventory of an area and ‘vegetation’ as the typical plant formation covering the soil at a special place, zoologists have no differentiating terms. In this context, fauna has two meanings:

Author “Gerd Müller-Motzfeld” has died before the publication of this book.

As the author of this chapter passed away before it was submitted, D. Mossakowski and U. Irmler took over proofreading.

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Table 13.1 Types of faunal change

Spacial dimension	Process	Time
Global	Evolutionary processes: Speciation, extinction	Millions of years
Supra-regional	Faunal exchange: Area dislocation, expansion, regression	Hundreds to thousands of years
Local	Topical: Change of species spectra, oscillations of area boundaries, succession	Years to decennia
	Ecological: Abundance change, stock fluctuation, dominance structure change	~ year

a qualitative (species composition) or a quantitative (dominance structure of a taxocoenosis) meaning (Müller-Motzfeld 1995). Therefore, the term faunal change must be analysed under different aspects. Short-term abundance fluctuations may be distinguished from medium-term directed changes in faunal composition (succession) or periodic oscillations of area borders by the methods of 'quantitative eco-faunistics' (Müller-Motzfeld 1990). 'Faunal exchange' refers to the long-term and species-rich restructuring of a species composition as took place several times during the Pleistocene in Central Europe (Müller-Motzfeld 1984). The evolution of new species or the extinction of species has global dimensions only. 'Species-loss' means the extinction of species if it exceeds 'the natural frame of evolutionary processes', e.g. the extinction of insular faunas or as a result of habitat destruction. Both dimensions—evolutionary processes and climatically induced faunal change—are well substantiated in carabid beetles (Coope 1979: Matthews 1976). Table 13.1 lists the main types of faunal change according to their space and time scales.

On the lowest level (ecological), changes of the actual quantitative composition of the fauna occur continually. Larsson (1939) distinguished three types of overwintering stages and seasons of reproduction in carabids. This alters the dominance structure during the course of a year, which is further affected by weather conditions or anthropogenic impact (e.g. agricultural measures, use of pesticides, etc.).

13.2 Causes of Faunal Change

Lasting faunal changes may be caused by ecophysiological adaptations, which may initiate an evolutionary process, or by the influence of climate change as occur even before anthropogenic impacts. The reactions of the fauna to accelerated climate change are complex, since all niche conditions are affected: competitors, predators, and parasites as well as the quality and availability of food. The following factors of the expected global climate change will have an impact on carabid fauna: (1) an increase of the mean annual temperature, (2) increased humidity due to increased precipitation, and (3) in particular on a regional scale, a sea level rise and related changes in the saline concentration of near shore habitats at the German North Sea and Baltic Sea coasts (Schellnhuber and Sterr 1993). Concerning the two latter components, there are significant differences between the North Sea coast and the Baltic Sea coast (e.g. tides and salt concentrations; cf. Chap. 7). Therefore, predictions of the expected faunal change must examine these differences together with knowledge of the ecological demands of the respective species when considering the expected regional climate trends.

Addionally, the current changing intensity of agricultural land-use has to be taken into account, including reductions of pesticides, set aside land, and green field margins, which produce synergetic effects with the climatic trend in some species with special demands (‘agro-steppe elements’). This is, for example, true for some field species which almost disappeared from Central Europe during the last century: *Poecilus punctulatus, Diachromus germanus,* and *Calosoma auropunctatum*. *Harpalus signaticornis*, which expanded since the 1990s again, has reached Mecklenburg-Western Pomerania coming from southern and eastern areas. Other species, such as *Anisodactylus signatus*, also seem to have expanded, but have not yet arrived in Mecklenburg-Western Pomerania. *Carabus auratus,* a typical element of the agrocoenoses, crossed the Elbe in the middle of the nineteenth century coming from the Atlantic area of Western Europe and proceeded eastwards even during a more continental climate period (Fig. 13.1). It is assumed that the expansion of *Carabus auratus* is partly caused by endogenous factors (Lindroth 1972). Compared with other *Carabus* species, *C. auratus* shows a remarkable change in behaviour. While after some futile attempts to crawl over them, most species walk around obstacles or change their direction. In contrast, *C. auratus* intensifies its effort. It is a good swimmer, too, which may at least partly explain its fast expansion. Nevertheless, in large parts of Central Europe a strong reduction in abundance occurred since the 1970s. It is well investigated that the decrease is the result of the increased use of biocides in agriculture during that period (Basedow 1998; Müller-Motzfeld 2000).

Horion (1938) already mentioned the impact of periodic climate fluctuations on the beetle fauna of Central Europe, whereas Gersdorf (1937) stressed anthropogenic causes as the reason for changes in the carabid fauna, especially in Mecklenburg-Western Pomerania. Since that time, the discussion focused on the importance of ‘anthropogenic’ and ‘natural’ (i.e. climatic) causes for faunal changes. Hammond (1974) analysed faunal changes in England and found a drastic decline in some carabid species caused by the use of biocides, whereas he could hardly prove climatic changes as reasons for the decline. Hengeveld (1985) supports these statements by an analysis of the Dutch carabid fauna. He distinguished the following three climatic periods: a relatively dry and warm period between 1930 and 1950, a period of high precipitation between 1950–1960, and a very dry period between 1960–1970.

Since the discussion on the relevance of human impacts on the global climate, climate factors have been noted as reasons for faunal changes. However, it is difficult to differentiate between ‘natural’ climatic changes in Central Europe, which rhythmically occurred during the last hundred thousand years, and global anthropogenic effects.

The present climate changes will result in fewer cold periods in winter and warmer periods in summer. Considering the combined effects of the increasing

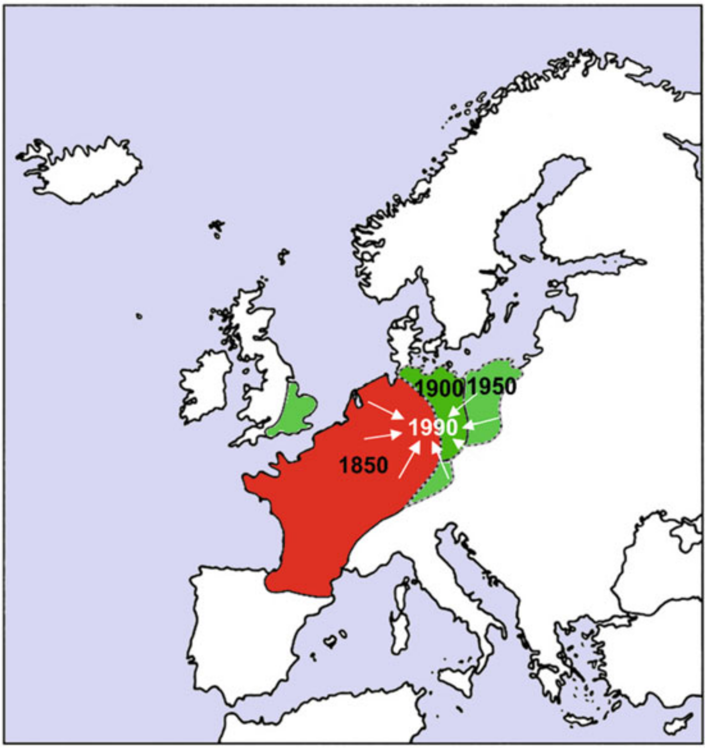

Fig. 13.1 Expansion of *Carabus auratus*. The species dispersed step by step from an area with an Atlantic-oceanic climate to the continental Baltic region. 1850 (red): *Carabus auratus* crossed the Elbe (1850), Oder (1900), and Weichsel (1950) rivers; since 1950 (light green): a drastic decrease of density in Central Europe; since 1990 (dark green): a new dispersal, re-colonisation of Schleswig-Holstein. Arrows: recent dispersal.

temperature, all environmental factors (e.g. increase of precipitation in humid areas, sea level rise, salinity change in the Baltic Sea) will affect the coastal carabids. The relevant data are compiled here in an expert system (Chap. 28) for selected species on the west-east gradient along the German North Sea and Baltic Sea coasts. As a basis for this compilation, extensive databases and actual information on the fauna of the respective areas were used (Bremen: Mossakowski 1991; Scheswig-Holstein and Lower Elbe: Gürlich et al. 1995; Irmler and Gürlich 2004; Mecklenburg-Western Pomerania: Müller-Motzfeld 1990).

13.3 Carabid Beetles of Mecklenburg-Western Pomerania: A Case Study

The carabid database of Mecklenburg-Western Pomerania contains 113,506 recordings for 338 species and enables us to quantify faunal changes for selected periods of the last decades. However, the recording intensity of the last period from 1975 to the present is about 10 times higher than for the preceeding periods (Table 13.2). This relation ('intensity factor') must be considered while interpreting the data according to the increase or decrease of species frequencies.

13.3.1 Increasing Records

Table 13.2 shows a list of species that obviously seem to increase. However, the increase in *Leistus rufomarginatus, Amara fusca, Nebria salina, Demetrias atricapillus, Microlestes maurus*, and *Notiophilus rufipes* is questionable considering the different recording intensities. Some species, e.g., *Carabus menetriesi* and *Bembidion milleri*, revealed no increase, but were overlooked due to wrong identification or occurrences in specific, rarely investigated habitats. A first view provides a confusing impression for some species and only climatic causes seem to be responsible for area changes of the species in Central and Northern Europe,

Table 13.2 Carabid records in Mecklenburg-Western Pomerania: species with increasing distribution. Current status: October 2005: 113,506 datasets

Species	Before 1900	1900–1950	1950–1975	After 1975
Carabus auratus	7	42	94	1055
Stenolophus mixtus	2	5	9	634
Leistus rufomarginatus	2	18	24	352
Amara fusca	3	12	14	70
Calathus rotundicollis	–	6	17	423
Nebria salina	–	27	3	218
Bradycellus verbasci	–	3	1	162
Demetrias atricapillus	–	7	12	90
Microlestes maurus	–	2	7	34
Notiophilus rufipes	–	2	1	18
Amara majuscula	–	–	1	46
Cymindis angularis	–	–	–	37
Dicheirotrichus rufithorax	–	–	–	34
Bembidion milleri	–	–	–	21
Carabus menetriesi	–	–	–	17
Bembidion ruficolle	–	–	–	11
Elaphropus parvulus	–	–	–	15
Porotachys bisulcatus	–	–	–	8
Sum of recordings	570	4000	5326	103,610

e.g. *Dicheirotrichus rufithorax, Amara majuscula, Stenolophus mixtus,* etc. (Lindroth 1972; Andersen 1986).

13.3.2 Decreasing Records

Species with clear decreases are listed in Table 13.3, taking the intensity factor into account. It is interesting that this process tends to exist for some species since 1993 (indicated with an *). It concerns typical agro-species, which drastically decreased during the last 100 years, e.g. *Dolichus halensis, Harpalus calceatus,* and *H. signaticornis,* or totally disappeared from Mecklenburg-Western-Pomerania, e.g. *Poecilus punctulatus, Diachromus germanus,* and *Amara tricuspidata*, but increased again since the 1990s. In these species of xerothermic open fields, in particular, it is difficult to determine whether the actual increase is a result of less intensive land-use or additionally due to the global climate change.

In Table 13.4, coastal species of Mecklenburg-Western Pomerania are listed which can be regarded as halobiontic (*Dychirius chalceus, D. salinus, Bembidion*

Table 13.3 Carabid records in Mecklenburg-Western Pomerania: species with decreasing distribution. Current status: October 2005: 113,506 datasets

Species	Before 1900	1900–1950	1950–1975	After 1975
Bembidion testaceum	2	–	–	–
Chlaenius nitidulus	3	6	–	–
Bembidion striatum	2	5	–	–
Dyschirius nitidus	1	7	–	–
Bembidion punctulatum	1	4	–	–
Paratachys bistriatus	1	2	–	–
Trichotichnus laevicollis	1	2	–	–
Acupalpus luteatus	–	1	–	–
Sphodrus leucophthalmus	1	9	1	–
Chlaenius sulcicollis	6	3	1	–
Chlaenius quadrisulcatus	1	5	1	–
Harpalus modestus	–	4	1	–
Ophonus rupicola	1	9	–	2
Limodromus longiventris	2	3	–	1
Agonum gracilipes	4	5	–	4
Harpalus melancholicus	1	5	–	4
Miscodera arctica	–	21	–	2
Dolichus halensis	3	9	1	10
Harpalus calceatus	1	18	3	21*
Poecilus punctulatus	2	23	–	6*
Amara tricuspidata	1	–	–	1*
Diachromus germanus	1	1	–	14*
Harpalus signaticornis	–	6	5	96*

Table 13.4 Carabid records in Mecklenburg-Western Pomerania: exclusive salt and coastal species. Current status: October 2005: 113,506 datasets

Species	Before 1900	1900–1950	1950–1975	After 1975
Amara strenua	1	–	–	–
Dyschirius impunctipennis	–	4	–	1
Agonum monachum	–	3	–	11
Dicheirotrichus gustavii	2	8	–	63
Dyschirius chalceus	1	2	1	44
Anisodactylus poeciloides	1	2	1	49
Bembidion polonicum	1	23	48	78
Cicindela maritima	1	23	15	112
Bembidion pallidipenne	1	12	6	121
Bembidion tenellum	1	10	5	131
Bembidion saxatile	2	24	55	161
Dyschirius obscurus	–	9	8	205
Amara ingénue	2	11	1	221
Bembidion transparens	–	1	5	255
Bembidion aeneum	–	4	–	259
Amara convexiuscula	1	7	25	275
Dyschirius salinus	3	6	2	328
Bembidion fumigatum	2	11	2	405
Dyschirius thoracicus	2	13	20	566
Bembidion minimum	3	9	17	1673

tenellum, B. aeneum, Anisodactylus poeciloides), halophilic (*Bembidion fumigatum, B. minimum, Dyschirius obscurus, D. impunctipennis, Amara strenua*) or halotolerant (*Bembidion transparens, B. saxatile, B. cruciatum ssp. polonicum, B. pallidipenne, Dyschirius thoracicus, Amara ingenua, A. convexiuscula, Cicindela maritima*). For some xerothermic species of dunes that are not included in Table 13.4, their preference for salt and coasts is sure, e.g. *Harpalus melancholicus, H. modestus, H. neglectus,* and *Amara quenseli* ssp. *silvicola*. The same is true for some other halotolerant ubiquitous species (e.g. *Bembidion varium* and *B. lunulatum*).

The first seven entries in Table 13.4 represent species, which have always been extremely rare or only locally present at the Baltic Sea coast due to their exclusive ecological demands. For the relative high number of recordings, a specific ‘intensity factor’ (~1:10) has to be taken into account since these species were particularly mapped within the project BIOSALT (2001–2003). In contrast, an increase is obvious for the last nine species of Table 13.4. The clear decline of some species in this group during the period from 1950 to 1975 can be explained by the specific situation in Mecklenburg-Western Pomerania with land-use intensification of the formerly extensively inundated salt grassland along the Baltic Sea coast that was meliorated to a large extent and, thus, desalinated. The most noticeable increase of recordings was revealed in the halophilic *Bembidion minimum*. An extension trend in the halophilic *Bembidion fumigatum* species since the 1980s was also observed in adjacent areas of Northwestern Germany (Handke 2000) and even as far as Switzerland (Marggi 1992). The situation of the oligohalobiotic *Bembidion aeneum* is more complicated. This species drastically increased in an area extending from the Weser marshland (Handke 1992) to the Central Baltic Sea coast. Its frequent occurrence on disturbed sites, in degraded or over-sanded inundation peat soils, and on specific field sites supports the thesis that a change of land-use instead of climate change caused this increase by creating habitats with raised osmotic values at the soil surface. Some years later, the *Bembidion aeneum* numbers decreased in some areas (Dülge et al. 1994; Främbs 1997).

An intermediate group of coastal species exists, which shows no change in record frequencies when the ‘intensity factor’ is taken into account. These species, such as *Bembidion saxatile, B. cruciatum polonicum,* or *Nebria livida*, are confined to silty soils and are often found at open cliffs of seacoasts (chalk, marl, or loam) (Schierding et al. 2013). Due to the microclimatic variety of these habitats, a reaction of these species to climate change cannot be expected in Central Europe.

In general, Müller-Motzfeld (1995) distinguished four phases of faunal change by analysing the Central European carabid fauna:

1. Phase 1 from the middle of the nineteenth century: Immigration of Atlantic species (*Carabus auratus, Leistus rufomarginatus, Amara fusca*), which is still continuing today and is verified by the immigration of species since the beginning of the twentieth century (*Calathus rotundicollis, Nebria salina*) (Fig. 13.2).
2. Phase 2 until the middle of the twentieth century: Maximum of thermophilic and wetland species, which were recorded for the last time during this period (*Chlaenius nitidulus, Bembidion striatum*).
3. Phase 3 following the middle of the twentieth century: Drastic decline of continental agro-species (*Poecilus punctulatus, Dolichus halensis,* and others).
4. Phase 4 since the 1970s: Increase of transgradient continental species (*Agonum gracilipes, Amara majuscula, Bembidion ruficolle*) and of thermophilic southern species (*Dicheirotrichus rufithorax, Elaphropus parvulus, Porotachys bisulcatus*).

   Furthermore, a fifth phase has to be added:
5. Phase 5 since the 1990s: Re-expansion of continental agro-species (*Poecilus punctulatus, Diachromus germanicus, Harpalus calceatus, H. signaticornis, Calosoma auropunctatum,* and others).

The development of agro-species (phase 5) may be better interpreted as a response to anthropogenic land-use effects than by general climate impacts. If all species are regarded, climate dependent changes are responsible for increased immigrations of Atlantic species in the west, while continental species immigrated in the east. This result is in agreement with new climate scenarios for the region of Mecklenburg-Western Pomerania (Freienkamp 2006).

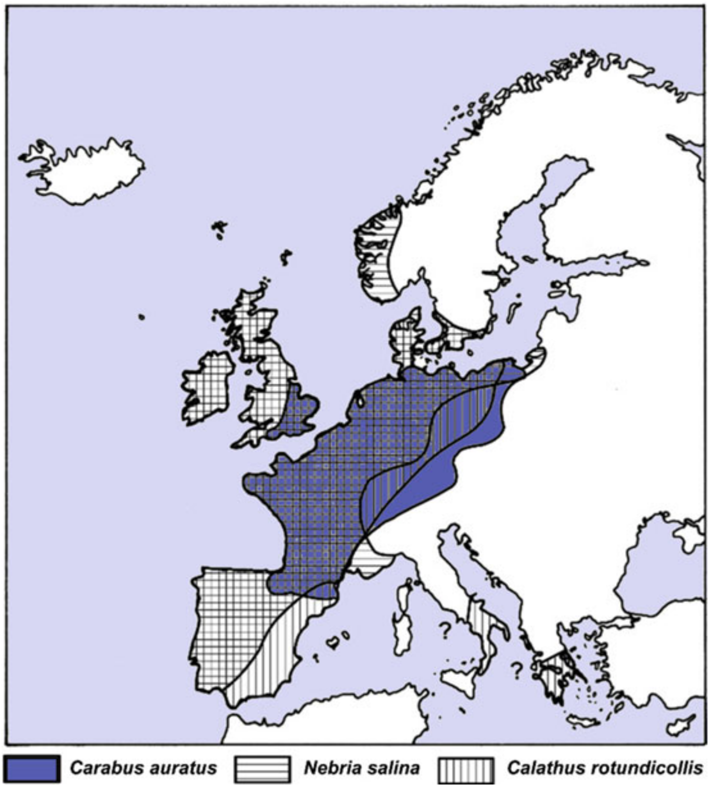

Fig. 13.2 Actual distribution area of species expanding from the Atlantic region

References

Andersen J (1986) Qualitative changes in the Norwegian carabid beetle fauna during this century. Acta Phytopathologica et Entomologica Hungarica 22:35–44

Basedow T (1998) Langfristige Bestandsveränderungen von Arthropoden in der Feldflur, ihre Ursachen und deren Bedeutung für den Naturschutz, gezeigt an Laufkäfern (Carabidae) in Schleswig-Holstein 1971-96. Schriftenreihe für Landschaftspflege und Naturschutz 58:215–227

Coope GR (1979) The Carabidae of the glacial refuge in the British Isles and their contribution to the post glacial colonisation of Scandinavia and the North Atlantic Islands. In: Erwin TL, Ball GE, Whitehead DE, Halpern AL (eds) Carabid beetles: their evolution, natural history and classification. Junk, The Hague, pp 407–424

Dülge R, Andretzke H, Handke K, Hellbernd-Tiemann L, Rode M (1994) Beurteilung nordwestdeutscher Feuchtgrünlandstandorte mit Hilfe von Laufkäfergesellschaften (Coleoptera: Carabidae). Natur und Landschaft 69:148–156

Främbs H (1997) Auswirkungen von Sturmfluten auf die Laufkäfer (Col. Carabidae) der Nordseeküste. Arbeitsberichte Landschaftsökologie Münster 18:47–61

Freienkamp F (2006) Klimawandel in Mecklenburg-Vorpommern–mögliche Szenarien. Report at the 3. Klimaschutzkongress Mecklenburg-Vorpommern. 08/09.06.2006

Gersdorf E (1937) Ökologisch-faunistische Untersuchungen über Carabiden der mecklenburgischen Landschaft. Zoologische Jahrbücher Systematik 70:17–86

Gürlich S, Suikat R, Ziegler W (1995) Katalog der Käfer Schleswig-Holsteins und des Niederelbegebietes. Verhandlungen des Vereins für naturwissenschaftliche Heimatforschung Hamburg 41:1–111

Hammond PM (1974) Changes in the British coleopteran fauna. In: Hawksworth DL (ed) The changing flora and fauna of Britain. Academic Press, London, pp 323–368

Handke K (1992) Zur Ausbreitung von *Bembidion aeneum* Germ. (Col. Carabidae) in der Bremer Wesermarsch. Zeitschrift Ökologie & Naturschutz 1:72–74

Handke K (2000) Veränderungen in der Insektenfauna der Bremer Flußmarschen von 1982-1999–Zeichen des Klimawandels. NNA Berichte 13:37–54

Hengeveld R (1985) Dynamics of Dutch beetle species during the twentieth century (Col. Carab.). J Biogeogr 12:389–411

Horion A (1938) Studien zur deutschen Käferfauna. II. Die periodischen Klimaschwankungen und ihr Einfluß auf die thermophilen Käfer in Deutschland. Entomologische Blätter 34:127–140

Irmler U, Gürlich S (2004) Die ökologische Einordnung der Laufkäfer (Coleoptera: Carabidae) in Schleswig-Holstein. Faunistisch-ökologische Mitteilungen Suppl 32:1–117

Larsson SG (1939) Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden. Entomologiske Meddelelser 20:277–560

Lindroth CH (1972) Changes in the Fennoscandian ground beetle fauna (Coleoptera, Carabidae) during the twentieth century. Ann Zool Fenn 9:49–64

Marggi W (1992) Faunistik der Sandlaufkäfer und Laufkäfer der Schweiz (Cicindelidae & Carabidae) Teil 1 Text. Dokumenta Faunistica Helvetiae 13:1–477

Matthews J-V (1976) Insect fossils from the Beaufort formation: geological and biological significance. Geol Surv Can 76-1B:217–227

Mossakowski D (1991) Zur Verbreitung der Laufkäfer im Lande Bremen. Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen 41:543–639

Müller-Motzfeld G (1984) Indikation und Zeitmaß von Faunenveränderungen demonstriert am Beispiel der Laufkäfer. Biologische Rundschau 22:369–378

Müller-Motzfeld G (1990) Quantitative Ökofaunistik im Dienste des Insektenschutzes. Entomologische Nachrichten u Berichte 34:109–117

Müller-Motzfeld G (1995) Klimatisch bedingter Faunenwechsel am Beispiel der Laufkäfer. Angewandte Landschaftsökologie 4:135–154

Müller-Motzfeld G (2000) Analyse von Gefährdungsursachen am Beispiel der Laufkäfer. Schriftenreihe für Landschaftspflege und Naturschutz 65:33–50

Schellnhuber H-J, Sterr H (eds) (1993) Klimaänderung und Küste. Springer, Heidelberg, p 400

Schierding M, Seer F, Irmler U (2013) Ground beetles of the Baltic Sea coast in Schleswig-Holstein (northern Germany)–impacts of environmental parameters and spatial use. Angewandte Carabidologie 10:23–34

Distribution of Spiders and Carabid Beetles Along a Geographical Gradient

14

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Abstract

Flooding conditions represent the major factor influencing the composition of the salt grassland ground beetle and spider communities at the North Sea and the Baltic Sea coasts. They lead to a decreasing species richness from high to low elevated sites. Above MHW level, two to three assemblages have been differentiated along the zonation of salt grassland at the western and eastern North Sea coast, which more or less correspond to the zonation of the vegetation. An additional zone exists in the lowermost parts of salt marshes below the MHW level characterised by beetle species. At sites protected against high floods, species can inhabit lower elevations than at sites exposed to the open sea. Surprisingly, exposition to the open sea also affected the zonation and altitudinal occurrence of species at the Baltic Sea although tides are lacking there. Salt content is certainly responsible for the decrease of several species from the western Baltic Sea to the eastern Baltic Sea.

The size reduction for two species between the present status and the two scenarios under increased sea level conditions was modelled. *Pogonus chalceus* represents a species living in the low elevated salt grassland, while *Erigone arctica* lives in the upper salt grassland. For the calculation, the length dimension between the MHW level and the dike was transferred into the elevation model of the Friedrichskoog foreland. A zonation index was used to estimate the

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theoretical habitat size. The present length dimension for *Pogonus chalceus* and *Erigone arctica* was drastically reduced under the conditions of scenario I and scenario II.

14.1 Introduction

Many studies exist on salt-influenced coastal habitats of Northern German coasts concerning the composition and zonation of communities (Heydemann 1960, 1962, 1967; Schultz and Müller-Motzfeld 1995; Meyer et al. 1997; Schaefer 1970; Weigmann 1973; Främbs et al. 2002; Irmler et al. 2002; Kinder et al. 2003; Finch et al. 2007). These studies usually differentiated the faunal zonation in correspondence with the zones of the vegetation. Regarding recent results based on data recorded by the present research project, two to three assemblages have been differentiated along the zonation of salt grassland at the western and eastern North Sea coast. They more or less correspond to the zonation of the vegetation (Irmler et al. 2002; Finch et al. 2007). After Dormann et al. (2008), an additional zone exists in the lowermost parts of salt marshes below the MHW level.

According to grazing experiments with sheep or cattle, the zonation changed mainly as a result of a changing sedimentation or light intensity on the soil floor (Irmler and Heydemann 1986; Andresen et al. 1990; Meyer et al. 1995). With respect to the sea level increase by global change, a 60% loss of habitat area for spider and ground beetle species of the lower and medium salt grassland was estimated for the eastern Wadden Sea (Irmler et al. 2002). This estimation was also found to be realistic for the western East Frisian Islands (Finch et al. 2007). However, these studies are either too imprecise or locally restricted to derive an outlook about what will happen under changing climatic and water level conditions along the entire length of the German coasts. It is well-known that faunal species occur either in the lower or upper salt grassland, but the elevation expansion of their niche and how it varies under different local environmental conditions has never been investigated. The present study, therefore, focused mainly on the elevation gradient and its local variance to study the expansion of the habitats, in particular, for typical coastal species. In addition, other environmental parameters, e.g., soil types, were analysed to evaluate the importance of water level changes for the occurrence of species. The following questions should be answered:

1. Which assemblages can be differentiated in salt grasslands along the German coasts?
2. How are they distributed on vertical and longitudinal gradients along the German coasts?
3. What main environmental factors are responsible for the occurrence of species?
4. Which factors produce the local variance in the vertical zonation and the species' composition?

14.2 Methods and Characterisation of the Study Sites

Spiders (Araneae) and ground beetles (Carabidae) are specifically adapted to coastal habitats and occur there in high species richness. Therefore, they were selected as representative animal groups with particular focus on coastal species. The spider and carabid fauna were studied in all study areas except Norderney and Sylt (cf. Chap. 4).

Environmental conditions of the study areas were measured by the zoological study groups and completed by data from the other groups (e.g. Chap. 6: Inundation regimes and Chap. 8: Soils). The environmental parameters were used to analyse the habitat preferences and the response of species to environmental conditions.

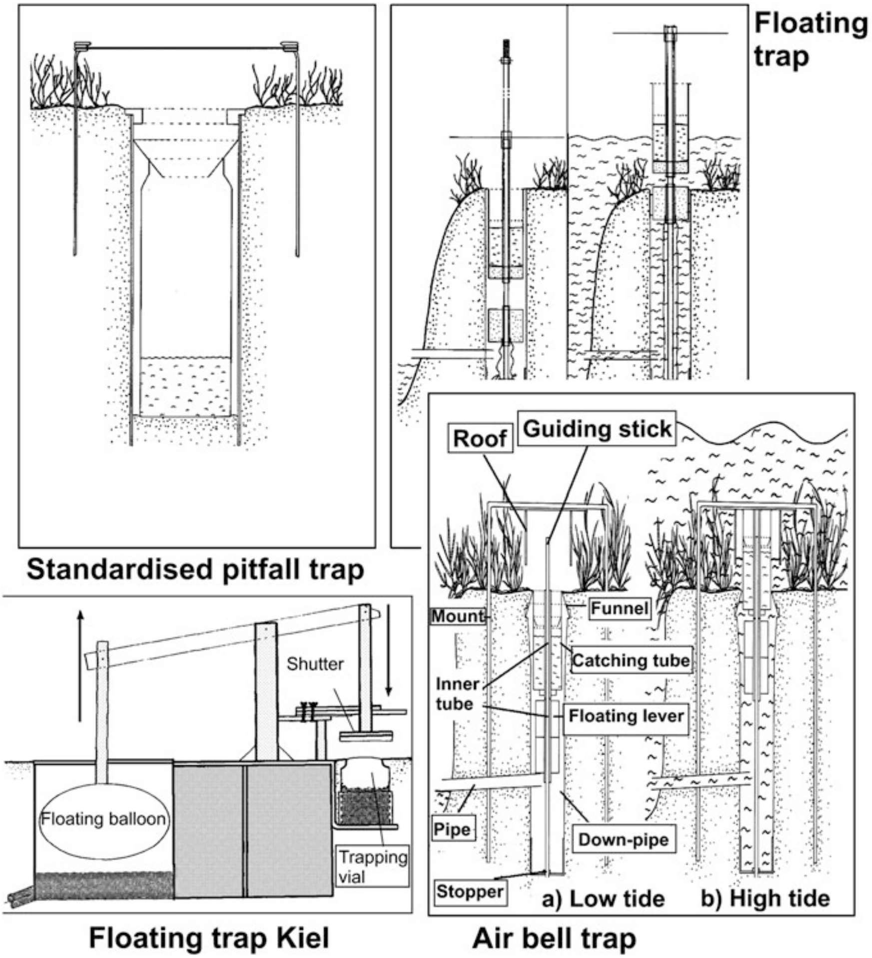
Nomenclature of both spiders and carabid beetles follows Platnick (2006); World Spider Catalog (2015); Trautner et al. (1997) and Müller-Motzfeld (2004), respectively.

14.2.1 Collecting Methods

Spiders and ground beetles were collected by pitfall traps (Barber 1931). For the later comparison of seasonality and zonation of the species, the zoological study groups made the following agreements: (1) pitfall traps were installed in intervals of 20 cm elevation beginning with 20 cm above MHW, (2) a number of five replicate traps were installed at each site, and (3) traps were emptied in 2 week intervals beginning on April, 15 in 1997 and ending on October, 28 in 1998. All groups had to change the traps on the same day, but a one-day delay was also accepted. Only at the North Sea coast, pitfall traps were not installed at all sites during wintertime from November to March 15 because of the rough weather conditions during winter. At Oxstedt, two additional sites were equipped with five replicate pitfall traps to study the spatial heterogeneity at equal elevations. Concerning upper circumference, fixation liquid, and other details (see Fig. 14.1), all groups used a standard version of pitfall traps.

The study of surface-active arthropods in periodically inundated habitats, such as salt marshes, has to overcome the difficulty of regular inundation by tides and/or floodwaters. Thus, the high frequency of flooding within the coastal zones of higher eulittoral and the lower supralittoral poses a methodological challenge for pitfall trapping. Trapping methods that are not susceptible to flooding but operate during low tides were necessary for collecting arthropods active in these zones. Four types of traps were used (Fig. 14.1).

Standard pitfall trap: The standardised pitfall trap was a glass (height 100 mm, diameter 690 mm) with a modified screw cap and a PVC ring (∅inside 560 mm, ∅outside 900 mm) at the opening, inserted in a long plastic tube (PVC tube in the soil; height 120 mm, diameter 900 mm, wall thickness 2.5 mm) and a transparent roof (partly not set during the summer because of grazing). The PVC ring that was 560 mm in circumference determines the effective opening width of the pitfall trap. A 2–4% solution of formaldehyde with detergent was used as a trapping liquid. Additionally, a funnel was placed inside the glass in order to hinder arthropods from


Standardised pitfall trap

Floating trap

Floating trap Kiel

Air bell trap

Fig. 14.1 Longitudinal sections across four types of floating pitfall traps

falling between the glass and the tube. The funnel fits exactly to the opening of the tube. Wire gauze prevents the catch of vertebrates by the pitfall traps. The distance between two traps was about 10 m in order to avoid mutual influences of their catching effect. The standardised trap was installed in habitats, which were potentially not flooded.

Floating trap Kiel: The floating trap used by the study group in Kiel covers the standard pitfall trap by a shutter at high water (Heydemann 1967; Meyer et al. 1995). The plunger is connected with a balloon lifted by high water in a tube while pressing the shutter down on the trap. A pipe connects the balloon-tube to a level lying lower than the trap site surface and guarantees the closure of the trap before the water reaches the trap site. The disadvantages of this design are the complicated construction and operation.

Floating trap Bremen: In 1997, the study group in Bremen used this type of floating trap, the design of which was taken from Främbs and Stahl (1997) and adapted to the specifications of the project (diameter, etc.). This trap is lifted when the water rises. A disadvantage is that tidal waves can still cause disturbances that wash out the cup, in particular when the guiding pole bar is too short, leading to false catch results.

Air bell trap: This type of floating trap is a further development of the floating trap Bremen, which was implemented to avoid the difficulties mentioned above. The study group in Bremen used the air bell trap from March 1998–2000. This new type of floating trap uses an air balloon to save the trap against inundation. The new trap is easier to construct and to operate. Moreover, it provides better protection of the catch than the other traps described above. For further details, see Dormann (2000). As in the floating trap Kiel, a pipe is connected to a lower elevated site to avoid water inflow before high water reaches the surface of the trap site.

14.2.2 What Do Pitfall Trap Catches Represent?

The pitfall trap method was intensively discussed, which should not be repeated here in detail. Doubtless, the catches of pitfall traps do not quantitatively represent the abundance of species per square metre. Therefore, many restrictions have to be kept in mind during the evaluation of such data. Nevertheless, pitfall trap data is obviously very useful in studies in which the recording of the occurrence and the dispersion of carabid and spider species are the aim of the research. There are no other methods that provide such good results for the species occurrence and assemblages with such a relatively low effort in time and work as pitfall trapping (Baehr 1984; Luff 1975). The amount of collected specimens of a species mainly depends on its abundance as well as on the animal's activity, which Heydemann (1956) described by the term 'activity density'. We prefer to denote the amount of collected animals as 'catch'. If not mentioned otherwise, a 'catch' is the accumulated number of specimens of a species in a single trap for a whole season.

14.2.3 Environmental Parameters Used to Characterise the Sites of the Fauna Studies

The *longitudinal co-ordinates* were taken from a digital map and reveal the decimal co-ordinate values (WGS84) of the study areas.

The *elevations* of all study sites were recorded by levelling measurements either before pitfall traps were installed, i.e., at Mellum, Wursten Coast, Friedrichskoog, and Sehlendorf Lagoon in 1997, or at the end of the study period, i.e., at Borkum, Wangerooge, Sundic Meadow, and Karrendorf Meadow. A second, more detailed elevation levelling was performed at the Wursten Coast in 1998/99 to document changes after 1 year which were assumed as a consequence of material aggregation by storm surges.

The co-ordinates of each point of the elevation measurement were determined by GPS and transferred to a GIS to make a detailed map of the area. The elevation data of the summer polder was taken from the project ‘Salt Marshes of Wursten Coast’ (Främbs et al. 2002) (Chap. 24).

All elevation measures refer to Mean High Water (MHW) corresponding to the German ‘Mitteltidehochwasser’ (MThw) at the North Sea and to NN at the Baltic Sea, which is near to MHW—with adequate accuracy. The data of Mecklenburg-Western Pomerania was calibrated originally to the Kronstadt gauge (HN). They are presented as Mean Water Level (MWL), which deviates from NN (Amsterdam gauge) by about 1 dm.

The data on *flooding dynamics* used in the faunal studies was estimated using the measured elevations of the pitfall traps and the official flooding data of the nearest gauges. The mean was calculated for the 2 years 1997 and 1998, although an expressed variance was observed between the 2 years. For example, at Mellum, the lower elevated area was flooded in the first half of September of both 1997 and 1998 by 0 and 15 times, respectively. At Friedrichskoog, flooding frequency at the lowest site amounts to 5 in September 1997, but 11 in 1998.

In addition to the calculation of flooding frequencies by the elevation data, pressure sensors were installed and flooding events were recorded by a data logger at Wursten Coast and Sehlendorf Lagoon. At Sehlendorf Lagoon, pressure sensor data (‘DKLog 200’ of ‘Driesen and Kern’, Bad Bramstedt) was recorded every 5 min and aggregated to half an hour average. In some cases, the flooding sensor data was revealed to be imprecise, because the data was influenced by sedimentation and flow speed. Therefore, at Wursten Coast, sensor data was controlled by flooding tubes at pitfall trap changing intervals. The tube openings were exposed 2 cm above the soil surface to avoid lateral rainwater inflow from the soil surface. If tubes were filled with water between the pitfall trap changing intervals, a flooding was assumed. At the North Sea, data refers to the flooding frequencies caused by the tide dynamics. At the Baltic Sea, coast tides are insignificant and, therefore, the flooding period was calculated instead of flooding frequency.

The gauges of ‘Borkum-Südstrand’ and ‘Wangerooge-West’ were taken as a reference for the study sites of these two islands. Calculations of flooding frequencies for Wursten Coast were performed on the basis of the data measured by the ‘Wasser- and Schiffahrtsamt Wilhelmshaven’ (gauge Schillig 1996–1999) and by the Lower Saxonian ‘Landesbetrieb für Wasserwirtschaft und Küstenschutz’, directory Norden (gauge Spieka-Neufeld 1981–2000). The gauge data of Friedrichskoog harbour (‘Amt für Ländliche Räume’, Heide, Außenstelle Büsum) that is located within 5 km distance from the study area was used to estimate the flooding dynamics in the Friedrichskoog foreland. For the Sehlendorf Lagoon, gauge data of the ‘Wasser- und Schiffahrtsamt’, Lübeck have been used to control the pressure sensor data. They were also adjusted by air pressure data of the station Westermarkelsdorf on the island of Fehmarn (Deutscher Wetterdienst). In the Hohwacht Bay, tides are very low and cannot be measured because the effects of wind and seiches are larger. All data of the Sehlendorf Lagoon refer to 1998 because pressure sensors were not installed in the first study year. The gauge of

Greifswald-Wiek was taken as being representative for Karrendorf Meadow and Sundic Meadow because a strong correlation was found between Karrendorf Meadow and Greifswald-Wiek for daily means ($r = 0.97$; Wohlrab 1997).

For the zoological investigations, soil and *salinity* data was used as listed in Chap. 8. Sand content of the soils was estimated from the soil type determined at each individual site of a pitfall trap. Sand content was derived from the different soil types listed in Arbeitsgruppe Boden (1994). As Arbeitsgruppe Boden (1994) published a range of sand contents for each soil type, the mean of the range was used. For the salinity data, the EC-values were used ranging between 0.1 and 7.5. If data on the elevation gradient was lacking at one site, the mean of the two adjacent sites was taken.

14.2.4 General Remarks on the Sites

The salt marshes of most study sites have been more or less strongly influenced by grazing. Only the sites of Mellum were never grazed. All sites at Oxstedt and at Sehlendorf Lagoon were under grazing in the past, but are not grazed at present or are extensively grazed for nature conservation management.

At Oxstedt, remarkable sediments were deposited after a storm flood on February 3, 1998. On February 20, the thicknesses of the layers were roughly categorised into three classes and mapped (Chap. 21).

The zoological study sites were characterised by the vegetation in cooperation with the botanists of the research project. The vegetation data was arranged to the scale of Londo (1975) or Braun-Blanquet (1964) to facilitate a comparison between faunal and vegetation data.

14.2.5 Statistical Analysis

Several indices were calculated to compare the zonation or annual occurrence of the species on a west—east gradient:

The mean elevation of a species occurrence was calculated by a zonation index (Z_i) (Irmler and Heydemann 1986):

$$Zi = \sum_{i=1}^{n} ni * hi/N, s.d. = \sqrt{\sum_{i=1}^{n} ni * (hi - Zi)^2/N}$$

with n_i = number of specimens at elevation i, h_i = elevation (in cm above MHW or MWL), N = total number of specimens in the study area, *s. d.* = standard deviation of Z_i.

The phenology index (P_i) was established in the same manner as the zonation index in order to characterise the mean annual occurrence of the species. In this calculation, the elevation zone of formula (1) was replaced by the subsequent numbers of the collection period.

Statistics were performed using the program package STATISTICA (StatSoft 1996). Correlation coefficients and significance were calculated by using Pearson's product-moment correlation consecutively after a test on normal distribution. For non-parametric data sets, Spearman rank correlation was used. Differences of the means were tested either by t-tests or a U-Test for parametric or non-parametric data.

Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) were performed using the program CANOCO for Windows version 4.0 (Ter Braak and Smilauer 1998). The eigenvalues of DCA are equal to the sample scores and are thus a measure of importance of ordination axes. According to Jongman et al. (1987), an eigenvalue higher than 0.5 denotes a good separation along the axis. The significance of environmental parameters was tested using the Monte Carlo Permutation test. Assemblages' differentiation was additionally supported by a cluster analysis using an unweighted pair group average as a fusion rule and percentage conformance as a distance measure.

Although the study groups agreed with the same sample size along the elevation gradient, sample sizes vary slightly because of dikes or other landscape characters and disturbances by flooding. Therefore, the rarefaction method was performed to estimate the species richness/1000 specimens or species richness/100 specimens in correlation with elevation using the computation program of Krebs (1999). Rarefaction species richness was only calculated for the lower site elevations between 10 cm and 60 cm above MHW/MWL in order to record data from sites with similar flooding conditions.

To establish a detailed elevation map for the Oxsted foreland and summer polder, a GIS program (ArcView 3.2) was used (for more details, see Chap. 24).

14.3 Results

14.3.1 Numbers of Specimens and Species

The total catch of spiders was 260,000 specimens of 187 species. Species richness varies distinctly between the localities: the highest species richness (107) was found on the island of Borkum, whereas the lowest richness (34) was observed at Berensch, a part of the Wursten Coast of the Lower Saxonian mainland with incomplete development of the upper salt marsh (Table 14.1).

Only 13 (7%) species were recorded at each research area, 51 species (27.3%) each were found in at least two thirds of the localities or a single locality. These findings reflect the different compositions of the individual communities, the differences in habitat heterogeneity of the research areas, the variation along the

Table 14.1 Total numbers of specimens and species of spiders (Araneae) in the study areas. Geographical gradient from west to east; North Sea. *Bo* Borkum, *Wa* Wangerooge, *Me* Mellum, *Be* Berensch, *Ox* Oxstedt (Wursten Coast); *Fk* Friedrichskoog, Baltic Sea: *Se* Sehlendorf Lagoon (Hohwacht Bay), *SW* Sundic Meadow, *KW* Karrendorf Meadow. Catch effort = accumulated number of 1 year traps for 1997 and 1998. Species richness/1000 ind. refers to elevations between 10 and 60 cm above MHW or MWL. Salt: halobiontic and halophilic species (species with salt preference >1, cf. Chap. 7); Flood: flood resistant species (flood resistance >1; cf. Chap. 7)

	North Sea						Baltic Sea		
	Bo	Wa	Me	Be	Ox	Fk	Se	SW	KW
Catch effort	70	53	85	40	50	60	80	60/67	60/62
Total species [*n*]	107	91	68	34	45	83	99	79	81
Species richness/1000 ind. ± s.d.	38.8 ± 2.8	44.1 ± 2.6	32.8 ± 2.2	18.6 ± 2.0	24.4 ± 2.1	31.6 ± 2.8	43.9 ± 2.8	25.9 ± 2.5	29.4 ± 2.5
Salt species [*n*]	11	14	15	10	13	12	12	12	11
Flood species [*n*]	8	8	6	6	8	6	7	6	7
Total specimens [*n*]	26,691	11,596	15,232	20,904	61,640	44,138	44,612	12,839	28,547
Salt specimens [*n*]	11,368	5405	4216	14,088	37,540	24,968	17,644	6891	14,075
Flood specimens [*n*]	2297	4677	3151	6890	34,499	3025	17,554	5944	6635

geographical gradient, and the different sampling intensities (number of sites studied).

Sixteen species have been found, which hitherto are either recorded only from saline habitats and are regarded as halobiontic or which have their maximum abundance in saline habitats and are regarded as halophilic (cf. Chap. 27 expert system). The following five spider species (3.2%) were the most frequent species and recorded in each study area: *Pardosa purbeckensis, Erigone longipalpi*s, *Oedothorax retusus*, *Erigone atra, Pachygnatha degeeri*. They account for more than 66% of the whole catch size. The richness of halobiontic and halophilic species per study area ranged between 15 at Mellum and 10 at Berensch of the Wursten Coast. The characteristic salt-preferring species occurred at nearly all study sites along the geographical gradient, but only 50% of all species were found in more than one or two study areas. Among the halobiontic or halophilic species, merely *Praestigia duffeyi* and *Erigone arctica* were not recorded for the Baltic Sea coast. At least *Praestigia duffeyi* is restricted to the Atlantic and North Sea coasts. Concerning the species richness estimated by the rarefaction method for the elevations between 10 cm and 60 cm above MHW/MWL, highest values were recorded at the western part of the gradient on the islands of Borkum and Wangerooge as well as at Sehlendorf Lagoon of the western Baltic Sea coast. However, this might be due to the more diverse habitat pattern of these areas, where dunes have been developed at higher elevation, than might be due to an overall west-eastern decrease of species richness.

Many species occurring in salt marshes originate from frequently flooded habitats. Only three of the eight flood resistant species (see Chap. 27) have been recorded at every study area of the west-east gradient.

The number of specimens varied extraordinarily between the study areas, e.g. catch numbers of *Pardosa purbeckensis* varied strongly between the study areas with 53 specimens at Friedrichskoog and 2590 specimens at Oxstedt for the 1998 annual catch size of traps.

More than 100,000 carabid beetles of 142 species were caught as a total of all study areas. Most species (76) were found at Karrendorf Meadow and the lowest number (22) at Berensch of the Wursten Coast (Table 14.2). These results also reflect the species richness estimated by the rarefaction method. Lowest values were found at Berensch, highest values at Karrendorf Meadow.

Seven species (4.9%) were found in each study area, including the two salt-preferring species *Bembidion minimum* and *Dyschirius salinus* (see Chap. 27). A total of 16 species is classified as halobiontic or halophilic. Among the salt-preferring species, *Bembidion aeneum* and *Amara convexiuscula* were also widely distributed at the North Sea and the Baltic Sea coasts, whereas *Bembidion normannum* and *Pogonus chalceus* were not found at the Baltic Sea coast in our material. *Dyschirius globosus* and *Bembidion minimum* were the most frequent species that occurred at each study area, while the overall most frequent species, *Dicheirotrichus gustavii*, was not found at the easternmost area of Karrendorf Meadow. A total of 37 species were only found in one study area. Except few rare salt-preferring species, i.e., *Dyschirius impunctipennis,* these species presumably

Table 14.2 Total numbers of specimens and species of carabid beetles in the study areas. Arrangement as in Table 14.1

	North Sea						Baltic Sea		
	Bo	Wa	Me	Be	Ox	Fk	Se	SW	KW
Catch effort	70	53	85	40	50	60	80	60/67	60/62
Total species [*n*]	64	67	65	22	42	65	49	69	76
Species richness/1000 ind. ± s.d.	33.3 ± 2.2	36.7 ± 2.5	13.8 ± 2.1	14.3 ± 1.6	22.4 ± 2.2	12.4 ± 1.7	22.9 ± 2.3	45.8 ± 1.6	36.4 ± 2.5
Salt species [*n*]	9	6	12	6	9	7	4	4	4
Flood species [*n*]	7	6	8	5	6	7	4	5	5
Total specimens [*n*]	9397	5136	42,105	3562	6874	25,151	6398	3588	6866
Salt specimens [*n*]	2095	1048	35,089	3494	5817	22,446	1654	171	2756
Flood specimens [*n*]	1729	810	35,169	3298	5775	22,083	1656	177	2770

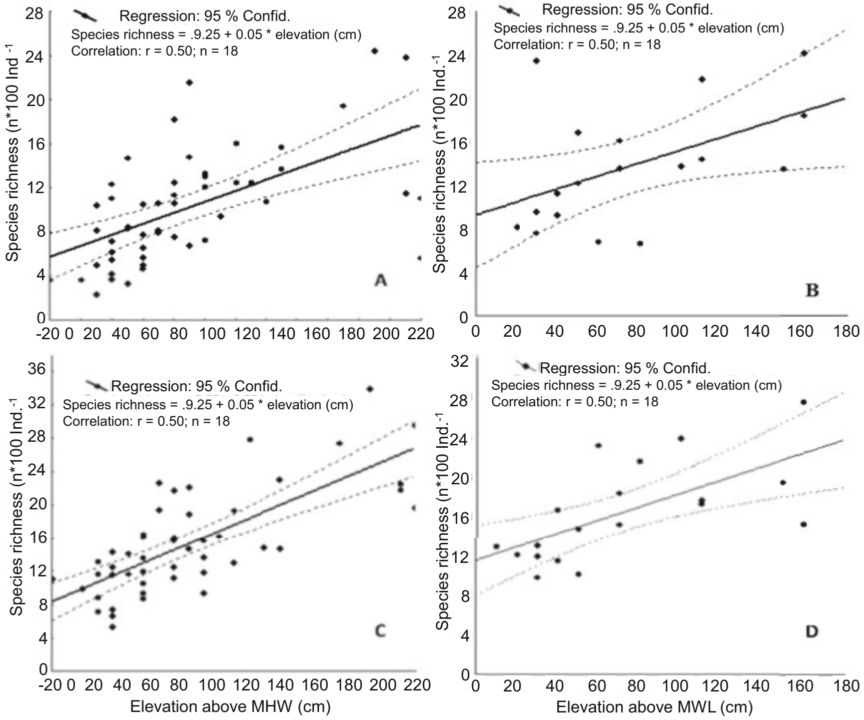


Fig. 14.2 Relation between elevation above MHW (North Sea) or MWL (Baltic Sea) and species richness. (**a**) Carabid beetles of the North Sea coast; (**b**) Carabid beetles of the Baltic Sea coast; (**c**) Spiders of the North Sea coast; (**d**) Spiders of the Baltic Sea coast

immigrated accidentally from adjacent habitats and cannot be regarded as typical for coastal salt grassland areas.

The total species richness can hardly be used to compare the different study areas because species richness is strongly correlated with elevation (Fig. 14.2). Low values were found at low elevations and high values at high elevations for both the North Sea and the Baltic Sea coasts. At some study areas, e.g., Berensch, the upper zones are not developed, which was the cause for the low values of species richness there. Overall, the increase of species richness revealed no differences between the different study areas meaning that total species richness of the areas is more or less similar. It is even similar if North Sea and Baltic Sea sites are compared. At 20 cm MHW/MWL, species richness is slightly lower at the North Sea coast than at the Baltic Sea coast but the difference is only 2 or 3 species. In the upper zone at 180 cm MHW, species richness of carabid beetles was calculated for both the North Sea and the Baltic Sea to be 15.7 and 20, respectively, whereas it was equal in spiders with 24 species. Richness of carabid beetles is usually slightly lower than spider species richness. Thus, species richness of salt grassland mainly depends on the development of zones. If only few zones are developed, total species richness is low, while the development of all potential zones caused high species richness.

14.3.2 Spider and Carabid Assemblages

For spiders and carabid beetles, five assemblages were differentiated by Cluster Analysis and DCA (Figs. 14.3 and 14.4). The results of the CCA revealed six environmental parameters to be significant for a distinction of the assemblages, but the results differ strongly between spiders and carabid beetles (Table 14.3). For carabid beetles, the environmental factors explain a higher percentage of the variation than in spiders. For Carabidae, elevation and flooding were the main factors, whereas temperature that is closely correlated with the longitudinal co-ordinates was the most significant explaining factor for spiders. In general, the elevation in salt marshes is of main importance for carabid beetles, but only the second important parameter for spiders. In contrast, the longitudinal co-ordinates are less important for carabid beetles.

As can be seen by the low eigenvalue of 0.42 for the first canonical axis, the differences between the five spider assemblages are low (Fig. 14.3). Assemblages 1 and 2 mainly cover the lower levels of salt grassland, but some higher elevated

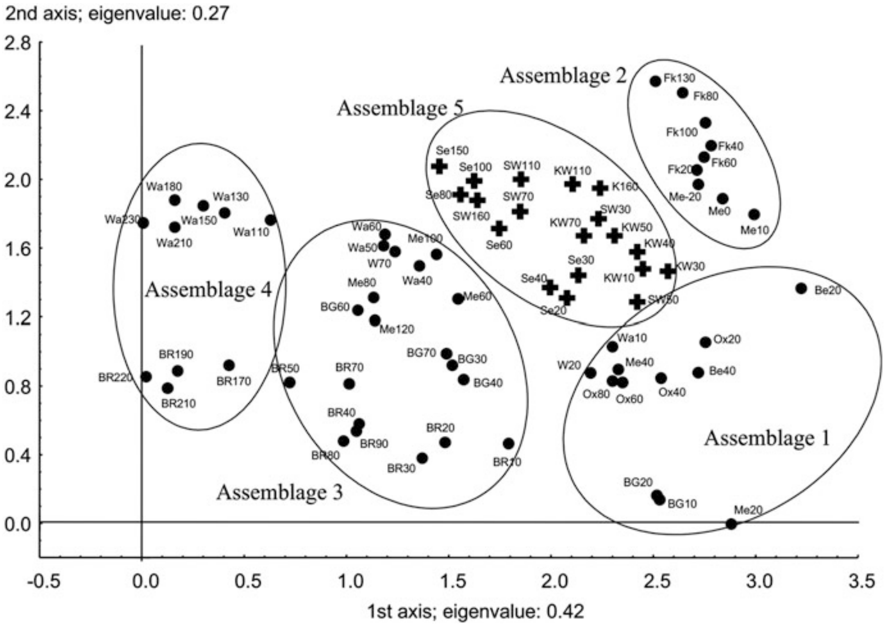


Fig. 14.3 Detrended Correspondence Analysis of spiders. Assemblages are formed by means of a cluster analysis (see text); ● sites at the North Sea coast; + sites at the Baltic Sea coast; for abbreviations of locations, see Table 14.1; *BR* Borkum Ronde Plate; *BG* Borkum Grüppenbeet

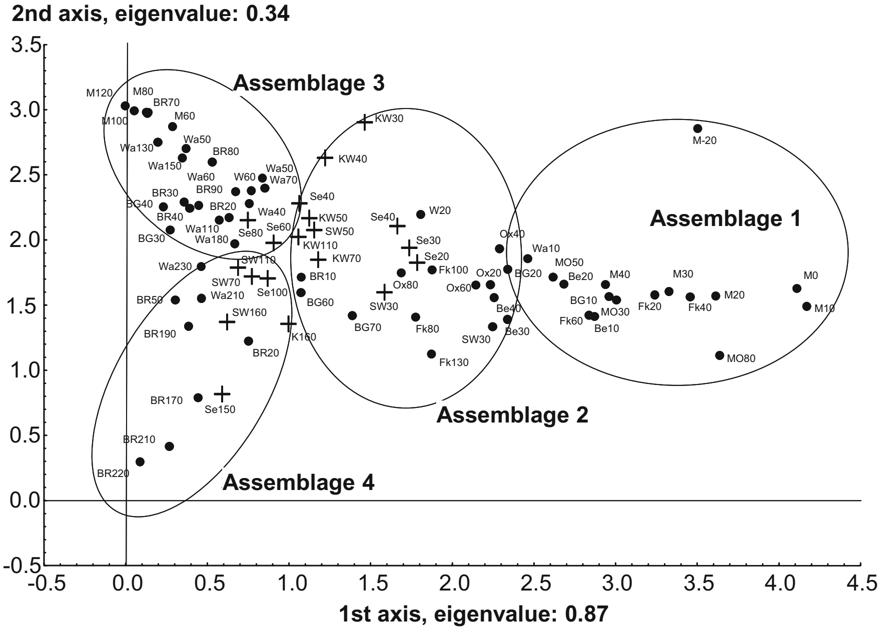


Fig. 14.4 Results of the Detrended Correspondence Analysis (DCA) of ground beetles. Groups are formed by means of a cluster anaysis (see text). • sites at the North Sea coast; + sites at the Baltic Sea coast; for abbreviations, see Table 14.1; *BR* Borkum Ronde Plate, *BG* Borkum Grüppenbeet, *MW* Mellum West, *ME* Mellum East

Table 14.3 Statistical results of CCA (F-values) for significant environmental factors

	Carabid beetles		Spiders	
Environmental factor	Rank	F–value	Rank	F–value
Elevation	1	9.80	2	5.99
Floods	2	7.11	6	1.53
Longitudinal co-ordinate	3	5.98	3	3.23
Salinity	4	4.82	4	2.81
Sand content	5	3.17	5	2.09
Temperature	6	2.69	1	6.00

sites were also included which may reflect the low influence of the elevation on the spider zonation. As the Baltic Sea sites exhibit a consistent assemblage, the continental climate or the lacking tides seem to be of higher influence on the specific composition of spiders than the elevation as observed at the North Sea coast. Compared to the carabid beetles, the low differences of spider assemblages on the elevation gradient at the North Sea can be explained by a higher mobility of spiders.

Only assemblage 4 at high elevations of 180 cm above MHW/MWL, on average, revealed a significant difference from the remaining assemblages. It is additionally

Table 14.4 Spider species composition of groups 1–5 and significant environmental factors; significant differences are indicated by different exponents

	1		2		3		4		5	
Assemblage	Mean	S.d.	Mean	S.d.	Mean	S.d.	Mean	S.d.	Mean	S.d.
Elevation (cm)	^{1}31.7	21.2	^{1}46.7	49.7	^{1}58.5	27.6	^{2}180.0	40	^{1}72.1	47.3
Salinity	^{1}5.3	0.5	^{1}4.8	1.6	^{2}3.2	1.2	^{3}1.3	0.7	^{2}3.0	2.0
Average temperature (°C)	^{2}8.9	0.2	^{3}8.5	0.4	^{1}9.1	0.1	^{1}9.0	0.1	^{3}8.2	0.2
Floods frequency (*n*)	^{1}54.7	32.6	^{1}85.8	100.4	^{2}17.5	16.8	^{2}0.4	0.6	^{2}23.3	35.5
Longitudinality (*n*)	^{1}2.3	0.8	^{2}3.3	1	^{3}1.4	0.5	^{3}1.6	0.5	^{4}6.0	0.9
Sand content (%)	^{1}20.9	4.5	^{2}40.5	23.5	^{2}52.1	29.9	^{3}92.5	0	^{2}48.3	26.9
Pardosa purbeckensis	35.5		2.5		13.5		1.4		10.9	
Oedothorax retusus	5.8		3.8		1.2		3.2		3.6	
Pachygnatha degeeri	4.0		1.8		5.2		1.5		1.8	
Erigone atra	3.3		3.6		2.1		4.3		5.6	
Pachygnatha clercki	3.3		1.1		1.3		0.2		2.1	
Argenna patula	1.9		2.3		1.3		0.2		1.1	
Erigone dentipalpis	1.0		2.2		0.5		0.8		1.3	
Bathyphanmtes gracilis	1.0		3.5		1.6		0.8		2.4	
Baryphyma duffeyi	9.0		0.9		0.5					
Erigone longipalpis	7.4		13.3		0.5		0.1		5.2	
Oedothorax fuscus	4.9		8.2		0.6		0.2		2.5	
Leptorhoptrum robustum	1.3		1.0		0.2				0.2	
Hypomma bituberculata	1.1		1.4		0.2				0.5	
Erigone arctica	0.3		6.4		0					
Silometopus ambiguus	0.4		2.2						0.6	
Dicymbium nigrum	0.4		2.1		0.1				1.8	
Arctosa leopardus	0.7				4.4		0.5		0.4	
Pardosa prativaga	0.9				7.2		0.8		1.9	
Alopecosa pulverulenta	2.2				8.3		8.3		2.3	

(continued)

Table 14.4 (continued)

	1		2		3		4		5	
Assemblage	Mean	S.d.	Mean	S.d.	Mean	S.d.	Mean	S.d.	Mean	S.d.
Trochosa ruricola	1.4		0.7		5.1		4.6		1.3	
Zelotes pusillus	0.4		0.2		1.9		4.9		0.5	
Zelotes latreillei	0.2				1.3		2.7		0.5	
Hahnia nava			0.2		1.1		2.6			
Zelotes electus					0.9		3.1		0.6	
Xerolycosa miniata	0.1				1.0		3.6			
Pardosa nigriceps	0.1		0.2		0.8		2.1			
Argenna subnigra					0.6		3.6		0.3	
Agroeca proxima					0.5		2.5			
Xysticus kochi					0.3		2.1		0.2	
Trochosa terricola	0.1		0.9		0.7		3.1		1.1	
Centromerita bicolor	0.6		0.6		0.7		1.1		2.5	
Pardosa palustris	0.8				1.3		0.3		3.7	
Pirata piraticus	0.4		0.5		1.6		0.6		3.3	

indicated by low flooding frequency and low salinity (Table 14.4). This assemblage is also characterised by a high sand content. Thus, it might represent the dune-like habitats at high elevated areas apart from the usual salt grassland. The remaining assemblages represent medium or low elevated sites. Assemblages 1 and 2 include sites with high salinity and high flooding frequency, whereas assemblages 3 and 5 represent sites with medium salinity and flooding frequency. The two first assemblages are significantly differentiated by their longitudinal co-ordinates, meaning that assemblage 1 is located in the western areas and assemblage 2 at the eastern areas of the North Sea coast. A similar differentiation is found between both assemblages 3 and 5, which are located at the westernmost and easternmost areas, respectively. As none of the other parameters reveal significant differences, except the mean annual temperature that is closely correlated to the longitudinal co-ordinates, the west-east gradient seems to be important for the composition of the spider communities on medium elevated sites.

The large number of species occurring in all assemblages also reflects the wide distribution of spider species along the elevation and longitudinal gradients. Only one species, i.e., *Praestigia duffeyi* can be regarded as typical for assemblage 1. Assemblage 2 is mainly characterised by three species, including the two salt-preferring species *Erigone arctica* and *Silometopus ambiguus*. In the remaining three assemblages, no salt-preferring species were frequently found. In particular, assemblage 5 on the easternmost medium elevated sites is characterised by species of wet grassland, e.g., *Pardosa palustris* and *Pirata piraticus*, showing that these sites are only weakly influenced by salt water during the vegetation period.

The four assemblages of carabid beetles were well separated by the DCA, which is indicated by an eigenvalue of 0.87 at the first axis (Fig. 14.4). According to Ter Braak (1986), eigenvalues higher than 0.5 are sufficient to discriminate assemblages of species.

The first axis differentiates the assemblages mainly according to the elevation level: Low elevated sites are placed at the right side, higher ones at the left side. In the first assemblage, only sites of the North Sea are found. The groups 2–4 included North Sea and Baltic Sea sites.

Assemblage 1 located on the lowest elevated sites of the North Sea coast is characterised by 6 species that can all be regarded as salt-preferring or flood tolerant species (see Chap. 27) (Table 14.5). Assemblages 2 and 3 represent the transitional zone between the lower elevated assemblage 1 and the highest elevated assemblage 4. They were located on medium elevated sites between 50 and 70 cm above MHW, on average. Although no significant difference in elevation is found, they are significantly separated by the salinity that is higher in assemblage 2 than in assemblage 3. Additionally, a difference seems to exist in the longitudinal co-ordinates. This can be associated with low elevated sites of the Baltic Sea and medium to high elevated sites at the North Sea in assemblage 2, while in assemblage 3 mainly high elevated sites of the North Sea are integrated. In assemblage 2, several species of the wet fresh grassland were frequent, i.e. *Bembidion properans* or *Agonum marginatum*. In contrast, in assemblage 3 several species of fresh or even dry grassland occurred, e.g. *Poecilus versicolor*. The last assemblage on the highest

Table 14.5 Carabid species composition of assemblages 1–4 and significant environmental factors; significant differences are indicated by different exponents

Environmental factor/ species	1		2		3		4	
	Mean	S.d.	Mean	S.d.	Mean	S.d.	Mean	S.d.
Elevation (cm)	125.6	24.2	^{2}51.3	31.8	^{2}69.4	34.3	^{3}147.1	41.5
Salinity	15.2	0.9	14.4	1.3	^{2}3.0	1.6	^{3}1.6	1.1
Average temperature (°C)	18.8	0.3	^{2}8.4	0.3	18.7	0.4	18.6	0.4
Flood frequency/year	187.6	76.5	^{2}38.3	33.8	^{2}11.5	15.2	^{2}0.4	0.8
Longitudinal co-ordinate (*n*)	18.1	0.5	^{2}10.2	2.1	^{2}19.1	2.6	^{2}19.6	2.5
Sand content (%)	14.7	17.5	^{2}30.8	22.1	^{2}14.4	27.9	^{3}87.1	15
Cillenus lateralis	4.5	16.1	0.4	1.1	0.1	0.6		
Dicheirotrichus gustavii	28	22.5	4.9	3.5	1.4	3.2		
Dyschirius thoracicus	1.1	3.5	0.4	1	0.9	4.9	<0.1	<0.1
Pogonus chalceus	24.8	15.5	3.8	3.3	1.7	2.1	0.4	0.9
Bembidion normannum	13.3	15.4	3	3.5	1.7	2.3	0.4	1
Dyschirius salinus	4.2	4.7	2.7	2.3	1.6	2	1	1.6
Bembidion minimum	8.1	10.1	13	10.4	2.5	3	0.4	0.9
Bembidion properans	1.8	2.6	2.8	3.3	0.3	0.8	0.2	0.6
Bembidion aeneum	1.5	2.2	4.2	2.2	1.7	2.2	<0.1	0.2
Agonum marginatum	0.1	0.3	1.7	2.2	1	2.2	<0.1	0.2
Dyschirius globosus	1	1.6	7	11.7	26.1	18.4	8	15.6
Pterostichus niger	0	0.1	2.1	3.6	5.7	6.6	3.2	3.7
Amara aenea	0.2	0.8	1.3	2	1.1	2.5	2	1.4
Poecilus versicolor	0.3	0.8	2	2.3	3.6	3	2.6	2.5
Amara spreta	0.3	1.1	1.3	2.6	0.9	2.5	2.2	2.6
Amara convexiuscula	0.1	0.2	0.4	0.9	1.4	2.7	0.4	0.9
Calathus melanocephalus	<0.1	0.3	2.6	3.8	2.8	3.9	5.3	3.6
Harpalus rufipes	0.4	1	1.7	2	2.1	2.3	2.1	1.1
Loricera pilicornis	0.6	1.4	3	3.6	2.4	4	2.4	4.9
Calathus fuscipes	<0.1	0	0.9	1.7	2.3	5.2	4.9	3.8
Calathus erratus	<0.1	0.2	0.7	1.5	2.7	7.1	9.5	17.7
Amara communis			1.4	2	1.4	2.4	2.6	2.6
Syntomus foveatus			0.3	1	0.2	0.8	1.3	1.5
Masoreus wetterhallii					0	0.2	2.2	3

elevated sites is characterised by species of dry grassland, i.e. *Calathus fuscipes* or *Calathus erratus* that are also frequently recorded from dune habitats. This is also particularly due to *Masoreus wetterhallii* that is typically found in dunes.

Although the carabid assemblages reflect a west-east gradient, the elevation is distinctly more important than in the spider assemblages. But both parameters are related for carabid beetles as can be seen by the shifting zonation of the assemblages on the west-east gradient (Fig. 14.5). Assemblage 1, representing the lowest elevated zone, occurred in the eastern part of the North Sea at higher elevated levels than in the westernmost part. Assemblage 2 indicates the high elevated sites at the western

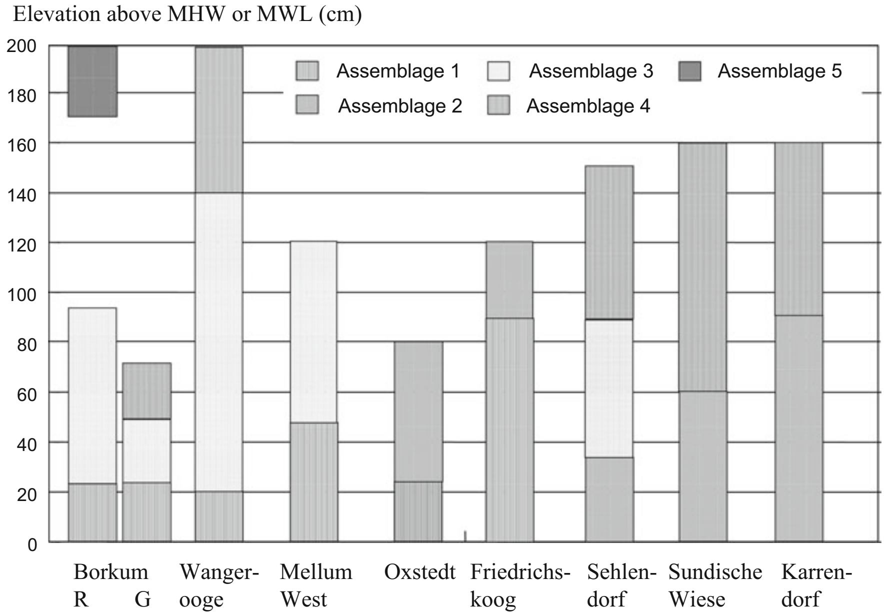


Fig. 14.5 Carabid assemblages in the elevation zones along a west-east gradient; *R* Ronde Plate, *G* Grüppenbeet, *n.d.* no data

North Sea coast but the low elevated sites at the Baltic Sea coast. Assemblage 4 was in fact scarcely found at the North Sea but was recorded there at still higher elevated sites than assemblage 2. It is supposed that it was not found on the eastern part of the North Sea coast because elevations higher than 140 cm were not investigated. At the Baltic Sea, this assemblage covers the uppermost part of the salt grassland down to a lower elevation of 50–80 cm above NN.

14.3.3 Geographical and Vertical Distribution of Species

The spiders and carabid beetles showed characteristic distributions along the geographical and vertical gradients, which are demonstrated for several typical coastal species in Fig. 14.6. The carabid species *Cillenus lateralis*, *Pogonus chalceus*, and *Bembidion normannum* were only found at the North Sea coast. *C. lateralis* is restricted to the lowest elevated sites and may be found only accidentally at higher elevated sites, e.g., in Oxstedt. For spiders, an ecologically similar species does not exist. Few spider species also inhabit elevations lower than 20 cm above MHW. They have their main habitat in higher elevated zones.

While salt content might be also responsible for the low catch of *D. salinus* at the Baltic Sea sites, the heterogeneous distribution of *B. aeneum*, *B. minimum,* and *D. globosus* must be explained by other parameters. Most of the typical coastal

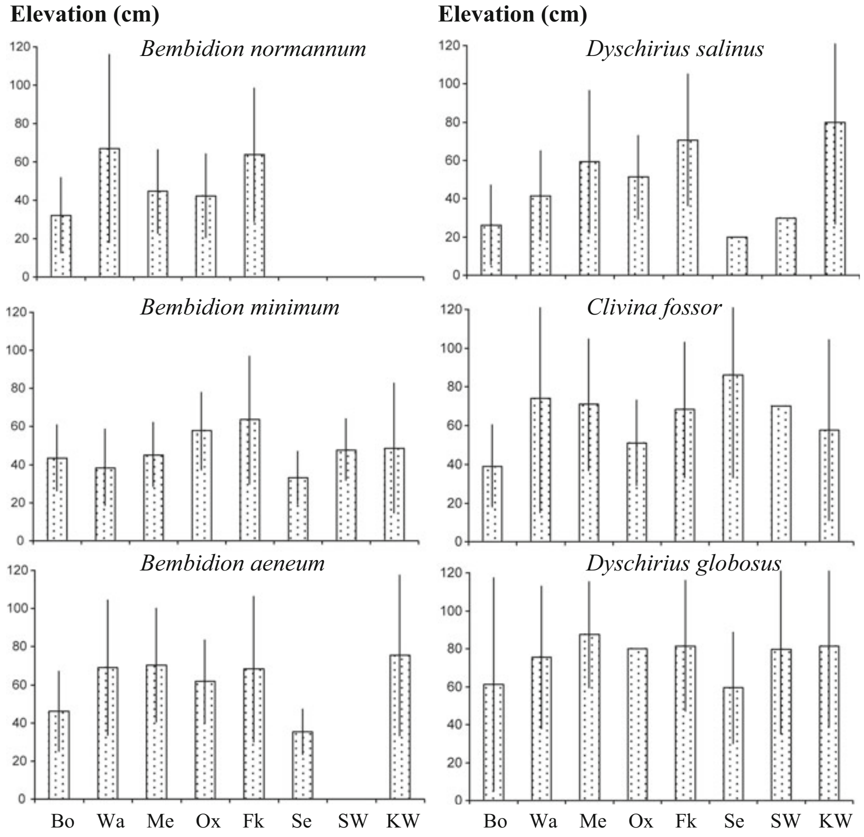


Fig. 14.6 Vertical distribution of six species of the salt marshes along a west-east gradient

spider species occurred at both the North Sea and the Baltic Sea. An interesting geographical distribution was found for *Silometopus ambiguus*. This species was not recorded in the westernmost areas of the North Sea and only rarely at the Baltic Sea. The catches were concentrated on the eastern North Sea areas at Oxstedt and Friedrichskoog. Most spider species were found in different catch numbers along the entire span of the geographical and vertical gradients.

14.3.4 Response of Species to the Environmental Parameters

The CCA showed that the environmental parameters determined in this study differently affect the occurrence of the assemblages. The importance of each factor for individual species of the salt grassland was analysed by the Spearman rank correlation. For the carabid beetles, seven groups were separated that differently respond to the ecological conditions of the investigated salt grasslands (Table 14.6).

Table 14.6 Results of the Spearman rank correlation of the carabid species. Only significant r-values are listed for species that were recorded with more than 10 specimens. *Elev* Elevation, *Flood* Flooding frequency, *Salt* Salt content, *Temp* Mean annual temperature, *Long* Longitudinal co-ordinate, *Sand* Sand content; $n = 76$

Species	Elev.	Flood	Salt	Temp.	Long.	Sand	Ecological preference
Dicheirotrichus gustavii	−0.55	0.66	0.75			−0.52	Species of the lower salt grassland
Pogonus chalceus	−0.51	0.61	0.62			−0.52	
Bembidion minimum	−0.31	0.34	0.39	−0.52	0.52	−0.56	
Bembidion normannum	−0.48	0.54	0.56	0.29	−0.3	−0.54	
Dyschirius salinus	−0.24	0.35	0.3	0.3	−0.34	−0.28	
Cillenus lateralis	−0.35	0.33	0.29				
Bembidion aeneum						−0.43	Flood and salt tolerant species
Bembidion properans				−0.34	0.36	−0.28	
Loricera pilicornis				−0.3	0.3	−0.24	
Clivina fossor				−0.3	0.28	−0.29	
Agonum marginatum				−0.44	0.45	−0.26	
Bembidion varium				−0.55	0.59		
Pterostichus strenuus				0.23	−0.28		
Pterostichus melanarius				−0.34	0.38		
Pterostichus nigrita				−0.45	0.42		
Bembidion lunulatum				−0.31	0.27		
Carabus granulatus		−0.23		−0.51	0.48		Flood sensitive species
Amara familiaris		−0.27		−0.46	0.45		
Amara plebeja		−0.31		−0.57	0.57		
Amara convexior		−0.34		−0.4	0.36		
Calathus melanocephalus	0.71	−0.7	−0.7			0.53	Species of the upper sandy salt grassland
Calathus fuscipes	0.54	−0.57	−0.49			0.43	

(continued)

Table 14.6 (continued)

Species	Elev.	Flood	Salt	Temp.	Long.	Sand	Ecological preference
Amara bifrons	0.6	−0.51	−0.5			0.38	
Amara communis	0.57	−0.54	−0.53			0.26	
Amara spreta	0.45	−0.41	−0.37			0.3	
Amara lunicollis	0.63	−0.63	−0.49			0.28	
Notiophilus aquaticus	0.29	−0.26	−0.29			0.26	
Calathus mollis	0.35	−0.38	−0.34			0.27	
Harpalus tardus	0.5	−0.46	−0.5			0.47	
Syntomus truncatellus	0.4	−0.34	−0.36			0.33	
Masoreus wetterhallii	0.49	−0.48	−0.42			0.46	
Amara curta	0.38	−0.36	−0.38			0.28	
Notiophilus germinyi	0.37	−0.33	−0.38			0.32	
Harpalus servus	0.38	−0.32	−0.32	0.26	−0.28	0.32	Species of the upper sandy salt grassland at the western coasts
Notiophilus palustris	0.35	−0.31	−0.27	0.35	−0.34	0.39	
Leistus terminatus	0.36	−0.31	−0.38	0.26	−0.33	0.35	
Trechus obtusus	0.44	−0.38	−0.43	0.28	−0.35	0.39	
Calathus erratus	0.36	−0.31	−0.36	0.4	−0.41	0.4	
Syntomus foveatus	0.48	−0.4	−0.46	0.27	−0.31	0.38	
Badister bullatus	0.37	−0.32	−0.4	0.4	−0.44	0.34	
Amara similata	0.25	−0.24	−0.24				Euryecious species of the upper salt grassland
Synuchus vivalis	0.26	−0.3	−0.31				
Amara aenea	0.39	−0.38	−0.36				
Dyschirius globosus	0.29	−0.34	−0.39				
Pterostichus niger	0.38	−0.42	−0.43				
Harpalus rufipes	0.44	−0.44	−0.46				
Poecilus versicolor	0.34	−0.45	−0.44				
Harpalus affinis	0.33	−0.35	−0.31	−0.37	0.34		Euryecious species of the upper eastern salt grassland
Pterostichus vernalis	0.25	−0.36	−0.24	−0.53	0.58		
Anisodactylus binotatus	0.36	−0.42	−0.34	−0.3	0.29		

Only six species can be regarded as typical for salt grassland because they prefer sites at low elevations, high flooding frequency, and high salt content. Most carabid species found in the coastal sites seem to avoid such conditions. They were positively correlated with elevation and negatively with flooding frequency and salt content. Nevertheless, there were also ten species that revealed no significant results correlating with these factors and thus can be regarded as tolerant to them. Among the species that respond negatively to the conditions of lower salt grassland, some species generally preferred sandy soils or sandy sites of the western coasts, whereas others showed an euryoecious occurrence in the upper salt grassland. 16 species revealed no significant results correlating with one of the environmental factors.

For spiders, nine preference groups were distinguished (Table 14.7). In total, only seven species seem to prefer lower salt grassland conditions with low elevation, high flooding frequency, and high salt content. Four species of the lower salt grassland occurred more frequently on the eastern coasts. These species were either distributed along the entire west-east gradient with higher abundance at the eastern North Sea coast, e.g., *Erigone longipalpis*, or were absent at the westernmost study areas, e.g. *Silometopus ambiguus*. Five species revealed positive correlations with the flooding frequency and can, therefore, be regarded as flood tolerant species. Within this assembly of species, *Erigone arctica* and *Walckenaeria kochi* are usually classified as species of coastal habitats or as halo-tolerant (Reinke and Irmler 1994). A large number of species showed no correlation with one of the factors that determine the conditions of the lower salt grassland. They seem to be euryoecious concerning these conditions, but they are either distributed on more western or more eastern coasts.

Compared to the carabid beetles, a lower number of species respond negatively to the conditions of the lower salt grassland. For both Carabidae and spiders, 45% and 32% of the species, respectively, avoid the lower salt grassland. Most species of this assembly of spiders correlated positively with the sand content. Finally, two spiders recorded from the salt grassland responded negatively with sand content. These species are usually classified as typical for wet grassland near fresh waters (Reinke and Irmler 1994). In this study, they occurred on peat soils of the Baltic Sea and seem to be tolerant to inundation or high salt contents.

Flooding frequency differed between the two study years and between sites. Thus, equal elevations among sites also differed in the number of flooding events. This can be seen for the two sites Mellum and Friedrichskoog that are both located at the North Sea coast (Fig. 14.7). At the 20 cm level, sites at Mellum were flooded approximately 50 times per year, whereas sites of the same level were flooded approximately 100 times at Friedrichskoog. The differences between the two study years also differed. While they differed distinctly at Mellum, Friedrichskoog revealed nearly no difference between the years.

The change of the zonation index between 1997 and 1998 was regarded for 60 comparisons (Table 14.8). The zonation index of 47 (79%) comparisons was higher in 1998 than in 1997, meaning that the species lived in higher zones in the year with the higher flooding frequency on an annual average. The mean lower zonation index was significant ($p < 0.05$) in 1997 rather than in 1998 if the

Table 14.7 Results of the Spearman rank correlation of the spider species. Only significant r-values are listed for species that were recorded with more than 10 specimens. *Elev* Elevation, *Flood* Flooding frequency, *Salt* Salt content, *Temp* Mean annual temperature, *Long* Longitudinal co-ordinate, *Sand*: Sand content; $n = 70$

Species	Elev.	Flood	Salt	Temp.	Long.	Sand	Ecological preference
Pardosa purbeckensis	−0.49	0.49	0.43			−0.67	Species of the lower salt grassland
Praestigia duffeyi	−0.35	0.46	0.37			−0.49	
Argenna patula	−0.29	0.43	0.37			−0.41	
Erigone longipalpis	−0.47	0.54	0.5	−0.58	0.57	−0.55	Species of the lower salt grassland on eastern coasts
Oedothorax retusus	−0.26	0.36	0.3	−0.48	0.57	−0.47	
Silometopus ambiguus		0.45	0.31	−0.48	0.48	−0.24	
Pachygnatha clercki	−0.24	0.28		−0.47	0.47	−0.44	
Erigone arctica		0.28					Flood tolerant species
Leptorhoptrum robustum		0.31				−0.35	
Oedothorax fuscus		0.34		−0.45	0.69	−0.39	
Walckenaeria kochi		0.31				−0.25	
Hypomma bituberculatum		0.31		−0.27	0.27		
Stemonyphantes lineatus				0.41	−0.45		Flood and salt tolerant species of the western coasts
Antistea elegans				0.31	−0.3		
Pirata latitans				0.34	−0.52		
Pirata hygrophilus				0.31	−0.37	0.29	
Walckenaeria antica				0.38	−0.33		
Walckenaeria atrotibialis				−0.27	0.27		Flood and salt tolerant species of the eastern coasts
Pardosa palustris				−0.26	0.29		
Gongylidiellum vivum				−0.35	0.34		
Dicymbium nigrum				−0.61	0.7		
Micrargus herbigradus				−0.28	0.47		
Araeoncus humilis				−0.68	0.71		

(continued)

Table 14.7 (continued)

Species	Elev.	Flood	Salt	Temp.	Long.	Sand	Ecological preference
Oedothorax apicatus				−0.53	0.65		
Bathyphantes approximatus				−0.27	0.37		
Agyneta decora				−0.27	0.31		
Trochosa terricola	0.42	−0.43	−0.41				Flood and salt sensitive species
Centromerita bicolor	0.27	−0.25	−0.37				
Euophrys frontalis	0.29		−0.26				
Micrargus subaequalis	0.28	−0.26					
Tiso vagans	0.32	−0.28	−0.42				
Centromerita concinna	0.31	−0.25	−0.26				
Trochosa ruricola	0.31	−0.38	−0.33			0.27	Flood and salt sensitive species on sandy salt grassland
Tenuiphantes tenuis	0.51	−0.36	−0.44			0.37	
Diplostyla concolor	0.52	−0.41	−0.44			0.38	
Ceratinopsis stativa	0.31	−0.33	−0.37			0.25	
Robertus lividus	0.32		−0.29			0.25	
Tapinocyba praecox	0.32	−0.3	−0.32			0.32	
Drassodes cupreus	0.43	−0.34	−0.38			0.4	
Xysticus cristatus	0.4	−0.45	−0.5			0.36	
Xysticus kochi	0.57	−0.48	−0.51			0.55	
Zelotes longipes	0.42	−0.39	−0.37			0.33	
Pardosa monticola	0.38	−0.43	−0.37			0.45	
Alopecosa pulverulenta	0.36	−0.42	−0.41	0.66	−0.46	0.33	Flood and salt sensitive species on sandy salt grassland of western coasts
Zelotes pusillus	0.42	−0.54	−0.41	0.49	−0.56	0.49	
Zelotes electus	0.51	−0.49	−0.45	0.39	−0.42	0.49	
Zelotes latreillei	0.5	−0.48	−0.45	0.43	−0.56	0.51	
Argenna subnigra	0.58	−0.59	−0.53	0.35	−0.41	0.63	
Xerolycosa miniata	0.37	−0.37	−0.3	0.48	−0.57	0.38	

(continued)

Table 14.7 (continued)

Species	Elev.	Flood	Salt	Temp.	Long.	Sand	Ecological preference
Agroeca proxima	0.49	−0.43	−0.43	0.38	−0.52	0.53	
Allomengea scopigera						−0.36	Species avoiding sandy grassland
Pardosa amentata						−0.3	

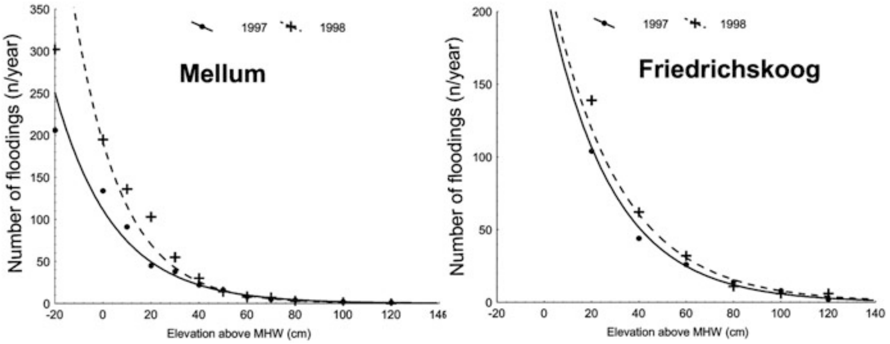


Fig. 14.7 Flooding frequency at the study areas of Mellum and Friedrichskoog

Algebraic sign test was used. In most cases, the differences between the 2 years were low with high variances. A significant higher zonation index in 1998 rather than in 1997 was found in 12 comparisons, but a significant lower one in only one comparison, on average. In contrast to 1997, populations shifted to an elevation zone in 1998 that was between 10 and 15 cm higher, which is less than the usual total expansion of the elevation habitat. If coastal species and non-coastal species are compared separately, both coastal and non-coastal species showed 4 and 9 significant shifts to higher elevations, respectively, which reflect that non-coastal species react more sensitively to a higher flooding frequency than coastal species. Overall, it seems that at low elevations an increase of flooding frequency between 40 and 50 floods per year is too low to cause a significant shift to higher elevations. The species remained more or less within their elevation habitat, although a weak trend to shift to higher elevations exists in some species as was indicated by the significant results of the Algebraic sign test.

The vertical distribution of species differed not only between the 2 years corresponding to the average annual flooding frequency but also within the annual seasons (Figs. 14.8 and 14.9). Generally, the species were recorded at higher elevations during the early part of the year and in autumn rather than during the summer months. If the seasonality of the zonation index of typical carabid species is compared between Mellum and Friedrichskoog, it can be seen that the seasonal

Table 14.8 Zonation index compared between 1997 and 1998 at three study areas of the North Sea coast. The upper species group of Carabidae and spiders indicate typical coastal species, whereas the lower group represents typical species of fresh grassland

	Wangerooge		Mellum West		Friedrichskoog	
Species	1997	1998	1997	1998	1997	1998
Carabidae						
Bembidion aeneum	26 ± 12	[a]110 ± 0		48 ± 19	58 ± 37	78 ± 30
Bembidion minimum	22 ± 7	[a]37 ± 24	30 ± 0	40 ± 4	67 ± 29	72 ± 35
Bembidion normannum	19 ± 18	[a]40 ± 27	29 ± 4	39 ± 12	46 ± 25	43 ± 24
Dicheirotrichus gustavii	17 ± 7	19 ± 10	11 ± 7	9 ± 6	44 ± 24	41 ± 19
Dyschirius salinus	16 ± 6	23 ± 14		58 ± 31	58 ± 26	63 ± 33
Dyschirius thoracicus				98 ± 11	76 ± 10	78 ± 13
Pogonus chalceus	18 ± 11	19 ± 16	14 ± 10	14 ± 12	42 ± 17	37 ± 14
Dyschirius globosus	60 ± 12	64 ± 21	10 ± 0	[a]93 ± 20	99 ± 24	107 ± 21
Amara aenea	141 ± 80	186 ± 48		107 ± 9	118 ± 22	103 ± 48
Calathus fuscipes	158 ± 76	193 ± 31		105 ± 18	105 ± 25	[a]130 ± 0
Calathus melanocephalus	177 ± 66	187 ± 46	30 ± 0	[a]97 ± 35	112 ± 24	115 ± 22
Clivina fossor	72 ± 39	[a]27 ± 22	30 ± 0	[a]92 ± 17	70 ± 35	89 ± 34
Loricera pilicornis	135 ± 75	52 ± 34	10 ± 12	[a]51 ± 38	68 ± 40	[a]118 ± 35
Spiders						
Argenna patula	21 ± 9	26 ± 20			49 ± 24	68 ± 29
Erigone longipalpis	16 ± 5	18 ± 10			60 ± 29	66 ± 32
Oedothorax retusus	24 ± 12	[a]45 ± 25			84 ± 33	85 ± 35
Pardosa purbeckensis	28 ± 17	33 ± 22			84 ± 36	58 ± 38
Pocadicnemis juncea	61 ± 27	63 ± 35			101 ± 21	73 ± 34
Silometopus reussi	65 ± 9	83 ± 43			98 ± 41	116 ± 29
Walkeneria vigilax	59 ± 13	73 ± 29			42 ± 30	40 ± 27
Diplostyla concolor	81 ± 50	121 ± 70			70 ± 42	77 ± 45
Erigone atra	40 ± 33	72 ± 52			82 ± 41	102 ± 34
Erigone dentipalpis	24 ± 15	[a]68 ± 30			93 ± 41	111 ± 29
Tenuiphantes tenuis	110 ± 71	122 ± 52			97 ± 33	109 ± 28

(continued)

Table 14.8 (continued)

	Wangerooge		Mellum West		Friedrichskoog	
Species	1997	1998	1997	1998	1997	1998
Oedothorax fuscus	22 ± 10	[a]59 ± 30			90 ± 32	92 ± 37
Pachygnatha degeeri	61 ± 34	70 ± 32			105 ± 25	104 ± 27

[a] indicates significant difference between 1997 and 1998

fluctuation is more expressed in Friedrichskoog salt grassland with high flooding frequency than at Mellum with lower flooding frequency. In particular, the two halobiontic *Bembidion* species exhibited high fluctuations at Friedrichskoog salt grassland (Fig. 14.9) as can be derived from the seasonally vertical occurrence. They overwinter at sites elevated higher than 100 cm above MHW and migrate to lower elevated sites between 30 and 60 cm above MHW in April. At Mellum, overwintering sites were located at lower elevations of 60 cm above MHW. In contrast to Friedrichskoog, elevation habitat in summer is equal for both species.

Thus, the different elevation niches of the two species are only revealed under flooding conditions as found in Friedrichskoog. Although seasonal fluctuation of the zonation index is not significant in *Dicheirotrichus gustavii* and *Pogonus chalceus,* a weak migration was observed at least at Friedrichskoog. However, it was much lower than for the *Bembidion* species that are well-known as good flyers. The elevation difference between early year and summer for both *D. gustavii* and *P. chalceus* was 40 cm and 10 cm, respectively. The much more conservative spatial behaviour of *D. gustavii* and *P. chalceus* can be associated with a high percentage of non-winged specimens in the population (Desender 1985). Nevertheless, a short vertical migration seems to exist also in these species under flooding frequency conditions as found at Friedrichskoog.

Spiders too, reflect high mobility concerning their vertical distribution. But a distinct seasonality cannot be derived from the seasonal fluctuation of the zonation index (Fig. 14.10). In general, they inhabited higher elevated sites early in the year and in autumn. But no constant elevation was found during the summer months. It seems that many species moved up and down corresponding to the flooding frequency. Indeed, for many species a significant correlation with the flooding frequency at the 40 cm level was determined, if all individual data from Mellum and Friedrichskoog are used, e.g., *Erigone longipalpis* ($r = 0.45$) and *Oedothorax retusus* ($r = 0.47$). Thus, spiders do not reveal an endogenous seasonality in their vertical occurrence, but a higher flexibility in vertical movement than carabid beetles.

At the Baltic Sea coast, too, a significant vertical shift was found for some typical coastal species (Fig. 14.10). Similar to the North Sea coast, *Bembidion minimum* exhibited a high seasonal vertical shift, in particular at Karrendorf Meadow (Fig. 14.12). The seasonal shift was less expressed at Sehlendorf Lagoon, but this might be associated with the landscape conditions. The species was recorded at

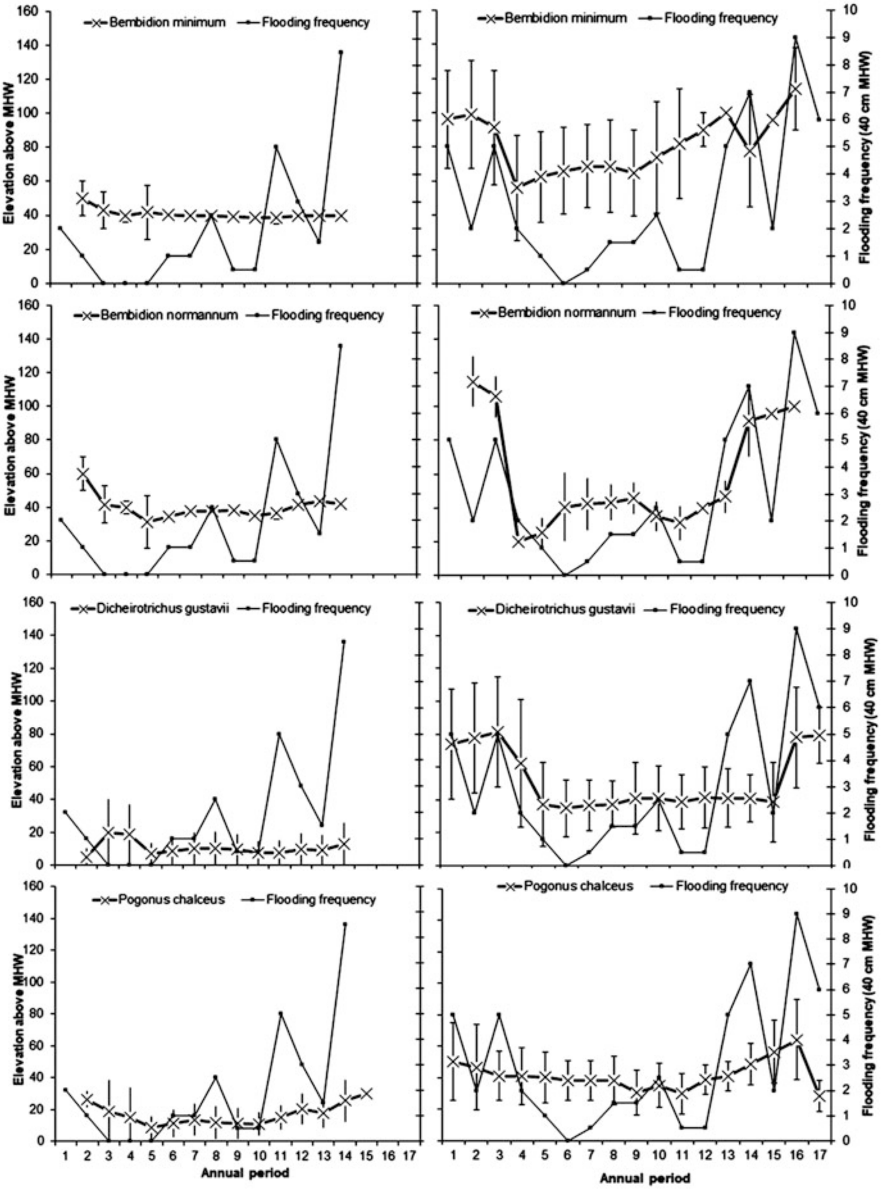


Fig. 14.8 Seasonal fluctuation of the zonation index of four typical coastal carabid species at Mellum (left) and Friedrichskoog (right) at the North Sea coast. Mean of the years 1997 and 1998. Annual periods are 2 week intervals beginning on March 15 with period 1

Sehlendorf Lagoon only during a short annual period in the salt grassland. It might have invaded from higher elevated sites that were not investigated by pitfall traps.

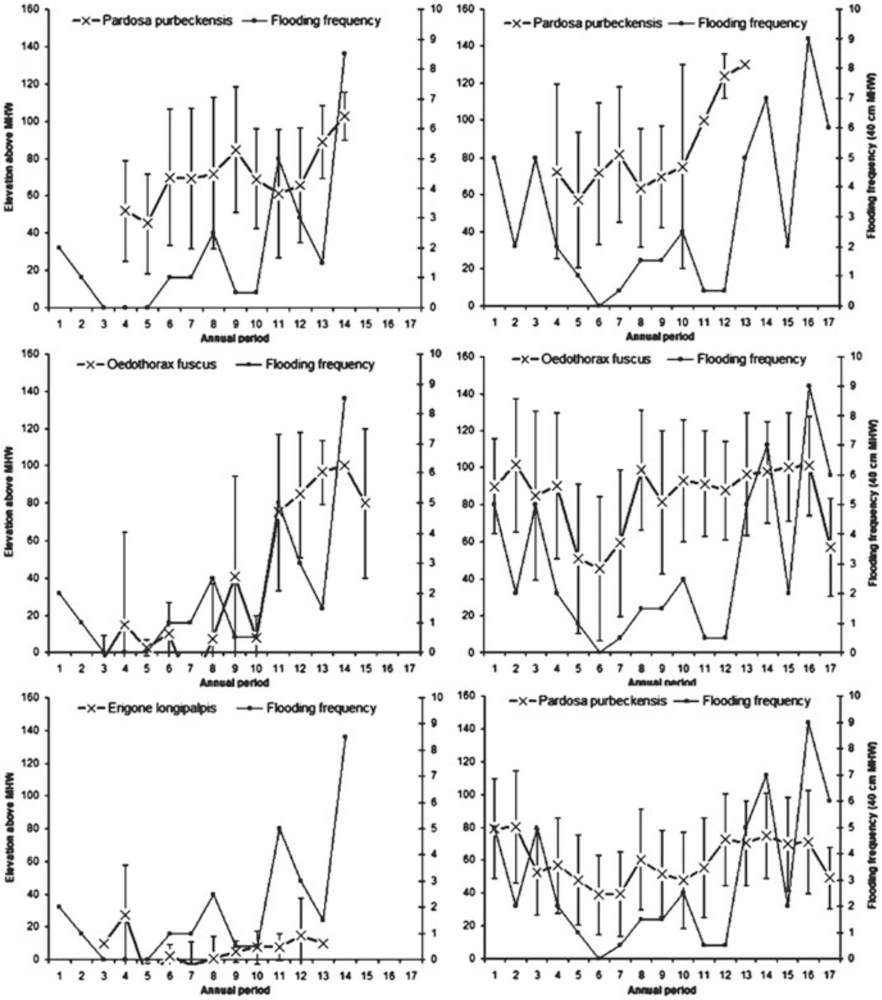


Fig. 14.9 Seasonal fluctuation of the zonation index of three typical coastal spider species at Mellum (left) and Friedrichskoog (right) at the North Sea coast. Mean of the years 1997 and 1998. Annual periods are 2 week intervals beginning on March 15 with period 1

Nevertheless, the vertical migration seems to be less expressed at Sehlendorf Lagoon than at Karrendorf Meadow as can also be seen in *Erigone longipalpis*. Whereas this species overwinters at Karrendorf Meadow at an elevation between 80 cm and 100 cm above MWL, no elevation shift was observed at Sehlendorf Lagoon.

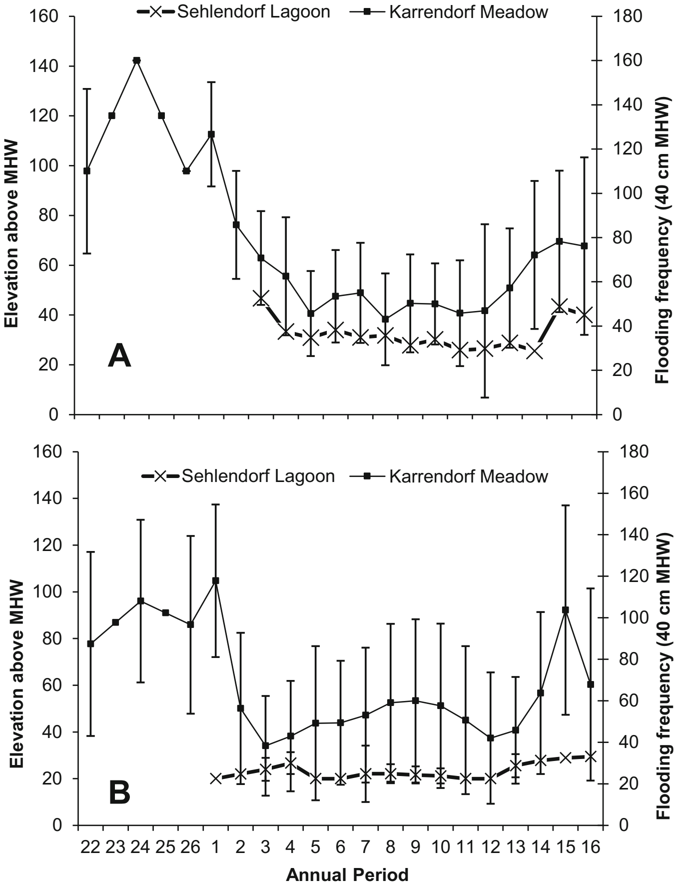


Fig. 14.10 Seasonal fluctuation of the zonation index (mean of the years 1997 and 1998) of carabid beetle, e.g., (**a**) *Bembidion minimum*, and spider, e.g., (**b**) *Erigone longipalpis*, at Sehlendorf Lagoon (western Baltic Sea) and Karrendorf Meadow. Annual periods were defined as 2 week intervals ending with period 26 at March 14 of sampling year 1997/98 and beginning with period 1 on March 15 of sampling year 1998/99

14.3.5 Seasonal Occurrence

Associated with the predicted increase of temperature, the seasonal occurrence of species was analysed by the phenology index. However, no significant results support the hypothesis that seasonal occurrence of species in the salt grasslands is related to the different mean annual temperatures of the study areas. The seasonal occurrence mainly depends on the general endogenous seasonal dynamics of the species and the locally specific flooding dynamics (Fig. 14.11). Comparing the phenology indices, the carabid species, e.g., *Pogonus chalceus* and *Bembidion aeneum*, and the spiders, e.g., *Argenna patula* and *Pardosa purbeckensis*, were

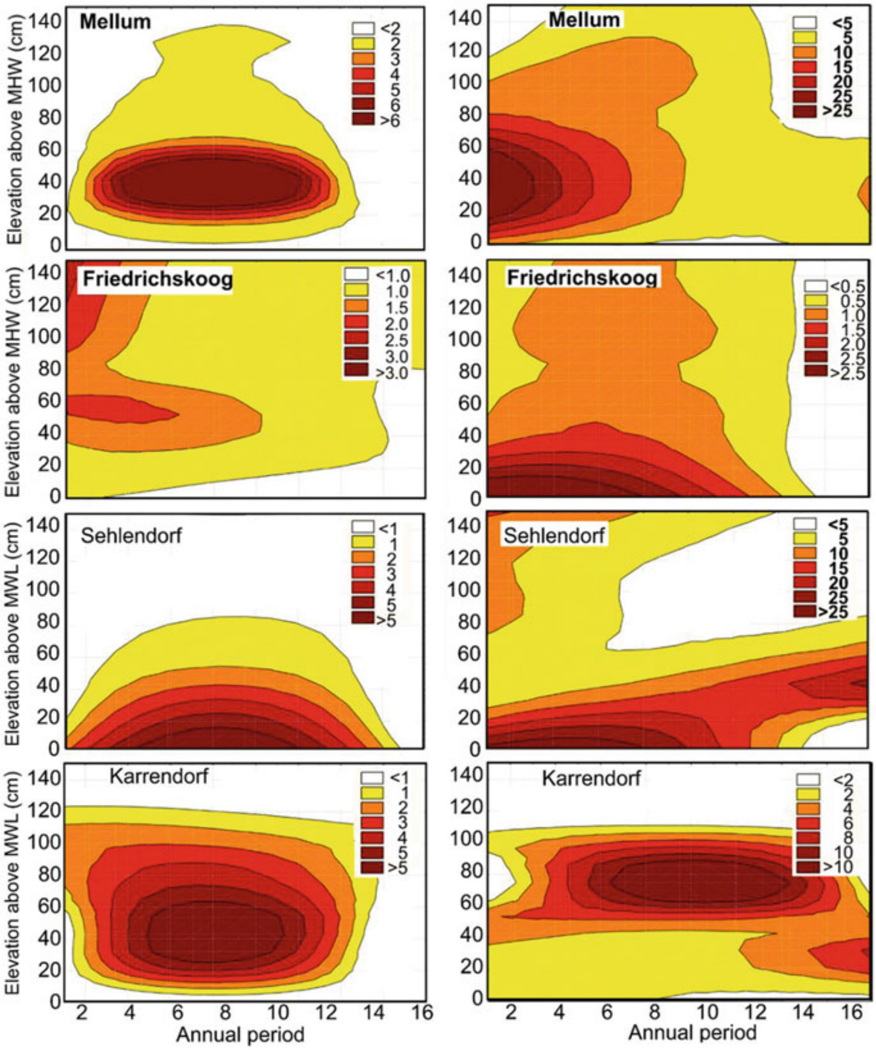


Fig. 14.11 Seasonal and vertical distribution of the carabid beetle *Bembidion minimum* (left) and the spider *Pardosa purbeckensis* (right) within the west-east gradient (Mellum: westernmost study area; Karrendorf: easternmost study area)

recorded in the early vegetation season with mean phenology indices of 4.9, 4.4, 5.9, and 5.6, respectively. These periods are in mid-May. The standard deviation between the study sites ranged between 0.7 and 1.4 periods, i.e., between 1.5 and 3 weeks. Representatives of the late year were the carabid beetles *Dicheirotrichus gustavii* and *Calathus melanocephalus* with mean phenology indices of 11.5 and 11.4, respectively, i.e., in the second half of August. Most species occurred between the periods 6 and 8.5, i.e., between the beginning of June to mid-July, e.g. *Bembidion minimum*, *Bembidion normannum*, *Dyschirius salinus*, *Erigone longipalpis*, *Oedothorax retusus*, *Erigone atra*, *Erigone dentipalpis*, and *Oedothorax fuscus*. All species showed a higher standard deviation within one study area than between the study areas.

14.4 Conclusions

Flooding conditions represent the major factor influencing the composition of the salt grassland community at the North Sea and the Baltic Sea coasts leading to a decreasing species richness from high to low elevated sites. Thus, the species richness of a foreland depends on the altitudinal expansion of the salt grassland. High elevated sites reveal more species that can invade to lower sites in periods with low flooding events. Another effect associated with the flooding conditions is represented by the exposition. At sites protected against high floods, species can inhabit lower elevations than at sites exposed to the open sea. Surprisingly, exposition to the open sea also affected the zonation and altitudinal occurrence of species at the Baltic Sea although tides are lacking there. Salt content is certainly responsible for the decrease of several species from the western Baltic Sea to the eastern Baltic Sea, e.g., *Dicheirotrichus gustavii*, while sand content is of lower importance.

The assemblages shift according to the overall flooding regime of the sites. Assemblages at low elevated sites of areas with few flooding events shift to high elevated sites of areas with high flooding frequency.

The inhabited salt grassland at Friedrichskoog demonstrates the size reduction for two species between the present status and the two scenarios under increased sea level conditions, if the present embankment remains (Fig. 14.12). *Pogonus chalceus* represents a species living in the low elevated salt grassland, while *Erigone arctica* lives in the upper salt grassland. For the calculation, the length dimension between the MHW level and the dike was transferred into the elevation model of the Friedrichskoog foreland. The zonation index with its standard deviation was used to estimate the theoretical habitat size. The present length dimension for both *Pogonus chlaceus* and *Erigone arctica* amounts to 140 m and 60 m, respectively.

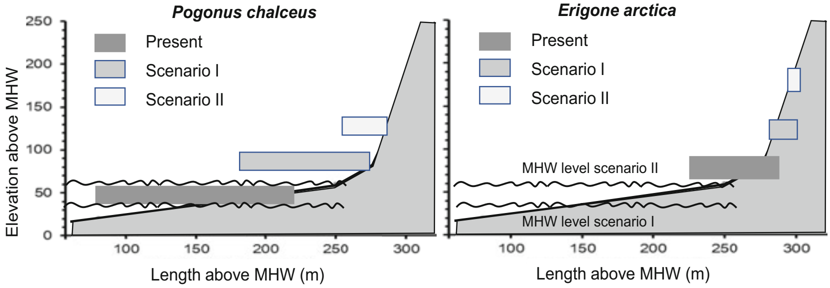


Fig. 14.12 Size of optional habitat in the salt grassland for *Pogonus chalceus* (Carabidae) and *Erigone arctica* (Araneida) at present and for the two scenarios

Under the conditions of both scenario I (sea level rise +35 cm, heavy floodings +33%) and scenario II (sea level rise +60 cm, heavy floodings +15%) the habitat size for *Pogonus chalceus* reduces to only 68% and 21%, respectively, while for *Erigone arctica* the values are 33% and 20%, respectively.

The general seasonal and vertical niches varied due to the local conditions. At areas exposed to high tide dynamics (Friedrichskoog), species occurred at higher elevations than at sheltered areas (Mellum). Seasonal migrations are more often expressed in species that are able to migrate (*Bembidion* species). Spiders are generally less fixed to a vertical occurrence than carabid beetles, which can be seen by the higher vertical fluctuation in correspondence to the flooding dynamics.

References

Andresen H, Bakker JP, Brongers M, Heydemann B, Irmler U (1990) Long-term changes of salt marsh communities by cattle grazing. Vegetatio 89:137–148

Baehr M (1984) Die Carabidae des Lauterbachtals bei Münsingen (Insecta. Coleoptera). Ein Querschnitt durch ein Flußtal der Schwäbischen Alb. 5. Beitrag zur Faunistik der Carabiden Württembergs. Veröffentlichungen für Naturschutz und Landschaftspflege Baden-Württemberg 57(58):341–374

Barber HS (1931) Traps for cave inhabiting insects. J Elisa Mitchell Sci Soc 46:259–266

Boden A (1994) Bodenkundliche Kartieranleitung. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart

Braun-Blanquet J (1964) Pflanzensoziologie, 3. Auflage edn. Springer, Wien, p 865

Desender K (1985) Wing polymorphism and reproductive biology in the halibiont carabid beetle *Pogonus chalceus* (Marsham) (Coleoptera. Carabidae). Biol Jb Dodonaea 53:89–100

Dormann W (2000) A new pitfall trap for use in periodically inundated habitats. In: Brandmayr P, Lövei G, Zetto-Brandmayr T, Casale A, Vigna Taglianti A (eds) Natural history and applied ecology of carabid beetles. Proc. IXth European Carabaridologist's meeting. Cosenza 1998. Pensoft Publishers, Sofia-Moscow, pp 247–250

Dormann W, Metzing D, Mossakowski D (2008) Klimafolgen und Küsten: Auswirkungen auf die Verteilung und Verbreitung von Laufkäfern der Salzwiesen (Carabidae). Insecta 11:51–62

Finch O-D, Krummen H, Plaisier F, Schultz W (2007) Zonation of spiders (Araneae) and carabid beetles (Coleoptera: Carabidae) in island salt marshes at the North Sea coast. Wetl Ecol Manag 15:207–228

Främbs H, Stahl R (1997) Eine aufschwimmende Bodenfalle zur Erfassung epigäischer Arthropoden in überflutungsgefährdeten Lebensräumen. Arbeitsberichte Landschaftsökologie Münster 18:287–289

Främbs H, Kinder M, Hielen B, Böhme B, Günther C, Rachor E, Cordes H, Mossakowski D (2002) Renaturierung salzbeeinflußter Lebensräume an der Nordseeküste. Salzwiesenprojekt Wurster Küste BfN-Skripten 68:326

Heydemann B (1956) Die Biotopstruktur als Raumwiderstand und Raumfülle für die Tierwelt. Verhandlungen der Deutschen Zoologischen Gesellschaft 20:332–347

Heydemann B (1960) Die biozönotische Entwicklung vom Vorland zum Koog. Vergleichendökologische Untersuchungen an der Nordseeküste. 1. Teil: Spinnen (Araneae). Akademie der Wissenschaften und Literatur Mainz. Abh. math.-naturwiss. Klasse 11:747–913

Heydemann B (1962) Die biozönotische Entwicklung vom Vorland zum Koog. Vergleichendökologische Untersuchungen an der Nordseeküste. 2. Teil: Käfer (Coleoptera). Akademie der Wissenschaften und Literatur Mainz. Abh. math.-naturwiss. Klasse 11:765–964

Heydemann B (1967) Die biologische Grenze Land–Meer im Bereich der Salzwiese. Franz Steiner, Wiesbaden, p 200

Irmler U, Heydemann B (1986) Die ökologische Problematik der Beweidung von Salzwiesen an der niedersächsischen Küste–am Beispiel der Leybucht. Naturschutz und Landschaftspflege Niedersachsen 11:1–115

Irmler U, Heller K, Meyer H, Reinke H-D (2002) Zonation of ground beetles (Coleoptera: Carabidae) and spiders (Araneida) in salt marshes at the north and the Baltic Sea and the impact of the predicted sea level increase. Biodivers Conserv 11:1129–1147

Jongman RHG, ter Braak CJF, Van Tongeren OFR (1987) Data analysis in community and landscape ecology. Cambridge University Press, Cambridge

Kinder M, Främbs H, Hielen B, Mossakowski D (2003) Regeneration von Salzwiesen in einem Sommergroden an der Nordseeküste: E + E Vorhaben "Salzwiesenprojekt Wurster Küste". Natur und Landschaft 78:343–353

Krebs CJ (1999) Ecological methodology. Computation program, 2nd edn. Benjamin/Cummings, San Francisco

Londo G (1975) Dezimalskala für die vegetationskundliche Aufnahme von Dauerquadraten. In: Schmid W (ed) Sukzessionsforschung. Cramer Verlag, Vaduz, pp 613–617

Luff ML (1975) Some features influencing the efficiency of pitfall traps. Oecologia 19:345–357

Meyer H, Fock H, Haase A, Reinke H-D, Tulowitzki I (1995) Structure of the invertebrate fauna in salt marshes of the Wadden Sea coast of Schleswig-Holstein influenced by sheep-grazing. Helgoländer Meeresuntersuchungen 49:563–589

Meyer H, Reinke HD, Irmler U (1997) Die Wirbellosenfauna unterschiedlicher Salzwiesen an der Wattenmeerküste in Schleswig-Holstein und Niedersachsen. Faunistisch-ökologische Mitteilungen 7:267–284

Müller-Motzfeld G (2004) Adephaga I: Carabidae. In: Freude H, Harde KW, Lohse GA, Klausnitzer B (eds) Die Käfer Mitteleuropas 2. Adephaga 1: Carabidae (Laufkäfer). Spektrum Verlag, Heidelberg

Platnick NI (2006) The world spider catalog. Version 7.0. Edited by Merrett P. Cameron HD http://research.amnh.org/entomology/spiders/catalog/index.html

Reinke HD, Irmler U (1994) Die Spinnenfauna (Araneae) Schleswig-Holsteins am Boden und in der bodenahen Vegetation. Faunistisch-Ökologische Mitteilungen Supplement 17:1–148

Schaefer M (1970) Einfluß der Raumstruktur in Landschaften der Meeresküste auf das Verteilungsmuster der Tierwelt. Zoologisches Jahrbuch für Systematik 97:55–124

Schultz R, Müller-Motzfeld G (1995) Faunistisch-ökologische Untersuchungen auf Salzstandorten bei Greifswald. Zeitschrift für Ökologie und Naturschutz 4:9–19

StatSoft (1996) Statistica für windows (computer-Programm-Handbuch). StatSoft Inc., Tulsa

Ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179

Ter Braak CJF, Smilauer P (1998) Canoco for windows version 4.0. Centre for Biometry, Wageningen

Trautner J, Müller-Motzfeld G, Bräunicke M (1997) Rote Liste der Sandlaufkäfer und Laufkäfer Deutschlands (Coleoptera: Cicindelidae et Carabidae) 2. Fassung. Stand Dezember 1996. Naturschutz und Landschaftsplanung 29:261–273

Weigmann G (1973) Zur Ökologie der Collembolen und Oribatiden im Grenzbereich Land-Meer (Collembola. Insecta–Oribatei. Acari). Zeitschrift für wissenschaftliche Zoologie Leipzig 186: 295–391

Wohlrab B (1997) Untersuchungen zum Stoffaustausch zwischen Küstenüberflutungsräumen und vorgelagertem Wasserkörper–ein Beitrag zu Stoffhaushaltsbilanzierungen im Renaturierungsgebiet Karrendorfer Wiesen (Greifswalder Bodden). Unpublished Diploma thesis. University Greifswald

World Spider Catalog (2015) World Spider Catalog. Natural History Museum Bern. Version 16. Accessed on 26, April 2015 from http://wsc.nmbe.ch

Predicting Carabid Beetle Distribution Shifts

15

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and Dietrich Mossakowski

Abstract

Selected common saltmarsh ground beetle species were analysed to find out future distribution patterns under the predicted climate scenarios. Distribution data were allocated to actual climate data and charged against data of the scenarios using the envelop technique (ecograms). The results revealed that species from the Atlantic region will distribute to the western study area. Few eastern distributed species will invade from the East and some species occurring on inland salt habitats may distribute to the northern coasts of Germany. Only one species may be extinct in the region due to northwards emigration. Additionally, few species will show eastward or westward shifts along the studied coastal region.

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15.1 Introduction

According to the climate scenarios of the German coasts for the year 2050, temperature might increase by 2.5 K and the seasonal distribution of precipitation might change (von Storch et al. 1998). Consequently, climate sensitive animals will react, e.g. cold adapted species distributed in a northern range will become extinct in the region, and species with a southern distribution will widen their area to the north. Under these conditions, coastal habitats may also be colonised from western, southwestern, and inland distributed species.

15.2 Methods

15.2.1 Distribution Patterns

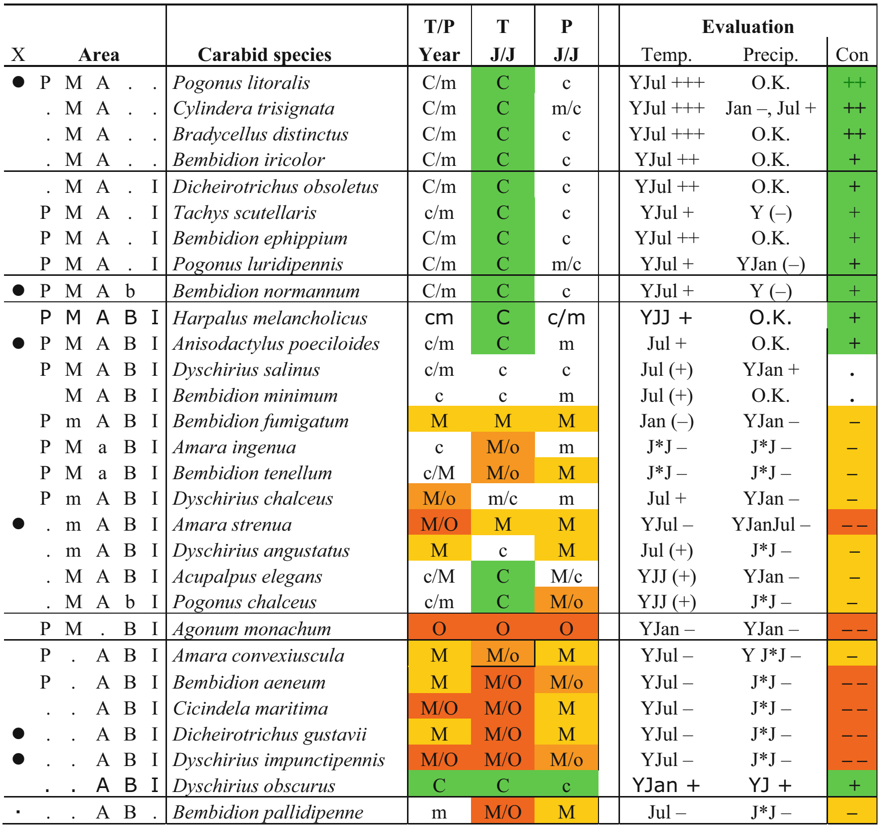
The analysis of the geographical pattern included carabid species that inhabit the German coast, coasts of adjacent regions, and similar salt habitats. Carabid species with only northern distribution were omitted, because a southward expansion is not expected.

Besides the pioneer work of Lindroth (1945), we digitalised further point maps for carabid beetles of other countries (Turin and Haeck 1977; Bangsholt 1983; Desender 1986; Desender et al. 2008; Turin 2000; Luff 2005) and used electronic sources, such as those for northwestern Germany (Start in 2001; Tolasch and Gürlich 2015) or those for entire countries, for example, for Ireland (Anderson and McFerran 2005), Britain (Luff 2005), Austria: ZOBODAT (Malicky 2015), Czech Republic (Zicha 2015), Germany (Bleich et al. 2015), and Italy (Ruffo and Stoch 2005). A basis for our distribution maps was the Europe-wide detailed maps on general distribution of carabid species (Turin and Haeck 1977).

Ecograms were calculated for 29 species, mainly for salt marsh species of the expert system and, in addition, species of other coastal habitats were included in Fig. 15.1 because they play a role in the discussion of salt preferring taxa (e.g. Müller-Motzfeld 2007).

15.2.2 Modelling Climate Effects

Characteristic coastal species were subsequently selected to model the climate effects under the given scenarios by the climate envelope technique. The envelope method is based on data of distribution, which were allocated to actual climate data and charged against data of the scenarios (for a description of the envelop method, see Chap. 10). Ecograms with combinations of temperature and precipitation values were performed for 29 species. Six species were selected in order to display their ecograms and distribution maps to represent the different patterns of geographical distribution found in the species groups.



X	Area					Carabid species	T/P Year	T J/J	P J/J	Evaluation Temp.	 Precip.	 Con
●	P	M	A	.	.	*Pogonus litoralis*	C/m	C	c	YJul +++	O.K.	++
	.	M	A	.	.	*Cylindera trisignata*	C/m	C	m/c	YJul +++	Jan –, Jul +	++
	.	M	A	.	.	*Bradycellus distinctus*	C/m	C	c	YJul +++	O.K.	++
	.	M	A	.	.	*Bembidion iricolor*	C/m	C	c	YJul ++	O.K.	+
	.	M	A	.	I	*Dicheirotrichus obsoletus*	C/m	C	c	YJul ++	O.K.	+
	P	M	A	.	I	*Tachys scutellaris*	c/m	C	c	YJul +	Y (–)	+
	P	M	A	.	I	*Bembidion ephippium*	C/m	C	c	YJul ++	O.K.	+
	P	M	A	.	I	*Pogonus luridipennis*	C/m	C	m/c	YJul +	YJan (–)	+
●	P	M	A	b		*Bembidion normannum*	C/m	C	c	YJul +	Y (–)	+
	P	M	A	B	I	*Harpalus melancholicus*	cm	C	c/m	YJJ +	O.K.	+
●	P	M	A	B	I	*Anisodactylus poeciloides*	c/m	C	m	Jul +	O.K.	+
	P	M	A	B	I	*Dyschirius salinus*	c/m	c	c	Jul (+)	YJan +	.
		M	A	B	I	*Bembidion minimum*	c	c	m	Jul (+)	O.K.	.
	P	m	A	B	I	*Bembidion fumigatum*	M	M	M	Jan (–)	YJan –	–
	P	M	a	B	I	*Amara ingenua*	c	M/o	m	J*J –	J*J –	–
	P	M	a	B	I	*Bembidion tenellum*	c/M	M/o	M	J*J –	J*J –	–
	P	m	A	B	I	*Dyschirius chalceus*	M/o	m/c	m	Jul +	YJan –	–
●	.	m	A	B	I	*Amara strenua*	M/O	M	M	YJul –	YJanJul –	– –
	.	m	A	B	I	*Dyschirius angustatus*	M	c	M	Jul (+)	J*J –	–
	.	M	A	B	I	*Acupalpus elegans*	c/M	C	M/c	YJJ (+)	YJan –	–
	.	M	A	b	I	*Pogonus chalceus*	c/m	C	M/o	YJJ (+)	J*J –	–
	P	M	.	B	I	*Agonum monachum*	O	O	O	YJan –	YJan –	– –
	P	.	A	B	I	*Amara convexiuscula*	M	M/o	M	YJul –	Y J*J –	–
	P	.	A	B	I	*Bembidion aeneum*	M	M/O	M/o	YJul –	J*J –	– –
	.	.	A	B	I	*Cicindela maritima*	M/O	M/O	M	YJul –	J*J –	– –
●	.	.	A	B	I	*Dicheirotrichus gustavii*	M	M/O	M	YJul –	J*J –	– –
●	.	.	A	B	I	*Dyschirius impunctipennis*	M/O	M/O	M/o	YJul –	J*J –	– –
	.	.	A	B	I	*Dyschirius obscurus*	C	C	c	YJan +	YJ +	+
·	.	.	A	B	.	*Bembidion pallidipenne*	m	M/O	M	Jul –	J*J –	–

Fig. 15.1 Evaluation of ecograms: Estimated influence of temperature and precipitation changes on the distribution of carabid species of the German coast. ●: Species displayed in Figs. 15.2, 15.3, 15.4, 15.5, 15.6, 15.7, 15.8, 15.9, 15.10, 15.11, and 15.12. *P* Pontic, *M* Mediterranean, *A* Atlantic, *I* Inland, *T* Temperature, *P* Precipitation; *C, M, O* Position of the distribution area in 2050, *C* more central, *M* more marginal, *O* out of recent climate values area, lower case: minor, upper case: major. *Y* Year, *Jan*: January, *Jul*: July, *YJJ*: Year, January and July, *J*J*: January–July combination

15.3 Results and Discussion

The distribution areas of the considered species were ordered into a few groups. In spite of the insufficient knowledge of biology and ecology, the species of the single groups were assumed to react similarly to the climate change.

P: Pontic distribution area. Only *Pogonus iridipennis* is a species with a purely pontic distribution area that may have the potential to spread to our region from the inland.

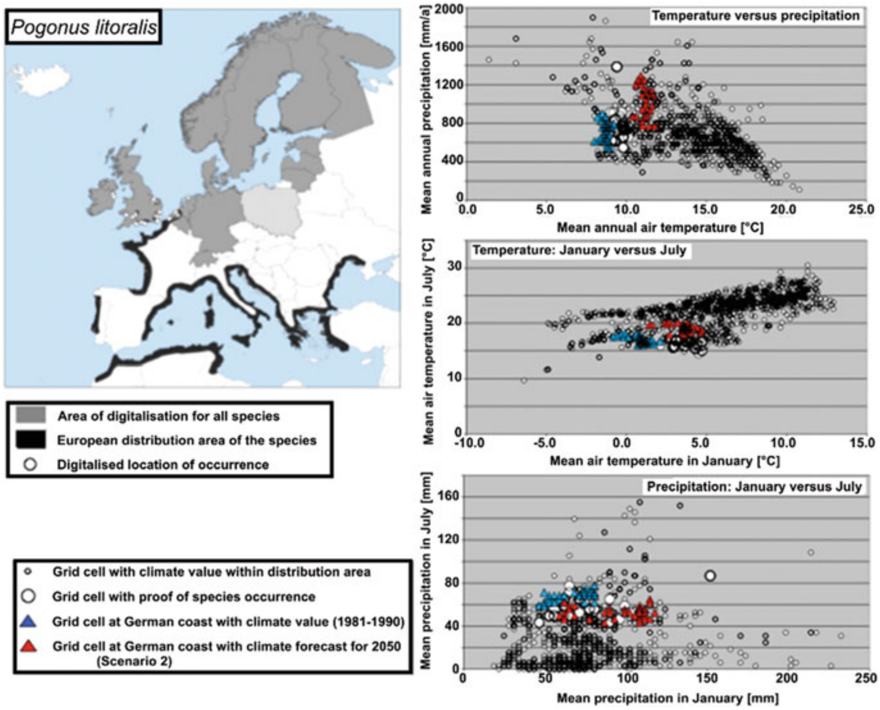


Fig. 15.2 Ecogram and distribution area of *Pogonus littoralis*. Area: Pontic-Mediterranean-Atlantic (PMA), not present in the project region

M: Halobiontic and halophilic species, which occur only in the Mediterranean area, are numerous, but were not considered except the two species with an additional inland distribution area: *Dyschirius extensus* and *Pterostichus cursor* that may potentially widen their area under climate change conditions (Fig. 15.1).

MA: Species with Mediterranean-Atlantic distribution restricted to coastal habitats.

Pogonus littoralis (Figs. 15.2 and 15.3) was selected to represent four species that reflect positive reactions to higher annual temperature and precipitation in January and lower values in July (Fig. 15.1). Only *Cylindera trisignata* shows a contradictory reaction with higher values in January. These species might widen their distribution area along the Atlantic coast in a long-term continuous process. The example of *Bembidion axillaris* demonstrates that the colonisation may also occur over long distances. This species was already found in The Netherlands far from its next known locations (Turin 2000).

Bembidion iricolor is enigmatic for this group because the German coast was first colonised in the twentieth century. Therefore, it can be expected that this species will spread to colder areas, particularly, under the changes of scenario 2.

MAI: Mediterranean-Atlantic species with inland distribution.

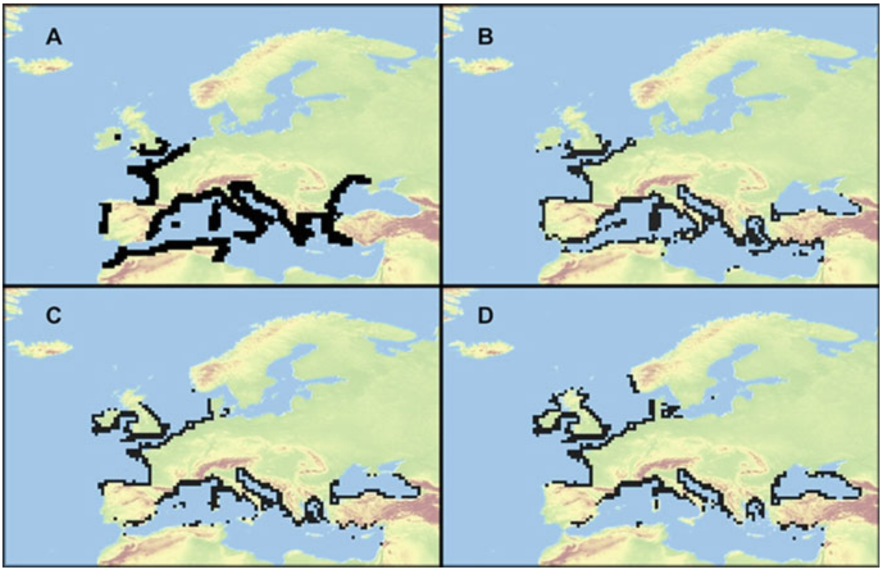


Fig. 15.3 Recent distribution area of *Pogonus litoralis* in Europe (**a**), and different area models: (**b**) for recent climate, (**c**) for scenario 1 (1.5 K, + 35 cm), and (**d**) for scenario 2 (2.5 K, + 55 cm)

These species will also benefit from the increasing temperature. *Dicheirotrichus obsoletus* and *Tachys scutellaris* have not yet reached the German coast today. In contrast to the above-noted group, these species might reach the German coast along the Atlantic coast as well as from the inland.

Although these species exhibit the same distribution pattern and a similar reaction to climate change, they have a different range in Germany. In contrast to the two species mentioned above, *Bembidion ephippium* and *Pogonus luridipennis* inhabit the coast of the North Sea. *P. luridipennis* additionally occurs in the salt habitats of German inland areas, while *B. ephippium* does not occur there (records of *P. luridipennis* from the Baltic Sea coast of Poland are not valid (Stachowiak 2008)).

MAb: Mediterranean-Atlantic species with occurrence at the northwestern Baltic Sea coasts.

Bembidion normannum (Figs. 15.4 and 15.5) occurs in large parts of the coasts of the study area. The position of the realised domain within the ecograms is in good congruence with the distribution data. The species will benefit from increasing temperatures; higher precipitations only indicate a tendency in negative direction. *B. normannum* was not listed by Lohse (1954) for the German Baltic Sea coast. The more recent discovery on Fehmarn (Tolasch and Gürlich 2015) is the southeastern-most location at the Baltic Sea coast and might be an indication for an actual dispersal. Records of *B. normannum* from the Baltic Sea coast of Poland are not valid (Stachowiak 2008).

PMABI: Mediterranean-Atlantic-Baltic species with inland distribution.

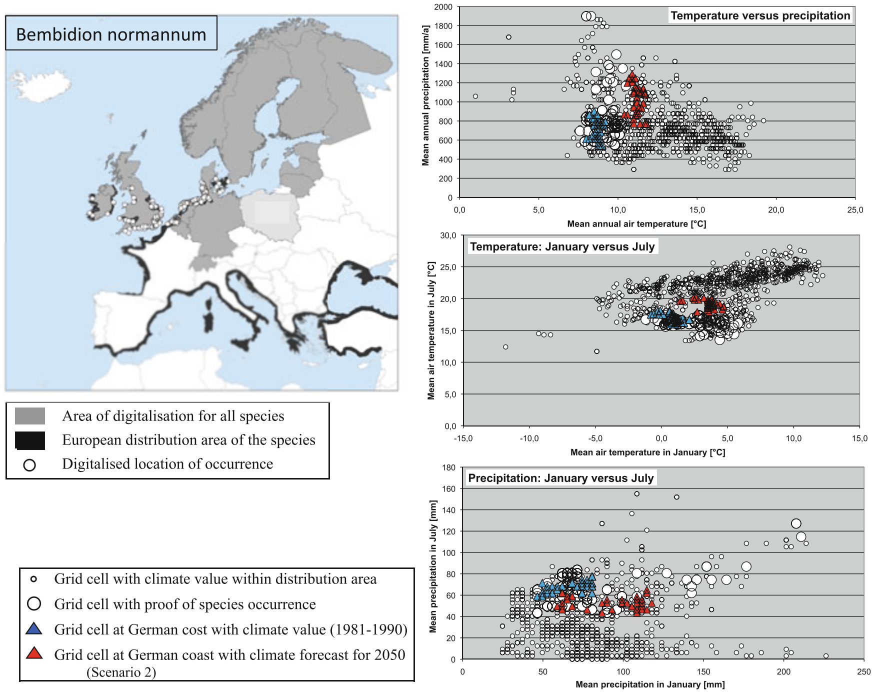


Fig. 15.4 Ecogram and distribution area of *Bembidion normannum*. Area type: Pontic-Mediterranean-Atlantic-Baltic (PMAB). This species is present in the project region but near the northern border of its ecological range

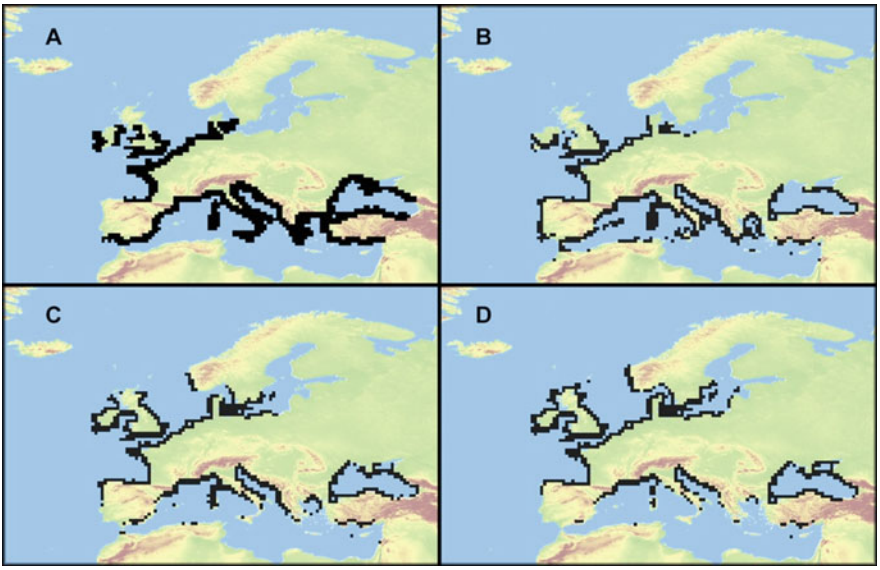


Fig. 15.5 Recent distribution area of *Bembidion normannum* in Europe (**a**), and different area models: (**b**) for recent climate, (**c**) for scenario 1 (1.5 K, + 35 cm), and (**d**) for scenario 2 (2.5 K, + 55 cm)

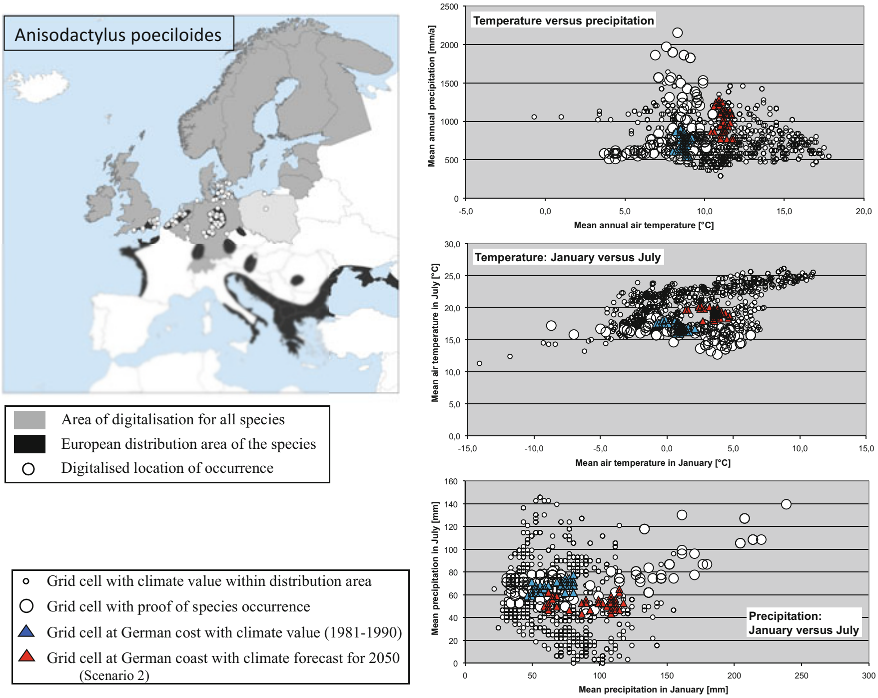


Fig. 15.6 Ecograms and distribution area of *Anisodactylus poeciloides*. Area type: Pontic-Mediterranean-Atlantic-Baltic (PMAB). This species is present in the project region but near the northern border of its ecological range

Twelve species show this distribution pattern. Although the response to climate change is similar as in the groups above, these species react differently. Only two species showed positive response to higher temperatures: *Harpalus melancholicus* that tolerates salt influence and *Anisodactylus poeciloides* (Figs. 15.6 and 15.7), a species yet absent at most parts of the German North Sea coast.

A moderate benefit was assumed for two species, *Dyschirius salinus* and *Bembidion minimum.* The remaining eight species will be influenced negatively by the changes predicted by scenario 2. *Amara strenua* was characterised as halobiontic in the expert system and as halophilic by Müller-Motzfeld (2007). It should be classified as halo tolerant because of its former confusion with the halobiontic *A. strandi* (Hieke 2004). The ecograms for *A. strenua* demonstrate the negative effects on these species (Fig. 15.8).

PM-BI: Mediterranean-Baltic species with inland distribution.

A single species, *Agonum monachum*, showed this pattern of distribution. All the point clouds in the ecograms were situated outside the recent points. This species has an extremely disjunct distribution. It will be negatively influenced by the higher annual temperature and higher January temperatures as well as by higher

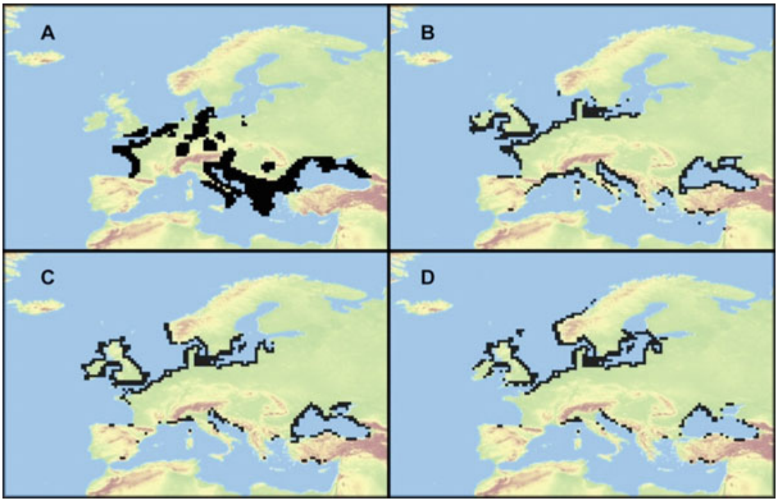


Fig. 15.7 Recent distribution area of *Anisodactylus poeciloides* in Europe (**a**), and different area models: (**b**) for recent climate, (**c**) for scenario 1 (1.5 K, + 35 cm), and (**d**) for scenario 2 (2.5 K, + 55 cm). Only coastal data is modelled

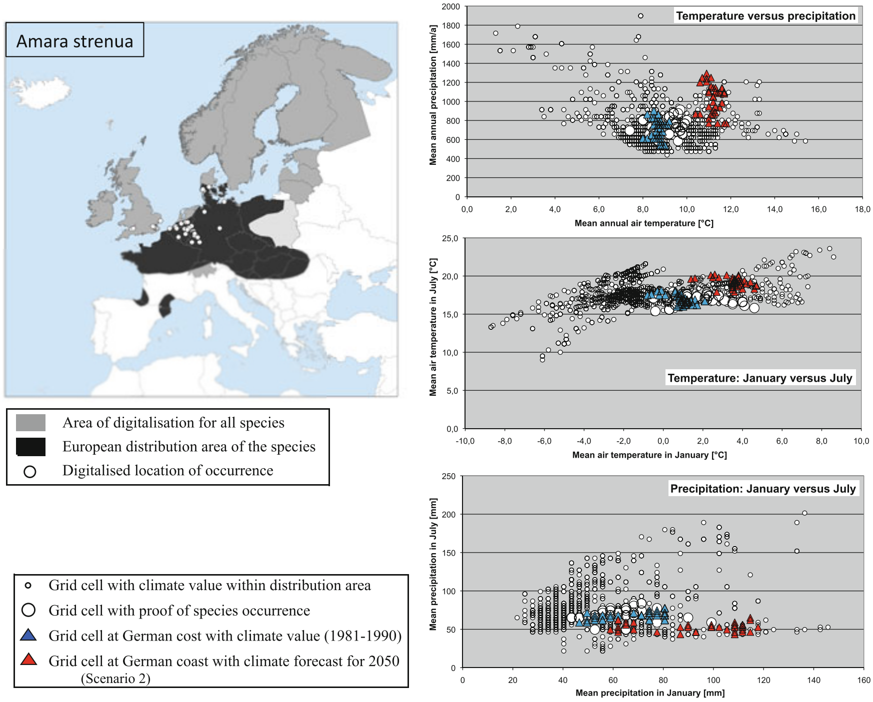


Fig. 15.8 Ecogram and distribution area of *Amara strenua.* Area type: (Mediterranean-) Atlantic-Baltic and Inland (mABI)

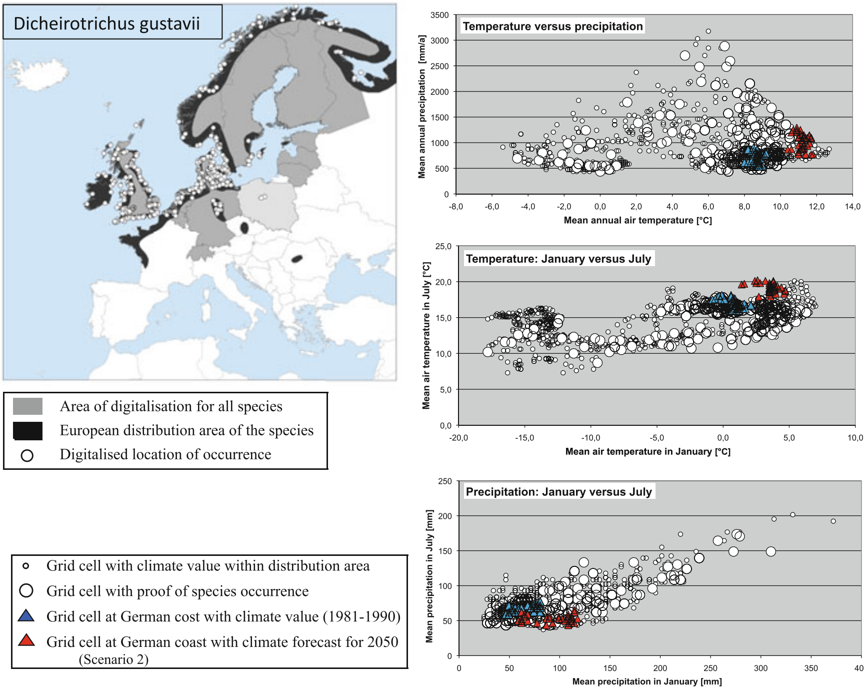


Fig. 15.9 Ecograms and distribution area of *Dicheirotrichus gustavii*. Area type: Pontic-Mediterranean-Atlantic-Baltic (ABI). This species is present in the project region but near the northern border of its ecological range

precipitation. The species inhabits only oligohaline reeds; thus, it is not likely that it will occur in alternative locations (Fig. 15.9).

ABI. Atlantic-Baltic species with inland distribution.

Six halobiontic or halophilic species were negatively influenced by higher annual and higher July temperatures as well as by a combination of January and July precipitation. Therefore, their realised living conditions will deteriorate; a decrease of populations will be the consequence and a long-term retreat to northern and northeastern regions is likely. *Dicheirotrichus gustavii* will suffer a decline in its southernmost distribution areas. Rising mean year and July temperatures have a negative influence, while January precipitation will have a positive one (Fig. 15.10).

Dyschirius impunctipennis may survive if the annual mean temperature is considered. However, the January versus the July temperatures lead us to assume that this species will become extinct (Figs. 15.11 and 15.12). *Cicindela maritima* demonstrates that a species is not threatened by climate change alone. This species

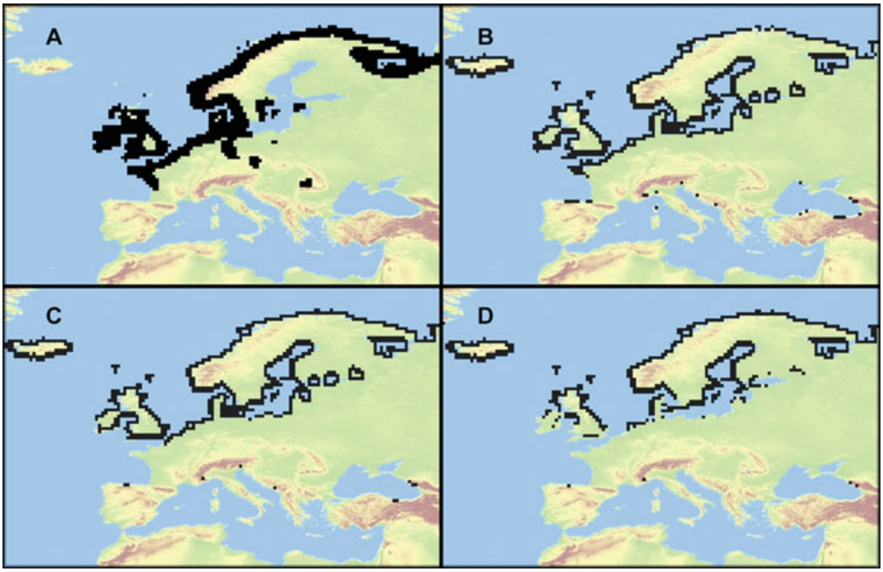


Fig. 15.10 Recent distribution area of *Dicheirotrichus gustavii* in Europe (**a**), and different area models: (**b**) for recent climate, (**c**) for scenario 1 (1.5 K, + 35 cm), and (**d**) for scenario 2 (2.5 K, + 55 cm). Only coastal data is modelled

is extinct at open-public beaches along the Baltic Sea coast (Schmidt 2002, 49). Nowadays, one can no longer imagine the occurrence of this species on the beach of the peninsula Priwall of Travemünde at Lübeck Bay although its former occurrence is well-documented (Lohse 1954).

AB: Atlantic-Baltic species.

Bembidion pallidipenne is affected by higher July temperatures, too. Its reaction is similar to that of the former group.

A: Atlantic species.

An exclusive Atlantic distribution pattern is known for three species that might be relatively independent from climate change due to their specific living demands: *Bembidion maritimum* from estuaries and *Cillenus lateralis* from at or below mean high water line. Both species depend on flooding—at least indirectly. No change is propagated for these species.

B: Baltic species.

The distribution area of *Bembidion transparens* will be restricted in the case of increasing temperature (Table 15.1).

The presentation of distributional data in maps is restricted (i) to special regions or countries (see above), or (ii) to generalised maps. Maps of the distribution over the entire European continent are singularities (Turin 2000).

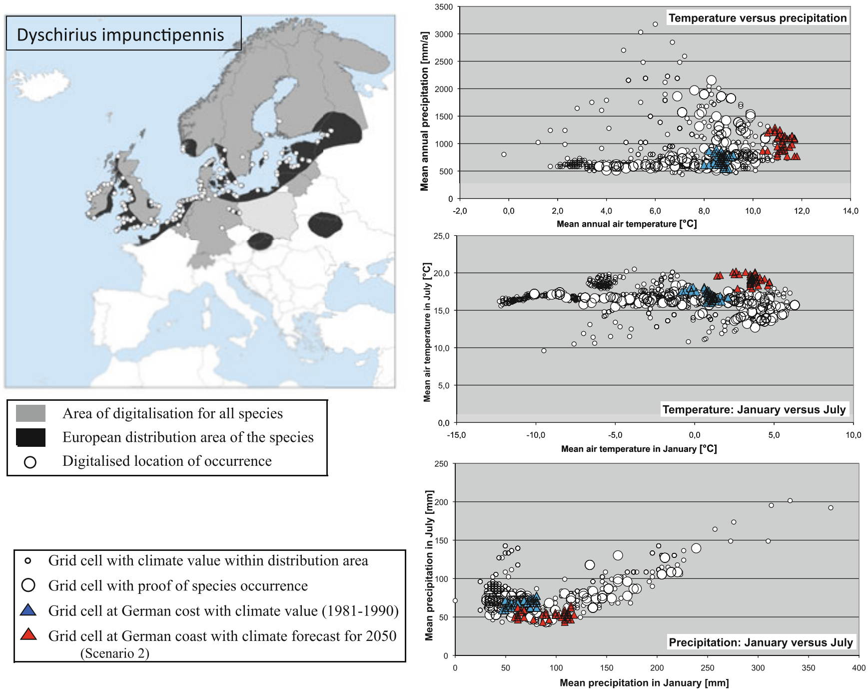


Fig. 15.11 Ecograms and distribution area of *Dyschirius impunctipennis*. Area: Atlantic-Baltic, local in the inland

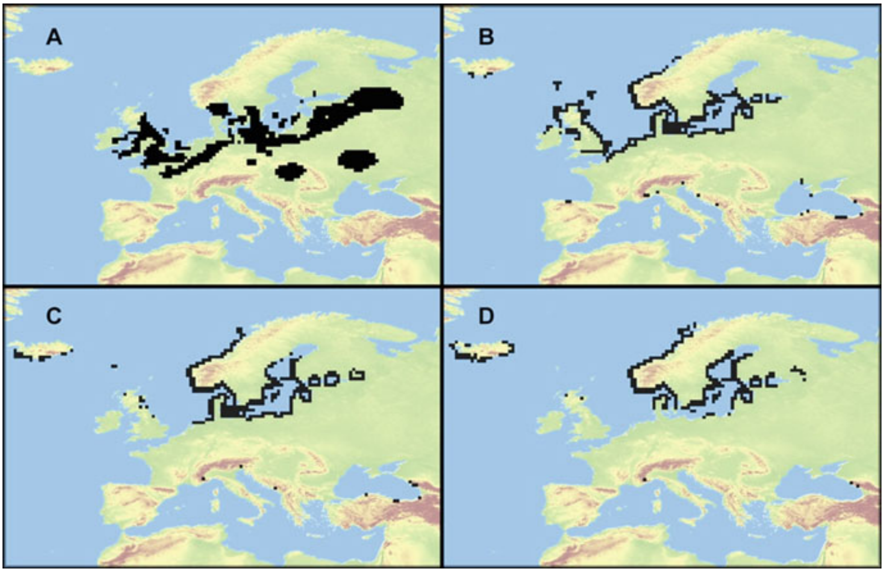


Fig. 15.12 Recent distribution area of *Dyschirius impunctipennis* in Europe (**a**), and different area models: (**b**) for recent climate, (**c**) for scenario 1 (1.5 K, + 35 cm), and (**d**) for scenario 2 (2.5 K, + 55 cm). Only coastal data is modelled

Table 15.1 Distribution, dispersal potential, and area changes of carabid beetles of the expert system (Chap. 27). Estimation of climate impact by means of biogeographical data. Sequence of species corresponds to actual distribution at Mediterranean (M), Pontic (P), Atlantic (A), and Baltic coasts (B). Ecogr: Ecogram, upper case: shown; Origin: C: Coast; L, W: In the inland, L: Local, W: Widespread, Geo capacity.: Geographical potential: +: Positive, −: Negative; Predict.: Predicted reaction, Colonisation from W: West, SW: Southwest or I: from the inland; /N: Decline to the North

Ecogr.	Distribution					Carabidae	Study area					Origin		Geo cap acit.	His cha	Predict.
							DK	NL	Nor Sea	Bal Sea	PL					
		M	a			*Bembidion axillare*		+	−	−		C				SW
		m	a		I	*Dyschirius extensus*			−	−		(C)	L	+		I
X	P	M	A			*Pogonus litoralis*		+	−	−		C		+		SW
x		M	A			*Bembidion iricolor*	+	+	+	−	.	C	(L)	+		
x		M	A		I	*Dicheirotrichus obsoletus*		+	−	−		C	L	+		SW
X	P	M	A		I	*Tachys scutellaris*		+	−	−		C	L	+		SW
x	P	M	A		I	*Bembidion ephippium*	+	+	(+)	−	?	C	(L)	+	−	
x	P	M	A		I	*Pogonus luridipennis*	+	+	+	−	+	C	L	+	−	
	P	M	A	.	I	*Bembidion aspericolle*			−	−		(C)	L	+		I
X	P	M	A	b		*Bembidion normannum*	+	+	+	−	?	C		+	+	
X	P	M	A	B	I	*Anisodactylus poeciloides*	+	+	−	+	+	C	L	+	−	(W, E)
x		M	A	B	I	*Dyschirius salinus*	+	+	+	+	+	C	(L)	+		
x		M	A	B	I	*Bembidion minimum*	+	+	+	+	+	C	L			
x	P	m	A	B	I	*Bembidion fumigatum*	+	+	(+)	+	+	C	W		+	
x	P	m	A	B	I	*Dyschirius chalceus*	+	+	+	(+)	+	C	L		−	/N?
x		m	A	B	I	*Amara strenua*	+	+	(+)	−	+		L			
X		M	A	B	I	*Acupalpus elegans*	(+)	+	−	−	+	C	L	+		
x		M	A	B	I	*Pogonus chalceus*	+	+	+	−		C	L	+		
	P	M	A	B	I	*Masoreus wetterhallii*	+	+	+	+	+		W	+		
	P	M	A	B	I	*Stenolophus mixtus*	+	+	+	+	+	C	W	+	+	

		mm	a	b	I	*Dyschirius globosus*	+	+	+	+	+		W			
	P	m	a	B	I	*Carabus clathratus*	+	+	(+)	+	+		W	–?	–?	
	P	m	a	b	I	*Omophron limbatum*	+	+	+	(+)	+		W	+	+	
		M	A	B	I	*Dyschirius thoracicus*	+	+	+	(+)	+	C	(W)			
x		M		B	I	*Agonum monachum*			–	(+)		C	L		(–)	E
X	P	m		B	I	*Amara strandi*	?		–	–	+		L	+		I, E
x	P		A	B	I	*Amara convexiuscula*	+	+	+	+	+	C	L	–		
x	P		A	B	I	*Bembidion aeneum*	+	+	+	+	+	C	(L)	–	+	/N
x			A	B	I	*Dicheirotrichus gustavii*	+	+	+	+	+	C	L	–		/N
X			A	B	I	*Dyschirius impunctipennis*	+	+	+	(+)	+	C	(L)	–	(–)	/N
	P		A	B	I	*Dyschirius obscurus*	+	+	+	(+)	+	C	(W)	–		
			A	B	I	*Amara quenseli silvicola*	+	+	(+)	(+)	+	C	(W)	–	–	
	P		A	B	I	*Amara majuscula*	+	+		+	+	C	W	+	+	
			a	b	I	*Blemus discus*	+	+	+	(+)	+	C	W	+	+	
			A			*Bembidion maritimum*	+	+	(+)	–		C			(+)	
			A			*Cillenus lateralis*	+	+	+	–		C		+		
				B		*Bembidion transparens*	+		–	+	+	C	W	+	–	E

The maps can only be as good as the data in the literature. A detailed distribution pattern of *Bembidion normannum* exemplifies the problem. Bangsholt (1983) and Turin (2000) present a generalised map of Europe in which the Baltic Sea coast from the Lübeck Bay up to Estonia is indicated to be colonised by this species. But the area of the species covers only the North Sea coast and the southwestern Baltic Sea coast with Fehmarn as an easternmost location.

Population dynamics are responsible for another problem. For some species, it is difficult to distinguish between annual fluctuations and long-term changes, e.g., a strong increase in records of *Bembidion aeneum* indicated a widening of the distribution area since the 1980s in semi-natural habitats (for estuarine salt marshes near Bremerhaven, see Mossakowski 1991), in anthropogenic marshes (for Bremen, see Handke 1992), and in regenerating salt meadows (for Mecklenburg-Western Pomerania, see Müller-Motzfeld 1997). In the meanwhile, the records decreased, which shows that this phenomenon can be interpreted as a fluctuation and not as a dispersion caused by climate change.

Summarising, three patterns of reaction to climate change can be differentiated: Many species will colonise the study region along the coasts, mainly from the southwest, in some cases from the east. This will be true for the majority of species, which live in saline habitats of the inland with a wide area in the Mediterranean region, and which occur more or less far to the north at the Atlantic coast (Fig. 15.1). The importance of this distribution route is demonstrated by the newfound *Bembidion axillare* in the Netherlands (Turin 2000), a halobiontic species of the Mediterranean region.

Only a small group of species may colonise the project area coming from an inland direction. But this pathway might be rarely verified because of the local and isolated occurrence of salt habitats in the European inland.

Another small group of species will decrease in numbers and, finally, retreat to the north. A local decline in our region is propagated: *Dicheirotrichus gustavii* is very abundant in salt marshes of the study region. This species has a northern distribution pattern and will suffer a decline in our region under rising temperatures. After a period of decline, it will be absent from the German coasts.

15.4 Relevance of Changes for the Ecosystem

The climate change will provoke many changes on the species level. This reorganisation of the coenoses may have important implications at the ecosystem level that cannot be estimated today. As a paradigm, the instance of a North American cicada may be cited. Pomeroy and Wiegert (1981) demonstrated that the extinction of a single species triggered important effects at the ecosystem level (Fig. 15.13).

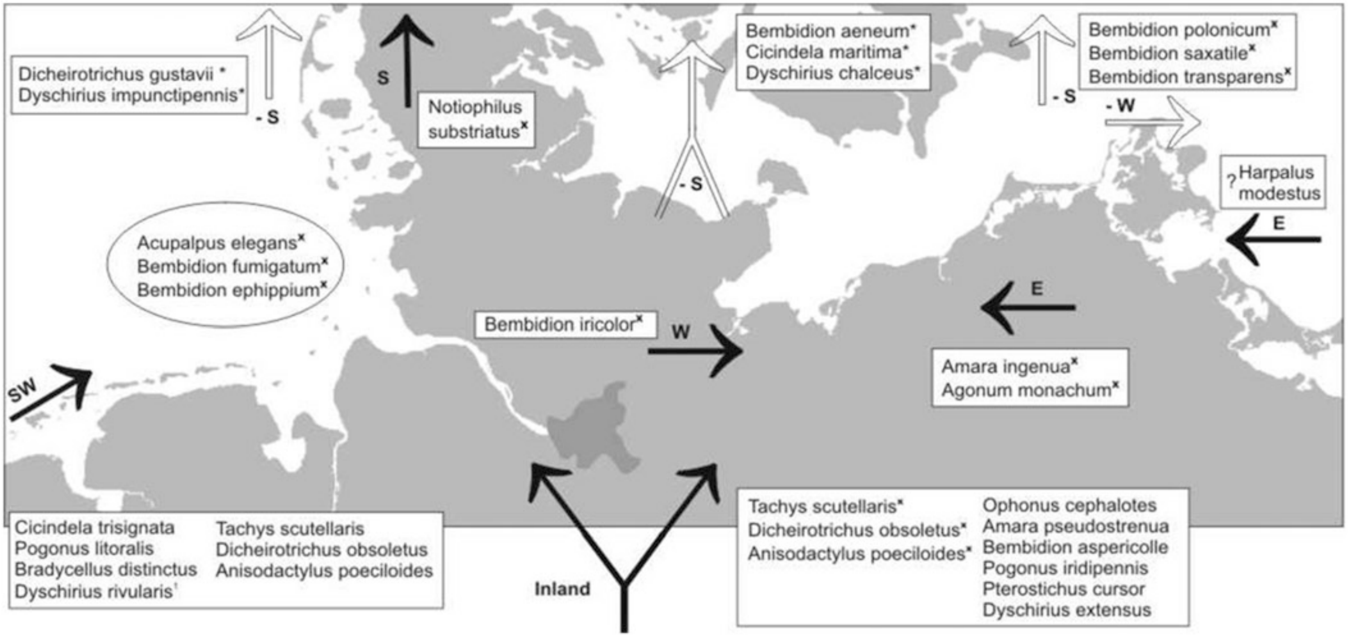


Fig. 15.13 Colonisation and retreat of carabid species as expected under climate change. Black arrows: colonisation from a direction; white arrows: retreat from a direction; Letters indicate cardinal directions, *s* Dispersal, −*s* Retreat from the south; * Present in coastal habitats in the whole area, *x* Only in some regions; An ellipse contains species with a potential to spread in the North Sea region

References

Anderson R, McFerran D (2005) Ground beetles of Ireland. http://www.habitas.org.uk/groundbeetles/index.html

Bangsholt F (1983) Sandspringernes og løbebillernes udbredelse og forekomst i Danmark ca. 1830-1981. Dansk Faunistik Bibliothek 4:1–271

Bleich O, Gürlich S, Köhler F (2015). Verzeichnis und Verbreitungsatlas der Käfer Deutschlands. http://www.colkat.de/de/fhl/

Desender K (1986) Distribution and ecology of carabid beetles in Belgium (Coleoptera, Carabidae). Koninklijk Belgisch Institut voor Natuurwetenschappen, Brussels

Desender K, Dekoninck W, Maes D (2008) Een nieuwe verspreidingatlas van de loopkevers en zandloopkevers (Carabidae) in België. Rapporten van het Institut voor Natuur- en Bosonderzoek, Brussel

Handke K (1992) Zur Ausbreitung von *Bembidion aeneum* Germ. (Col. Carabidae) in der Bremer Wesermarsch. Zeitschrift Ökologie & Naturschutz 1:72–74

Hieke F (2004) Zabrini. In: Müller-Motzfeld G (ed) Die Käfer Mitteleuropas: Adephaga 1. Carabidae (Laufkäfer), 2nd edn. Spektrum, Berlin

Lindroth CH (1945) Die fennoskandischen Carabidae. II. (Karten). Göteborgs Kungl. Vetenskaps och Vitterhets-Samhälles Handlingar. Wettergren & Kerber, Göteborg

Lohse G-A (1954) Die Laufkäfer des Niederelbegebietes und Schleswig-Holsteins. Verhandlungen des Vereins für naturwissenschaftliche Heimatforschung Hamburg 31:1–39

Luff M (2005) Provisional atlas of the ground beetles (Coleoptera Carabidae) of Britain. Biological Records Centre, Huntingdon. https://core.ac.uk/download/files/79/59617.pdf

Malicky M (2015) ZOBODAT. http://www.landesmuseum.at/sammlungen/gruppe-natur/zobodat-zoologisch-botanische-datenbank.html

Mossakowski D (1991) Zur Verbreitung der Laufkäfer im Lande Bremen. Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen 41:543–639

Müller-Motzfeld G (1997) Renaturierung eines Überflutungssalzgrünlandes an der Ostseeküste. Schriftenreihe für Landschaftspflege und Naturschutz 54:239–263

Müller-Motzfeld G (2007) Die Salz- und Küstenlaufkäfer Deutschlands–Verbreitung und Gefährdung. Angewandte Carabidologie 8:17–27

Pomeroy LR, Wiegert RG (1981) The ecology of a salt marsh: ecological studies, vol 28. Springer, New York

Ruffo S, Stoch, F (ed) (2005) Checklist e distribuzione della fauna italiana. Memorie del Museo Civico di Storia Naturale di Verona, 2nd serie Sezione Scienze della Vita, 16

Schmidt J (2002) Habitatpräferenzen küstentypischer Laufkäfer der Mecklenburgischen Ausgleichsküste. Unpublished Diploma thesis, Universität Rostock, pp. 136

Stachowiak M (2008) Przegląd systematyczny biegaczowatych Polski (*Coleoptera*, *Carabidae*)–Wersja skrócona. Accessed 25 Sept 2016 entomo.pl/coleoptera/carabidae/index.php

Tolasch T, Gürlich S (2015) Verbreitungskarten der Käfer Schleswig-Holsteins und des Niederelbegebietes. http://www.entomologie.de/hamburg/kart

Turin H (2000) De Nederlandse loopkevers. Verspreiding en ecologie (Coleoptera: Carabidae). Nederlands Fauna 3. KNNV Uitgeverij, Utrecht

Turin H, Haeck J, Hengeveld,R (1977) Atlas of the carabid beetles of the Netherlands. Amsterdam. North-Holland Pub Co

von Storch H, Schnur R, Zorita E (1998) Szenarien & Beratung. Anwenderorientierte Szenarien für den norddeutschen Küstenbereich. Abschlußbericht FKZ 01 LK 9510/0

Zicha O (ed) (2015) Biological Library–BioLib. http://www.biolib.cz/en/taxonmap/

Part III

Experimental Assessments of the Effects of Climate Change on Habitats and Their Organisms

Field Experiment: Effects of Increased Temperature on a Tidalic Fluvisol

16

Hans-Peter Blume, Ulrich Irmler, Udo Müller-Thomsen, and Ulrich Pfisterer

Abstract

An experimental approach was executed in one salt marsh in western Schleswig-Holstein to analyse the reaction of soil processes under a 5°K higher temperature conditions using a heating construction installed in 1 m depth. Microbial activity and soil faunal changes were studied. Changes in soil processes caused only by the temperature increase were small or neglectable. Higher temperatures will lead to increasing dryness of the soil, but increase of the sea level will cause more flooding events. Overall, the increasing sea level will have higher influence on the soil processes than temperature.

16.1 Introduction

The effects of increased soil temperatures on soil-biological activities, soil temperature, water, redox potential, nutrients, and gas dynamics in a Tidalic Fluvisol were analysed by a field experiment (Figs. 16.1, 16.2, 16.3, 16.4, and 16.5). Referring to climate scenario 2, an increase of an average 2.5 K annual temperature in the year 2050 was assumed. The experiment was performed on a Gleyi-sali-tidalic Fluvisol (calcaric) (*oxidierte Salzrohmarsch*; 50 cm above MHW, loamy sand to sandy loam, 1.4–0.6% org. m., 3–4% lime, >100 cm permanent reduced conditions, dense

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Fig. 16.1 PE tubes laying in the salt marsh of Hedwigenkoog. Experimental and reference sites (each measuring 3 x 3 m)

Fig. 16.2 Platform to heat the experimental site. Stage with photovoltaic device for the production of electric power for the control system, logger and pump; solar panel for water heating and station acclimation

vegetation cover, 70 annual floodings) of the upper salt meadow of the Hedwigenkoog foreshore (Chap. 3). The experiment pursues the following questions: 1) what are the effects of the expected temperature increase on the chemical processes in a Tidalic Fluvisol, 2) which changes will be expected for the biological processes in the soils, and 3) which effects will be expected on greenhouse gases.

Fig. 16.3 Gauging station in the tidal flat. The station was fitted with a photovoltaic device and Plexiglas bonnets to gather net gas emissions

Fig. 16.4 Plexiglas bonnets were used to gather net gas emissions. The mast was fitted with a control device. Inlet tubes for cooling bonnets from above when flooded

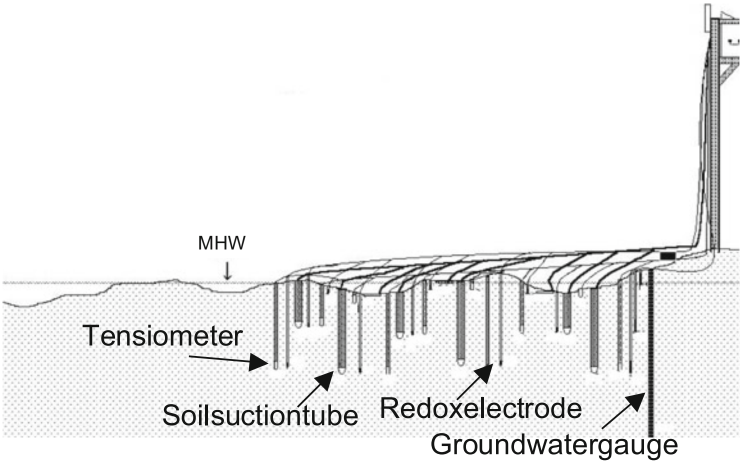

Fig. 16.5 Schematic diagram of installations to measure climate and soil dynamics. Tower with data logger, three totalizers, photo voltage installation, and water tank. *GW*: ground water gauge, *R1–R9*: redox electrodes; *BZ*: Ag/AgCl electrode; *T1–T9*: tensiometers; *S1–S9*: suction tubes for soil solution; *C0–C3*: temperature sensors

Some of the presented results were published in Blume and Müller-Thomsen (2007).

16.2 Methods

The soils were continuously heated to about 2 K (using a plastic tube with circulating warm water in 3–6 cm soil depth at a distance of 10 cm like a floor heating). The heated soil area was compared with a similar, not heated control area, and with a protothionic Hypersali-tidalic Fluvisol (*marines Übergangswatt*; 20 cm below MHW, 500–600 annual floodings, mean tidal amplitude of 3.3 m, loamy sand, 1.6–1.2% org. m., 2–4% lime, some bushes of *Spartina*).

The heating installation lasted from 15.08.97 until 04.02.99 (only interrupted in winter 97/98) on an area of 14 m^2. A higher temperature of 0.5 K was effective even beneath 1 m depth. The measured effects, however, can only be expected if the sedimentation intensity develops equally to the assumed rising sea level and without rise of the groundwater table. A detailed description of the chemical and physical methods in the field and in the lab is given in Blume and Müller-Thomsen (2007).

Microbial activity was determined using the DMSO-reduction-method (Alef 1991). Feeding activity of the soil mesofauna was measured using the bait lamina test (von Törne 1990). As feeding substrate, a mixture of wheat bran and agar-agar was used. In total, 48 replicate lamina baits were exposed for 14–30 days and calculated for a daily mean. After the end of the heating experiment, the soil fauna was sampled on April 24, 1999 in 10 replicates on the control and the heated sites each taking a 0.03 m^2 soil core of 4 cm depth. The soil fauna was extracted using a Macfadyen apparatus (Macfadyen 1962) for 2 weeks (dryness process beginning at 25 °C and ending at 65 °C, temperature increment 5 °C day^{-1}).

The emission of the so-called greenhouse gases, including carbon dioxide, i.e., methane and nitrous oxide, were also studied under the influence of soil heating. For these measurements, we followed the method of "closed soil covers" (plastic caps of 589 cm^2 and 27 l volume, after Hutchinson and Moiser 1981, which were changed every 2 h, and which changed their vertical position during low and high tides).

16.3 Results and Discussion

16.3.1 Importance of Higher Soil Temperatures for Soil Organisms

The simulated heating of the topsoil by about 2 K has increased the average contents of microbial carbon from 180 mg/kg soil mass at 140 mg, which is an increase of 80% (Fig. 16.6).

The carbon increase was expected. A corresponding strong increase of microbial activity, however, could not be found.

For the feeding activity of the soil animals, an increase of average 30% in spring and an absolutely low level in autumn and winter were found (Fig. 16.7). No significant differences between the heat and the control area were found by the sign-test (r = 6, p = 0.51) or Wilcoxon-test (W = 33, p = 0.21). The CO_2-concentration in the air directly above the soil surface might have favoured the biomass production of the vegetation, which means an increased food supply for soil organisms.

The densities of the different species and groups of the soil fauna are listed in Table 16.1. The statistical analysis using the U-test revealed no significant results

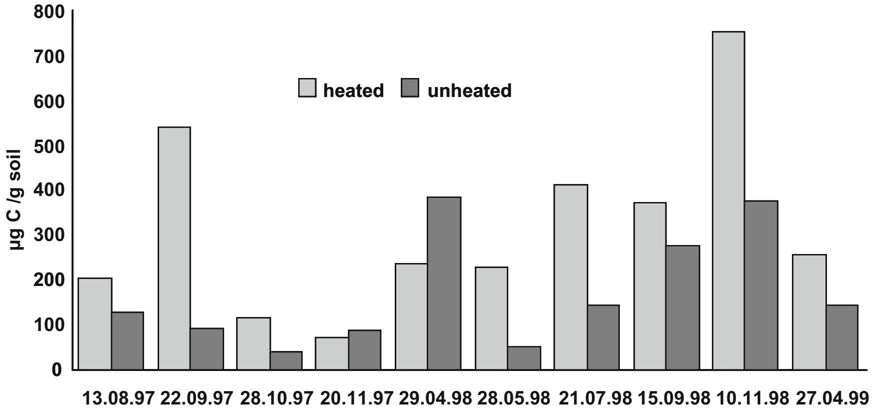

Fig. 16.6 Contents of microbial carbon in the topsoil of a normal and a heated Gleyi-sali-tidalic Fluvisol (fumigation-extraction method after Vance et al. 1987)

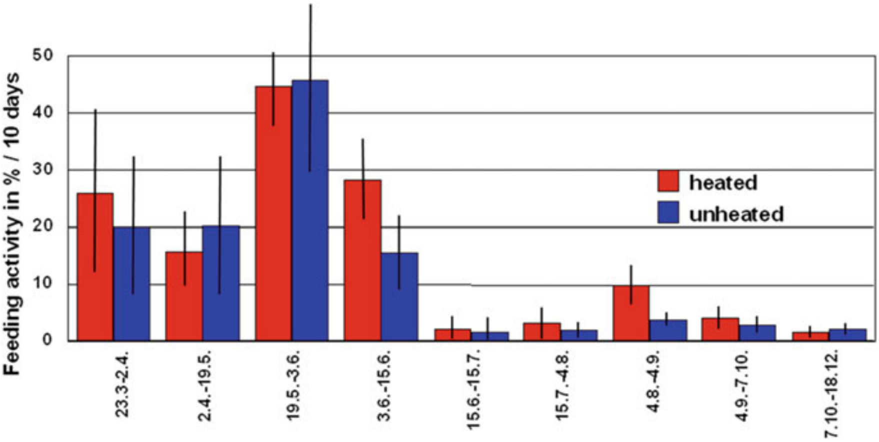

Fig. 16.7 Feeding activity of soil mesofauna in the topsoil (1–8 cm) of a normal and a heated Gleyi-sali-tidalic Fluvisol. Small bait test after von Törne 1990

between the heated and control site for both the total density of mesofauna and prostigmatic (control: 880 ± 725 ind. m^{-2}; heated 760 ± 1123 ind. m^{-2}; $U = 45$, $p = 0.78$) and cryptostigmatic mites (control: 120 ± 193 ind. m^{-2}; heated: 40 ± 126 ind. m^{-2}; $U = 31$, $p = 0.17$) on the control and heated site, respectively. In contrast, the density of Collembola (control: 2800 ± 2537 ind. m^{-2}; heated: 1320 ± 2946 ind. m^{-2}; $U = 21$, $p = 0.02$) was significantly lower on the heated site compared to the control site.

Among the cryptostigmatic mites (Oribatida), only *Trichoribatides incisellus* could be identified to species level. According to Weigmann (1971), this species is typical for the *Puccinellia* salt grassland but seems to be salt-tolerant and also inhabits salt grassland at the Baltic Sea coast. Among Collembola, several species were characteristic species of salt grassland, e.g., *Folsomia sexpunctata*, *Archisotoma pulchella* and demand saline and flooded soils of the coast. Little is known about the temperature demand for coastal species of oribatids and Collembola. Weigmann (1973) mentioned that *Tullbergia krausbaueri* needs 45–60 days at 12 °C for egg development. According to these values, total development would likely be fast if the temperature in the soils increases slightly.

The microbial activity has obviously increased in the subsoil, too, because lowered redox potentials in relation to the unheated soil were found.

16.3.2 Importance of Increased Soil Temperatures for the Supply of Water and Oxygen

The heating stimulated evapotranspiration, which led to a temporarily dry topsoil. Thus, the content of available water was reduced, which was still intensified by a higher salt concentration in the soil solution that increased the osmotic potential.

Table 16.1 Means (ind. m^{-2}) of soil faunal species or groups in the control and the heated area

Species	Control	Heated	Total	Species/group	Control	Heated	Total
Collembola				**Acari**			
Archisotoma pulchella	40	80	60	Gamasina	320	520	420
Brachystomella parvula	1720	680	1200	Uropodina	560	240	400
Entomobrya nivalis	0	40	20	*Trichoribates incisellus*	120	40	80
Folsomia sexoculata	800	360	580	Total Acari	1000	800	900
Onychiurus sp.	80	120	100				
Tullbergia affinis	120	40	80	**Remaining Insecta**			
Tullbergia krausbaueri	40	0	20	Elateridae larv.	0	80	40
				Empidoidea larv.	40	40	40
				Meotica hanseni (Staphylinidae.)	0	120	60
Total Collembola	2800	1320	2060	Total Insecta	40	240	140
Total soil fauna	3880	2480	3180				

Such changes in soil moisture have no long-lasting effects, because they are balanced by excessive precipitation events and by flooding. The postulated increase of the flooding frequency may also shorten this effect.

An increased dryness of the topsoil in summer temporarily increased the redox potentials and the oxygen supply. Because flooding events might increase under climate change conditions, these effects might last only for a short time, similar to the effects of the reduced water supply. In the subsoil, however, the redox potentials decreased as a consequence of the simulated heating, because soil organisms were more active. Thus, in the subsoil the root ability decreased for those plants, which need a sufficient oxygen supply in the root zone.

16.3.3 Importance of Increased Soil Temperatures for Plant Nutrient Supply

The availability of nutrients in Gleyi-sali-tidalic Fluvisols is controlled by seawater, which contains 1.2 g Ca, 0.4 g K, 1.3 g Mg, 2.7 g SO4, and 4 g B per litre, on average (Becher 1998). This is a high amount of Ca, K, and Mg as well as a high supply of SO_4 and B (Schlichting et al. 1995). In spite of higher soil temperatures and a subsequent higher need for nutrients, stronger changes will not be expected. This is even true for SO_4, which is reduced by microorganisms in the subsoil and immobilised as metal sulphide. Lower sulphate concentrations were not found in the Cr-horizon. In spite of an increased SO_4-reduction as a consequence of a higher microbial activity, the supply of SO_4 will remain constant.

Statements referring to the supply of available nitrogen are more difficult. The contents of nitrate and ammonium in the soil solution continuously changed strongly in the topsoil during the vegetation period between 0.2 and 1.3 mg l^{-1}, and in the subsoil between 0.1 and 2.9 mg l^{-1}. These values are low compared to average offers in the rooting zone (Schlichting et al. 1995). The higher soil temperatures decreased the NO_3- as well as the NH_4^+ contents of the soil solution: the certainly stronger mineralisation of organic matter effects no increase of available nitrogen as a consequence of a significantly higher microbial biomass. A higher N-uptake by plants and soil organisms and an increased loss by NH_3-evaporation in the alkaline milieu (in spite of a slightly changed denitrification) evidently work against this process. This means that the certainly existing lack of N might increase.

In spring and autumn, the incubation of the field samples with increased temperatures of about 1 K (part 4 of the project) led (compared with the field experiment) to an increased N-mineralisation rate at (?) all sites with similar vegetation structure. In spite of the small temperature difference, the constant incubator temperature may mainly cause this evident effect.

The nutrients P, Mn, and Fe were not investigated. As their mobility is highly redox-dependent, their availability will change strongly but their concentrations will be sufficient in any case.

16.3.4 Importance of Increased Soil Temperatures for the Emission of "Greenhouse" Gases

As a result of an assimilation of CO_2 by plants during the day and the respiration by roots during the night in the vegetation period, as well as the annual soil respiration (mainly by microbes), we found an annual net-emission of 700 g CO_2 m^{-2}, or a mean daily emission of 1.9 g m^{-2} from the surface of the Gleyi-sali-tidalic Fluvisols. Referring to an average annual temperature of 8.4 °C, this is a moderate value (Schlichting et al. 1995). A simulated raised temperature of 2 K leads to an annual net-emission of 880 g m^{-2} or a mean daily net-emission of 2.4 g m^{-2} (Fig. 16.8). This increase had been expected as a consequence of the temperature increase by 2 K (Blume et al. 1991), but means an additional pollution of the atmosphere. In Gleyi-sali-tidalic Fluvisols with higher clay and humus contents of the Sönke-Nissen-Koog foreshore (Chap. 8), an annual net-emission of 860 g m^{-2} was found (Müller-Thomsen 1997). With an increased temperature of 2 K, a value of 1080 g m^{-2} could be expected in soils with higher clay contents, which is still a moderate increase.

In the neighbouring Hypersali-tidalic Fluvisol, the net-CO_2-emission is even significantly lower, because a great amount of CO_2 is solved in the seawater. With a decrease of the CO_2-solubility with increasing water temperatures, CO_2-emission from the tidal area into the atmosphere will increase.

The annual mean net-methane-emission from the Gleyi-sali-tidalic Fluvisol was negative with -14 g m^{-2} h^{-1} (Fig. 16.8), as airborne methane was absorbed by soil and vegetation. From the clay- and humus-rich North-Frisian Gleyi-sali-tidalic Fluvisol (Chap. 8) with a Cr-horizon in higher position (70 cm instead of 100), no annual net-methane-emission was found (Müller-Thomsen 1997). It is true that methane is produced in the strongly reduced horizon (rH lower 10) of that Fluvisol (Pfisterer et al. 1997), but, rising to the soil surface, it is oxidised by microbes again. Giani et al. (1996) found only low methane emissions from salt meadows to the atmosphere, too. In contrast, daily flooded beach soils emit methane into the atmosphere.

In the Gleyi-sali-tidalic Fluvisol, a small nitrous oxide emission of 20–120 g m^{-2} h^{-1} into the atmosphere was observed in summer (Fig. 16.8), while in other months nitrous oxide that developed in soils of the tidal area seems to be bound. In the North-Frisian Gleyi-sali-tidalic Fluvisol, the nitrous oxide emissions were slightly increased (Müller-Thomsen 1997) but still absolutely insignificant.

Generally, salt meadows influence atmospheric CO_2-pollution, but this is not true for methane and nitrous oxide. In contrast to the salt meadows, the daily flooded tidal marsh areas with their significantly greater extents will exhibit increased emissions as a consequence of higher temperatures.

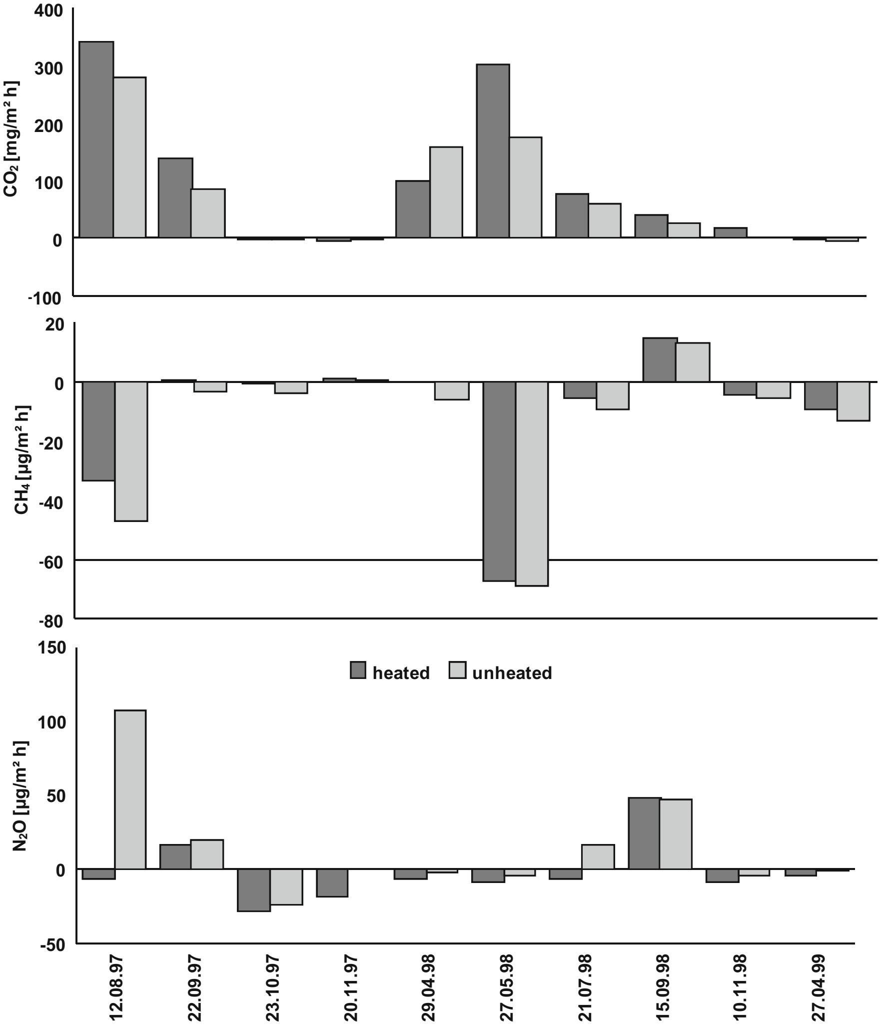

Fig. 16.8 Net gas fluxes of CO_2, CH_4, and N_2O of a normal and a heated Gleyi-sali-tidalic Fluvisol adjacent to the Hedwigenkoog in form of daily mean values

16.3.5 Possible Effects of Increased Soil Temperatures on Pedogenesis

Higher soil temperatures have positive effects on soil organisms if specific temperature limits are not exceeded. If the average groundwater table does not change, the intensity of litter decomposition will increase, but a stronger humification or humus-accumulation will not occur, because raised temperatures stimulate a higher decomposition rate than biomass production (Mohr et al. 1972), The formation of soil structure by animals and microbes will certainly increase (Witkamp and Frank 1970). The assumption that a higher soil temperature will develop a more intensive and deeper-reaching bioturbation depends on the question, whether in addition to the mesofauna, the burrowing macrofauna also benefit from the higher temperatures. However, in salt marshes, earthworms mainly responsible for bioturbation in other habitats are absent because they are very sensitive to salt water (Piearce and Piearce 1979). Perhaps the transformation of Fluvisols into Gleysols by destroying the textural layering will be more intensive.

Acids develop on a high degree due to an intensive mineralisation of organic matter. Besides carbonic acid, partly emitted as CO_2, strong mineral acids, such as sulphuric acid and nitric acid, are formed, which possibly could intensify carbonate solution. A subsequent decalcification of the Gleyi-sali-tidalic Fluvisol is uncertain. It depends to a great extent on the degree of the increasing temperature of the tidal water, which is not only influenced by the air temperature but also by the Gulf Stream. In more southern locations, the sediments of the daily flooded tidal areas actually show (in case of an equal texture) higher contents of carbonates (Schleswig-Holstein 3–8%, Belgium 30–35%), which could be caused by a stronger biological formation of carbonate with increased water temperatures (Brümmer et al. 1970).

Processes of acidification and a subsequent silicate weathering and clay formation will appear. Regarding the postulated strong sedimentation, a quick neutralisation of intensively developing acids will occur.

The formation of sulphides will intensify, since a raised temperature in the reduced subsoil will intensify the microbial reduction of sea water sulphates. During dry periods in summer, increased temperatures will shrink faster loamy soils that will develop wider and deeper cracks. This process will increase the oxidation of ferrous sulphide along the aggregate surfaces, followed by a formation of ferrihydrite. A more intensive formation of sulphides in the reduced subsoil and concurrently an intensified formation of ferrihydrite on aggregate surfaces on the walls of animal and root channels will intensify the redoximorphism of the coastal Fluvisols.

16.4 General Conclusions

According to climate scenario 2 (Chap. 2), the CO_2 concentration of the atmosphere will increase to 550 ppm, the mean sea level will rise by 55 cm combined with a 30 cm higher tidal range. Wind and storms will blow more often from 300° with an increase by 10%; storm tides will occur 15% more often with increased effects of 15%. The annual average temperature will rise by 2.5 K and precipitation will increase by 15% in winter.

How will this scenario affect the site conditions of the upper salt meadow on the investigated Gleyi-sali-tidalic Fluvisol with 70 annual floodings in the Hedwigenkoog foreshore? It is assumed that the sea level on the west coast of Schleswig-Holstein has risen in the last centuries by about 20 cm/century and that many of the salt meadows of the same size have “grown” by sedimentation. As a consequence, their surface levels remained equal compared with the sea level

(R. Köster, verbal information). It remains an open question, if they will follow the postulated stronger sea level increase of 50 cm in 50 years (see Chap. 6).

The investigated Gleyi-sali-tidalic Fluvisol is situated 380 m in front of the 8.6 m high winter dike. Located 2.2 m above sea level, it is actually a high salt meadow with 20–30 cm above the normal level of the salt meadows and it has a loamy sand to sandy loam texture. The tide-exposed foreshores are about 10 km long and mostly composed of sandy areas that offered a high amount of sedimentation, today even stronger than the generally postulated 20 cm/century. Thus, it seems realistic that in this area (under the postulated conditions of scenario 2), the tidal area sands are displayed in eastern direction and deposited with a thickness of 55 cm in the actually developing salt meadow area. Under this presumption, the surface level would be in a balance with the rising sea level. Furthermore, it can be assumed that the sediments with a loamy sand to sandy loam texture are deposited together with seaborne organic matter contents of 0.6–1.2% and carbonate contents of about 4%. Under such conditions, after 50 years a Gleyi-sali-tidalic Fluvisol (*oxidierte Salzrohmarsch*) will develop which shows nutrient reserves and both water and air capacities similar to the actually known values.

Under such conditions, it can be assumed that mainly the temperature increase of 2.5 K, besides an increase of 15% (or about 50 mm) precipitation in winter times, will support the activities of soil organisms as well as the soil water, elements, and gas dynamics.

A main question is posed: Which consequences will evolve from the postulated rising sea level, if no balance by sedimentation results? This case is expected at the North Sea coast, where actually only a small or no sedimentation is found, e.g., in North Friesland.

The postulated rise of the sea level by 55 cm combined with no sedimentation will increase the groundwater table by at least 55 cm. As scenario 2 predicts an increased tidal range by 30 cm and more frequent and longer-lasting storm tides, the mean groundwater table will increase to 70 cm. This corresponds with an only moderate water permeability of 10 cm d^{-1} in the subsoil of the investigated Gleyi-sali-tidalic Fluvisol, which decelerates drainage of the soils during low tide. Therefore, after 50 years the future soil conditions are expected to be as in the investigated Hypersali-tidalic Fluvisol, which is elevated 70 cm lower than the investigated Gleyi-sali-tidalic Fluvisol.

Under these conditions, flooding frequency will increase from 70 times per year to approximately 500 to 600 times per year. The soil will non-seasonally remain flooded. The reduced Cr-horizon will end directly below the soil surface and vegetation will have completely changed. The ecosystem will be extremely poor regarding plant and animal species. Water, element, and redox dynamics will be similar to those of the actual Hypersali-tidalic Fluvisol. As the soil temperatures will have increased by 2 K, stimulated processes like sulphate reduction and methane-production will occur more intensively.

A complete loss of sedimentation, however, will only occur at a few locations of the North Sea coast, presumably at tidal areas situated between the East-Frisian islands and the mainland. However, the proportion of Gleyi-sali-tidalic Fluvisol area on total tidal area will increase, if a twice higher sedimentation during the future 50 years will occur (as the 20 cm assumed for the past centuries). The studied Gleyi-sali-tidalic Fluvisol having a permanently reduced Cr-horizon beginning at 100 cm will change to a Fluvisol with a 20–30 cm higher elevated reduced horizon. The impacts of the postulated increased temperatures would be less serious, depending on the activities of soil organisms, if the higher temperature in the main ecosystem is partly compensated by a low oxygen supply.

References

Alef K (1991) Methodenhandbuch Bodenmikrobiologie. Ecomed, Landsberg/Lech

Becher G (1998) Der Salzgehalt im Wattenmeer. In: NSHW UBA (ed) Umeltatlas Wattenmeer, vol 1. Ulmer, Stuttgart

Blume H-P, Müller-Thomsen U (2007) A field experiment on the influence of the postulated global climatic change on coastal marshland soils. J Plant Nutr Soil Sci 170:145–156

Brümmer G, de Groot A, Zschuppe K (1970) Untersuchungen zum Carbonatgehalt mariner, brackischer und fluviatiler Schlicke im Nordseeküstenbereich. Mitteilungen der Deutsche Bodenkundliche Gesellschaft 10:306–307

Blume H-P, Bayern L, Friedrich F (1991) Correlations between the microbial activity, and water, air, temperature and nutrient status of different soils under different use. In: Overdiek D (ed) Esser G. Modern Ecology. Elsevier, Amsterdam, pp 321–346

Giani L, Dittrich K, Martsfeld-Hartmann A, Peters G (1996) Methanogenesis in saltmarsh soils of the North Sea coast of Germany. Eur J Soil Sci 47:175–182

Hutchinson GL, Moiser AR (1981) Improved soil cover method for field measurement of nitrous oxide fluxes. J Soil Sci Soc Am 45:311–316

Macfadyen A (1962) Soil arthropod sampling. In: Caswell H (ed) Advances in ecological research. Academic Press, London, pp 1–34

Mohr E, van Baren F, van Schuylenborgh G (1972) Tropical soils, 3rd edn. Mouton, The Hague

Müller-Thomsen U (1997) Wasser-, Gas-, Salz- und Nährstoffdynamik zweier Standorte im Deichvorland Norddeutschlands. FTZ Westküste der Universität Kiel, report 16

Pfisterer U, Khan H, Müller-Thomsen U (1997) Verteilung von Methan und Lachgas, sowie Sulfat-, Nitrat- und Ammoniakkonzentrationen in Böden der Salzwiese und des Watts Nordfrieslands. Mitteilungen der Deutschen Bodenkundliche Gesellschaft 85:985–988

Piearce TG, Piearce B (1979) Responses of lumbricidae to saline inundation. J Appl Ecol 16:461–473

Schlichting E, Blume H-P, Stahr K (1995) Bodenkundliches Praktikum, 2nd edn. Parey/Blackwell, Berlin

Vance E, Brookes P, Genkinson G (1987) An extraction method for measuring soil microbial biomass. Soil Biol Biochem 19:703–708

Von Törne E (1990) Assessing feeding activities of soil living animals 1. Bait Lamina Test Pedobiologia 34:89–101

Weigmann G (1971) Faunistisch-ökologische Bemerkungen über einige Oribatiden der Ostseeküste und des Binnenlandes von Norddeutschalnd (Insecta: Collembola–Acarai: Oribatida). Ein Beitrag zur Erforschung ungestörter Biotope. Faunistisch-Ökologische Mitteilungen 4:11–20

Weigmann G (1973) Zur Phänologie von Collembolen im Einflußbereich des Meeres. Faunistisch-Ökologische Mitteilungen 4:185–198

Witkamp M, Frank ML (1970) Effects of temperature, rainfall, and fauna on transfer of Cs, K, Mg, and mass in consumer-decomposer microcosms. Ecology 51:465–474

Field Experiment: Effects of Microclimate Modification on Soil Organisms and Aggregate Formation in Dune Sand

17

Detlev Handelmann, Thiemo Klittmann, and Gerhard Weidemann

Abstract

The reaction on soil temperature increase by future climate scenarios was studied using a field experimental approach in coastal dunes. In this experiment microclimate was changed by using square plots uncovered as control and covered by coarse and fine gauze. Mean monthly temperature under covered plots differed from control plot depending on the temperature seasonality (maximum 2°C). Differences between covered plots were not significant. Among the soil animals, only nematodes showed a clear increase in density in the upper soil (0–8 cm) under gauze plots. The findings support the hypothesis that a modification of the microclimate affects the biotic community and hence indirectly the aggregate formation in dune sand.

17.1 Introduction

The aggregate formation in dune sand and hence the stabilisation of dunes is an ecosystemic process, which results from the interactions of organisms with the substrate (van Dieren 1934; Koehler and Weidemann 1995). The hypothesis underlying our experiment was that a microclimate change, mainly by temperature raise,

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Author "Gerhard Weidemann" has died before the publication of this book.

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would intensify the activity of soil organisms in dune sand and by this way induce an increased aggregate formation.

17.2 Methods

On the island of Norderney, 18 experimental plots measuring 2 x 2 m, which were planted with cuttings of *Calammophila baltica* (set 7 x 7 cm apart), were established in a dune field. 12 of these plots were roofed by metal frames (2 x 2 x 0.5 m) and covered with gauze of 3.5 mm or 1.5 mm mesh width in order to modify the microclimate, especially the temperature, in the plots by changing reflection and transmission of radiation. The remaining six plots were not roofed and served as controls (Fig. 17.1).

On the one hand, the influence of the gauze on soil humidity (by interception of precipitation) was obviously minimal as could be demonstrated by comparison of the actual water content of soil samples from gauze treatments and control plots. On the other hand, wind speed was definitely reduced thus causing an adverse effect on air exchange near the soil surface. Furthermore, photosynthetic active radiation was reduced by 25% under the gauze.

In spite of the small overall temperature increase, the microclimate alteration due to the gauze treatments resulted in significant changes on the level of the biotic community and on the level of the ecosystem process of 'biogenic sand stabilisation'. Since there was no relevant difference between the two different gauze treatments, the respective findings are united here (Fig. 17.2).

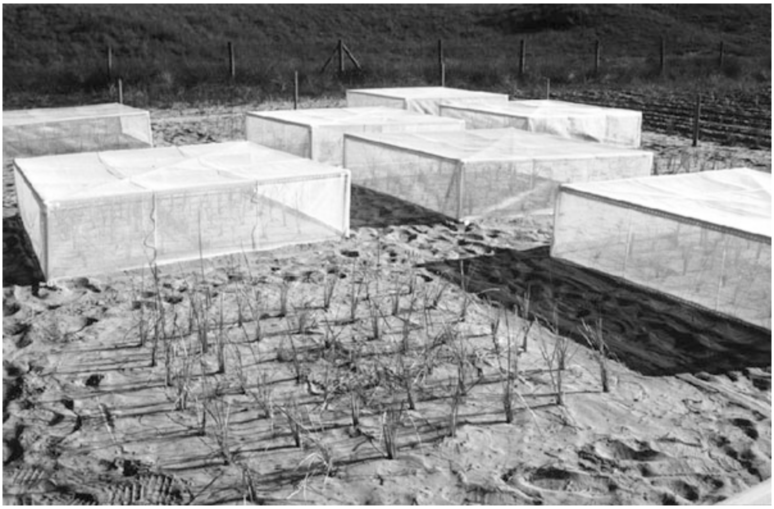

Fig. 17.1 Experimental plots. In the foreground, a control can be seen showing the *Calammophila* plants planted in a grid of 7 x 7 cm distance. In the background, experimental plots are set up with gauze covered metal frames

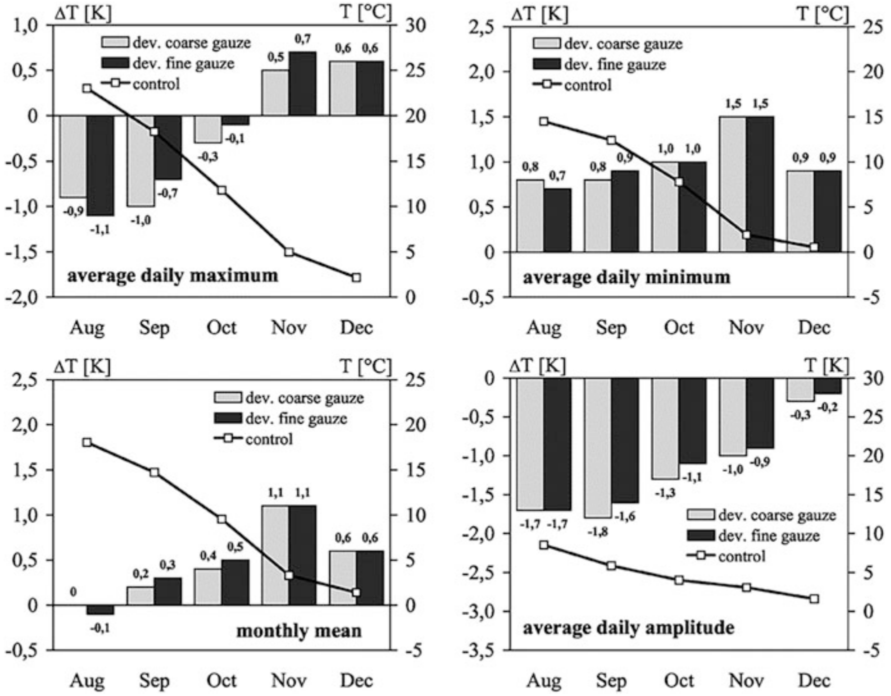

Fig. 17.2 Soil temperature effect of the gauze cover shown as average daily maxima, minima, mean, and amplitudes. The values for the controls are given in °C (T, right ordinate), whereas the gauze treatments are shown as a deviation from the control (ΔT, left ordinate). Soil depth 4 cm, *n* = 2, period: August–December 1998

17.3 Results and Discussion

As expected, the biomass of *Calammophila baltica* showed a seasonal periodicity in all treatments with a maximum for the shoot in July and for the root later in autumn. There was a tendency to higher biomass values under both gauze treatments from July of the second year on, but they were significant only at single dates (Fig. 17.3).

Microbial biomass, which was determined in the second year at 0–8 in–and cm and 8–16 cm soil depth, was weakly but not significantly raised in the upper soil of the gauze treatments (Fig. 17.3).

Among the soil animal groups studied, only nematodes showed a clear increase in density in the upper soil (0–8 cm) under gauze (Fig. 17.4), while the densities of collembolans and gamasid mites did not markedly differ between the three treatments (Fig. 17.4). However, by a rank-correlation analysis, it could be demonstrated that the density of soil microarthropods (Collembola and Gamasina)

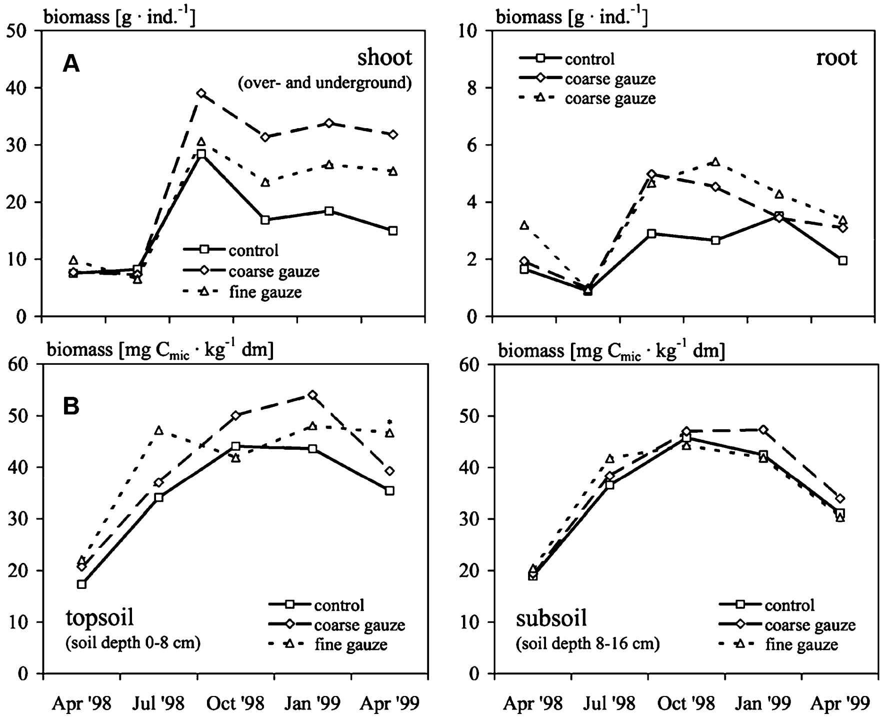

Fig. 17.3 (**a**) Mean plant biomass of *Calammophila baltica* (g · ind^{-1}), no significant deviation from the control (*ANOVA*, 1-factorial and 2- factorial with iteration, $p \leq 0.05$); (**b**) Mean microbial biomass, significant deviation from the control (*ANOVA*, 1-factorial) * $p \leq 0.05$; no significant deviation from the control after 2-factorial *ANOVA* with iteration; $n = 6$

at almost all sampling dates was significantly correlated with plant biomass (Fig. 17.5). Since the latter was higher in the gauze treatments in most cases, this finding can be interpreted as an indirect influence of microclimate alteration on the soil microarthropods. In the same way, the increase of microbial biomass and of nematode density might be understood as a result of the increase of the root biomass of *Calammophila* in the gauze treatments. According to Klittmann (in Handelmann 2001), who determined the nematodes, 59% of the species found were microphytophagous (bacterial or fungal feeders). Similarly, Goralczyk and Verhoeven (1999) reported that the nematode community of dunes with permanent grass cover consists of nearly 50% of bacterial feeders.

In all treatments, the percentage of aggregated soil particles in the soil matrix as well as the mean aggregate size as a measure of soil texture development clearly increased in the course of the study. Both parameters showed higher values in the upper soil (0–8 cm) of the fine gauze variant than in the control towards the end of the study (Fig. 17.6).

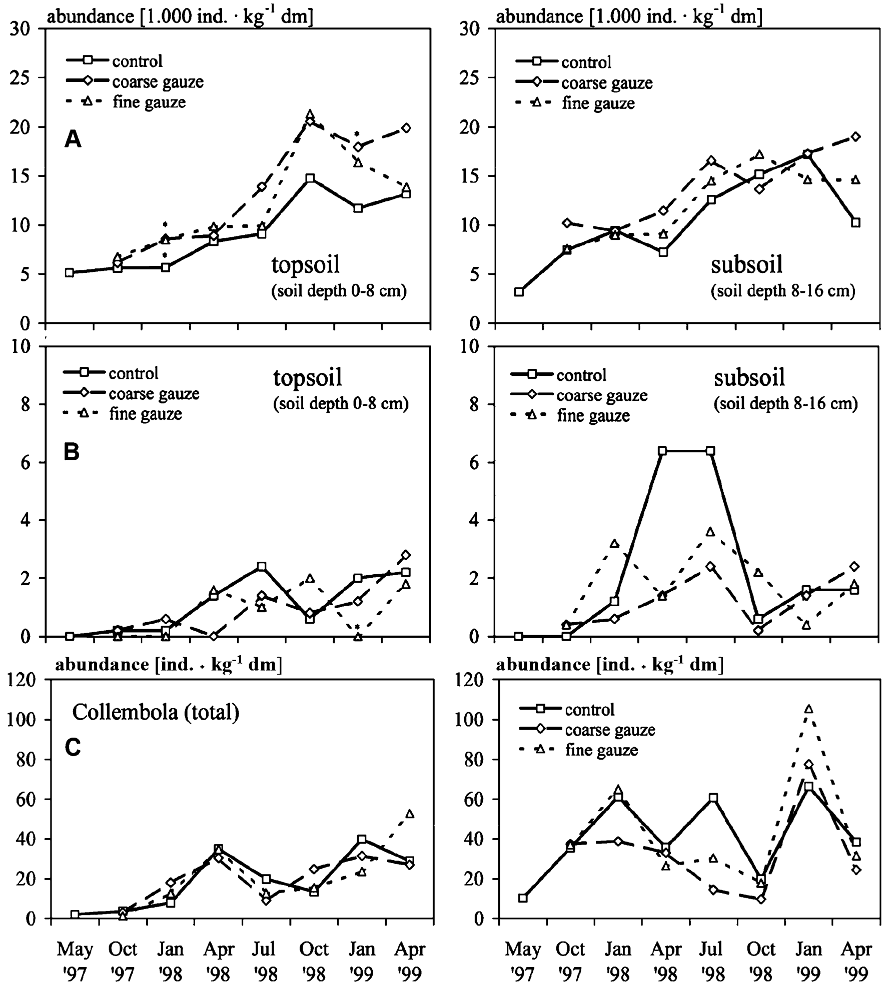

Fig. 17.4 (**a**) Total abundance of Nematoda, (**b**) Gamasina (predatory mites) and (**c**) Collembola in top and subsoil; median, $n = 6$; significance of deviation from the control (*H*-Test) * $p \leq 0.05$

Our findings support the hypothesis that a modification of the microclimate affects the biotic community and hence indirectly the aggregate formation in dune sand. It cannot be assumed, however, that the minimal temperature increase, which was induced by the gauze cover, is alone responsible for this effect. According to the model of the optimum curve, a minimal change in the intensity of an ecological factor affects a population only in the worst range of its ecological potential (see, e.g., Begon et al. 1998; Bick 1998; Tischler 1993). Concerning temperature, the soil organisms under study do not likely live at their worst level.

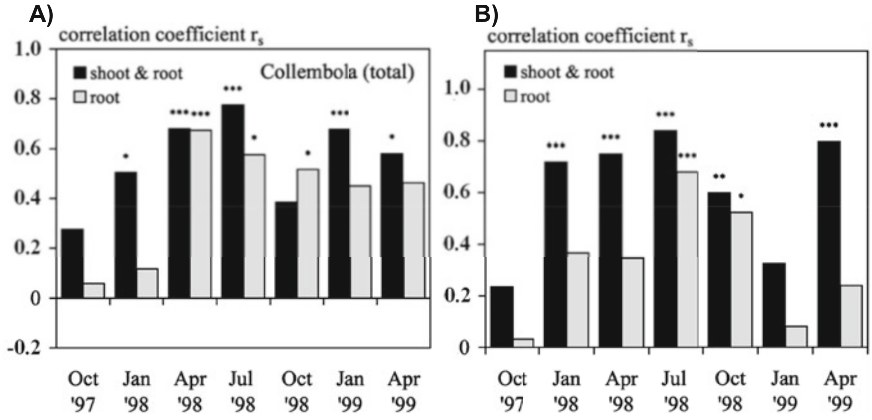

Fig. 17.5 (**a**) Rank correlation of total abundances of Collembola (springtails) with subterranean plant biomass and (**b**) rank correlation of total abundances of Gamasina (predatory mites) with subterranean plant biomass; Correlation coefficient r_S. Soil depth 0–16 cm, $n = 18$, significance for $r_s \neq 0$ (2-sided question), * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.005$

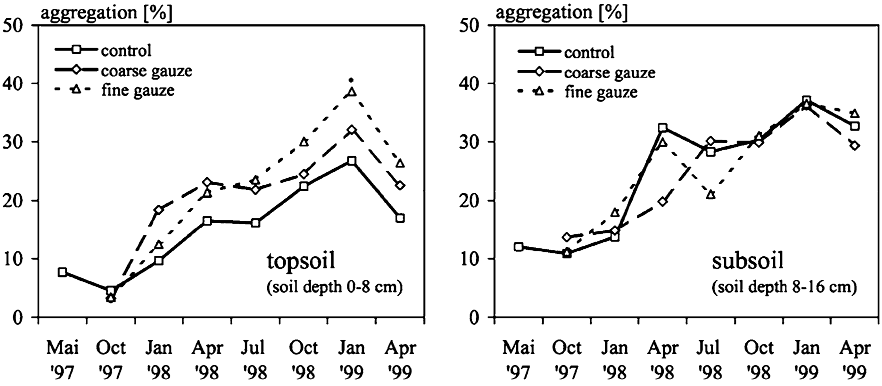

Fig. 17.6 Aggregation of sand as weight percentage of aggregates (particle size ≥ 0.63 mm) in the soil matrix; mean values, $n = 6$; significant deviation from the control (*ANOVA*, 1-factorial and 2-factorial with iteration), * $P \leq 0.05$

Therefore, the whole complex of abiotic factors, which were changed by the gauze cover, must be responsible for the observed effects. For Råbjerg Mile, a migrating dune in northern Jutland (DK), Anthonsen et al. (1996) stated that an increase in vegetation cover could be observed during a period of a slight (ca. 0.3 K) temperature increase, 9% increased precipitation and reduced storm intensity. The latter two factors presumably are responsible for the vegetation expansion on Råbjerg Mile. However, an area of 1.35 km^2 is hardly comparable with our 4-m^2 plots.

Nevertheless, reduction of wind intensity and hence mitigation of an important stress factor in coastal dunes was also a substantial effect of the gauze cover. Furthermore, the radiation was reduced. According to Grace (1996), it is generally assumed that the production of plant biomass is decreased by high wind velocity. Moreover, transpiration of plant stands is greatly influenced by wind and radiation (Penman 1948, cit. in Begon et al. 1998). The weakening of both factors in connection with a slight temperature increase might have supported the biomass production of *Calammophila*. Living roots of *Ammophila* are quickly colonised by bacteria and fungi and after a few weeks also by actinomycetes (Watson and Williams 1974). This should also apply to *Calammophila*. The rhizosphere microflora is favoured by root exudates and dead plant material. This has a positive effect on the mineralisation of dead organic matter and on the availability of bioelements for plants (Clarholm 1985). The latter is increased by bacterial feeding nematodes (and ciliates), which, on the one hand, keep populations of bacteria in logarithmic growth phase and, on the other hand, excrete superfluous nitrogen (Ingham et al. 1985; Trofymow and Coleman 1982; Wardle and Lavelle 1997).

Among the microarthropods, Collembolans are mainly feeders of fungi and bacteria. Their abundance increased in all variants in the course of the study and hence their influence on their food organisms. Fungi occurring in dunes are either saprophytes or symbionts (VA-mycorrhiza) (Nicolson and Johnston 1979; Klittmann and Albers 1999). By feeding on the hyphae, they are activated to grow and to metabolise. Furthermore, mycorrhiza stimulates the growth of its host plant (Koske and Polson 1984). Finally, the predatory gamasid mites influence the population dynamics of their prey, e.g., collembolans and nematodes. Thus, *Calammophila*, soil microflora, and soil fauna constitute an interacting system of mutual support under the influence of a modified microclimate. This also promotes the build-up of soil aggregates. The different types of aggregates in dune sand, which can be distinguished, are mainly glued together by mucous polysaccharides, which are excreted by bacteria, algae, and roots (Forster 1979; Forster and Nicolson 1981). Regarding these interrelations, the following effect chain can be deduced: plant roots (+ dead organic material) - > bacteria - > soil aggregates. The biotic community controls the build-up of soil aggregates in dune sand depending on the microclimate. Together with the ability of Marram Grass to collect and to hold back sand on the macro-level, this leads to sand stabilisation (Fig. 17.7).

Whether the results of our experiment allow predictions of the behaviour of coastal dune ecosystems under real conditions of climate change as forecasted by von Storch et al. (1998) and which consequences have to be drawn are discussed in Chap. 28.

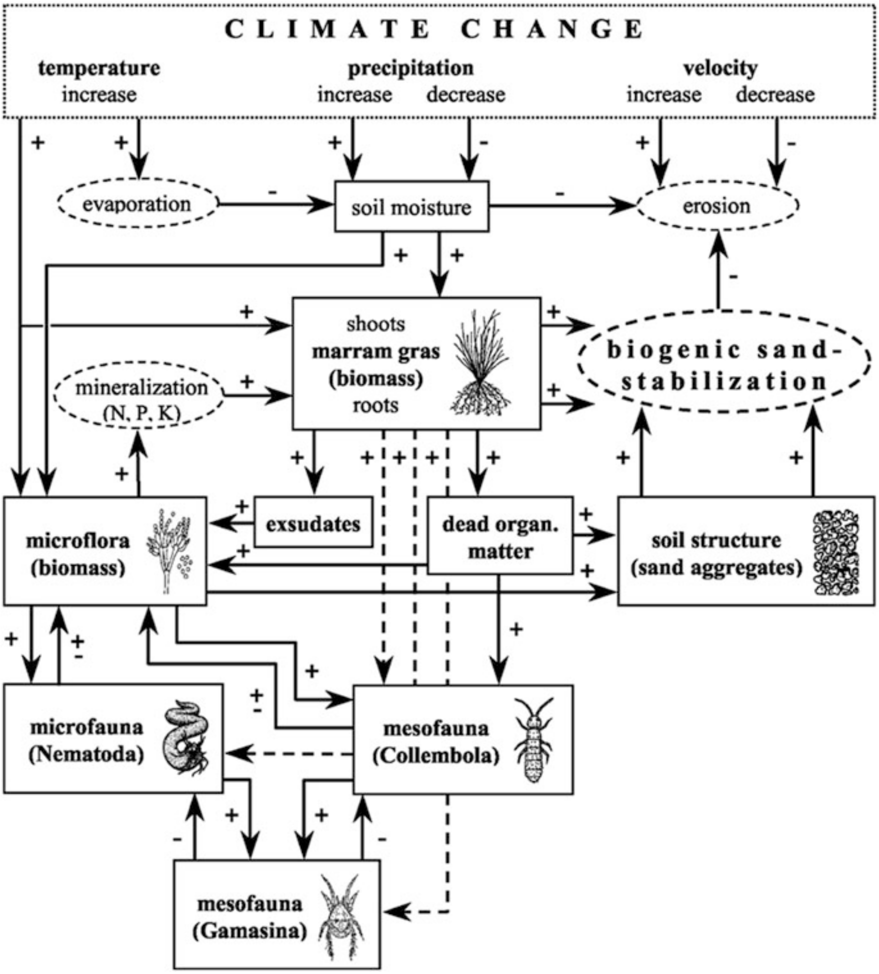

Fig. 17.7 Interaction model of biogenic sand stabilisation and climate impact. Rectangles contain ecosystem compartments, ovals illustrate processes, and arrows symbolise positive or negative effects and backlashes. Dashed line arrows indicate influences of the habitat

References

Anthonsen KL, Clemmensen LB, Jensen JH (1996) Evolution of a dune from crescentic to parabolic form in response to short-term climatic changes: Råbjerg Mile, Skagen Odde, Denmark. Geomorphology 17:63–77

Begon ME, Harper JL, Townsend CR (1998) Ökologie. Spektrum, Heidelberg

Bick H (1998) Grundzüge der Ökologie, 3rd edn. Fischer, Stuttgart

Clarholm M (1985) Possible roles of bacteria, protozoa and fungi in supplying nitrogen to plants. In: Fitter AH, Atkinson D, Read DJ, Usher MB (eds) Ecological interactions in soil: plants, microbes and animals. Blackwell, Oxford, pp 35–365

Forster SM (1979) Microbial aggregation of sand in an embryo dune system. Soil Biol Biochem 11: 537–543

Forster SM, Nicolson TH (1981) Aggregation of sand from a maritime embryo sand dune by microorganisms and higher plants. Soil Biol Biochem 13:205–208

Goralczyk K, Verhoeven R (1999) Bodengenese als Standortfaktor für Mikrofauna–Ciliaten und Nematoden in Dünenböden. In: Koehler H, Mathes K, Breckling B (eds) Bodenökologie interdisziplinär. Springer, Berlin, pp 105–118

Grace J (1996) Wind. In: Brunold C, Rügesegger A, Brändle R (eds) Stress bei Pflanzen. Haupt, Bern, pp 173–188

Handelmann D (2001) Folgen eines Klimawandels für die biogene Sandstabilisierung in Küstendünen. Dissertation, Universität Bremen, FB 2

Ingham RE, Trofymow JA, Ingham ER, Coleman DC (1985) Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. Ecol Monogr 55:119–140

Klittmann T, Albers J (1999) Die Großpilze in den Küstendünen von Houstrup Strand (West-Jütland). Faunistisch-ökologische Mitteilungen Supplement 26:49–60

Koehler H, Weidemann G (1995) Biogenic dune sand stabilization. In: VanDijk HWL, Hurkmans WEG (eds) Management and preservation of coastal habitats. EUCC, Leiden, pp 83–98

Koske RE, Polson WR (1984) Are VA mycorrhizae required for sand dune stabilization? Bioscience 34:420–424

Nicolson TH, Johnston C (1979) Mycorrhiza in the Gramineae III: Glomus fasciculatus as the endophyte of pioneer grasses in a maritime sand dune. Trans Br Mycol Soc 72:261–268

Penman HL (1948) Natural evaporation from open water, bare soil and grass. Proc R Soc A 193: 120–145

Tischler W (1993) Einführung in die Ökologie, 4th edn. Gustav Fischer, Stuttgart

Trofymow JA, Coleman DC (1982) The role of bacterivorous and fungivorous nematodes in cellulose and chitin decomposition in the context of a root/rhizosphere/soil conceptual model. In: Freckman DW (ed) Nematodes in soil systems. Univ. of Texas Press, Austin, pp 117–137

Van Dieren JW (1934) Organogene Dünenbildung. Martinus Nijhoff, den Haag

von Storch H, Schnur R, Zorita E (1998) Szenarien & Beratung. Anwenderorientierte Szenarien für den norddeutschen Küstenbereich. Abschlußbericht

Wardle DA, Lavelle P (1997) Linkages between soil biota, plant litter quality and decomposition. In: Cadisch C, Giller KE (eds) Driven by nature: plant litter quality and decomposition. CAB International, Wallingford, pp 107–124

Watson ET, Williams ST (1974) Studies on the ecology of actinomycetes in soil VII. Actinomycetes in a coastal sand belt. Soil Biol Biochem 6:43–52

Expected Vegetation Dynamics in Salt Marshes at the North Sea Coast Under Changed Inundation Conditions as an Effect of Climate Change

18

Irene Vagts

Abstract

The changing flooding regime under future climate conditions affects the zonation of saltmarsh vegetation. This effect was studied by a field experimental approach. Vegetation was transplanted from upper to lower zones and the changes in the composition of the vegetation compared to not transplanted control plots. The change in the vegetation depended from the grassland management (ungrazed, grazed, semi-natural, and natural). Overall, higher inundation frequencies can be regarded to have a severe impact on the competitive ability of the upper salt marsh plant species. The vegetation borders shift to the upper zone. The results of the grazed salt marshes revealed that multiple stresses mean higher impact on the salt marsh vegetation.

18.1 Introduction

In coastal ecosystems, different drastic impacts can be expected under climate change conditions (Warrick et al. 1993; Schellnhuber and Sterr 1993; Bazzaz 1996; Warrick et al. 1996; Lozán et al. 1998). Extinction of sensitive selected species or altered competitive relationships will have drastic effects on ecosystems; the scale depends on species attributes and the succession stage of the impacted ecosystems (Bazzaz 1996).

Sea-level rise, an increase in inundation frequencies and duration, severe storm events, more serious wave attacks, and changed erosion and sedimentation

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conditions will affect the coastline in the future (Beukema et al. 1990). Recent estimations of sea-level rise in the North Sea region published about 55 cm (mid estimate) for the year 2100 (Sterr 1998; von Storch et al. 1998).

The zonation of plant species and vegetation communities along the vertical gradient in salt marshes reflects the ecological gradient of inundation, salinity, and soil aeration (Adam 1990). Stress increases for species and coastal systems through a higher frequency of inundations combined with the effect of salinity and a root environment under reduced conditions (DeLaune et al. 1993). Due to the changed hydrologic regime, a drastic influence in the vertical vegetation zonation will be probable (Dijkema et al. 1990; Huiskes 1990; Dierssen 1993). Stress to plants under inundation can be expressed in different ways. Inundation inhibits gas exchange, changes of stomatal closure lead to altered nutrient allocation and death of fine roots, whereas lower rates of photosynthesis and growth efficiency change flowering and senescence. Two stress strategies—tolerance or avoidance—can lead to species survival. Under changed inundation conditions, plant species either already possess adaptations, such as aerenchymas, and to survive they migrate to more suitable habitats or they become extinct (Ungar 1991; van Diggelen 1991; Brändle 1996). Many authors explain the different potential of individual species to cope with anaerobic water logging conditions (Cooper 1982; Groenendijk et al. 1987; Armstrong et al. 1991, 1994) with the different manifestations of ecophysiological and morphological adaptations (Rozema et al. 1988). Justin and Armstrong (1987) pointed out that there is a difference between the influence of water logging and flooding. The significance of results from water logging experiments is limited and transplantation experiments in the field open a more realistic simulation frame. Transplantation studies of single species (Stalter and Batson 1969; Snow and Vince 1984) or two species assemblies (Groenendijk et al. 1987) were used to examine the reactions of plant species to inundation. In this study, vegetation-turf transplantation experiments were carried out to predict the vegetation development under the influence of increasing flooding as a consequence of climate change.

18.2 Material and Methods

18.2.1 Study Area

The present investigations were performed in different salt-marsh types in the Wadden Sea-area of Northwest Germany (1997–1999). Grazed and abandoned man-made mainland salt marshes, ungrazed semi-natural mainland, and natural island salt marshes (except parts grazed by geese) were investigated (Table 18.1). The study area of the mainland salt marshes is part of the Wursten Coast, situated south of Cuxhaven (8° 34′ E, 53° 48′ N). The study area of the island salt marshes is situated on the uninhabited island of Mellum (8° 10′ E, 53° 43’N), which is located in the German Bight of the North Sea. Mean high water (MHW) on Mellum is about +1.5 m NN and in the mainland salt marshes about +1.6 m NN.

Table 18.1 Features of the investigated salt-marsh types

Location	Berensch	Arensch	Oxstedt	Cappel	Mellum
Age (years)	70	70	100	40	45
Grazing	Intensive until 1998 (sheep), extensive since 1999	Abandoned since 1994	Abandoned since 1996	No (geese?)	No (geese?)
Hydrology	Drainage	Drainage	Drainage	Tidal creek	Tidal creek
Aeration	++	++	++	+	+++
Nutrients	Rich	Rich	Rich	Rich	Poor
Sedimentation	Artificial	Artificial	Artificial	Semi-natural	Natural
Soil material	Silt	Silt	Silt	Silt	Sand

The '*grazed salt marsh'* (Berensch) was intensively grazed by sheep (5–7 sheep ha^{-1}) until 1998. In 1999, the grazing intensity was lowered. The soil type was identified as a polyhaline salt marsh with a relatively high nutrient pool. Because of an extensive ditch system, the topsoil layer was sometimes well aerated. The site was characterised by a low vegetation structure and a homogenous vegetation pattern. The dominant vegetation types were Puccinellietum maritimae and a species poor Armerio-Festucetum litoralis. Species that are sensitive against trampling and grazing were missing. A decreasing gradient of grazing intensity existed from the dike to the tidal flats; the highest and lowest parts were rarely influenced by grazing or were ungrazed. In the higher parts, patches of Artemisietum maritimae and Agropyretum litoralis were sprinkled. The ungrazed lower parts were occupied by Spartinetum anglicae and Salicornietum brachystachyae (Table 18.2).

The *semi-natural mainland salt marsh* (Cappel) developed in front of a new embankment and since then natural tidal creeks developed. Except for the well-aerated banks of the tidal creeks, the soil exhibits low ventilation. The vegetation along the tidal creeks was characterised by mosaic patterns of Spartinetum anglicae, Puccinellietum maritimae with *Cochlearia anglica*, Suadetum macrocarpae, and Halimionetum portulacoidis. The lower salt marsh was dominated by Puccinellietum maritimae with *Spartina anglica* and *Aster tripolium*. *Plantago maritima* and *Triglochin maritimum* were frequently occurring species in this area. Armerio-Festucetum litoralis covered the upper parts and Agropyretum litoralis forms patches on the highest parts beside creeks (Table 18.2).

The young polyhaline *island salt marsh* (Mellum) was built up from a sand-mud flat and was temporarily aerated up to oxygen rich in the upper parts, where a regosol gley was featured. Nutrient reserves, soil moisture, and salinity showed a clear gradient from the lower to the upper parts with greater amplitude than in the mainland marshes.

The lower part of the natural island salt marshes on sandy soil was characterised by Salicornietum strictae and Spartinetum anglicae. The dense shrub layer of Halimionetum portulacoidis occupied the middle parts with a dominance of *Atriplex*

Table 18.2 Vegetation assembly of investigation sites

Investigation sites at Wurster Coast			
1 Abandoned salt marsh, mainland (Arensch)	m > NN	**3** Abandoned salt marsh, mainland (Oxstedt)	m > NN
Agropyretum litoralis	2.0	Agropyretum litoralis	2.4
Armerio-Festucetum maritimae	1.9	Armerio-Festucetum litoralis	1.9–2.2
Puccinellietum maritimae	1.8	Puccinellietum maritimae	1.8
Spartinetum anglicae/ Puccinellietum maritimae	1.5	Spartinetum anglicae/ Puccinellietum maritimae	1.5
2 Grazed salt marsh (Berensch)		**4** Semi-natural salt marsh (Cappel)	
Agropyretum litoralis	2.0	Armerio-Festucetum litoralis	2.15
Puccinellietum maritimae	1.8	Puccinellietum maritimae	1.70
Spartinetum anglicae/ Puccinellietum maritimae	1.7	Spartinetum anglicae/ Puccinellietum maritimae	1.65
Investigation sites at Mellum			
5 Island salt marsh (Mellum)	m > NN		
Agropyretum litoralis	2.15		
Halimionetum portulacoides K-L1927	1.89		
Spartinetum anglicae/Spartinetum anglicae	1.51		

portulacoides, *Limonium vulgare*, and *Suaeda maritima* and the upper parts by Agropyretum litoralis (Table 18.2).

18.2.2 Field Experiments

Experimental investigations were made on the basis of the IPCC and the local scenario of sea-level rise (Warrick et al. 1996; von Storch et al. 1998) to simulate impacts of an increased inundation frequency on salt-marsh vegetation. Changed flooding frequencies involve a combined impact of inundation, soil aeration, and salinity.

Transplantation experiments were carried out since 1997. The plots were transplanted in April 1997 along vertical gradients in mainland and island salt marshes with different soil types (Fig. 18.1 and Table 18.3). Turfs with a size of 1 m^2 and a depth of about 40 cm were transplanted and used to investigate the dynamics of salt-marsh vegetation and the development of populations under simulated sea-level rise conditions on permanent plots. Elevation steps of transplantation depend on the vegetation types. One data set consists of three replicates and un-transplanted control plots, each. Although it was necessary for transportation to cut the plots in six pieces, turfs were little influenced by transplantation due to a careful reconstruction of the plots. Internal transplantations were undertaken to

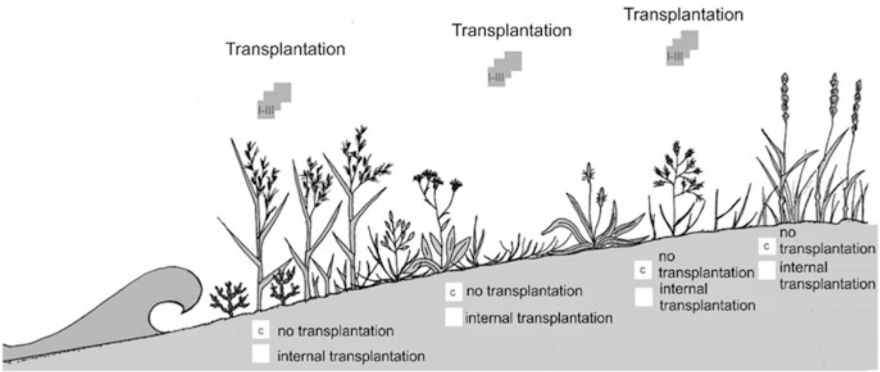

Fig. 18.1 Transplantation design. Transplantations were done from higher to lower vegetation units; *c* control

Table 18.3 Number of inundations (*n*) and inundation frequencies (%) at the different study sites

	Elevation (m NN)																									
	+2.4		+2.2			+2.15			+2.00			+1.90			+1.80			+1.70			+1.65			+1.50		
Loc-ation	Cont.		Tr.	Cont.		Tr.	Cont.		Tr.	Cont.		Tr.	Cont.		Tr.	Cont.		Tr.	Cont.		Tr.	Cont.		Tr.	Cont.	
	%	n	%	%	n	%	%	n	%	%	n	%	%	n	%	%	n	%	%	n	%	%	n	%	%	n
Ar.										100	91 →	138	100	126 →	144	100	182 →							238	100	433
Be.										100	91 →				200	100	182 →	140	100	255						
Ox.	100	24 →	188	100	45 →							280	100	126 →	144	100	182 →							238	100	433
Ca.							100	52 →										100	490	255 →	115	100	293			
Me.							100	24 →				275	100	66 →										416	100	275

Ar. Arensch, *Be*. Berensch, *Ox.* Oxstedt, Ca. Cappel, *Me*. Mellum; *Co.* Control, *Tr.* Transplanted; arrows indicate transplantation from site 1 to site 2

estimate the effect of transplantation. The results show that transplantation shock can be neglected. The total number of plots amounts to 73.

The plots were examined for the following parameters: *community level*: species abundance/dominance (percentage, <5% also abundance), canopy height, horizontal structure (drawings); *population level*: phenology, biomass, growth, seedling-establishment; *site-factor level:* inundation frequency and duration, elevation data, soil conditions, salinity.

For statistical analysis, the log transformed data of vegetation relevés were used in a Correspondence Analysis (CA) with Canoco 3.12 (Ter Braak 1987). Species nomenclature is according to Wisskirchen and Haeupler (1998), vegetation communities to von Glahn et al. (1989) and Schaminée et al. (1998).

18.3 Results

18.3.1 Vegetation Dynamics

Due to the increasing flooding frequency, the vegetation assembly changed in different directions. The intensity of interspecific interactions and the direction of vegetation dynamics depend on flooding frequency, soil characteristics, land use, contact vegetation, and initial floristic composition (Fig. 18.2, Table 18.5).

	Arensch	Berensch	Oxstedt	Cappel	Mellum	*n*
Control plots (c)	4	3	5	3	3	18
Control plots (internal transpl.)	4	3	5	3	3	18
Inundation plots (I-III)	9	6	12	6	4	37
Erosion plots (I-III)	9	6	12	6	4	37
∑n	26	18	34	18	14	110

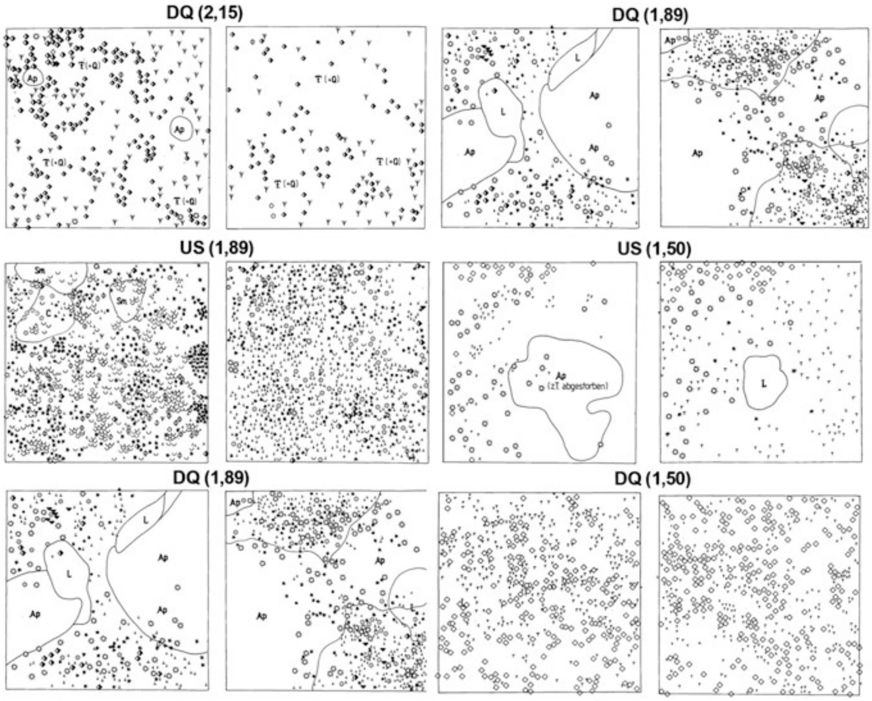

Fig. 18.2 Development of canopy structure on an island salt marsh. *DQ* control plots, *US* transplants under changed inundation, transplantation from +1.89 m NN to +1.5 m NN

18.3.1.1 Grazed Salt Marsh

In the first year after the transplantation, the vegetation reacted in correspondence with the increasing flooding frequency, but in the second year, reduced grazing intensity counteracted this process.

18.3.1.2 Abandoned Salt Marsh

In the upper salt marsh, the transplantation along the environmental gradient affects a decrease of the coverage of *Elymus athericus*. Sublayer species formerly suppressed by competitors, such as *Festuca rubra*, *Agrostis stolonifera,* and *Artemisia maritima*, benefit from the better light conditions. Species with fast-growing stolons (*Atriplex portulacoides*) and species with aerenchymas (Justin and Armstrong 1987; Ellenberg et al. 1991), such as *Aster tripolium*, benefit from the changed abiotic conditions (Table 18.4, Table 18.5).

18.3.1.3 Semi-natural Salt Marsh

The experimentally increased flooding frequency influenced the coverage of *Festuca rubra* and *Puccinellia maritima* in the upper salt marsh: the presence of *Festuca rubra* was eliminated, coverage with *Puccinellia maritima* increased, *Salicornia* spp. and *Spartina anglica* invaded. In the lower part, *Triglochin maritimum* or *Puccinellia maritima* were favoured, whereas species like *Spergularia maritima, Atriplex portulacoides, Plantago maritima,* and *Atriplex prostrata* were extinguished (Tables 18.4 and 18.5).

18.3.1.4 Natural Island Salt Marsh

The upper island salt-marsh vegetation changed under higher inundation frequencies. *Elymus athericus* and the dominant species *Festuca rubra* disappeared or only few individuals remained, whereas the fruticose *Atriplex portulacoides* with the ability of rapid lateral spreading grew vigorously in the absence of fast-growing competitors, now forming the shrub layer together with co-dominance of *Suaeda maritima* and *Limonium vulgare*. *Spergularia maritima* and *Salicornia* spp. invaded. Species composition changed from Agropyretum litoralis to Halimionetum portulacoidis. Since the first year after the increased inundation frequency, the vitality of *Elymus athericus* was obviously reduced. In the lower parts, *Atriplex portulacoides* and *Spergularia maritima* disappeared, the coverage with *Limonium vulgare* was reduced, and *Salicornia stricta* was stimulated by the more frequent inundations. *Spartina anglica* invaded from the surrounding vegetation (Table 18.4, Table 18.5).

The average Ellenberg indicator values of soil moisture (Fig. 18.3) and of light increased during vegetation development and more salt-tolerant species benefit under higher inundation frequencies.

18.3.2 Correspondence Analysis

A correspondence analysis (CA) of the vegetation relevés from 1997 until 1999 separates two groups and clarifies the vegetation dynamics (Fig. 18.4). The first axis

Table 18.4 Vegetation development under simulated sea-level rise. *Transp* transplant, *Agrop litor* Agropyretum litoralis, *Arm-Fest litor* Armerio-Festucetum litoralis, *Pucc mar* Puccinellietum maritimae, *Spart/Pucc* Spartinetum anglicae/Puccinellietum maritimae, *T* Transition, *Halim portul* Halimonietum portulacoidis

	Vegetation assemblies				
Berensch	Agropyr. litor.→	Transp.	Arm-Fest. lit/Pucc. mar→	Transp.	Spart./ Pucc.
m > NN	2	1.8	1.8	1.7	1.7
Species					
Elymus althericus	■	-			
Artemisia maritima	○	+			
Festuca rubra	○	0	●	++	
Cochlearia anglica	▪	+			
Glaux maritima	○	0	●	-	
Spergularia maritima	○	0	○	0	▪
Suaeda maritima	○	0	○	0	▪
Puccinellia maritima		↑	■	0	■
Aster tripolium		↑		↑	○
Salicornia ramosissima			○	0	○
Spartina anglica				↑	●

Arensch	Agropyr. litor.→	Transp.	Arm-Fest. lit→	Transp.	Pucc. mar. →	Transp.	Spart./ Pucc.
m > NN	2	1.9	1.9	1.8	1.8	1.5	1.5
Species							
Elymus althericus	n	--					
Artemisia maritima	○	++	o	u			
Festuca rubra	▪	+	■	---			
Atriplex prostrata	○	--	▪	0	▪		
Cochlearia anglica	○	+	o	+		↑	
Atriplex portulacoides	○	++	o	0	o	0	
Aster tripolium	▪	++	o	0	●	-	○
Suaeda maritima	○	0	o	0	o	0	○
Atriplex littoralis	▪	0			▪		
Glaux maritima	▪	+	o	+	o	0	
Puccinellia maritima	▪	0	o	+++	●	++	●
Salicornia ramosissima	▪	0	o	++	o	+	●

(continued)

Table 18.4 (continued)

Arensch	Agropyr. litor.⟶	Transp.	Arm-Fest. lit⟶	Transp.	Pucc. mar. ⟶	Transp.	Spart./ Pucc.
Spergularia maritima	▪	0	o	0	o	0	
Plantago maritima			●	+	o	0	
Triglochin maritimum			●	+	□	-	
Limonium vulgare					▪	+	
Spartina anglica					▪	+	□

Oxstedt	Agro. litor.⟶	Transp.	Arm.-Fest. lit.→	Transp.⟶	Arm.-Fest. lit.⟶	Transp.	Pucc. mar.⟶	Transp.	Spart./ Pucc.
m > NN	2.4	2.2	2.2	1.9	1.9	1.8	1.8	1.5	1.5
Species									
Elymus altherticus	■	0							
Agrostis stolonifera	○	+	●	+	■	-			
Festuca rubra	▪	+	■	+	○	0	●	+	○
Aster tripolium	○	0	○	0	▪	0	▪		
Atriplex littoralis	▪	0	○	+	▪	0	▪		
Atriplex prostrata	▪	0	▪	0	○	0	○		
Suaeda maritima		↑	○	0	○	-	○	0	○
Plantago maritima			▪	0	○	0	○	-	
Glaux maritima				↑	▪	+++	■	0	
Puccinellia maritima	▪			↑	▪	0	▪	---	□
Salicornia ramosissima	▪		▪	0			▪	+	○
Spergularia maritima	▪			↑				0	
Triglochin maritimum					○	0		↑	●
Spartina anglica								↑	●

Cappel	Arm.-Fest. lit⟶	Transp.	Pucc. mar.⟶	Transp.	Spart./ Pucc.
m > NN	2.15	1.7	1.7	1.65	1.65
Species					

(continued)

Table 18.4 (continued)

Cappel	Arm.-Fest. lit⟶	Transp.	Pucc. mar.⟶	Transp.	Spart./ Pucc.
Festuca rubra	□	┼			
Spergularia maritima	○	-	○	┼	
Triglochin maritimum	▪	0	○	+	
Atriplex portulacoides	○	0	○	┼	
Plantago maritima	○	0	▪	┼	
Puccinellia maritima	■	+	■	0	●
Aster tripolium	●	0	●	-	○
Atriplex prostrata	○	0	▪	┼	▪
Cochlearia anglica	○	0	○		▪
Suaeda maritima	○	0	○	0	○
Salicornia ramosissima		↑	○	0	▪
Spartina anglica		↑	○	0	□

Mellum	Agro. lit.⟶	Transp.	Hali. port.→	Transp.⟶	Spart./ Pucc.
m > NN	2.15	1.89	1.89	1.51	1.51
Species					
Elymus althericus	●	--			
Festuca rubra	■	---			
Artemisia maritima	o	0			
Cochlearia anglica	o	0			
Atriplex portulacoides	o	++	□	┼	●
Suaeda maritima	o	+++	o	0	
Limonium vulgare	▪	+	●	0	●
Spergularia maritima		↑	o	┼	
Salicornia ssp.		↑	o	++	●
Puccinellia maritima			o	0	▪
Spartina anglica				↑	●

□ Dominant, ● …, ■ Common, ○ …, ▪ rare, ┼ extinct, ↑ new, +++ very strong increase, ++ strong increase, + increase, 0 constant, - decline, -- strong decline, --- very strong decline

describes the series along the elevation gradient corresponding to the abiotic gradient of inundation and salinity. The second axis reflects the sequence of development explained by competition. According to the analysis, the following parameters separate the upper, middle, and lower salt marsh independent from the salt marsh type: the lower and middle salt-marsh vegetation is mainly influenced by abiotic conditions, the upper salt-marsh vegetation by competition.

In the scatter diagram, the points of control plots are localised close together and show no vegetation change during the investigation period.

On the island salt marsh of Mellum, the changed environmental conditions have a severe impact on the vegetation. The transplanted vegetation developed in the direction of the lower salt-marsh vegetation with a shift in vegetation composition

Table 18.5 Plant strategy types

Study area	Ber	Ar/Ox	Cap	Mel	Ber	Ar/Ox	Cap	Mel	Ecological attributes								
Salt marsh/ Ecological group	high	high	high	high	low	low	low	low	M	S	N	G	Str	L-f	Grwth-form	Lat spr.	Aer en.
1																	
Sueda maritima	0	+	0	+	0	0	0	0	8=	8	7	4	SR	T	succ		
Salicornia ramosissima	abs	0	+	-	0	+	0	+	8=	9	5	4	SR	T	succ		
Salicor. dolichostachya	abs	0	+	abs	0	+	0	+	9=	8	4	4	SR	T	succ		
2																	
Spartina anglica	abs	abs	+	abs	+	+	0	+	9=	8	3	1	SC	HG	rept rhiz	++	x
Triglochin maritimum	abs	abs	0	abs	abs	+	+	abs	7=	8	5	3	CSR	H	ros	+	x
Limonium vulgare	abs	abs	abs	+	abs	abs	abs	0	7=	8	5	2	S	H	ros	+	x
Plantago maritima	abs	+	0	abs	abs	0	-	abs	7=	7	5	3	CSR	H	ros	+	x
3																	
Aster tripolium	+	+	0	abs	+	+	-	abs	x=	8	7	1	CR	HT	sem hib		x
Cochlearis anglica	-	+	0	0	abs	+	abs	abs	8=	8	7	1	CR	BH	sem		
4																	
Puccinellia maritima	+	0	+	abs	0	+	0	0	8=	8	5	5	CR	H	stol	+++	
Spergularia marina	0	0	-	+	0	0	-	-	7=	8	5	5	CSR	HC	stol	+++	
Glaux maritima	0	+	abs	abs	-	0	abs	abs	7=	7	5	5	CR	H	rhiz stol	++	
5																	
Atriplex portulaccoides	abs	+	0	+	abs	0	-	-	7=	8	7	1	SC	C	frut caesp rhiz	+++	
6																	
Atriplex littoralis	abs	0	abs	abs	abs	abs	abs	abs	x=	7	9	2	R	T	scap		
Atriplex prostrata	abs	0-	0	abs	abs	abs	-	abs	6	7	9	1	R	T	scap		
7																	
*Festuca *littoralis*	0	+	-	-	+	abs	abs	abs	6=	7	5	5	CSR	H	rhiz		+++
*Agrostis *maritima*	abs	+	abs	abs	abs	abs	abs	abs	7-	6	5	5	CR	H	stol		+++
8																	
Elymus athericua	-	-	abs	-	abs	abs	abs	abs	5-	6	5	2	C/SC	HG	rept rhiz		+++
Artemisia maritima	+	+	abs	0	abs	abs	abs	abs	5=	7	7	2	SC	CH	suff scap		++

(continued)

Table 18.5 (continued)

Ecological groups: (1) inundation-tolerant, low growing annuals, grazing-tolerant, oligo-mesotraphent; (2) water logging-tolerant, medium-height, perennials with aerenchymas, grazing sensitive, oligo- (meso) traphent; (3) inundation/water logging-tolerant biennials, grazing sensitive, meso-eutraphent; (4) inundation-tolerant, disturbance-tolerant, low growing perennials, oligo-mesotraphent; (5) water logging-sensitive Chamaephyte, grazing sensitive, oligo- (meso) traphent; (6) water logging-sensitive and grazing sensitive annuals (ruderals) eutraphent; (7) inundation and salinity sensitive low growing, disturbance-tolerant perennials, oligo-mesotraphent; (8) tall growing, water logging-sensitive, medium grazing sensitive, meso-traphent.

Ber Berensch, *Ar* Arensch, *Ox* Oxstedt, *Cap* Cappel, *Mel* Mellum; *Low* lower salt marsh, *High* upper salt marsh; Vegetation development under study conditions (*abs* absent, 0 constant, – decrease, + increase); *M* moisture value, indicators of extreme dryness, often restricted to places, which dry out completely (Ellenberg et al. 1991); *S* salt indicator value, 0 salt sensitive . . . .9 euhaline-hypersaline (Ellenberg et al. 1991); *N* nitrogen value, 1 indicators of sites poor in available nitrogen . . . ..9 in extremely rich situations (Ellenberg et al. 1991); *G* Grazing and trampling sensitivity (1 sensitive . . . ..5 not sensitive); Strategy type after Grime et al. (1988); Life form following Ellenberg et al. (1991); Growth-form following Mueller-Dombois and Ellenberg (1974); Lateral spreading (+ . . . ..+++ intensity)

The different colours underline the change of occurrence 0 = yellow, no change; + = green; – = orange

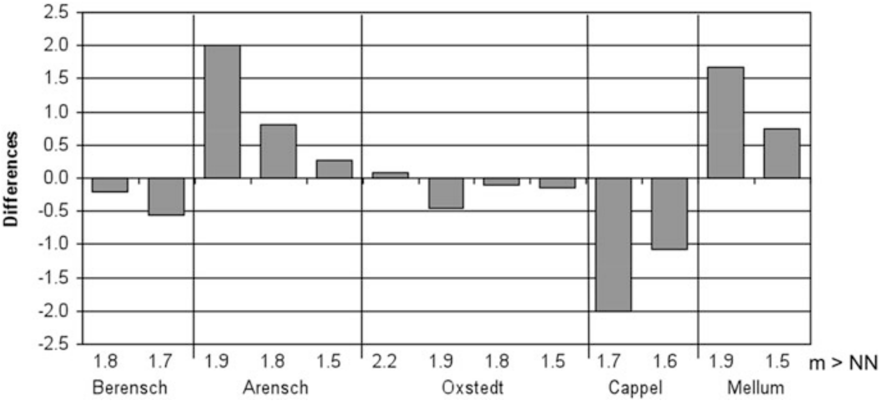

Fig. 18.3 Changes of mean moisture values calculated according to Ellenberg et al. (1991) during the vegetation development at five locations with reference to elevations (m above NN)

and structure. This is also visible in the upper and middle abandoned salt marshes of the mainland (Arensch, Oxstedt, and Cappel). The lower salt marshes are not severely influenced by a higher inundation.

The pattern in the CA of the grazed mainland salt marshes (Berensch) reveals two influencing factors: the effect of an increased inundation frequency in the first year and the altered direction of development in the second year under changed grazing management.

The analysis shows the major influence of inundation and competition. Higher inundation frequencies can be regarded to have a severe impact on the competitive ability of the upper salt marsh species.

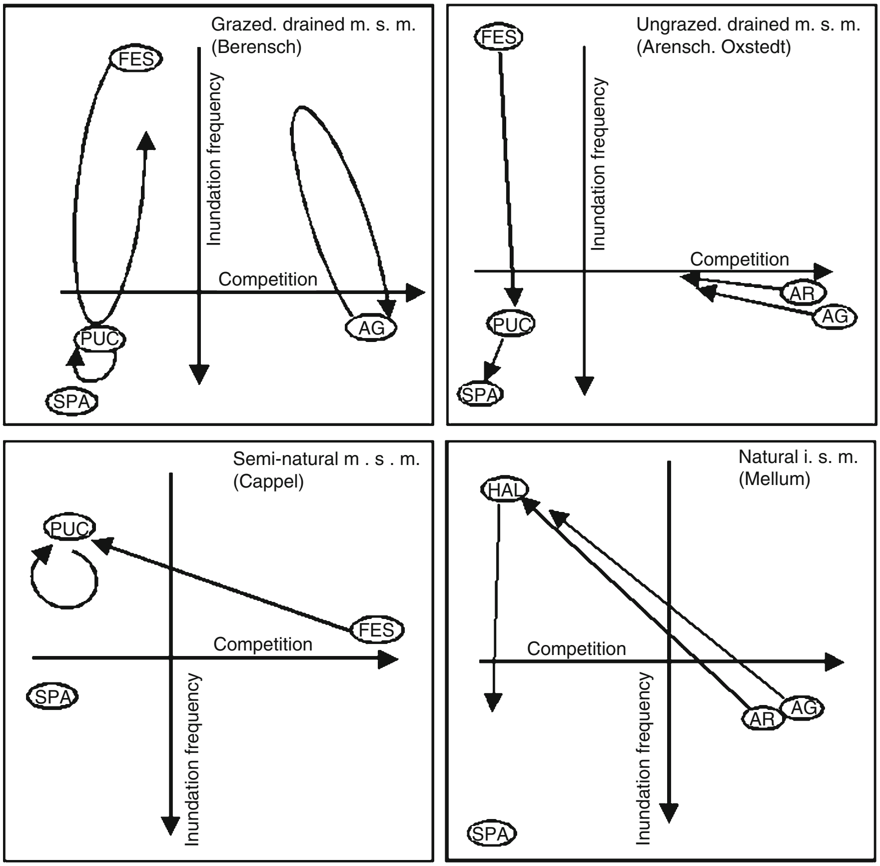

Fig. 18.4 Ordination diagram referring to correspondence analysis of vegetation dynamics (1997–1999) under increased inundation frequency. The arrows represent the intensity of factors influencing vegetation development. *AG* Agropyretum litoralis, *AR* Artemisietum maritimae. *FES* Armerio-Festucetum, *HAL* Halimionetum portulacoidis, *PUC* Puccinellietum maritimae, *SPA* Spartinetum anglicae

18.4 Discussion

Vegetation dynamics are determined by the species pool, which is specific for each distinguished salt-marsh type, the species immanent attributes and traits. Hence, higher inundation frequencies expected under climate change cause different degrees and directions of responses in the salt-marsh vegetation. Assembly rules (in this case flooding tolerance, competitive ability for light and nutrients, trampling and grazing tolerance) affect the window of sensitivity and specify which species from the species pool could exist under the environmental conditions and form the community (Keddy 1990, 1992).

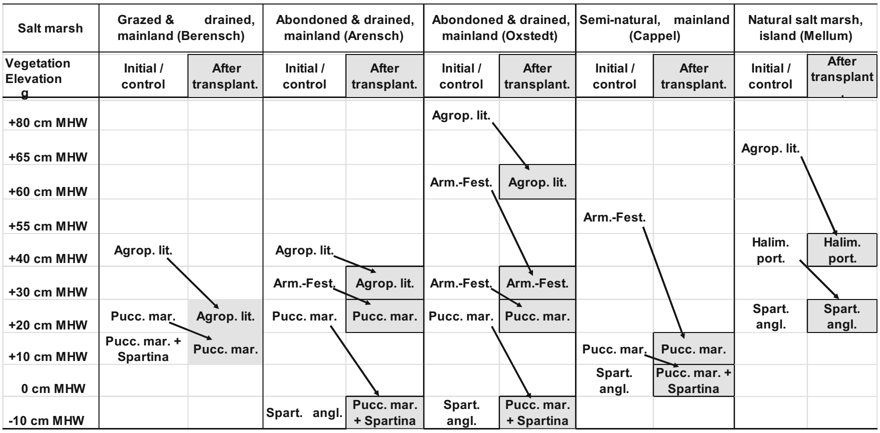

Fig. 18.5 Impact of higher inundation frequency on vegetation development: *Agrop. lit.* Agropyretum litoralis, *Halim. port.* Halimonietum portulacoides, *Arm.-Fest.* Armerio-Festudetum, *Spart. angl.* Spartinetum anglicae

Eight ecological groups were distinguished on the basis of species attributes and strategy types (Fig. 18.5). Only few species occurred in the upper and lower salt marsh under grazing conditions: mainly disturbance-tolerant species and disturbance, water logging or inundation-tolerant species. In abandoned sites, a clear boundary between the distribution pattern of groups from the upper and lower salt marsh existed. The lower salt marsh is dominated by water logging or inundation-tolerant species (groups 1–3), whereas in the upper salt marsh a high patch diversity of dominant competitive species was found (groups 7 and 8). In semi-natural salt marshes with low soil aeration, water logging and inundation-tolerant species groups also occurred at higher elevation, while the water logging-sensitive species were restricted to small areas along the tide-creek banks (groups 4 and 5). In natural island salt marshes on sandy soil, eutraphent annuals (r-strategists) (group 6) were mainly absent and the water logging and grazing sensitive but salinity tolerant Chamaephyte *Atriplex portulacoides* (group 5) was dominant. Prolonged inundation favours annuals and species with aerenchymas or lateral spreading capacity (groups 2 and 3) and deleted or weakened inundation and water logging-sensitive species (groups 6, 7, and 8). Early succession stages benefited from higher flooding conditions.

Clear differences existed between the vegetation development of the island and the mainland salt marshes due to different nutrient state. N and P limited island and young salt marshes (Kiehl et al. 1997; van Wijnen and Bakker 1999), whereas the nutrient pool was sufficient for *Elymus athericus* requirements on mainland salt marshes. On areas with nutrient poor soils in island salt marshes, with an internal bio-element flux by drift line material from the lower to higher elevations (Gerlach 1999), the effect of increased inundation frequencies was much stronger than on the mainland salt marshes on nutrient rich soils. Multiple stresses impact the vegetation. Nutrient limitation (van Wijnen and Bakker 1999) like on Mellum is probably responsible for the intensity of stress, because nutrients improve the tolerance against salinity and flooding (Jefferies et al. 1979). If *Elymus athericus* is weakened by increased inundation frequencies, the assembly of the upper salt marsh will change and either species with a higher elasticity from lower salt marshes, i.e. *Atriplex portulacoides*, will invade (Bockelmann and Neuhaus 1999) and form a new sublayer or the lower salt-marsh vegetation drifts to the upper parts.

In grazed salt marshes, the influence of an increased inundation frequency can be counteracted by a reduced grazing intensity. Bakker (1989) pointed out that under grazing pressure the upper border of lower salt-marsh species shifts upwards and after cessation of grazing vice versa. In this case, the lower border of the upper salt-marsh species was determined by their morphological and physiological constitution, and the occurrence of competitive or facilitating species. The border of the well-drained middle salt marshes shifted to lower elevation with a decreasing number of competitive species. Semi-natural mainland salt marshes have a tide-creek-system with suboptimal drainage compared to the ditches of man-made salt marshes. The vegetation borders shift to the upper zone. Trampling and grazing-tolerant species with aerenchymas occur with a great number in such ungrazed areas and form a further competition factor for the dominant species of the upper salt marsh plants, e.g., *Elymus, Artemisia,* and *Festuca*. Positive interactions, such as co-occurrence, can facilitate the environment (oxidation) for different plants—also under these species-rich conditions (Salzman and Parker 1985; Bertness and Hacker 1994; Levine et al. 1998).

Survival of the salt marshes under changed climate conditions depends on sedimentation and erosion processes, whether the vertical growth can keep pace with the rate of sea-level rise. It is expected that erosion of the sea-edge results in cliff formation and a loss of man-made mainland and barrier island salt marshes (Dijkema et al. 1990; Dijkema 1994; Bakker et al. 1997). Changed hydrodynamic conditions and sediment characteristics can lead to a negative sedimentation balance (Bartholomä and Flemming 1996). In accreting regions, salt marshes can survive due to topographical change.

The mainland salt marshes bordered by dykes have no sufficient regeneration space to remain and to allow a shift of species. Thus, a loss of a part of the salt marshes can be expected. Species of the lower salt marsh show a higher elasticity than the species from the upper salt marsh. Therefore, the vulnerability of salt marshes corresponds with the increasing elevation level. A tendency to earlier succession stages will be possible in salt marshes (Bazzaz 1996). The productivity of species will decrease with decreasing nutrient availability and with the destruction of competitive tall growing species.

Ecological and taxonomic diversity will decrease, because species richness is negatively correlated with stress that increases with a decrease in salt marsh elevation (Brewer et al. 1997).

References

Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge

Armstrong W, Justin SHFW, Beckett PM, Lythe S (1991) Root adaptation to soil water logging. Aquat Bot 39:57–73

Armstrong W, Brändl R, Jackson MB (1994) Mechanisms of flood tolerance in plants. Acta Botanica Neerlandica 43:307–358

Bakker JP (1989) Nature management by grazing and cutting. Kluwer, Dordrecht

Bakker JP, Esselink P, van der Wal R, Dijkema K (1997) Options for restoration and management of coastal salt marshes in Europe. In: Urbanska KM, Webb NR, Edwards PJ (eds) Restoration Ecology and sustainable development. Cambridge University Press, Cambridge, pp 286–322

Bartholomä A, Flemming BW (1996) Zur Sedimentdynamik in den ostfriesischen Rückseitenwatten und den Veränderungen durch natürliche und anthropogene Einflüsse. Schriftenreihe der Schutzgemeinschaft Deutsche Nordseeküste 1:70–89

Bazzaz FA (1996) Plants in changing environments: linking physiology, population, and community ecology. Cambridge University Press, Cambridge, p 312

Bertness MD, Hacker SD (1994) Physical stress and positive associations among marsh plants. Am Nat 144:363–372

Beukema JJ, Wolff WJ, Brouns JJWM (1990) Expected effects of climatic change on marine ecosystems. Kluwer, Dordrecht, p 221

Bockelmann A-C, Neuhaus R (1999) Competitive exclusion of *Elymus athericus* from a high stress habitat in a European salt marsh. J Ecol 87:503–513

Brändle R (1996) Überflutung und Sauerstoffmangel. In: Brunold C, Rüegsegger A, Brändle R (eds) Stress bei Pflanzen. Haupt, Bern, pp 133–148

Brewer S, Levine JM, Bertness MD (1997) Effects of biomass removal and elevation on species richness in a New England salt marsh. Oikos 80:333–341

Cooper A (1982) The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. New Phytol 90:263–275

DeLaune RD, Pezeshki SR, Patrick WH Jr (1993) Response of coastal vegetation to flooding and salinity: a case study in the rapidly subsiding Mississippi River deltaic plain, USA. In: Jackson MB, Black CR (eds) Interacting stresses on plants in a changing climate. Springer, Berlin, pp 211–230

Dierssen K (1993) Mögliche Auswirkungen von Klimaänderungen auf die Vegetationsentwicklung in Küsten-Salzrasen. In: Schellnhuber H-J, Sterr H (eds) Klimaänderung und Küste. Einblick ins Treibhaus, Springer, pp 189–195

Dijkema KS (1994) Auswirkung des Meeresspiegelanstieges auf die Salzwiesen. In: Lozán JL, Rachor E, Reise K, von Westernhagen H, Lenz W (eds) Warnsignale aus dem Wattenmeer. Blackwell, Berlin, pp 196–200

Dijkema KS, Bossinade JH, Bouwsema P, de Gloopper RJ (1990) Salt marshes in the Netherlands Wadden Sea: rising high-tide levels and accretion enhancement. In: Beukema JJM, Wolff WJ, Brouns JWM (eds) Expected effects of climatic change on marine coastal ecosystems. Kluwer Academic Press, Dordrecht, pp 173–188

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1991) Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18:248

Gerlach A (1999) Winter driftline debris on the Wadden island of Mellum, Germany, distribution, quantity and decomposition. Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen 44(2–3):707–724

Grime JP, Hogson JG, Hunt R (1988) Comparative plant ecology. Unwin Hyman, London

Groenendijk AM, Spieksma JG, Vink-Lievaart MA (1987) Growth and interactions of salt-marsh species under different flooding regimes. In: Huiskes AHL, Blom CWPM, Rozema J (eds) Vegetation between land and sea. Geobotany, vol 11, pp 236–259

Huiskes AHL (1990) Possible effect of sea level changes on salt-marsh vegetation. In: Beukema JJ, Wolff WJ, Brouns JJWM (eds) Expected effects of climatic change on marine ecosystems. Kluwer, Dordrecht, pp 167–172

Jefferies RL, Davy AJ, Rudmik T (1979) The growth strategies of coastal halophytes. In: Jefferies RL, Davy AJ (eds) Ecological processes in coastal environments. Blackwell, Oxford, pp 243–268

Justin SHFW, Armstrong W (1987) The anatomical characteristics of roots and plant response to soil flooding. New Phytol 106:465–495

Keddy PA (1990) The use of functional as opposed to phylogenetic systematics: A first step in predictive ecology. In: Kawano S (ed) Biological approaches and evolutionary trends in plants. Academic Press, London, pp 388–406

Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. J Veg Sci 3:157–164

Kiehl K, Esselink P, Bakker JP (1997) Nutrient limitation and plant species composition in temperate salt marshes. Oecologia 111:325–330

Levine JM, Brewer JS, Bertness MD (1998) Nutrients, competition and plant zonation in a New England salt marsh. J Ecol 86:285–292

Lozán JL, Graßl H, Hupfer P (eds) (1998) Warnsignal Klima. Das Klima des 21. Jahrhunderts. Wissenschaftliche Auswertungen, Hamburg

Mueller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation ecology. Wiley, New York

Rozema J, Scholten MCT, Blaauw PA, Diggelen J (1988) Distribution limits and physiological tolerances with particular reference to the salt marsh environment. In: Davy AJ, Hutchings MJ, Watkinson AR (eds) Plant population ecology. Blackwell, Oxford, pp 137–164

Salzman AG, Parker MA (1985) Neighbors ameliorate local salinity stress for rhizomatous plant in a heterogeneous environment. Oecologia 65:273–277

Schaminée JHJ, Weeda EJ, Westhoff V (1998) De vegetatie van Nederland. Deel 4: Plantengemeenschappen van de kust en van binnenlandse pioniermilieus. In: Opulus, Upsala

Schellnhuber H-J, Sterr H (1993) Klimaänderung und Küste. Einblick ins Treibhaus, Springer

Snow AA, Vince SW (1984) Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. J Ecol 72:669–684

Stalter R, Batson WT (1969) Transplantation of salt marsh vegetation, Georgetown, South Carolina. Ecology 50:1087–1089

Sterr H (1998) Auswirkung auf den Meeresspiegel. In: Lozán JL, Graßl H, Hupfer P (eds) Warnsignal Klima. Das Klima des, vol 21. Jahrhunderts. Wissenschaftliche Auswertungen, Hamburg, pp 201–206

Ter Braak CJF (1987) CANOCO, a FORTRAN program for Canonical Community Ordination. Wageningen, ITI-TNO

Ungar I (1991) Ecophysiology of vascular halophytes. CRC Press, Boca Raton

van Diggelen J (1991) Effects of inundation stress on salt marsh halophytes. In: Rozema J, Verkleij JAC (eds) Ecological responses to environmental stresses. Tasks for Vegetation Science 22:62–75

van Wijnen HJ, Bakker JP (1999) Nitrogen and phosphorus limitation in a coastal barrier salt marsh: the implications for vegetation succession. J Ecol 87:265–272

von Glahn H, Dahmen R, von Lemm R, Wolff D (1989) Vegetationssystematische Untersuchungen und großmaßstäbliche Vegetationskartierungen im Außengroden der niedersächsichen Nordseeküste. Drosera 89:145–168 von Storch H, Schnur R, Zorita E (1998) Anwendungsorientierte Szenarien für den norddeutschen Küstenbereich. Abschlußbericht 01 LK9510/0 unpublished

Warrick RA, Barrow EM, Wigley TML (eds) (1993) Climate and Sea Level Change. Cambridge University Press, Cambridge

Warrick RA, Le Provost C, Meier MF, Oerlemans J, Woodworth PL (1996) Changes in sea level. In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) Climate change 1995. The science of climate change. Contribution of Working Group I to the second assessment report of the Intergovernmental Panel of Climate Change. Cambridge University Press, Cambridge, pp 359–406

Wisskirchen R, Haeupler H (1998) Standardliste der Farn- und Blütenpflanzen Deutschlands. Ulmer, Stuttgart

Effects of Sedimentation and Erosion on the Development of Vegetation

19

Irene Vagts

Abstract

The future change in inundation frequencies as cause of the climate change will affect sedimentation processes at the North Sea salt marshes. An experimental approach was performed to find the reaction on higher erosion by storm surges or higher sedimentation on the vegetation. The re-colonisation of plants on plots with experimental supply of sediments as well as on plots with totally removed vegetation was analysed. Re-colonisation after high sedimentation was significantly faster after erosion. Re-colonisation on sediment plots required only some weeks, whereas it required one or two vegetation periods on erosion areas. Vegetation on transplanted erosion plots developed similar associations as those adjacent to control plots. In general, the cover was lower on the erosion plots than on the control areas.

19.1 Introduction

The extension of salt marshes depends on the quantity and quality of sediments, on sedimentation dynamics, and the resulting sedimentation—resulting in an erosion balance. A positive sedimentation balance leads to horizontal or vertical salt marsh growth (Allen and Pye 1992).

Micro-algae and Cyanobacteria perform the first biotic stabilisation of sediments (Packham and Willis 1997). The quality of sediments engenders the species assemblage and the structure of salt marshes. The stabilisation of soils and sediment

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capture by the settling of plants act against processes of erosion (Larcher et al. 1985; Grumblat 1987). Sedimentation and erosion are very important for communities of coastal habitats. This is true, in particular, for glasswort mudflats and salt marshes. If sand drift and erosion by wind are included, dune communities are also affected by sedimentation and erosion.

A positive sediment balance in salt marshes existed in many areas up to the present, in particular, at the North Sea Coast (Grumblat 1987), although geographical and zonal differences exist. Sedimentation and erosion depend on the exposition of the habitat against sea and wind, elevation, and vegetation cover (Gray 1992). Humans influence the system by digging tide-creeks, building brushwood groynes in the foreland, establishing sand trapping facilities, and planting grasses in the dunes. Sedimentation also highly depends on grazing management as grazed salt marshes had lower sedimentation than ungrazed saltmarshes (Andresen et al. 1990).

Climate change will impact the conditions of sedimentation and erosion in the future. An important question will be whether sedimentation keeps pace with erosion.

A short-term relocation of sediments may be caused by ice drift or storm surges. Permanent changes of sedimentation may be triggered by an increase of energy input (sediment composition and morphology) (Bartholomä and Flemming 1996) and will have consequences for salt marshes.

The extant dikes restrict sediment dislocations. Thus, it is questionable whether the present existing salt marshes may maintain their dimensions (Bartholomä and Flemming 1996; Dijkema 1997; Neuhaus et al. 1998), because the predicted rising storm surges will increase erosion.

19.2 Methods

The influence of sedimentation on the development of vegetation was studied by field experiments and surveys as well as lab work.

After a heavy storm surge in March 1998, high amounts of sediments were deposited in parts of the study area of the Wursten Coast. The re-colonisation of plants in these areas was registered using labelled plots (storm surge plots).

Study sites under natural conditions were compared with those filled up experimentally with sediments.

Sediments were taken from the nearby mudflat and were used to fill up plots at different levels of the salt marsh (sediment plots, control plots). Vegetation dynamics were studied under these conditions (Hölscher 1999). The focus of this experiment was to monitor the regeneration capability of plant species, populations, and vegetation composition as well as the speed of resettlement. Experimental sites followed a gradient in relation to the MHW level, dominated by *Spartina anglica, Puccinellia maritima, Festuca rubra,* and *Elymus athericus.*

The input of diaspores by sediment deposition was registered using the method of germination on outdoor beds of the Biological Garden of the University of Bremen.

The rate of sedimentation was studied at the Wursten Coast in the course of the years 1998 and 1999 for the evaluation of the actual development in the foreland.

Erosion was investigated in spring 1997 when the vegetation was completely destroyed on plots along an elevation gradient by removing the total biomass above the ground together with the soil layer of the upper two cm. These plots were transplanted to lower areas along a vertical gradient. Regeneration of the plants and the vegetation was studied from 1997 to 1999 (for more details, see Chap. 18).

19.3 Results

19.3.1 Sedimentation

Vegetation development differed strongly depending on the elevation above MHW. Within a few weeks, re-colonisation of areas disturbed by artificial sedimentation was found for many species.

19.3.1.1 Elevation-Dependent Development

Low elevation between +1.5 to +1.7 m NN, dominance of *Spartina anglica*.

In general, the artificially filled sediments were washed away at these low-level habitats. Therefore, little disturbance was found. At places where the additional sediments remained until summer, jaggy vegetation developed partly with a strengthened incidence of the therophytes *Atriplex prostrata* and *Salicornia europaea* agg. *Puccinellia maritima* and *Spartina anglica* built up a low coverage at the waste ground. *Suaeda maritima* occurred frequently. After a rapid regeneration, the vegetation of these areas equalled those of the surroundings and no changes in phenology were found.

Elevation between +1.8 and + 1.9 m NN, dominance of *Puccinellia maritima*.

The deposited sediments persisted over the whole vegetation period as a hardened layer of about 1–3 mm thickness. Some plants penetrated this layer by vertical growth using new built desiccation cracks. Analogous vegetation, such as in the surrounding contact zone, grew up on the experimental plots during the vegetation period.

A rapid regeneration by *Aster tripolium, Glaux maritima, Plantago maritima, Suaeda maritima,* and *Triglochin maritimum* was found on the waste ground. Therophyte plant species were enhanced, in particular, *Atriplex* species (mainly *Atriplex prostrata*) and *Suaeda maritima. Atriplex prostrata* grew remarkably on the experimental plots resulting in higher coverage and higher growth. Compared with control areas, flowering of *Suaeda maritima* shifted for 1 month from August to July on experimental plots.

Grazing had an important impact on vegetation of this elevation level. Because of heterogeneous grazing intensity, particularly in the control area, this effect is reflected in the vegetation height and in the number of plants with parts eaten away. A quick reaction was found for *Puccinellia maritima*, *Festuca rubra*, and *Glaux maritima* depending on the cover before. Grass species spread specifically by vertical growth through sediment layers. Compared with the control plots, an insular pattern developed at experimental plots with numerous specimens of *Salicornia, Suaeda,* and *Glaux.* In particular, the development of *Salicornia* und *Suaeda* was favoured.

The thickness (2–3 cm) of the artificially deposited mudflat layer persisted. The surface was covered by an irregular pattern of cracks. Vegetation-free areas were rapidly re-colonised in the course of the vegetation period. At this elevation, *Atriplex* species were enhanced, too. A higher number of seedlings of therophytes, such as *Salicornia, Suaeda*, and *Cochlearia*, were found. *Puccinellia maritima, Spergularia,* and *Suaeda* were able to regenerate quickly.

Elevation at +2.0 m, dominated by *Elymus athericus*.

The thickness of 2–3 cm of the deposited mudflat sediments persisted during the vegetation period as a cracky layer. *Elymus athericus* dominated on the control areas already in spring. The vegetation structure of experimental plots differed remarkably. The regeneration power of *Elymus athericus* is weak which can be derived from the lower cover than in the control. In contrast to control areas, *Elymus* could not built-up dominance, which consequently led to a shift of species prevalence. *Artemisia maritima, Atriplex prostrata*, *A. littoralis, Festuca rubra,* and *Suaeda maritima* exploited the space and light offer.

The artificial deposition of mudflat sediments to the experimental plots resulted in a direct destruction of the vegetation, but also changed the habitat conditions by addition of nutrients, on the one hand, and a reduction of nutrient uptake, on the other hand, by the destruction of the vegetation, wetness, and salinity. Thus, therophytes and nitrogen indicators (*Atriplex littoralis, Atriplex prostrata*, *Suaeda maritima*) were enhanced.

The deposited mudflat sediments remained longer as a layer on higher elevations with fewer floods than at lower elevations with numerous floods. Therefore, the number of disturbances differs along the elevation gradient.

A vegetative colonisation happened by rapid vertical growth through the artificial sediment layer by stolones as well as by an input of vegetative diaspores that were washed out from surrounding habitats. Short-living and rapid growing species, such as therophytes and hemi-cryptophytes, were enhanced. Tolerance against sediment cover differed among species. In general, those species, which were dominant before the experimental disturbance, displayed a high regeneration power. Bare soil areas were colonised by species of sub-layers when the formerly dominant species formed jaggy stocks. *Elymus athericus* was found to be the species that was most sensitive to disturbances.

19.3.1.2 Diaspores in the Sediment

In the mudflat samples, therophytes (*Salicornia europaea* agg. 53%, *Suaeda maritima* 29%) account for the main part of diaspores. All other species had less than 10%.

19.3.1.3 Deposit of Sediments by a Heavy Storm Surge

A heavy storm surge in winter 1998 brought up a thick sediment layer on the salt marshes of the study area Oxstedt Fallow (Oxstedter Brache). A rapid development of the vegetation started in the same manner as on the experimental plots. Similar vegetation as in the surroundings developed after one vegetation period. Seedlings of *Atriplex prostrata*, *A. littoralis, Suaeda maritima*, *Salicornia europaea* agg., and *Aster tripolium* could be detected on the affected areas. Re-colonisation after the disturbance event was significantly faster than on the erosion areas. Re-colonisation required only some weeks, whereas it required one or two vegetation periods on erosion areas.

19.3.1.4 Rate of Sedimentation

The balance of sedimentation was positive in the study area (Wursten Coast). Our own measurements gave similar results as found by Arens et al. (1997), who found a sedimentation between +1 m above NN to more than +2 m NN within 37 years at Cappel foreland, which equals an average rate of 2.7 mm per year. In our 15-month period, seasonal fluctuations occur due to shrinking and swelling processes. The maximum deposit of 4.91 cm (from February 1998 to June 1999) was found in higher elevations (study area Oxstedt at 2.4 m NN, Berensch at +1.7 m NN). Outstanding high rates are due to storm surges like that of February 1998. The sedimentation rate is lower in upper salt marshes with pasture than in those without grazing (Figs. 19.1 and 19.2).

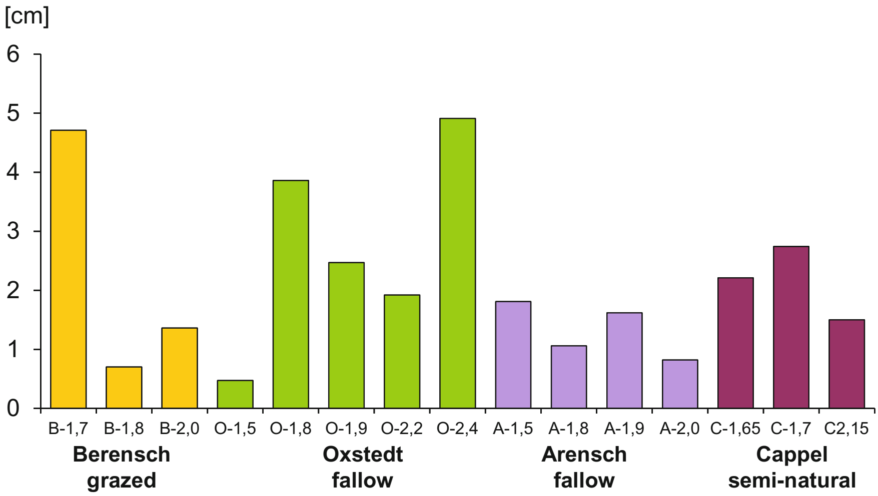

Fig. 19.1 Balance of sedimentation—erosion at sites of the Wursten Coast calculated on the basis of measurements in a 15-month period

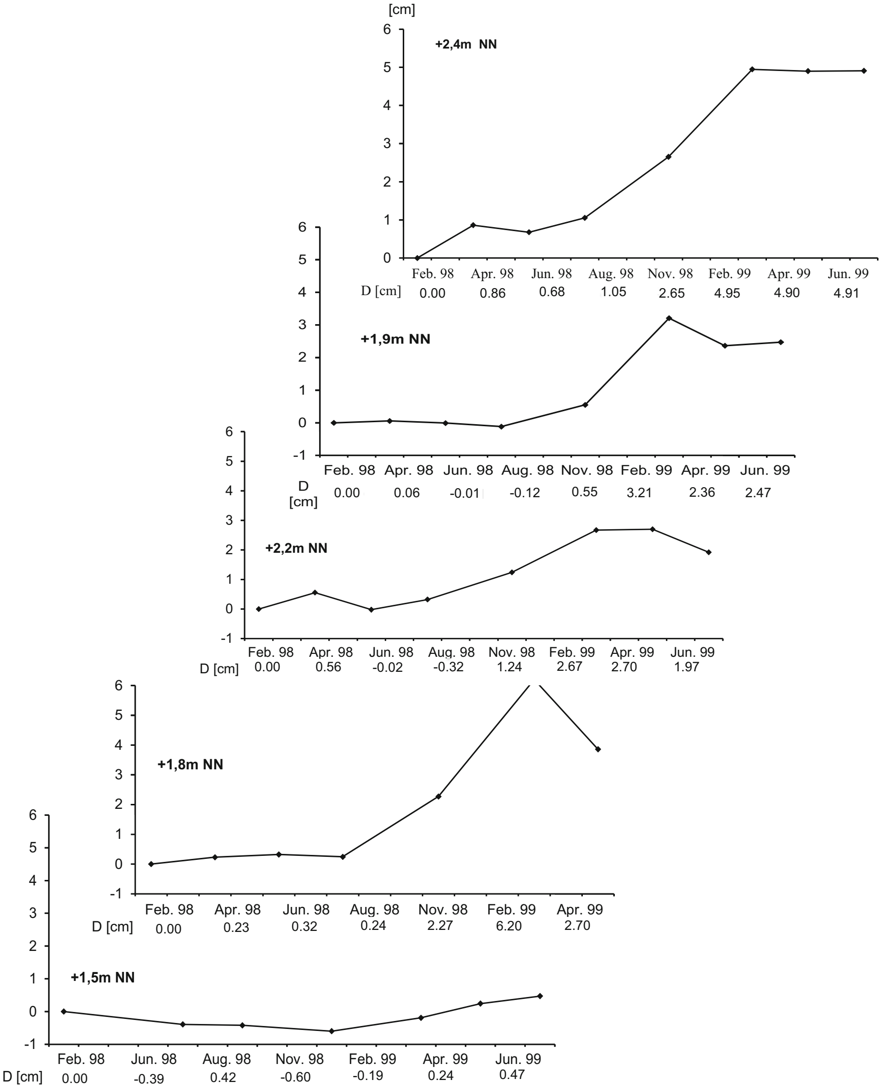

Fig. 19.2 Sediment measurements along an elevation gradient at Oxstedt Fallow

19.3.2 Erosion

The vegetation on the transplanted erosion plots explicitly developed similar associations as those adjacent to the plots. In general, the cover was lower on the erosion plots than on the control areas.

Immediately after transplantation and destruction of the vegetation, many perennial species regenerated or immigrated from adjacent sites by stolones or rhizomes.

Species with rapid growth colonised faster than those with lower growth rates. The high reproductive therophytes colonised the bare soil areas in the first spring after disturbance in high specimen numbers. Thus, the therophytes *Salicornia europaea* agg. and *Suaeda maritima* settled on all erosion areas except those in the upper zones (+2.2 m NN).

At the MHW level, Spartina anglica immigrated from the associations around the erosion plot. This species and *Puccinellia maritima* have high cover values and were able to colonise the disturbed areas together with very few other species.

19.3.2.1 Development at Wursten Coast

Elevation of the Puccinellietum maritimae at +1.8 m NN.

Puccinellia maritima, *Glaux maritima*, *Triglochin maritimum*, and *Aster tripolium* were able to regenerate at this elevation. Many species that were transplanted from Armerio-Festucetum into the Puccinellietum displayed an elastic reaction towards the changed environmental conditions. *Festuca rubra* did not regenerate on these erosion plots.

A transition community of Puccinellietum maritimae and Armerio-Festucetum was present in the salt marsh at this elevation under grazing. *Festuca rubra* occurred at this elevation due to pasturing and was able to regenerate on erosion areas under these deviating conditions. It disappeared on erosion plots at +1.8 m NN in the fallow of Oxstedt.

Elevation of the Agropyretum litoralis at +2.4 m NN.

Agropyretum litoralis is dominated by *Elymus athericus*. A very differentiated response to the transplanted erosion plots occurred. *Elymus athericus* showed a poor regeneration on the erosion plots. With increasing degradation of *Elymus athericus*, colonisation of other species increased because of the high space and light resources. The immigration species are those of the adjacent community. Transplantation of the Agropyretum into the Armerio-Festucetum led to a low development of *Elymus athericus* and in return to a strengthened development of *Festuca rubra*. From adjacent Halimionetum portulacoidis vegetation, species repossessed the plot and repressed other immigrating species.

19.3.2.2 Other Conditions

Therophytes (*Salicornia* agg. and *Suaeda maritima*) and fast-growing grasses dominated erosion plots in grazed areas.

In fallow areas, *Spartina anglica* colonised erosion plots at low elevations upcoming from surrounding vegetation. Therophytes, such as *Salicornia* agg. and *Suaeda maritima*, used bare soil areas to colonise depending on the elevation. *Glaux maritima* was already found on all erosion plots in the starting year. It showed a high tendency to spread on plots above +1.8 m NN. *Puccinellia maritima* colonised new established bare soil areas quickly due to its stolones. This process is much faster at low elevations than at higher ones. The settlement starts from surrounding vegetation and by regeneration of damaged stolones of the soil surface.

In waterlogged salt marshes, *Puccinellia maritima* exhibited high cover at all erosion plots. *Salicornia europaea* agg. occurred at open areas but with low cover.

Triglochin regenerated on all erosion plots. *Atriplex portulacoides* immigrated into the upper areas during the last study year. In the upper zones of +2.15 m NN, *Festuca rubra* settlings were not able to spread over the erosion plots.

19.3.2.3 Mellum

The effects of erosion were strong on sandy soils with good aeration at the island of Mellum. Besides *Salicornia stricta*, which dominates the areas at +1.5 m NN, *Limonium vulgare* spread over these erosion plots. Therophytes, such as *Suaeda maritima* and *Salicornia europaea* agg., colonised the bare soil areas quickly, in particular, in the zone at +1.9 m NN with low influence of the sea. *Elymus athericus* was considerably weakened; only a few small growing specimens occurred at this elevation. In contrast, *Atriplex portulacoides* spread on erosion plots of this high elevation. *Festuca rubra* did not gain ground, but stolones of *Puccinellia maritima* and *Glaux maritima* expanded from the surrounding areas.

Deviation in phenology could be documented at the erosion plots. *Elymus athericus* possessed a significantly higher proportion of specimens with fruits. *Puccinellia maritima* flowered on the erosion plots at +1.9 m NN, but not on the control area. The vegetative development of *Aster tripolium* at the erosion plots in the lower salt marsh (+1.5 m NN) was lower than in the control plots. The converse result was found at higher elevation (+1.8 m NN).

19.3.2.4 Ordination

An indirect ordination compared the vegetation data of erosion plots with those of permanent plots. The vegetation of the transplanted erosion plots showed a succession away from the starting point and developed similar patterns as the vegetation in the new surroundings (Fig. 19.3).

19.3.3 Sedimentation and Erosion as Disturbance Processes

A strong sedimentation or erosion event may be interpreted as disturbance producing new habitats free from vegetation (Grime 1979). Deposits of floating refuse and sediment create bare areas that can be re-colonised. Storm surges lead to small or large bare areas within the existing vegetation. In the case of total destruction of the surface biomass, a secondary succession (miniaturised succession) will start (Miles 1978; Grime 1981). By destruction of dominant plants, resources became free for species poor in competition (Denslow 1985) (Figs. 19.4 and 19.5). Disturbance interrupts the exclusion by competition; therefore, it is necessary to sustain species diversity. Disturbances of small areas are found more often than those of large areas (Bazzaz 1983).

Biological and ecological qualities of the formative plant species change in the course of succession on disturbed areas. The vegetation cover increases in height and density; in consequence, the microclimate and reproductive strategies of the plants change. At the starting point, short-living therophytes with a transient seed bank and rapid growing hemi-cryptophytes with stolones colonise the disturbed areas

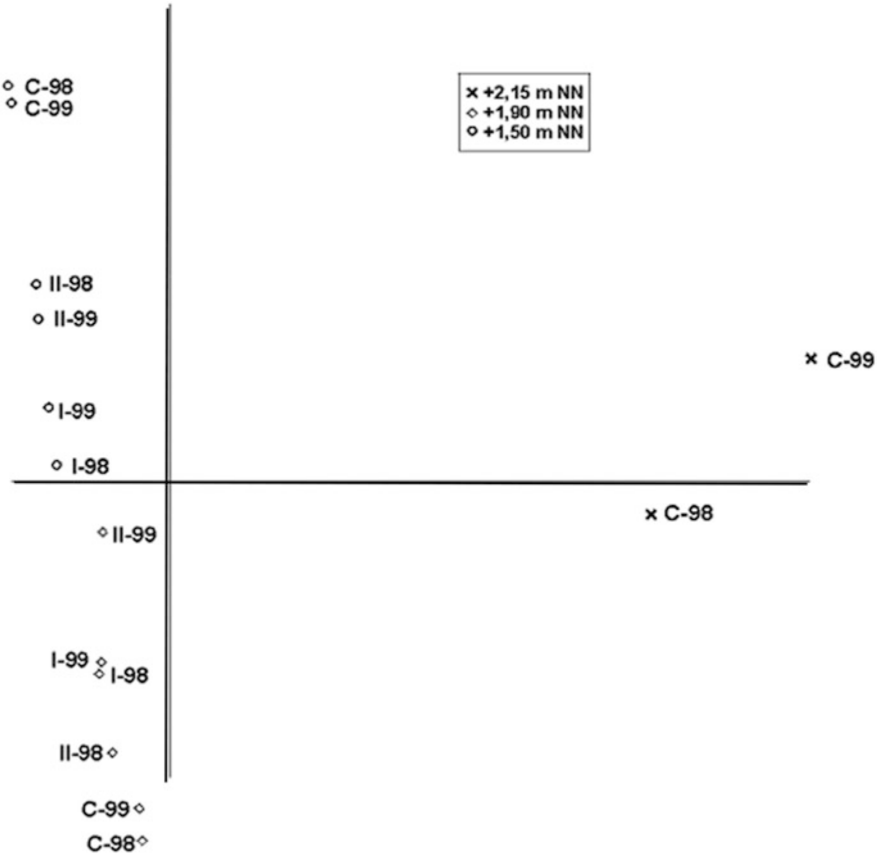

Fig. 19.3 Ordination diagram of the vegetation development under the influence of changed erosion and flooding; *C* control, *I-III* transplanted erosion plots

(Rabotnov 1995). Plants rapidly regenerate on small-disturbed areas. As a consequence of disturbances, interactions between animals and plants also change. Vegetation under sub-optimal conditions may react on grazing differently than that of a large and dense stock implicating a retroaction of the vegetation (Thompson et al. 1997). Space and time selection may also cause changes in the genetic structure.

Vegetation development depends on the dimension and frequency of disturbances. According to Connell (1978), an intermediate degree of disturbance leads to a maximum species diversity. Small gaps in the stock were colonised by species of adjacent habitats, whereas large gaps were settled by species that migrate over long distances. Systems influenced by disturbances were rapidly colonised by short-living species with high production of seeds and a transient seed bank (ruderals). Slow-growing species need a more stable habitat. Pioneer species were eliminated by perennial species with high competition power in the period of stabilisation after a disturbance event (Grime 1979; Bernhardt 1993). As disturbed

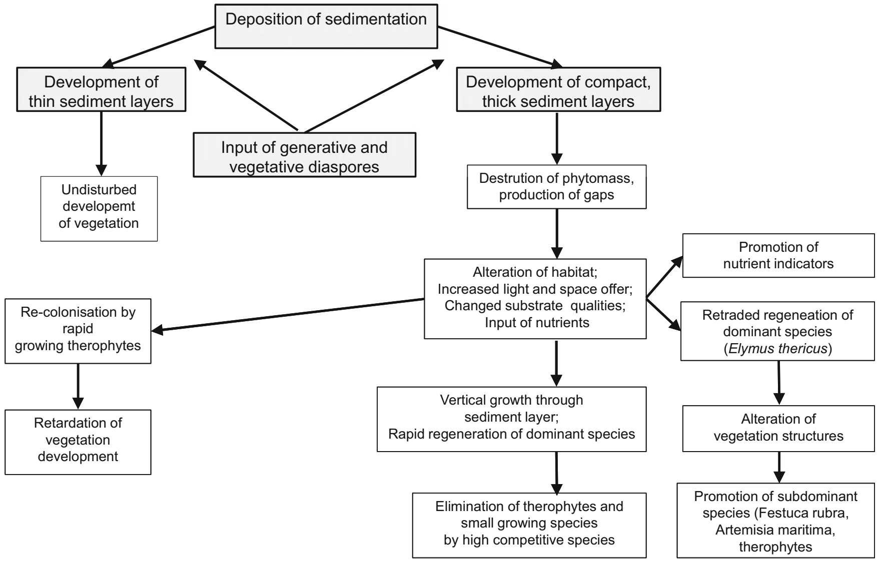

Fig. 19.4 Implications of disturbance processes by sedimentation events in salt marshes

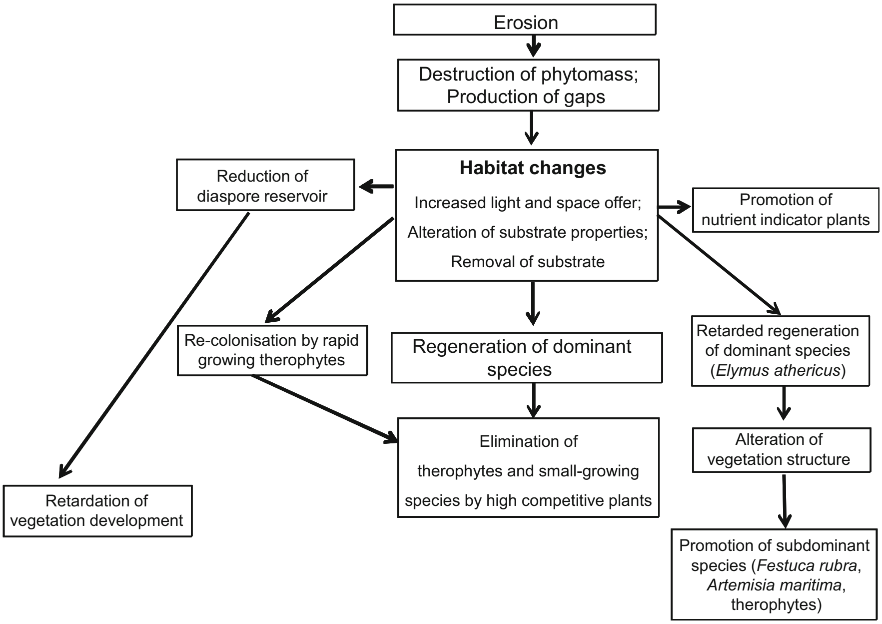

Fig. 19.5 Effects of disturbances by erosion in salt marshes

areas were rapidly re-colonised by lateral dispersal from the adjacent habitats, their vegetation becomes similar to the undisturbed surrounding vegetation (Hartman 1988).

Re-colonisation happened as the interplay between habitat conditions, species qualities, and the reservoir of diaspores. The input of diaspores most importantly influences the succession of the vegetation. The input of diaspores into the tidal foreland is controlled by the floating refuse of diaspores, by wind, and by the sediment.

Fragmentation and restriction of space at sites abundantly covered with vegetation may function as resource limiting factors, and, together with competition, enhance only a few strongly competitive species; thus, a dominant cover eliminates weaker competitors. Further disturbance delivers restricted resources and allows the invasion of pioneer species. The emergence of bare areas gives access to light, water, and nutrients, which may be the limiting factors on sites with dense vegetation (Paine and Levin 1981). Flexibility in architecture and allocation enables plants to make better use of the resources (McConnaughay and Bazzaz 1992).

A higher sedimentation rate leads to short-termed disturbances. Newly created bare places were rapidly re-colonised. Not only the amount of sediment, but also its composition is of crucial importance as could be shown by the studies of Flemming and Nyandwi (1994). They found that a decrease in fine-grained sediment input is correlated with an increase of the sea water level and the dislocation of barrier islands towards the mainland. Moreover, alterations of the sediment composition induce a modification of the habitat. Sandy soils have lower nutrient contents, better air ventilation, and a higher sensitivity against flooding events. Strong erosion may lead to a total loss of salt marsh areas, whereas light erosion offers long-term bare small areas and in consequence, establishments of vegetation patterns with more pioneer plants and successions.

References

Allen JRL, Pye K (eds) (1992) Saltmarshes: morphodynamics, conservation and engineering significance. Cambridge University Press, Cambridge

Andresen H, Bakker JP, Brongers M, Heydemann B, Irmler U (1990) Long-term changes of salt marsh communities by cattle grazing. Vegetatio 89:137–148

Arens SE, Heddinga P, Meyer C, Ragutzki G (1997) Untersuchungen zur Vorlandsentwicklung an der Wurster Küste. Forschungsstelle Küste (NLÖ), Wilhelmshaven. (unpublished report)

Bartholomä A, Flemming BW (1996) Zur Sedimentdynamik in den ostfriesischen Rückseitenwatten und den Veränderungen durch natürliche und anthropogene Einflüsse. Schriftenreihe der Schutzgemeinschaft Deutsche Nordseeküste 1:70–89

Bazzaz FA (1983) Characteristics of populations in relation to disturbance in natural and manmodified ecosystems. In: Mooney HA, Gordon M (eds) Disturbance and ecosystems: components of response. Springer, Heidelberg, pp 259–276

Bernhardt K-G (1993) Untersuchungen zur Besiedlung und Dynamik der Vegetation von Sand-und Schlickpionierstandorten. Dissertationes Botanicae 202. J. Cramer, Stuttgart

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Denslow JS (1985) Disturbance-mediated coexistence of species. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, London, pp 307–321

Dijkema KS (1997) Impact prognosis for salt marshes from subsidence by gas extraction in the Wadden Sea. J Coast Res 13:1294–1304

Flemming BW, Nyandwi N (1994) Land reclamation as a cause of fine-grained sediment depletion in backbarrier tidal flats (Southern North Sea). Neth J Aquat Ecol 28:299–307

Gray AJ (1992) Saltmarsh plant ecology: zonation and succession revisited. In: Allen JR, Pye K (eds) Saltmarshes: morphodynamics, conservation and engineering significance. Cambridge University Press, Cambridge, pp 63–79

Grime JP (1979) Plant strategies and vegetation processes. Wiley, Chichester

Grime JP (1981) The role of seed dormancy in vegetation dynamics. Ann Appl Biol 98:555–558

Grumblat J-D (1987) Auswirkungen von Beweidungsformen und Mahd auf sedimentation und erosion. In: Kempf N, Lamp J, Prokosch P (eds) Salzwiesen: Geformt von Küstenschutz, Landwirtschaft oder Natur? Tagungsband der Umweltstiftung WWF-Deutschland, 2nd edn. Husum Druck- und Verlagsgesellschaft, Husum, pp 375–380

Hartman JM (1988) Recolonisation of small disturbance patches in a New England salt marsh. Am J Bot 75:1625–1631

Hölscher T (1999) Regenerationsverhalten und jahreszeitliche Entwicklung von Gefäßpflanzenarten der Wurster Küste unter experimentell veränderten Sedimentationsbedingungen. Unveröffentlichte Diplomarbeit Fachbereich 2 (Biologie) Universität Bremen

Larcher W, Höbl E, Fuchs T, Ulmer VE (1985) The influence of vegetation on erosion and accretion in salt marshes of the Oosterschelde, The Netherlands. In: Van Eerdt MM (ed) Ecology of coastal vegetation, vol 62. Dordrecht, Stuttgart, pp 367–373

McConnaughay KDM, Bazzaz FA (1992) The occupation and fragmentation of space: consequences of neighbouring shoots. Funct Ecol 6:711–718

Miles J (1978) Vegetation dynamics. Chapman and Hall, London

Neuhaus R, Dijkema K, Reinke HD (1998) Die Gefährdung der Flora und Fauna an Küsten durch den Meeresspiegelanstieg. In: Lozán JL, Graßl H, Hupfer P (eds) Warnsignal Klima. Das Klima des 21. Jahrhunderts. Wissenschaftliche Auswertungen, Hamburg, pp 313–317

Packham JR, Willis AJ (1997) Ecology of dunes, salt marsh and shingle. Chapman & Hall, London

Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and dynamics of pattern. Ecol Monogr 51:145–178

Rabotnov T (1995) Phytozönologie–Struktur und Dynamik natürlicher Ökosysteme. UTB–Große Reihe. Aus dem Russischen von A. Netschajev. Überarbeitung des deutschen Textes. Feddes Repertorium 106(5–8):494

Thompson K, Bakker JP, Bekker RM (1997) The soil seed banks of North West Europe. In: Methodology, density and longevity. Cambrige University Press

Tide Simulation Experiment

20

Ulrich Irmler

Abstract

An experimental approach was performed under controlled laboratory conditions to find the effects of the increasing sea level on two carabid species. Inundation frequencies were executed in three basins with transplanted salt marsh. The inundation frequencies were arranged according to the two climate scenarios and a control basin under present inundation conditions. The results showed that the two species *Pogonus chalceus* and *Dicheirotrichus gustavii* reacted differently on the changed inundation scenarios. A moderate increase of the sea level will affect no significant reactions. On heavy increase both species will evade to higher zones. In *Dicheirotrichus gustavii* this evasion is weak but combined with significant higher activity.

20.1 Introduction

As can be seen from the field data (Chaps. 14 and 28), flooding is a major parameter which induces the zonation of most spider and carabid species. Multiple adaptations develop to overcome the time of submergence (Chap. 11). From the field data, however, the reaction of species on changing tide dynamics cannot be derived. Thus, an experiment was performed which combines field conditions in salt grassland with artificially induced variable tide dynamics. As carabid beetles showed a higher segregated zonation due to flooding in salt grasslands and they are easier to handle in mark-and-re-catch experiments than spiders, only carabid species were used in this experiment, which investigates the influence of future flooding dynamics on the

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fauna of low elevated salt grassland. Two main questions are investigated by the experiment: (i) Do higher tides result in a species shift to higher elevations? (ii) Do carabid species react on higher tides with changing movement behaviour?

20.2 Experimental Design

The two ground beetle species—*Dicheirotrichus gustavii* and *Pogonus chalceus*—were selected in order to study their reaction to artificial tide dynamics. The experiment was performed in three 5 x 5 m basins during 1999 on the campus of Kiel University (Figs. 20.1 and 20.2). The basins were planted with salt marsh sods in 1998, a year before the experiment started, to have similar vegetation conditions as in the field. They were connected with a salt water tank. The salt water had a salinity as usually found in the North Sea (Chap. 7) and was pumped from this tank into the basins under controlled conditions to simulate the expansion of the flooded area and the time of flooding. The basin's ground had a sloping floor to guarantee a continuous flooding from the low edge to the high edge that was 50 cm higher in elevation. Water inflow and outflow was regulated separately for each basin to provide different flooding conditions. The simulated tide conditions referred to the three scenarios of sea level change for the year 2050 (Chap. 2): Scenario (1) assumes no additional human impact and proposes a sea level increase of 15 cm plus 10 cm at higher tides; Scenario (2) assumes low additional human impact and proposes a sea level increase of 35 cm plus 20 cm at higher tides; and Scenario (3) assumes high additional human impact and proposes a sea level increase of 55 cm plus 30 cm at higher tides.

Fig. 20.1 One of the three tide simulation basins with the control panel in the centre for flooding regulation. The salt water tank is located under the panel

Fig. 20.2 Tide simulation basin half-filled at weekly flood conditions for scenario 1

Concerning the official tide measurements of the gauge at Friedrichskoog (54°01.41’N, 8°50.13′E), salt marshes at an elevation of 20 cm MHW are flooded between three and four times a week, on average. At an elevation of both 40 cm and 60 cm MHW, it results in 0.9 times and 0.7 times per week, respectively. Estimating the simulated tides of the three scenarios at a site of approximately 60 cm MHW elevation in the middle of the basin’s slope, the following tide conditions were established in the basins:

Basin 1: one flood per week filling half of the basin with salt water simulates the conditions of scenario 1;

Basin 2: two floods per week simulate the conditions of scenario 2. The basin was half-filled and three quarters filled during the two separate floods;

Basin 3: three floods per week simulate conditions of scenario 3. The basin was half-filled, three quarters filled and totally filled during the three separate floods.

Each basin was divided into five zones and three columns to differentiate 15 quadrants. The lowest zone was permanently flooded, while the remaining four zones were provided with pitfall traps. The distance between traps was 1 m in the vertical and 1.25 m in the horizontal direction. The pitfall traps were empty without conservation liquid to catch specimens alive. The caught specimens were released for future re-catch. Each basin was stocked with both 154 and 84 *Pogonus* and *Dicheirotrichus* marked specimens, respectively. Specimens were individually marked by milled points on the elytra. Additionally, 172 unmarked *Dicheirotrichus* specimens were also exposed, because marking was impossible due to the soft elytra. Marking of specimens was performed using the scheme described by Mühlenberg (1993), which enables the marking of up to 1000 individual specimens. Pitfall traps were the same as used for the catches in the field (Chap. 14). Sampling periods were set at weekly intervals between June and September and pitfall traps were controlled every second day during the sampling periods.

In addition to the occurrence of the specimens in one of the four zones, the direction of their movement was determined. Only specimens that were caught at least two times were taken into account. A specimen that was found in two vertically adjacent pitfall traps was assumed to use two zones, whereas a specimen found in horizontally adjacent pitfall traps was assumed to use two columns. Therefore, migration in a vertical direction refers to the number of used zones, while the number of used columns represents a horizontal movement direction. The radius of activity was measured using the distance between pitfall traps of re-caught individuals per time and activity by using the relation between total catch to total population density.

20.3 Results

The number of exposed specimens, catch, and re-catch results is listed in Table 20.1. As can be seen from the total catch, in some basins more specimens were caught than were exposed at the beginning of the experiment, indicating that a number of specimens was already introduced with the salt marsh sods. The number of re-caught specimens differed considerably between the three basins, in particular for *Dicheirotrichus gustavii*. In basins 1 and 2, the low number of specimens that was only caught a few times more than once prevents a further statistical analysis of used zones and columns for this species.

In the field, *D. gustavii* and *P. chalceus* colonised elevation levels between approximately 40 and 50 cm above MHW (Irmler et al. 2002). This elevation preference for low elevated salt marshes was also realised in the basins with the tide conditions of scenario 1 (Table 20.2, Fig. 20.3). *D. gustavii* was most frequently found in slightly higher elevations at zone three, whereas *P. chalceus* was more often recorded at slightly lower elevations between zones two and three. It may be assumed that this difference reflects the slight difference in the field, where *P. chalceus* was found at 44 cm above MHW, on average, while *D. gustavii* was

Table 20.1 Results of exposed and caught specimens of the two investigated ground beetle species

	Dicheirotrichus gustavii			*Pogonus chalceus*		
	Basin 1	Basin 2	Basin 3	Basin 1	Basin 2	Basin 3
Exposed (marked/unmarked)	84/172	84/172	84/172	154/0	154/0	154/0
Total catch	160	208	432	120	115	198
Re-catch of marked specimens	25	28	82	91	96	92
Re-catch more than once	3	8	34	28	34	36

Table 20.2 Results of colonised zones and vertical and horizontal movement of the two investigated ground beetles

	Basin 1		Basin 2		Basin 3	
	Mean	SD	Mean	SD	Mean	SD
Pogonus chalceus						
Used zone	2.0	0.8	1.9	0.7	2.8*	0.9*
Used number of zones	1.8	0.8	2.1	0.6	2.1	0.8
Used number of columns	2.0	0.8	2.2	0.8	2.0	0.8
Radius of movement (m day^{-1})	0.06	0.05	0.13*	0.14*	0.11*	0.11*
Dicheirotrichus gustavii						
Used zone	3.0	0.5	3.1	0.6	3.6*	0.7*
Used number of zones	1.3	0.6	1.7	0.5	1.7	0.8
Used number of columns	2.0	1.0	2.2	0.4	2.1	0.7
Radius of motion (m day^{-1})	0.09	0.08	0.15	0.19	0.35	0.46

SD Standard deviation; * statistically significant with $p < 0.05$

found at 47 cm above MHW on average (Irmler et al. 2002). For both species, the colonised zones were located at a higher elevation in the basin with more and higher floods corresponding to scenario 3. This difference amounts to approximately 1 zone compared to the basin with the tide conditions of scenario 1. This difference, however, is only significant for the conditions of scenario 3. The number of used zones and columns showed no difference between the three basins. This means that food exploitation is likely the same in all investigated scenarios. In contrast, activity was higher in the basins of scenario 2 and 3. This is at least statistically significant for *P. chalceus*, but it also seems true for *D. gustavii* compared to the conditions of basin 1, although a statistical significance could not be verified due to the low number of re-caught specimens in basin 1.

Considering these results, the following model of reaction to the increasing sea level can be assumed (Fig. 20.3): For tide conditions of scenarios 1 and 2, the two species remain at their mean preferred elevation in the salt marsh, that is, according to Irmler et al. (2002), at an elevation of 44 ± 23 cm MHW for *P. chalceus* and 47 ± 20 cm MHW for *D. gustavii*. The other behavioural difference between the scenarios is reflected by the higher activity in scenarios 2 and 3.

It seems that both species try to remain at their current residence as long as possible. The conditions of scenario 3 seem to be too extreme to maintain this behaviour. A movement to higher elevations is, thus, supposed under these conditions. Nevertheless, a change of behaviour already starts under the conditions of scenario 2 because activity increases. This change of behaviour is certainly a result of more frequent floods and provokes a changed energy balance with a higher demand for food. In scenario 2, this behaviour is clearly obvious. The two species remain at their current elevation, but already increase their activity.

The observed behaviour of the two carabid beetles was also found in *Orchestia gammarellus*, a beach hopper (Amphipoda) species common in salt grasslands. This species was not purposely released for the experiment, but was certainly introduced

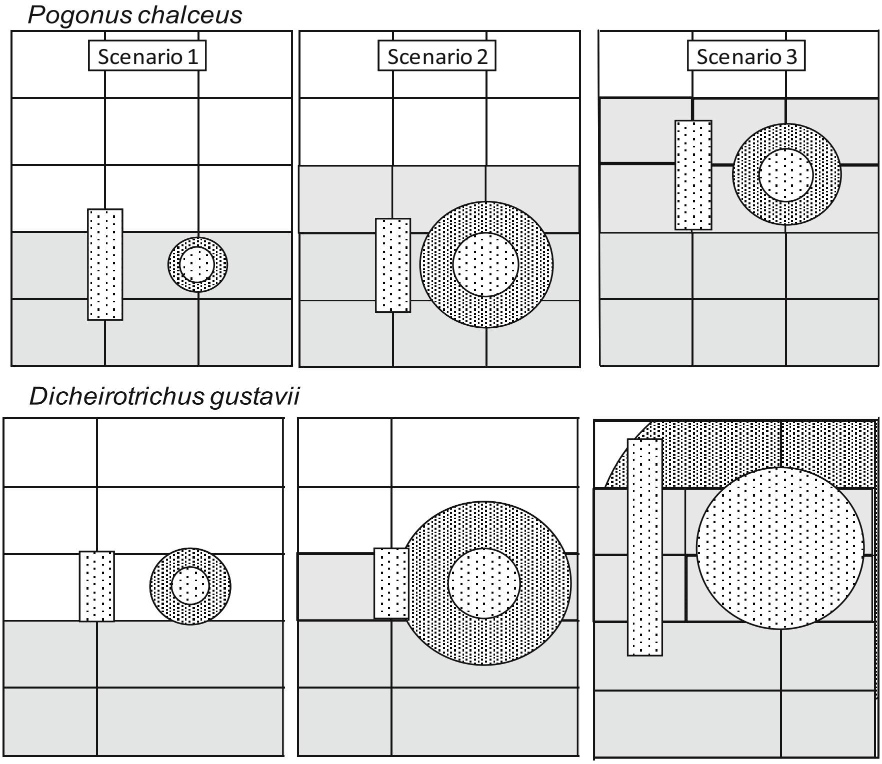

Fig. 20.3 Modelled behaviour of *Pogonus chalceus* and *Dicheirotrichus gustavii* under the tide conditions of the three scenarios. Mean weekly flooded area is indicated by the grey area. The left column indicates the preferred elevation referring to the mean and standard deviation. The circles represent the radius of movement in m week^{-1}. Distance of rows is 1 m; distance between columns is 1.25 m

by the planted grass sods and developed in the basins in high number. *O. gammarellus* showed a similar elevational distribution as the carabid beetles (Fig. 20.4). Under the conditions of scenario 3, the species preferred the highest elevation zones ¾ and 1 (zonation index 3.1), while under scenarios 2 and 1, most specimens were found in the lower zones (zonation index 2.3–2.4). The activity behaviour could not be calculated for *O. gammarellus* because the total number of specimens was unknown.

20.4 Discussion

Species living permanently in the salt grassland of the North Sea coast have to adapt to the tide conditions with frequent flood events. They must be either tolerant against inundations at least for several hours or steadily immigrate from higher elevated sites

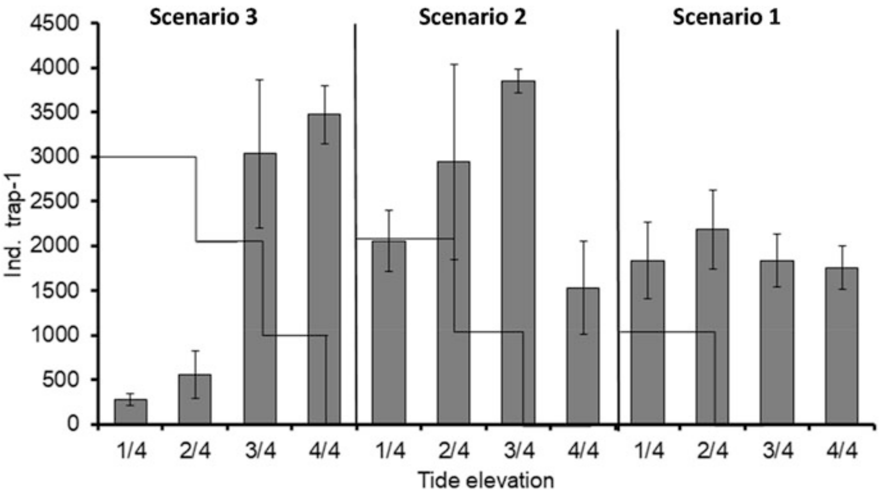

Fig. 20.4 Total catches of *Orchestia gammarellus* in 1999 for the four levels of submergence simulated in the three scenarios with the number of floods (1–3) per week

after extinctions of populations. Tolerance against inundation can be based on morphological, physiological, or behavioural adaptations (Chap. 11). In carabid species, e.g. *Pogonus chalceus*, a dimorphic wing development is temporarily developed in the population with a part of the specimens with well-developed wings and another part with rudimentary wings (Desender 1985). Thus, during unfavourable flooding conditions at least a part of the population can leave the area to inhabit other more favourable sites. Physiological adaptations to the salt grassland were often based on a wide osmotic potential, which was found, for example, in small soil arthropods such as Collembola (Weigmann 1973; Witteveen et al. 1988). Morphological adaptations can be developed by a dense pubescence on the body surface to retain air for respiration during the inundation, such as in *Dicheirotrichus gustavii* (Foster and Treherne 1979). The spider *Erigone longipalpis* survived inundations with salt water of 4 days (Bethge 1973). Many behavioural adaptations are found for beetle species, e.g., survival in soil crevices by *D. gustavii*, with dial activity at night which is suppressed under long submergence (Foster 1983). The higher activity behaviour in scenarios 3 and 2 may be the result of the longer suppression of predation in these basins and the subsequent higher activity when the beetle can predate again under emergence conditions. Tidal dependent migrations were never found (Heydemann 1979). These findings are not astonishing because inundations in the salt grassland are irregular and the distances are too long to avoid submergence by regular migrations.

However, Irmler and Heydemann (1985) found tide dependent shifts of the population in the spider *Erigone longipalpis*, which means that the specimens had not migrated with the tides but the mean elevation of the population shifts depending on the annual mean height of the tides. This shift might be either caused by small distance movements or by the extinction of parts of the population. An increase from approximately 60–120 annual tidal inundations resulted in a shift of 10 cm altitude by the population, which is a high value if the flat surface of the salt grassland is taken into account. The observed change in *Erigone longipalpis* corresponds with the findings in the present experiment and may also explain the population shift of this spider. The behaviour of *Orchestia gammarellus* supported these findings and shows that it is not only true for high active carabid beetles. According to our findings in the experiment, specimens perform small distance movements to higher elevations if tidal inundations become more frequent. In total, the whole population will shift to higher elevated sites. In the experiment, an increase of two floods per week resulted in a shift of approximately 10 cm elevation. Because the mentioned inundation tolerant species nearly inhabit the same area in the salt grassland, this value might reflect the general potential of species living in the lower zone of the salt grassland.

However, a much more severe problem might result from the increasing activity combined with increasing inundation events, because higher activity also means a higher energy supply demand. According to the experiment, activity increases energy demand by two to four times the present level. As the biomass of prey does not increase to the same extent, a decrease of specimens in the population must occur. Thus, both factors—decreasing space by an increasing sea level and increasing activity—will result in a decreasing number of specimens in the population depending on the foraging behaviour of the individual species.

References

Bethge W (1973) Ökologisch-physiologische Untersuchungen über die Bindung von *Erigone longipalpis* (Araneae, Micryphantidae) and das Litoral. Faunistisch-Öologische Mitteilungen 4:223–240

Desender K (1985) Wing dimorphism and reproductive biology in the halobiont carabid beetle *Pogonus chalceus* Marsham (Coleoptera, Carabidae). Biol Jaarboek Dodonaea 53:89–100

Foster WA (1983) Activity rhythms and the tide in a salt marsh beetle *Dicheirotrichus gustavii*. Oecologia 60:111–113

Foster WA, Treherne JE (1979) Adaptive strategies of air-breathing arthropods from marine salt marshes. In: Jeffries RL, Davy AJ (eds) Ecological processes in coastal environments. Blackwell Scientific Publications, Oxford, pp 165–175

Heydemann B (1979) Responses of animals to spatial and temporal environmental heterogeneity within salt marshes. In: Jeffries RL, Davy RJ (eds) Ecological processes in coastal environments. Blackwell, London, pp 145–163

Irmler U, Heydemann B (1985) Populationsdynamik und Produktion von *Erigone longipalpis* (Araneae, Micryphantidae) auf einer Salzwiese Nordwestdeutschlands. Faunistisch-Ökologische Mitteilungen 5:443–454

Irmler U, Heller K, Meyer H, Reinke H-D (2002) Zonation of ground beetles (Coleoptera: Carabidae) and spiders (Araneida) in salt marshes at the North and the Baltic Sea and the impact of the predicted sea level increase. Biodivers Conserv 11:1129–1147

Mühlenberg M (1993) Freilandökologie, 3. Auflage edn. Verlag Quelle & Meyer, Heidelberg, p 512

Weigmann G (1973) Zur Ökologie der Collembolen und Oribatiden im Grenzbereich Land-Meer (Collembola, Insecta–Oribatida, Acari). Z wiss Zool Leipzig 186:295–391

Witteveen J, Verhoef HA, Huipe TEAM (1988) Life history and egg diapause in the intertidal collembolan *Anurida maritima*. Ecol Entomol 13:443–451

Storm Surges as Natural Experiments

21

Wolfgang Dormann and Dietrich Mossakowski

Abstract

Under the future climate conditions an increased number of storm surges are predicted. The present study investigated the effects of storm surges on the salt marsh fauna at Wursten coast. Carabid beetles were recorded before and after a storm event and drifting beetles were collected out off the water during the storm surge 'Kerstin'. Sieving of beetles at the drift line during half an hour resulted in 427 specimens of 21 carabid species. Five out of six special salt marsh species suffered in the year after the storm surge but with variance depending on site and elevation, only *Dicheirotrichus gustavii* showed partly an increase in numbers. Storm surges expel carabid beetles from the foreland, the polder, and the main dike.

21.1 Introduction

Storm surges greatly influence the development of coastal regions. Their destructive potential was the reason not only to construct sea walls of about 8–9 m above NN but also to build barrages as well as stone or concrete fortifications at the foot of the dikes in order to prevent flooding and erosion. These measures have a direct and important impact on the habitat and on the dynamics and species composition of arthropods. Figure 21.1 demonstrates a comparison of natural salt marsh habitats with different fortified coasts. The salt marshes of Mellum provide living space for numerous species, which are partly highly adapted to this habitat (Fig. 21.1a, b). In contrast,

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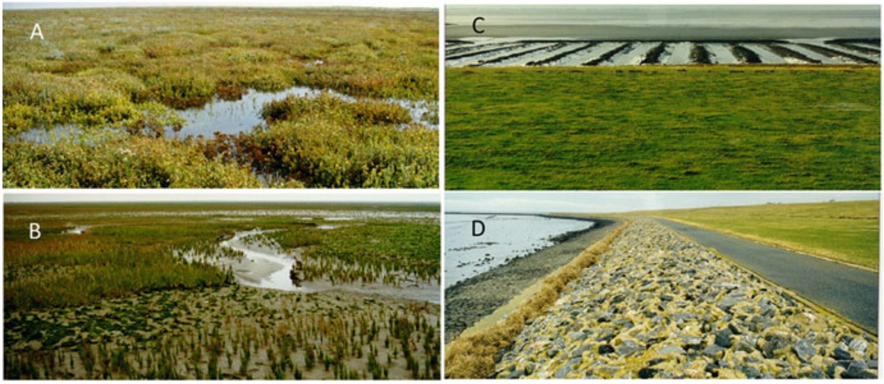

Fig. 21.1 (**a, b**): Natural salt marshes at the island of Mellum, (**c, d**): man-made measures against storm surges at the southern Wursten Coast. (**a**) Large-scale area of salt marsh, (**b**) Lower salt marsh with tide-way, (**c**) Land reclamation area with ditch beds, (**d**) Erosion protection by stone packs

concrete fortification as in parts of the southern Wursten Coast prevent any settlement over many kilometres of the coastline (Fig. 21.1d).

The influence on arthropods was often underestimated because storm surges occur mainly in the winter season (October–February) when most arthropods hibernate in the soil.

Remarkable amounts of sediments can be deposited, in particular at salt marsh cliffs and along the margins of tidal gullies (Chap. 19 and Sect. 21.3).

In general, storm surges are random events due to the coincidence of diverse circumstances by chance. Therefore, their power, track, frequency, and length are not predictable (Von Storch and Woth 2011). Their frequency is not subject to cyclic behaviour. The number of storm surges at the Wursten Coast varied greatly from year to year as shown by the data of the reference gauge at Spieka-Neufeld (Fig. 21.2; Absolute numbers (>0) range from 2–34, 1–4, and 1–1, respectively).

The frequency of storm surges at the Wursten Coast during the last four decades was characterised in three classes following Lüders and Luck (1976). An outstanding high number of storm floods occurred in the 90s. In addition to their frequency, date, intensity, and wind direction are the main parameters that control the drift of arthropods and the changes in the salt marsh area. The dike of the summer polder in front of the Wursten Coast has its lowest point at 3.43 m above NN and was flooded by surges 1.5 times per year (range 0–9) on average.

The basis of the main dike was neither flooded directly nor reached by salt water under normal tides or most storm surges. Only heavy storm surges higher than 3.43 m NN can overwhelm the summer dike. Therefore, normally no arthropods were found at the foot of the main dike that were characteristic for the salt marshes in front of the summer dike or at a small margin of the ‘Ententief’ within the summer polder. Moreover, the wrack line was normally found in front of the summer dike and only after heavy storm surges at the main dike.

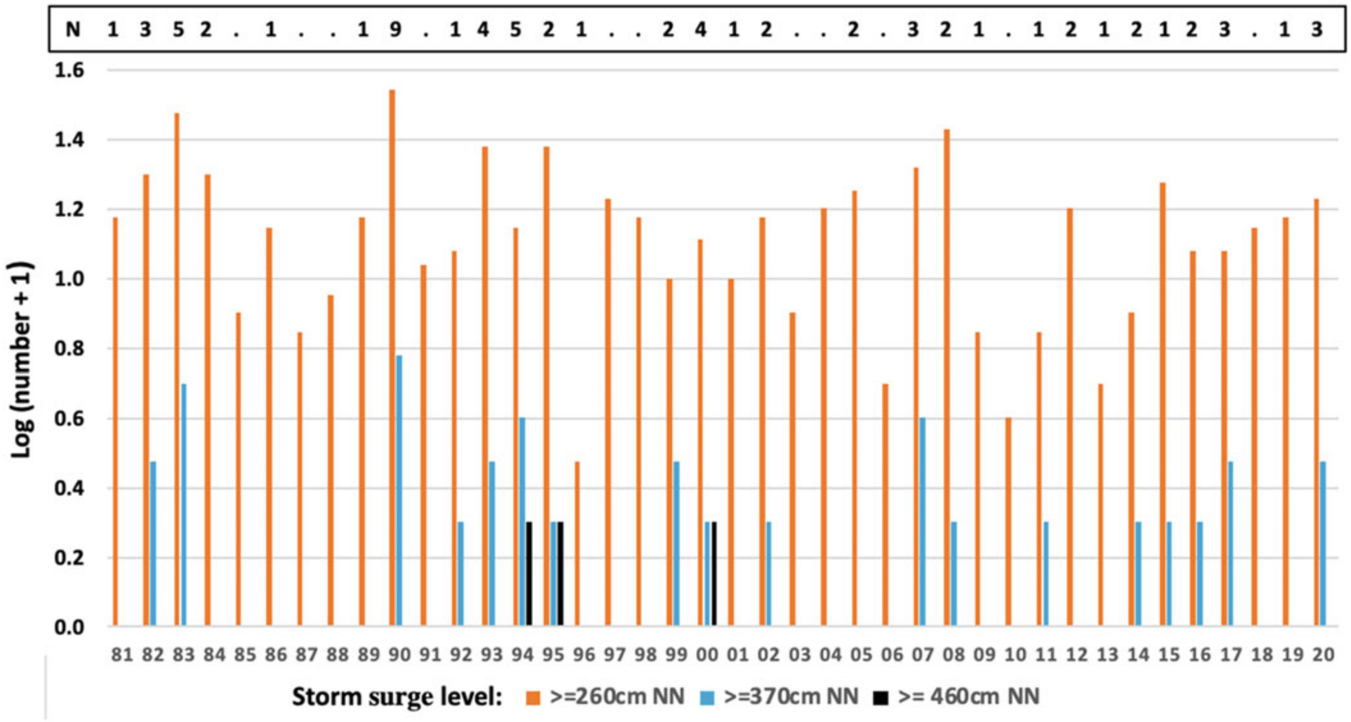

Fig. 21.2 Frequency of storm surge events registered at the water level gauge 'Spieka-Neufeld' of the southern Wursten Coast. *N* numbers of floods that overflow the summer dike (>343 cm NN) per year (November–October)

21.2 Methods

Samples were taken by (1) wrack sifting, (2) pitfall traps, and (3) hand sifting out of the water: (1) Quantitative wrack samples were collected after the storm surge 'Kerstin'. Wrack was collected at the tide line in 0.2 m long sections parallel to the main dike of Oxstedt and at Berensch Dune as well as in a 0.5 m section at Arensch Cliff (indicated in Fig. 4.8). The amount of wrack at the two former locations was so big that the length of the section must be restricted. The material was sifted completely and the beetles were extracted by a photo-eclector in the laboratory. The results of the samples were extrapolated to a 10 m tide line. (2) In addition to the sites used for the gradient evaluation, pitfall traps were exposed at 13 sites in 1999 at the foreland of Berensch and Oxstedt (both with six sites in the gradient with 5 traps each) and at the 'Ententief' creek within the polder (one site with 5 traps). Air bell traps were used at all sites up to 80 cm above MHW. (3) Hand sifting was performed directly in the incoming waters during the heavy storm surge 'Kerstin' on January 30, 2000 at the foot of the main dike of Oxstedt and the Berensch dune. All specimens that drifted on or immediately below the surface of the water were sampled by a sieve in a 1–2 m broad section for about half an hour.

Several storms were named in 1997 and 1998, but they did not influence the summer polder (Table 21.1). Anatol and Lothar were classified as hurricanes, but their impact on the summer polder differs clearly. The wrack deposited by Lara was removed by the offices as usual in the warm season to protect the dike. Because this is not done regularly in winter, the wrack thrown in by Anatol will have been covered up by that of Kerstin. In consequence, arthropods found in the wrack in January 2000 may have drifted in by either Anatol or Kerstin. But we can exclude that beetles could have developed in between there.

Normal distribution was tested with the Kolmogorov-Smirnov-Test with Lilliefors correction (Hemmerich 2018), and the significance of differences by a t-test (PAST4.08, Hammer et al. 2001) in the case of normal distribution or Mann–Whitney U-test (Statskingdom 2007), respectively. Significant differences were marked by a star ($\alpha = 0.05$). The slope of straight lines was calculated with PAST4.08.

Table 21.1 Storm surges at the Wursten Coast (Gauge Spieka-Neufeld data) within the period under discussion. The lowest point of the summer dike lies at +343 cm NN. Overflow in cm above NN (NN + 160 = MHW). Wrack at the main dike

Storm	Date	Overflow	Wrack
(several)	1998	No	– –
Lara	Feb. 05, 1999	434, 375	++
Anatol	Dec. 03, 1999	478	++
Lothar	Dec. 25/26, 1999	No	– –
Martin	Dec. 27/28, 1999	No	– –
Kerstin	Jan. 29/30, 2000	401	++

21.3 Results and Discussion

21.3.1 The Impact of Lara on Species and Specimens

This evaluation only takes the halobiontic and halophilic species into account that also contain the species with highest catch numbers in the foreland of the summer dike. The observed pattern is complex, whereby significant differences occurred between the years, the sites, and the elevations (Fig. 21.3, Tables 21.2 and 21.3).

Besides the effects of year, the single species were differently affected by site or elevation (Fig. 21.3).

Site: Three species, *Pogonus chalceus, Bembidion normannum,* and *Dyschirius salinus* occurred predominantly at the Berensch site;

Elevation: The catch numbers of two species, *Bembidion minimum* and *B. aeneum,* depend on the elevation of the site, both species were abundant at higher elevations. Additionally, they differ significantly between years in six of eight cases. In contrast to the two previous species, *Dicheirotrichus gustavii* occurs preferentially at the lower elevation level of 20 cm. This species displayed contradictory results at different sites and elevations but the Generalised Linear Analysis (GLM) for this

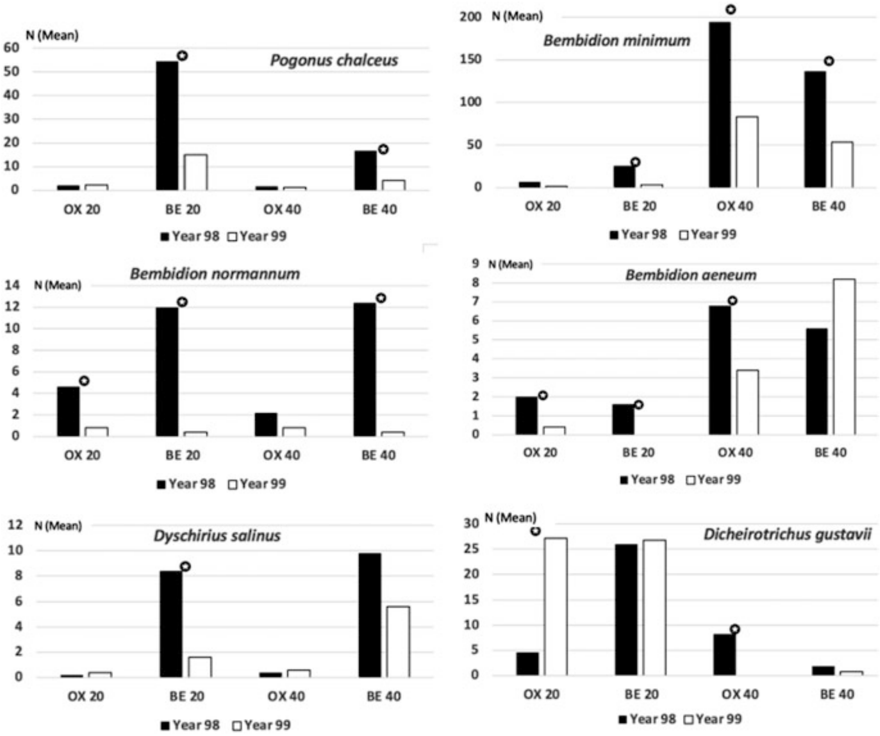

Fig. 21.3 Mean numbers of carabid species in the foreland at different years, sites, and elevation. Three species occurred predominantly in one site (Berensch, left), three others one elevation (20 or 40 cm above MHW, right), respectively

Table 21.2 Slopes of the straight lines for the relations of year, site, and elevation. Generalised Linear Model (GLM) analysis for one species, one factor. *S* Significance level $\alpha = 0.05$

GLM	Year			Site			Elevation		
(1 species, 1 factor)	Slope	*p*	S	Slope	*p*	S	Slope	*p*	S
Bembidion aeneum	−1.0	0.3634		−0.7	0.5269		0.3	<0.0001	✪
Bembidion minimum	−55.4	0.0132	✪	16.7	0.4854		5.4	<0.0001	✪
Bembidion normannum	−7.0	0.0002	✪	−4.2	0.4889		−0.0	0.8232	
Dicheirotrichus gustavii	13.4	0.0209	✪	6.1	0.3187		−0.4	0.1595	
Dyschirius salinus	−2.75	0.1382		−6.1	0.0002	✪	0.1	0.4124	
Pogonus chalceus	−13.05	0.0178	✪	−20.9	<0.0001	✪	−0.6	0.0247	✪

Table 21.3 Estimation of Carabid beetle sensitivity to drift caused by storm surges. The first 11 salt marsh species were separated from the rest. Sensit. Estimated sensitivity against drift. *S* Strong, *M* Medium, *P* Probably, + Increase, Σ: Summarised catches of 65 pitfall traps, each from an elevation series at Berensch and Oxstedt, respectively, plus that of 'Ententief'. In the lower part, only species caught by a sieve were included. Numbers in italics represent the total catch, including omitted species. Sieve: Beetles were collected by sieving the incoming water during the Kerstin event. Threat: Red List of *W* Wadden Sea, *L* Lower Saxony, *D* Germany; Status: 0 Extinct, 1 Critical, 2 Endangered, 3 Vulnerable, *P* Susceptible, *V* species of the warning list, *V** species of the advance warning list with different endangerment in the focus area

		Method			Threat
	Sensit.	∑ 13 x 5 traps		Sieve	W L D
Period		1998	1999	Feb. 30, 2000	
Species					
Amara convexiuscula	P	16	1	0	
Bembidion aeneum	S	741	116	**64**	3 - -
Bembidion iricolor	S	52	4	**14**	3 2 2
Bembidion minimum	S	4625	1696	**12**	
Bembidion normannum	S	1242	313	**5**	
Cillenus lateralis	M	15	0	0	P 2 2
Dicheirotrichus gustavii	M+	418	729	0	- - V*
Dsychirius chalceus		6	1	0	P 1 1
Dyschirius impunctipennis		0	1	0	2 3 2
Dyschirius salinus	M	317	86	**2**	- - V*
Pogonus chalceus	M	989	169	0	- - V*
Agonum fuliginosum		0	0	**1**	
Amara aenea	S	10	0	**34**	
Amara communis	M	35	10	**7**	
Amara familiaris	M	12	0	**2**	
Amara lunicollis		3	2	**1**	
Amara plebeja	S	3	7	**10**	
Amara similata		1	0	**1**	
Bembidion lampros		0	0	**1**	
Bembidion properans	S	233	26	**31**	
Bembidion varium		2	5	**1**	
Clivina fossor	P	57	48	**2**	
Dyschirius globosus	M	839	652	**3**	
Dyschirius lüdersi	P	16	5	**1**	
Pterostichus strenuus	S	171	36	**225**	
Pterostichus vernalis	S	14	4	**9**	
Species, total N		*58*	*39*	21	
Specimens, total N		*10,569*	*4663*	427	

species gave a significant increase in numbers considering years beside the main influence of site (Table 21.2).

All six species show at least single significant differences between years (Fig. 21.3). In the GLM analysis, four species displayed significant changes

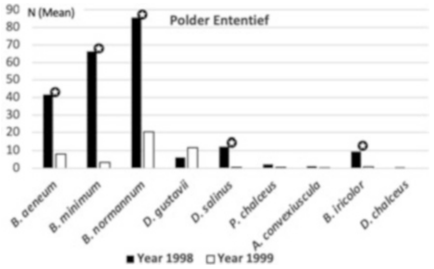

Fig. 21.4 Carabid numbers (mean) of a site within the 'Ententief' summer polder in two consecutive years, before (1998) and after (1999) the Lara storm surge event. Halobiontic and halophilic species were included

considering year, three species a more or less strong reduction but only one species, *Dicheirotrichus gustavii*, an increase after the storm surge Kerstin (Table 21.2). The highest slope in our data was found for the decrease in numbers of *Bembidion minimum* in the sequence of years (Table 21.2).

Interestingly, the only species with an increase in numbers was the only one, which hibernates as larva. We assume that larvae in their soil quarter are better protected against washing-off by storm surges. Therefore, the hibernation stage may play an important role for drift sensitivity in general.

The GLM analysis of the foreland data resulted in a strong site difference for two species, *Dyschirius salinus* and *Pogonus chalceus,* and a lower one for *Bembidion normannum* (Fig. 21.3). These high catch numbers at Berensch versus the very low ones at Oxstedt indicate habitat differences between the sites at the same elevation level.

The dispersion of salt marsh species is known to depend on the elevation gradient (Chap. 27). *Bembidion aeneum, B. minimum,* and *Dicheirotrichus gustavii* showed such differences in the GLM analysis (Table 21.2).

Clear habitat difference between sites in front of the summer dike at the same elevation was not expected but certainly such between before and behind the summer dike. The lower extent of flooding within the polder resulted in the occurrence of additional species, like *Bembidion iricolor,* which is sensitive to flooding and prefers a low salt content of the soil. These conditions were only realised within the summer polder.

The data from the 'Ententief' polder (Fig. 21.4) supports the statements made before on the influence of storm surges although they resulted only at one elevation level.

We hypothesise that a lot of beetles were washed out of their hibernation quarters in the ground and transported by the waves across the summer dike onto the wrack of the foot of the main dike foot and that many of the beetles living in the summer polder also suffered the same fate. Thus, the pitfall catches of the species concerned have been reduced in the season after the Lara event in February, more than a month before the season began. We assume that the specific carabid beetles of the salt marshes survived the surges because of their high resistance to survive in and under water for long periods that has been demonstrated by Heydemann (1967) and Irmler (Chap. 20) in their experiments.

Such partly dramatic changes require a clear case although the pattern is rather complex. In general, differences in abundance between successive years were interpreted to be caused by differing weather conditions. Den Boer (1977) described changes in the amount of several carabid species in his long-term studies on heathery habitats that were correlated with weather conditions. Nearly a full generation of the carabid species *Carabus auronitens* skipped due to temperatures too cold for propagation (Hockmann et al. 1998). Främbs and Mossakowski (2001) also found a weather effect in one species' propagation in a study on restoring peatland. Heydemann (1962a) did not mention similar results in his extensive study on salt marshes and polders. But the mentioned findings differ clearly to ours because we found this effect in a series of relevant species. Because there were no drastic weather differences between the years under study, it makes sense to link the differences mainly to the storm surges. In an initial study, Främbs 1997already found evidence of drifted carabid beetles but from less extensive data.

Due to these findings, beetles were collected by Wolfgang Dormann from the incoming water during the Kerstin event and along the wrack line to prove the hypothesis that they were drifted in high numbers.

21.3.2 The Impact of Anatol and Kerstin

The winter season 1999/2000 brought two deep pressure systems, Anatol and Kerstin, which induced storm surges heavy enough to overflow the summer dike (Table 21.1). 21 species were sampled directly from the incoming waters at the foot of the main dike and Berensch Dune (Table 21.3) when the storm Kerstin pushed the sea into the summer polder. The power of water and waves washed a lot of beetles out of their hibernating quarter in the ground. Hand sampling data and the results of the quantitative eclector analyses of the wrack material demonstrate that this happened along the whole path of the storm surge: in front of the summer dike, within the summer polder, and at the dike foot. *Cillenus lateralis* is a specific species living in the tidal flats in front of the salt marshes (Främbs 2002; Mossakowski and Dormann 2011). Hence, it is never found in the summer polder under normal circumstances. The low number of drifted specimens of this species depends on the low density of the population at the Wursten Coast. Other species, like *Bembidion minimum* and *Dicheirotrichus gustavii,* occur as well in front and behind the summer dike but in higher numbers in the foreland. *Bembidion iricolor* is a strong indicator that the beetles of the summer polder are also pushed out of the ground. Finally, *Notiophilus substriatus* in the flood line material demonstrates that beetles hibernating at the dike were also washed out. This species is mainly found along the embankments in the northernmost part of its distribution area (Heydemann 1962b).

We performed an estimate in order to classify the impact of storm surges on the species that was based on (i) direct records of 21 species, which were found drifting in the incoming water of the 'Kerstin' event (Table 21.3), (ii) indirect confirmation such as the occurrence in wrack at the tide line, (iii) a comparison of the total catch numbers of 13 sites with five traps each, and (iv) their occurrence in the salt marshes and other habitats at the Wursten Coast in our data and those published by Främbs (2002).

Nine Carabid species are classified to suffer strongly, 11 species suffer weakly, and five species presumably suffer under storm surges. Four of these species showed

Table 21.4 Quantitative wrack samples (Eclector samples) after Kerstin storm surge at three locations of the Wursten Coast. *Cliff* Geest Cliff north of Arensch, *Dune* Berensch Dune, *Dike* Main dike. Numbers in italics correspond to the total sample, inclusive species < 5 specimens in the lower part that were omitted

Location	Cliff	Dune	Dike	Cliff	Dune	Dike
Sampled wrack, width [m]	0.5	0.2	0.2			
Date	March 23, 2000					
Width foreland [m]	80	400	400	Extrapolation to drift line of 10 m		
Width polder [m]	–	1750	1270			
Species, total N	*6*	*25*	*23*			
Specimens, total N	*11*	*407*	*585*	*22*	*2035*	*2925*
Bembidion aeneum		2	3		10	15
Bembidion iricolor		4	5		20	25
Bembidion minimum	1	63	147	2	315	735
Bembidion normannum		18	25		90	125
Cillenus lateralis			1			5
Dyschirius salinus			1			5
Amara aenea	1	16	21	2	80	105
Amara communis		3	8		15	40
Amara plebeja		15	16		75	80
Bembidion properans		48	34		240	170
Clivina fossor		11	2		55	10
Dyschirius globosus		2	8		10	40
Poecilus versicolor		7	5		35	25
Pterostichus strenuus	2	185	264	4	925	1320
Pterostichus vernalis		17	20		85	100

an increase in numbers (one halobiontic), 16 a decrease including the majority of halobiontic and halophilic species (Table 21.3, first block).

The wrack material studied during the Kerstin event and later could not be distinguished from that of the Anatol event because the wrack was not removed in winter. Wrack is generally removed at the earliest in March. Therefore, drifted specimens from Anatol's wrack may have survived. Nonetheless, they were drifted specimens. None of the winter-active carabid species was found in our drift material.

Eight species of the drift material are threatened or threatened with extinction (Table 21.3). The level of threat will increase because of the predicted 10–15% increase of storm surges (Von Storch et al. 1998).

Species composition and the number of specimens depend on the storm direction and on the situation in front of the flood line. Kerstin induced a storm surge direct from the west.

Thus, the enormous differences in collected beetles at the three sites correspond with the breadth of the areas in front of flood lines. In the wrack at the Geest cliff, only one specimen of the most common salt species was found (Table 21.4) because the terrain in front of the cliff is built up by areas at a high level where no such species live.

21.3.3 Storm Surge Impact on Area Proportions

The effects of storm surges shall be described using the specific example of the Wursten Coast including the erosion and deposition of sediments as well as the pattern of sedimentation.

However, it should be taken into account that sedimentation does not happen on average; local deviations were observed in particular at locations that were exposed to floods (Figs. 21.5 and 21.6). Due to this fact, a higher rate of sedimentation may occur in the western part of the summer polder due to storm surges.

Storm surges develop eroding forces, which destroy salt marshes at the seaside of coastal habitats. The loss of areas is not compensable for arthropods landwards because of the highly fixed coastline due to the presence of dikes (Fig. 21.1). The

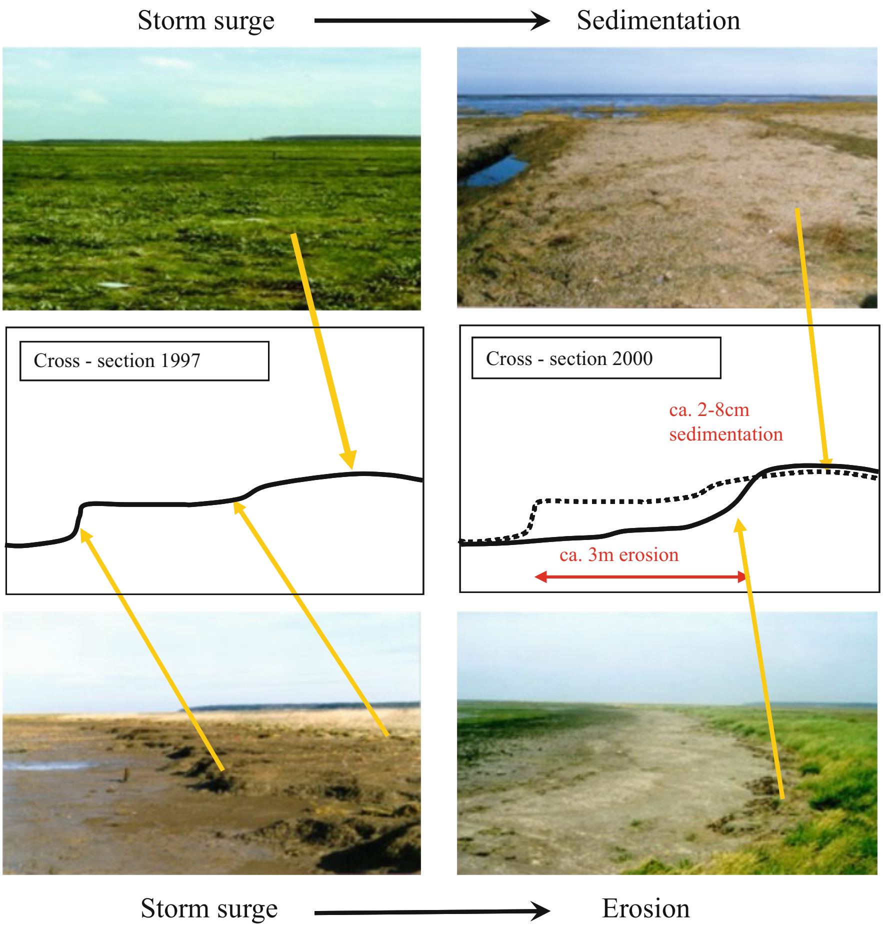

Fig. 21.5 Area changes due to storm surges at the study sites of Oxstedt Fallow in the period from 1997 to 2000

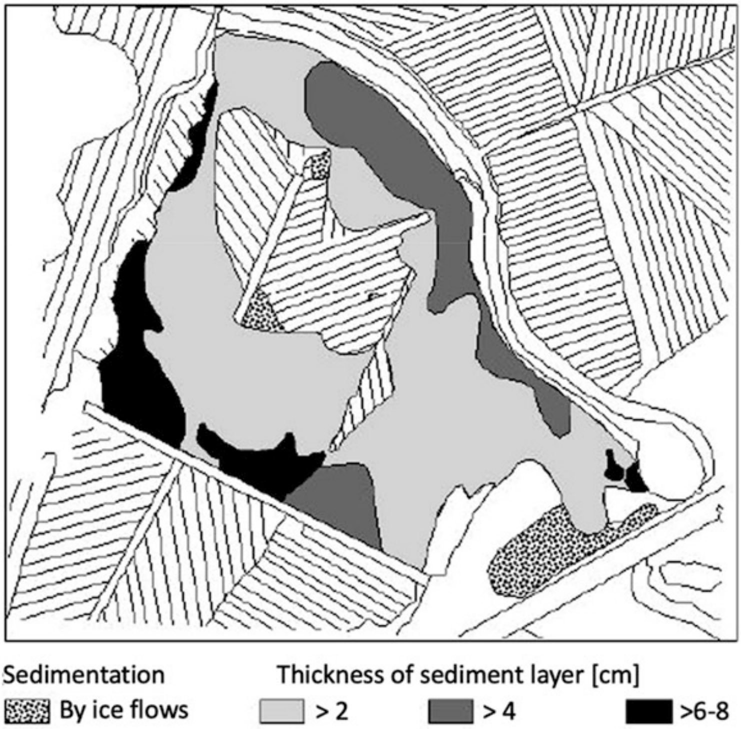

Fig. 21.6 Distribution of sediment deposits in the foreland of Oxstedt Fallow on February 20, 2000 after the storm surge Kerstin (January 29/30, 2000)

decrease of numbers in animal species caused by storm surge drift may be balanced partly by high reproductive rates of salt marsh species (Heydemann 1967) but the loss of area in front of the dike reduces the salt marshes step by step with the consequence that their existence as large area habitats is threatened. The impact of erosion on salt marshes and their fauna was studied by simulations using Oxstedt Fallow as an example (see Chap. 25).

References

Den Boer PJ (1977) Dispersal power and survival. Carabids in a cultivated countryside. Miscellaneous Papers, Agricultural University, Wageningen 14:1–190

Främbs H (1997) Auswirkungen von Sturmfluten auf die Laufkäfer (Col. Carabidae) der Nordseeküste. Arbeitsberichte Landschaftsökologie Münster 18:47–61

Främbs H (2002) Terrestrische Arthropoden: Landwanzen, Laufkäfer, Webspinnen. In: Främbs H, Kinder M, Hielen B, Böhme B, Günther C-P, Rachor E, Cordes H, Mossakowski D (eds) Renaturierung salzbeeinflusster Lebensräume der Nordseeküste, vol 68. BfN-Skripten, Germany, pp 129–181

Främbs H, Mossakowski D (2001) Dynamik von Laufkäfer-Gemeinschaften (Coleoptera, Carabidae) nach Wiedervernässungsmaßnahmen im Leegmoor. Angewandte Landschaftsökologie 38:107–162

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4(1):9. https://www.nhm.uio.no/english/research/infrastructure/past/

Hemmerich W (2018) StatistikGuru: Normalverteilung online prüfen. https://statistikguru.de/rechner/normalverteilung-rechner.html

Heydemann B (1962a) Die biozönotische Entwicklung vom Vorland zum Koog. Vergleichend-ökologische Untersuchungen an der Nordseeküste, II. Käfer (Coleoptera). Akademie der Wissenschaften und Literatur Mainz, Abhandlungen der mathematisch-naturwissenschaftliche Klasse 11:765–964

Heydemann B (1962b) Der Einfluß des Deichbaus auf die Larven und Imagines von Carabiden und Staphyliniden. Berichte Wanderversammlung der Deutschen Entomologen 9:237–274

Heydemann B (1967) Die biologische Grenze Land—Meer im Bereich der Salzwiesen. Franz Steiner, Wiesbaden, p 200

Hockmann P, Horstmann B, Van Den Boom A, Landwehr M, Bechtel A, Kliewe V, Baumgartner R, Mond S, Fennemann U, Kurz D, Weber F (1998) The age structure in a local population of Carabus auronitens under the influence of an abiotic key factor for reproduction. In: Baumgärtner J, Brandmayr P, Manly BFJ (eds) Population and community ecology for insect management and conservation. Balkema, Rotterdam, pp 145–156

Lüders K, Luck G (1976) Kleines Küstenlexikon. In: Natur und Technik an der deutschen Nordseeküste. Verlagsbuchhandlung August Lax, Hildesheim, p 240

Mossakowski D, Dormann W (2011) A plea for using qualitative aspects in the interpretation of ecological field data as revealed by carabid beetle assemblages of a pristine salt marsh. Zookeys 100:273–286

Statskingdom (2007) Mann Whitney U test calculator. http://www.statskingdom.com/17Umedian_mann_whitney.html

Von Storch H, Woth K (2011) Sturmfluten. http://www.hvonstorch.de/klima/pdf/hammerl.woth.pdf

Von Storch H, Schnur R, Zorita E (1998) Szenarien & Beratung. Anwenderorientierte Szenarien für den norddeutschen Küstenbereich. Abschlußbericht FKZ 01 LK 9510/0.1

Part IV

De-embankments and Its Effects on the Vegetation and Fauna

De-embankments at the North Sea and the Baltic Sea Coasts

22

Dietrich Mossakowski

Abstract

De-embankment may be a suitable management to mitigate damages of strong storm events on coastal habitats. This chapter provides an overview over de-embankments along the Atlantic and Baltic Sea coasts. In total 185 individual de-embankments were listed along the coasts from Spain to Eastern Germany including Great Britain. The history and the success of few de-embankments were described in detail.

22.1 Introduction

Embankments along salt marsh coasts have a long tradition (Charlier et al. 2005). They serve to protect against flooding by the sea in order to produce new re-colonisation areas, normally for agricultural use, which were formerly lost by storm surges. Although protection of the hinterland was used as an argument to build up new dikes for land reclamation, public opinion changed against land reclamation in the second half of the last century. The importance of salt marshes for marine sedimentation was accepted as a fundamental shelter against storm surges as sedimentation provokes an up-growth of salt marshes to compensate for the rising sea level. Moreover, a specific and endangered flora and fauna lives in salt marshes, which promotes a worldwide interest in these habitats for nature conservation and scientific studies.

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The public debates between nature conservancy and traditional coast protection resulted in two kinds of consequences: (i) the philosophy and practice of new embankments changed in the last decades (Sect. 22.2) and (ii) a lot of de-embankments were propagated and realised (Sect. 22.3). Thus, both strategies are outlined in this chapter. De-embankments were often used to study the changes of vegetation (Wolters et al. 2005; Wolters 2006). Seiberling et al. (2009) focused on the restoration of salt grassland vegetation at the coasts of Central Europe. Only very few embankments, e.g. Heydemann (1962), as well as de-embankments were investigated by zoologists, in particular those studying arthropods (Sect. 22.4).

Like in other fields of ecology, a lot of terms are used. Rupp-Armstrong and Nicholls (2007) propagate the term ‘managed realignment’ instead of ‘managed retreat’ and ‘set back’ which were in use in England. They list terms like ‘outdiking’, ‘outbankment’, ‘de-embankment’, and ‘depolderisation’ as used in Central Europe (German: ‘*Deichrückverlegung*’, ‘*Deichöffnung’,* or ‘*Ausdeichung’*). We prefer to use the term de-embankment to make clear that only the measures are in focus, which include the opening of an embankment ranging from a small sluice up to the full destruction of a dike. Additionally, sites with natural breaches are included.

A geographical restriction is necessary at least caused by differences in salt marsh structures in well-studied regions, e.g., the United States of America (overview in Atkinson et al. 2001). This chapter disregards the technical problems of de-embankments and their solutions (e.g. Van Oevelen et al. 2000; Simenstad 2002; English Nature 2003; Van Duin et al. 2007; Doody 2008; Esteves 2014).

22.2 Former Classical to Modern Embankments

A change in the embankment philosophy can be demonstrated by comparing embankment approaches at the Central European North Sea Coast.

Important embankments were realised in the last century. One of the best known is the closure of the Zuiderzee in 1932. The resulting Ijsselmeer is now used for touristic activities. Fortunately, it was used as a research field experiment to study the succession (Haeck 1971; Van 1973). Large embankments were also carried out in the second half of the twentieth century, e.g., an embankment in 1969 closed the Lauwersmeer, another large bay in the Netherlands. In 2003, the National Park Lauwersmeer was created due to the developed flora and fauna of the brackish water (Meijer 1971, 1973, 1974, 1980).

Unexpected consequences of embankments occurred, for example, in the German Leybucht, where in 1950 a sea dike (Störtebekerdeich) and later, in 1958, a summer polder called Hauener Hooge were constructed. Here, a change in sedimentation followed the embankment which induced problems in ship transfer (Müller 1960: Wadden sea and its fauna; Dahl and Heckenroth 1978: Birds and vegetation; Wilkens et al. 1983; Irmler and Heydemann 1986; Andresen et al. 1990: Vegetation, spiders, beetles, etc.). After a controversial discussion, the plan of a full embankment of the Leybucht was rejected. Instead, the Leybuchthörn was built: a dike was closed

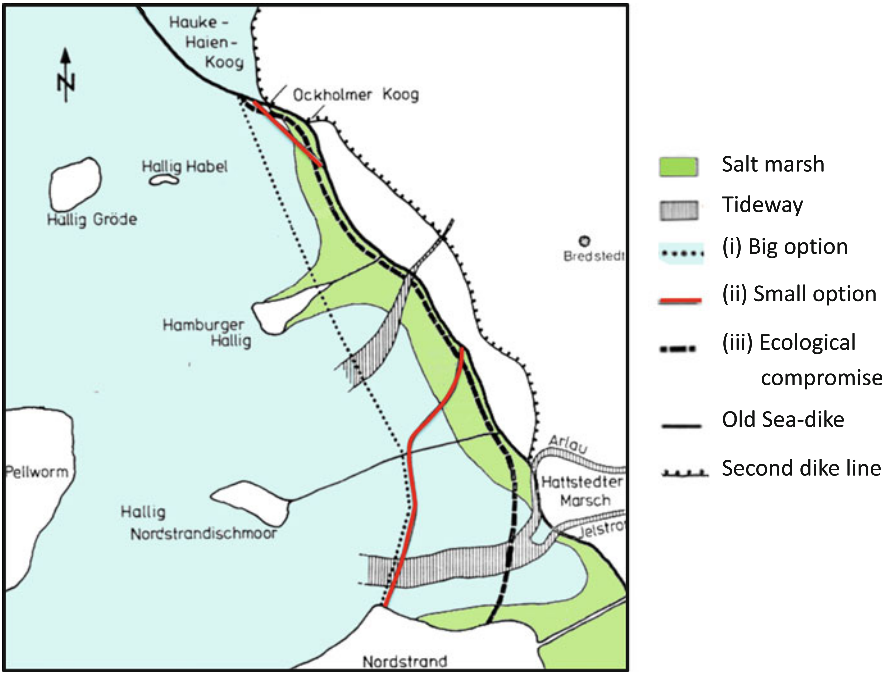

Fig. 22.1 Options under discussion for the Beltringharder embankment measure before decision. Option (ii) was realised. Adopted from Heydemann (1981), modified (with kind permission of the Nordfriisk Instituut, Bredstedt)

in 1987 (Meyer 2001), while the summer dike of the Hauener Hooge was removed (see Sect. 22.3).

At the Schleswig-Holstein coast, the Hauke-Haien-Koog embankment was finished in 1960. It was built in front of the salt marshes, directly in the Wadden Sea. It was the first one, which is used as water repository in the case of storm surges, etc., as a nature conservation area, and only partly for agricultural purposes (Heydemann 1960, 1962, 1967). Another embankment at the German North Sea Coast was executed in the Meldorfer Bucht (Meldorf Bay); this embankment was finished in 1978. It serves to achieve a better protection of the hinterland against floods and a shorter front line of the seawall.

A paradigm for modern embankments was revealed in the construction of the Beltringharder Koog, which was finished in 1987 and put totally under nature conservation in December 1991 as a salt-water habitat (Schmidt and Abraham 1997). Three options were discussed for this new dike (Heydemann 1981), illustrated in Fig. 22.1; the maximal option could be prevented.

The two sluices in the new embankment had different functions (Fig. 22.2): (1) Holmer Siel is the outlet of the Aarlau River and the Aarlau reservoir that contain brackish to fresh water and were under free succession at its southern bank; (2) Lüttmoorsiel should enable the existence and development of salt marshes

Fig. 22.2 The Beltringharder Koog was finished in 1987 in front of the old sea dike, the isle of Nordstrand, and its causeway. Satellite photo (Google Earth) from 2008. Salt-water lagoon under tidal influence. Lüttmoor Lake with brackish to fresh water

behind the new dike as a salt-water lagoon. This regulated tidal exchange (RTE) works all the time, except during storm surges (Bruns 1997; Hagge et al. 1998). In the first years after embankment, the inflow of salt water was very low (tidal range about 3.5 m in front of the dike, only about 0.4 m inside (ABPmer White Papers 2011)). Consequently, glycophytes were established and replaced salt marsh species in the upper zones. Therefore, the tidal management was changed in 1994 to achieve similar levels inside and outside the polder. The northernmost part, Lüttmoor Lake, was managed by moderate intensive grazing (sheep, cattle) with remaining salt influence (Wolfram et al. 1998).

This measure was accompanied by comprehensive studies on vegetation and fauna. It was an instructive example demonstrating that an artificial construction can create valuable new habitats.

22.3 De-Embankment Sites

An excellent overview on de-embankments in Europe together with the resulting changes of vegetation is presented by Wolters (2006), who also displayed the geographic positions.

Meanwhile, a lot of new measures have been performed. The list in Table 22.1 is mainly based on Wolters (2006); Rupp-Armstrong and Nicholls (2007), and the interactive databank presented by the ABPmer's Online Marine Registry (OMReg 2021) website (Former: Managed Realignment Guide (OMReG) (ABP Marine

Table 22.1 Natural breaches and managed de-embankments in Europe in geographical order (W to E). *MB* Managed realignment, *RTE* Regulated Tidal Exchange, *SB* Sea Wall Breach, *NB* Natural Breach, *SR* Managed Seawall Removal, *sR* Summer dike removal, *LL* Land lowering, *DL* Dike lowering, *UR* Unregulated, * in column tide: outside of polder, * in column year: not realised. *A* Arthropods, *Aq*: Aquatic fauna, *Ag* Algae, *B* Benthos, *C* Collembola, *Ca* Carabid beetles, *D* Dragonflies, *F* Fish, *I* Invertebrates, *H* Hoverflies, *L* Lepidoptera, *O* Birds, *R* Amphibia and Reptiles, *S* Spiders, *V* Vegetation, *p* Part. Measures are classified under the following terms: *MB* 'Managed Realignment (also called Managed Retreat or De-Embankment in Europe) involves deliberately breaching or removing sea walls to allow tidal waters from adjacent coasts or estuaries onto the land'. (OMReg). *RTE* 'Regulated Tidal Exchange (RTE) encompasses a range of techniques to develop intertidal habitats behind permanent sea defences, particularly where walls will remain in place and/or as part of a phased realignment strategy' (OMReg)

						Tide			
Wolters	OM Reg	Location/Country	Region	Measure	ha	Tide m	Year	Geogr. coordinates	BIO
		Spain							
	OM	(Veta la Palma)	Andalucia	RTE	3200		1990	36°58'13"N 06°13'46"W	
	OM	Rio de la Rubia	Cantabria	MB:SR	47		2009	43°22'45"N 04°19'05"W	VB
	OM	Marismas Vega de Jaitzubia	Bidasoa	MB:SR	23	4.4	2004	43°21'00"N 01°48'44"W	B
		France							
		Polder Graveyron	Arcachon Bay	NB			1996	44°40'52"N 01°02'38"W	
		Ile Nouvelle	Gironde	NB	265		2000	45°09'45"N 00°41'20"W	
		Mortagne sur-Gironde	Gironde	NB			1999	45°28'10"N 00°48'34"W	
	OM	Polder de Sébastopol	Ile de Noirmoutier	RTE			1999	46°56'27"N 02°09'13"W	VO(A)
	OM	Aber de Crozon	Bretagne	MB:SR, RTE			1980	48°14'07"N 04°25'58"W	
		Polder de Sables-d'Or-les P.	Gulf of St. Malo				Open	48°38'03"N 02°24'52"W	
		Ploubalay	Gulf of St. Malo	NB			'90/'06	48°34'54"N 02°09'47"W	

(continued)

Table 22.1 (continued)

						Tide			
Wolters	OM Reg	Location/Country	Region	Measure	ha	Tide m	Year	Geogr. coordinates	BIO
77	OM	Polder de Carmel	Baie des Veys	NB, RTE	30	6	1991	49°21'23"N 01°08'24"W	
		Renclotures du Mollenel	Somme Bay	NB	9.75		<2006	50°10'48"N 01°39'16"W	
		England and Wales							
14		Carnforth Marsh	Morecambe Bay	RTE	51.2	8.4		54°07'N 02°47'W	
	OM	Glasson	Conder	RTE	6.4	8.3*	2005	53°59'39"N 02°49'45"W	
	OM	Hesketh Out Marsh	Ribble Estuary	B: SB	180	7.9	2008	53°43'13"N 02°53'15"W	VOIF
	OM	Ynys-hir	Dyfi	MB:SB	6		2010	52°33'07"N 03°56'17"W	
23		Gwent Levels	Ely, Cardiff Bay	TRE	10.8			51°26'48"N 03°09'59"W	
	OM	Cone Pill	Severn	MB: SR	50		2001	51°41'46"N 02°33'45"W	
		Tutshill	Congresbury Yeo	MB: SB	2		2011	51°23'30"N 02°53'42"W	
	OM	Walborough	Axe (Somerset)	RTE	4.5	11.2*	2004	51°19'02"N 02°59'05"W	V
	OM	Bleadon Levels	Axe (Somerset)	MB	13	11.2	2001	51°18'38"N 02°59'06"W	VOI
10		Brue Pill	Weston Bay, Som.	MB		11.6	1990	51°13'N 2"59'W	
	OM	Steart Peninsula	Parrett Estuary	MB: SR	475		2014	51°13'29"N 03°00'05"W	
33	OM	Pawlett Hams	Parret	MB: SB	4.8	11.1	1994	51°12'13"N 03°00'55"W	
34	OM	Porlock Bay	North Somerset	NB	75	11.1	1996	51°12'58"N 03°36'24"W	
		Pillmouth River	Torridge, Devon	SB		7	2000	51°01'49"N 04°11'55"W	
	OM	Pillmouth (Phase 1 & 2)	Torridge	MB: SB	12.9	5.9	2001	50°59'48"N 04°10'45"W	

	OM	Annery Kiln	Torridge	MB: SB	3.8	5.7	2000	50°59'14"N 04°11'41"W	
	OM	Watertown Farm	Yeo	MB: SB	1.5	5.9	2000	50°59'43"N 04°11'51"W	
	OM	Clapper Marshes	Camel	RTE	10		2011	50°30'35"N 04°49'04"W	
	OM	Treraven Meadows	Camel	RTE	14		2007	50°30'43"N 04°49'31"W	IO
35	OM	Ryan’s Field	Hayle	RTE	6.2	5.8	1995	50°10'35"N 05°25'59"W	V
18		Cotehele River	Tamar, Cornwall	SB	15	4.2	2002	50°29'N 04°13'W	
36	OM	Saltram (Blaxton Meadow)	Plym	RTE	4.2	4.7*	1995	50°23'05"N 04°05'09"W	VO
	OM	South Efford Marsh	Avon	RTE	17		2011	50°18'21"N 03°50'44"W	
	OM	Goosemoor	Glyst	RTE	6.3	1.1	2004	50°40'55"N 03°27'13"W	VOB
	OM	Black Hole Marsh	Axe (Devon)	RTE	6	3	2009	50°43'09"N 03°03'39"W	
	OM	Lymington Estuary	Lymington	RTE	21		2009	50°45'54"N 01°32'23"W	
	OM	Lepe	Dark Water	RTE	4	3.2	2006	50°47'14"N 01°21'29"W	
	OM	Thorness Bay	The Solent, I. Wight	MB: SB	7	3.4	2004	50°44'22"N 01°21'04"W	
42	OM	Thornham Point	Chichester Harbour	MB: SB	6.9	4.4	1997	50°50'00"N 00°54'54"W	V
15	OM	Chalkdock Marsh	Chichester Harbour	RTE	3.25	4.4*	2000	50°48'26"N 00°52'39"W	V
	OM	Cobnor Point	Chichester Harbour	MB: SB	6.5		2013	50°46'53"N 00°54'25"W	O
	OM	Medmerry	Sussex Coast	MB: SB	450		2013	50°45'03"N 00°49'27"W	VOFR
	OM	Rye Harbour Farm	Rother	RTE	17		2011	50°55'59"N 00°45 54"E	
4		Barksore I	Medway Estuary	NB			1908	51°22'48"N 00°40'56"E	

(continued)

Table 22.1 (continued)

						Tide			
Wolters	OM Reg	Location/Country	Region	Measure	ha	Tide m	Year	Geogr. coordinates	BIO
28		Milfordhope 10	Medway Estuary	NB			1908	51°23'31"N 00°40'07"E	
17		Copperhouse 6	Medway Estuary	NB	1.9		1897	51°23'31"N 00°35'16"E	
12		Burntwick 5	Medway Estuary	NB	71.3		1897	51°25'02"N 00°40'20"E	
31		Oakham 13	Medway Estuary	NB			1897	51°25'13"N 00°37'58"E	
	OM	Barking Creek A13	Thames	MB: SR	0.04	3	2006	51°31'41"N 00°04'51"E	
	OM	Barking Creek/ Barrier	Thames	MB: SR	1	7	2006	51°31'00"N 00°05'49"E	
	OM	Stanford Wharf, London Gw.	Thames	MB: SB	27	5.7	2010	51°30'10"N 00°26'47"E	
	OM	Vange Marsh	Thames	RTE	1	0.7/ 5.7*	2006	51°33'23"N 00°29'51"E	
	OM	Millennium Terraces	Thames	SR	0.5		1998	51°30'08"N 00°00'27"E	
13		Canvey Point	Thames Estuary	NB	23	5.2	1874	51°31'13"N 00°37'48"E	
	OM	Bowers Marsh	East Haven Creek	RTE	10		–	51°32'40"N 00°32'24"E	
09		Bridgemarsh Island A-C	Crouch Estuary	NB	149	5	1928	51°38'16"N 00°44'24"E	
29		North Fambridge A+B	Crouch Estuary	NB	70	5	1897	51°38'49"N 00°39'21"E	

16		Clementsgreen Creek	Crouch Estuary	NB	4	5	1897	51°38'16"N 00°38'03"E	
08	OM	Brandy Hole	Crouch	MB: SB	12	5	2002	51°37'39"N 00°38'38"E	V
46	OM	Allfleet's Marsh, Wallasea I.	Crouch	MB: NB	113	5	2006	51°36'59"N 00°50'11"E	VOBR
32	OM	Orplands	Blackwater	MB: SB	38	4.7	1995	51°43'11"N 00°52'04"E	VOB
30	OM	Northey Island	Blackwater	MB: SB	0.8	4.8	1991	51°43'09"N 00°42'54"E	VS
44	OM	Tollesbury	Blackwater	MB: SB	21	4.7	1995	51°46'03"N 00°50'25"E	VOBFS
01	OM	Abbots Hall	Blackwater	MB: SB	84	4.7	96/02	51°47'05"N 00°50'44"E	VOBFRS
37		Sampson's Creek	Blackwater	NB	4	4.7	1945	51°47'23"N 00°53'45"E	
02		Aldboro Point	Colne Estuary	NB	7	4.5	1921	51°50'00"N 00°59'09'E	
05		Barrow Hill	Colne Estuary	NB	23	4.5	1953	51°48'10"N 00°56'25"E	
19		Ferry Lane	Colne Estuary	NB	6	4.5	1945	51°51'07"N 00°51'32"E	
20		Fingringhoe Marsh A + B	Colne Estuary	NB	78	4.5	1897	51°49'31"N 00°57'28"E	
	OM	Deveraux Farm 1	Hamford Water	MB: SB	15	3.8	2010	51°51'27"N 01°14'45"E	
47		Walton Central	Hamford Water	NB	73	3.8	1938	51°52'47"N 01°16'16"E	
40		Stone Marsh	Hamford Water	NB	30	3.8	1874	51°53'00"N 01°15'58"E	
26	OM	Horsey Island	Hamford Water	RTE	1.2	3.8*	1995	51°52'31"N 01°13'46"E	
39		Skipper's Island	Hamford Water	NB	37	3.8	1953	51°52'33"N 01°12'59"E	
21a		Foulton Hall A	Hamford Water	NB	66	3.8	1896	51°55'06"N 01°15'37"E	
21b		Foulton Hall B	Hamford Water	NB	34	3.8	1921	51°54'42"N 01°15'14"E	
45	OM	Trimley Marsh	Orwell	MB: SB	16.5	3.6	2000	51°58'56"N 01°17'03"E	VOB
25		Hemley	Deben Estuary	NB	31	3.6	1953	52°02'13"N 01°20'26"E	
48		Woodbridge	Deben Estuary	NB	15	3.6	1953	52°05'17"N 01°19'14"E	

(continued)

Table 22.1 (continued)

						Tide			
Wolters	OM Reg	Location/Country	Region	Measure	ha	Tide m	Year	Geogr. coordinates	BIO
24	OM	Havergate Island	Ore	MB: SB	8.1	3.6	2000	52°04'40"N 01°32'11"E	VOB
	OM	Lantern Marsh (North)	Ore	MB: SB	29	2.3	1999	52°07'33"N 01°35'24"E	V
11		Bulcamp Marsh	Blyth (Suffolk)	N	100	2	1945	52°19'49"N 01°34'17"E	
06		Blackshore Mill	Blyth (Suffolk)	N	<1	2	1953	52°19'28"N 01°39'27"E	
	OM	Halvergate 5 Mile Reach	Yare	MB Relocated	0.5	?	2005	52°34'43"N 01°37'33"E	
07	OM	Brancaster West Marsh	North Norfolk	MB: SR	7.5	6.5	2002	52°58'20"N 00°37'53"E	V
43		Titchwell	North Norfolk	MB: SB	36	6.5	2011	52°58'13"N 00°36'53"E	O
22	OM	Freiston	The Wash	MB: SB	66	6.8	2002	52°57'53"N 00°05'33"E	VOIF
03	OM	Alkborough	Humber	MB: SB	370	5.9	2006	53°41'29"N 00°40'38"W	VOBF
27	OM	Chowder Ness	Humber	MB: SR	15	6.9	2006	53°41'30"N 00°28'54"W	OBF
41	OM	Paull Holme Strays	Humber	MB: SB	80	6.0	2003	53°42'30"N 00°13'10"W	Vobfdlch
	OM	Welwick	Humber	MB: SB	54	4.6*	2006	53°38'50"N 00°00'34"E	OIF
38	OM	Seal Sands	Tees	RTE	9	4.6*	1993	54°37'10"N 01°12'01'W	OB
	OM	Warkworth	Coquet	TE	0.4	4.2	2009	55°20'38"N 01°36'08"W	O
	OM	Almouth 1	Alne	MB: SB	8	4.2	2006	55°23'28"N 01°37'20"W	VOCa
	OM	Almouth 2	Alne	MB: SB	20	4.2	2008	55°23'48"N 01°36'53"W	VOCa
	OM	Goswick Farm (Beal)	South Low River	RTE	4.5	4.2	2010	55°41'02"N 01°53'02"W	
		Scotland							
	OM	Skinflats	Firth of Forth	RTE	11		2009	56°03'20"N 03°44'02"W	
	OM	Kennet Pans	Firth of Forth	MB: SR	8.2		2007	56°04'40"N 03°44'14"W	

	OM	Black Devon Wetlands	Forth/Black Devon	RTE	28	5.5*	2ßßß	56°06'00"N 03°46'37"W	
	OM	Mains of Dun	Montrose Basin	MB: SB	0.3	4,2	1997	56°42'35"N 02°31'57"W	
	OM	Nigg Bay	Cromartry Firth	NB: SB	25	3.6	2009	57°44'20"N 04°01'59"W	VOB
		Belgium							
	OM	Yzer Mouth	Yzer	SR:1300, LL	50		2001	51°08'54"N 02°44'18"E	SCa
		Prosperpolder	Zeeschelde	MB: SR	145		2010	51°20'10"N 04°13'43"E	
	OM	Paardeschor	Zeeschelde	MB, LL	12	5.13	2004	51°20'02"N 04°15'12"E	
	OM	Lillo-Potpolder	Zeeschelde	MB: 160+170	8		2012	51°18'07"N 04°17'46"E	
	OM	Ketenisseschor	Zeeschelde	MB: SR+LL	36	5.27	2002	51°16'57"N 04°18'46"E	VOB
		Kruibeke Polders	Zeeschelde	RTE: 4x	650		2013	51°10'05"N 04°19'15"E	
		Durmevallei	Durme	RTE	205		Plan	51°06'35"N 04°09'23"E	
	OM	Lippenbroek	Zeeschelde	RTE	10	1.5/ 2.5*	2006	51°05'08"N 04°10'18"E	VOBF
		Vlassenbroek & Wal-Zwijn	Zeeschelde	RTE	102		2015	51°03'20"N 04°08'19"E	
	OM	Paddebeek	Zeeschelde	MB: SR	1.6	3.26	2003	51°00'54"N 04°02'02"E	
		Paardeweide	Zeeschelde	DL	85		2012	51°00'39"N 03°58'33"E	
	OM	Bergenmeersen	Zeeschelde	RTE, DL	41		2013	51°01'06"N 03°57'59"E	
		Wijmers 1	Zeeschelde	RTE	159		2013	51°00'40"N 03°56'47"E	
		Wijmers 2	Zeeschelde	SR	28		2015	51°00'23"N 03°56'48"E	
	OM	Heusden	Zeeschelde	MB: 2x25m	13	4.8	2006	51°01'28"N 03°47'23"E	
		Diljemonding	Dilje	RTE	207		2013	51°03'31"N 04°26'11"E	
		Bovendijle	Bohelden	DL	60		S 2017	50°59'28"N 04°36'32"E	
		The Netherlands							
63		(Zwarte Polder, Herdijke ZP)	Zeeuws Vlaanderen	MB	65		*1995	51°23'09"N 03°25'50"E	

(continued)

Table 22.1 (continued)

						Tide			
Wolters	OM Reg	Location/Country	Region	Measure	ha	Tide m	Year	Geogr. coordinates	BIO
62		Verdronken Zwarte Polder	Zeeuws Vlaanderen	NB	43		1802	51°23'13"N 03°26'24"E	V
55		(Hellegatpolder)	Westerschelde	MB	125		*1995	51°21'39"N 03°56'50"E	
		Saeftinghe, Verdronken Land	Westerschelde	NB	3200		1570/84	51°21'16"N 04°10'14"E	
61		Sieperdaschor	Westerschelde	NB	100	5.5	1990	51°20'17"N 04°11'32"E	VB
54		Hedwigepolder	Westerschelde	MB	320		*1995	51°20'30"N 04°12'52"E	
49		Boonepolder/ O Zwakepold.	Westerschelde	RTE	80		2007	51°27'00"N 03°55'00"E	
52		(Everingepolder)	Westerschelde	MB	235		*1995	51°24'05"N 03°52'04"E	
51		Dordtse Biesbosch	Haringvliet	MB 2x	100	0.7	2005	51°44'13"N 04°40'36"E	
	OM	Tiengemeten	Haringvliet	MB:50-60 m	450	0.3+	2007	51°44'41"N 04°17'22"E	
	OM	Sophiapolder	Noord river	MB	77		2012	51°50'21"N 04°39'54"E	
	OM	Klein Profijt	Oude Maas	MB +LL:22+2	6	1.1	2005	51°50'05"N 04°26'50"E	
	OM	de Kerf	Mainl. C. N Holland	MB	6	1.9	1997	52°41'06"N 04°38'15"E	VCa
	OM	Bunkervallei, de Slufter	Island of Texel	MB: 10 m	3	2.1	2002	53°09'36"N 04°49'18"E	
	OM	Groene Hoek, de Slufter	Island of Texel	MB: 50+15	13	2.1	2002	53°09'11"N 04°50'09"E	
57	OM	Kroon's Polders	Vlieland	MB: 10 + 10	85	2.1	1996	53°15'22"N 04°57'41"E	VOBF
53	OM	Groene Strand	Isl. of Terschelling	MB	23	2.1	1996	53°21'52"N 05°12'06"E	VO
	OM	Bildtpollen	Friesland	MB: 15, sR	60		2009	53°19'00"N 05°39'00"E	V

58		Noarderleech N Fr Butendiks	Friesland	MB:3x20–40	135	2	2001	53°19'54"N 05°44'24"E	VO
		Holwert West	Friesland	? SR	51		2004	53°22'43"N 05°52'48"E	
56	OM	Holwerder Summerpolder	Friesland	MB: 12 m	28	2	1989	53°23'01"N 05°53'53"E	V
59		Paezemerlannen	Friesland	NB	100	2	73/79	53°24'15"N 06°06'11"E	V
50	OM	Breebaart	Dollard Estuary	RTE	63		2001	53°17'31"N 07°04'43"E	VOF
		Germany, North Sea							
66	OM	Hauener Hooge	Ley Bay	MB: sR	80	2.8	1994	53°30'56"N 07°04'45"E	vobcsCa
69p	OM	Lütetsburger Sommerpold.	Mainl. E Friesland	MB:sR:0.40	15	2.8	1982	53°40'02"N 07°14'53"E	
70p		(Munster Summerpolder)	Mainl. E Friesland	Rejected			–	53°40'57"N 07°26'18"E	
68p	OM	Langeooger Sommerpold.	Island of Langeoog	MB: sR	215	3.1	2003	53°44'53"N 07°32'09"E	VAgSCa
		Langwarden Groden	Mainl. E Friesland	MB: sR	70		2015	53°36'40"N 08°19'23"E	
	OM	Vorder-/ Hinterwerder Pold.	Weser	MB: SB	30	0.9/ 4.3*	1997	53°07'29"N 08°39'18"E	VOBF
	OM	Rönnebecker Sand	Weser	MB: SB+LL	34	0.7/ 4.3*	2002	53°12'55"N 08°29'08"E	
	OM	Kleinensieler Plate	Weser	MB: SB+LL	58	−0.2/ 4*	2000	53°27'24"N 08°29'04"E	VOBF
	OM	Tegeler Plate Polder	Weser	MB: SB	150	4.4	1997	53°27'48"N 08°30'31"E	Ca
	OM	Luneplate	Weser	RTE	215	4.2*	2008	53°28'58"N 08°31'06"E	VOBSCa
	OM	Dorum Sommerpolder	Wursten Coast	MB: sR	4	3.2	2001	53°44'43"N 08°31'14"E	VO
	OM	Dorum-Cappel-Neufeld	Wursten Coast	MB: sB	74	3.2	2007	53°45'41"N 08°31'50"E	VOCa

(continued)

Table 22.1 (continued)

						Tide			
Wolters	OM Reg	Location/Country	Region	Measure	ha	Tide m	Year	Geogr. coordinates	BIO
	OM	Cappel-Spieka-Neufeld	Wursten Coast	MB: sB	71	3.2	2007	53°46'09"N 08°32'12"E	VOCa
	OM	Berensch/Spieka-Neufeld	Wursten Coast	RTE	280	1/3.2*	1995	53°48'26"N 08°33'29"E	VOAq
		Altengammer Hauptdeich	Elbe	No measure but cited in literature				53°25'28"N 10°16'08"E	
65	OM	Wrauster Bogen Warwisch	Elbe	MB: SR	2.2	3.6	1991	53°25'30"N 10°07'58"E	V
	OM	Riepenburg, Zollenspieker	Elbe	MB: SR	1		1995	53°24'N 10°12'E	Ca
	OM	Kreetsand	Elbe	MB: SR	26	3.9	1999	53°29'54"N 10°02'46"E	
	OM	Spadenländer Spitze	Elbe	MB: SB	7.5	3.9	2000	53°30'06"N 10°03'33"E	V
	OM	Billwerder Insel	Elbe (estuary)	MB: SR	20	3.6	2008	53°30'42"N 10°03'57"E	VO
	OM	Hahnöfersand	Elbe	MB: SR+LL	104	3.5	02/'04	53°32'51"N 09°42'11"E	Ca
		Hetlingen-Giesensand	Elbe	RTE			2007	53°36'03"N 09°37'48"E	Ca
		Neuwerk Polder	Neuwerk	MB: UR	53		2004	53°55'13"N 08°30'44"E	SCa
	OM	Beltringharder Koog	North Friesland	RTE	853	0.4/ 3.5	1988	54°33'03"N 08°53'45"E	voifsCa
		Denmark							
	OM	Geddal Strandenge	Limfjord	MB: SR + LL	140	0.4	1992	56°32'43"N 08°45'42"E	
	OM	Viggelsø	Odense Fjord	MB: SB	66	0.3	1993	55°28'07"N 10°27'40"E	
		Germany, Baltic Sea							
	OM	Kleines Noor	Flensburg Fjord	MB: SB	14	0.3	2002	54°52'33"N 09°35'27"E	

	OM	Strandseenlandsch. Schmoel	Kiel Bay	MB: SB	40	0.3	1989	54°23'58"N 10°26'55"E	
	OM	Pepelower/ Tessmansd. W.	Salzhaff	MB: SB	120	0.2	2002	54°02'50"N 11°35'28"E	
	OM	Polder Roggow	Salzhaff	MB: SB	40	0.2	2002	54°04'37"N 11°37'37"E	
		Riedensee	Mecklenburg coast	NB	10	0.2	1995	54°08'58"N 11°40'45"E	
74 p		(Sundische Wiese)	Darss-Zingst penin.	MB: SR:8 km	130	0.2	2017	54°25'35"N 12°54'52"E	VSCa
		Bruker Holz	Greifswald Bodden	NB; RTE		0.2	2007	54°10'58"N 13°19'37"E	
67	OM	Karrendorfer Wiesen	Greifswald Bodden	MB: SR	350	0.2	1993	54°09'54"N 13°23'22"E	VOSCa
		P. Eisenhammer E Labedow	Greifswald Bodden	NB	25	0.2	1995	54°05'58"N 13°25'21"E	
76	OM	P. Friedrichshagen, Ziesetal	Greifswald Bodden	NB; MB: SR	90	0.2	95/'99	54°05'02"N 13°30'26"E	VCa
72	OM	Polder Freetz	Island of Rügen	MB: SR	180	0.2	2002	54°21'01"N 13°31'37"E	
71	OM	Polder Neuensien (SWpart)	Island of Rügen	MB: SB	40	0.2	2002	54°21'38"N 13°38'25"E	
75		Zickerniss-Niederung	Island of Rügen	NB		0.2	1995	54°18'50"N 13°42'24"E	
	OM	Polder Wehrland	Peenestrom	MB: SR	113	0.2	2004	53°58'24"N 13°50'28"E	
	OM	Teilpolder Waschow	Peenestrom	MB: SR	66	0.2	2004	53°58'01"N 13°50'55"E	
	OM	Anklamer Stadtbruch	Oderhaff	NB, UR	1750	0.2	2004	53°48'38"N 13°51'19"E	

Environmental Research Limited, a subsidiary of Associated British Ports Holdings Ltd.), which offers a lot of information including geographical coordinates and a visualisation of the locations. A compact overview on English de-embankments, in particular, was given by Armstrong (2011). The topics of the references cover a wide field: natural breaks without technical management (included in Wolters 2006) to technical aspects (e.g. OMReg), restriction to special regions as described in a report of English Nature (1992, a series of historical sea wall failures in Essex), and a review paper on selected sites worldwide at estuaries (Van Oevelen et al. 2000).

Many other projects are planned or under implementation (e.g. Goeldner-Gianella 2007a, b; OMReg downloads, DEFRA/Environmental Agency 2002, ComCoast). Many projects of defence removals are realised along the inland part of rivers, but are neglected here (Table 22.1).

22.4 Arthropod Studies on De-Embankment Sites

Although the number of de-embankments is high, numerous data only exists for aquatic animals and birds (e.g. Atkinson et al. 2001; Castelijns et al. 1997; Eertmann et al. 2002). Only few studies considered arthropods.

Along the North Sea Coast, the big estuaries are influenced by tides and by a fluctuating gradient of increasing freshwater conditions upstream. De-embankments were studied along streams in Belgium and along the estuary of the Schelde River (Hendrickx et al. 1998: spiders; Desender and Maelfait 1999: spiders, carabid beetles, etc.), in Germany along the Ems River (Assmann and Terlutter 1999; Terlutter 1999) and at the Elbe estuary (Gürlich 1999: Carabidae). Bonn et al. (2002) published a comparison of the significance of tidal influence on spiders and carabid beetles along the three major German rivers.

22.4.1 Spain

For this country, papers on saltmarsh arthropods considering de-embankments are not available.

22.4.2 France

Pétillon et al. (2008) published a comprehensive study on the salt marshes of the Mont Saint-Michel region. They compared salt marshes with natural and managed (cutting and sheep grazing) land use as well as salt marshes dominated by the *Elymus anthericus* using the spider and carabid fauna.

22.4.3 United Kingdom

A lot of work was done on benthic invertebrates, e.g. fish and birds (see OMReg data base; e.g. Evans 1997; Evans et al. 2001; Reading et al. 2000; Atkinson et al. 2001). But studies on arthropods were performed only in very few projects.

Pétillon and Garbutt (2008) published a study on restoration using spiders. They compared managed realignment sites of different age (Abbotts Hall, Tollesbury, and Northey Island) with adjacent natural sites. They published the following results: ‘The natural salt marshes were characterized by a relatively low species richness, the dominance of late-successional stage species such as *Pirata piraticus*, and the exclusive presence of large species preferring a closed vegetation cover like *Arctosa fulvolineata* and *Pardosa nigriceps*. Restored habitats were characterised by greater species richness than the adjoining reference habitats, at least during the first years of succession. This is probably due to a more heterogeneous habitat, favouring pioneer species (mainly linyphiids). Restored habitats were also suitable for some halophilic species, in terms of both presence (*Enoplognatha mordax* and *Erigone longipalpis*) and greater abundance (*Pardosa purbeckensis*). Although these results need to be confirmed by a long-term survey, they argue for maintaining a maximum of successional stages in salt marshes as they increase the diversity of halophilic spiders’ (Pétillon and Garbutt 2008).

Northeast coast of England: Eyre and Luff (2005) studied carabid, rove, and phytophageous beetles in salt marshes, dunes, and dune slacks at the northeast coast of England. The sites included two of the managed realignments of our list (Almouth and Beal). The number of carabid species was lowest in salt marshes compared with other habitats. Only four halobiontic or halophilic species were found at all or most sites (*Dicheirotrichus gustavii, Bembidion minimum*, and *Dyschirius salinus*). *Cillenus lateralis* was found with low frequency. Eyre and Luff (2005) stated that the effects of seawater inundation on farmland and dune slacks will cause a change in species assemblage and will severely limit species richness.

22.4.4 Belgium

Ijzer estuary: In the Flemish Nature Reserve ‘The Yzer-rivermouth’ at Nieuwpoort, restoration was carried out in the period from 1999–2004 that comprised ‘the complete demolition of the former military harbour and the digging off of the dredging spoil-dumps’ in order ‘to restore mud flats, salt marshes and sand dunes’ (Herrier et al. 2005; Deboeuf and Herrier 2002).

Desender et al. (2006) sampled carabid beetles and spiders in three subsequent years after the beginning of restoration on old salt marsh and dune stands as well as on newly developed sites. No uniform tendencies were observed in the changes between the years independent of different sampling efforts.

Additionally, Desender et al. (2007) published the results of a continuous study since 1989 on ground beetles as ‘early warning-indicators’. This study is of particular value because the estuary of the Ijzel River was explored continuously since 1989 by these authors so that long historical data exists.

The old salt marsh sites were characterised by a high presence of halophilic and halobiontic carabid species (*Pogonus chalceus, Dyschirius salinus, Dicheirotrichus gustavii, Bembidion minimum, Dicheirotrichus obsoletus,* and *Cillenus lateralis*). In contrast, the occurrence of these species was relatively uneven in the newly restored sites, e.g., at one new site, four species displayed the highest or second highest numbers of all places. Therefore, this site resembled the series of the old sites. The characteristic salt marsh species, *Dyschirius salinus*, could not be found in the restored sites.

River Schelde: Hendrickx et al. (1998) published the results of an investigation on the spider fauna along a gradient of the tidal part of the Schelde River. In salty and brackish sites of downstream Antwerp, high numbers of only two halobiontic species, *Baryphyma duffeyi* and *Pardosa purbeckensis*, occurred.

Desender and Maelfait (1999) published data on terrestrial amphipods, isopods, carabid beetles, and spiders sampled from coastal sites, which were located along a gradient along the Scheldt River. They found 98 carabid, 45 spider, 9 isopod, and 2 amphipod species. The faunal composition changed abruptly between the coastal and inland salt marshes although all sites were influenced by tides. Salinity is the major factor controlling the distribution of species along this gradient. However, salinity can be only partly responsible for the faunal change as the highest change occurred within the brackish zone.

22.4.5 The Netherlands

Although numerous de-embankments were realised in The Netherlands (De Leeuw and Meijer 2002) and an excellent knowledge of the fauna is present (Turin et al. 1991; Turin 2000; Turin et al. 2022), monitoring studies on restoration sites are not available, except one note on the monitoring of carabids at the DeKerf site (De Leeuw and Meijer 2002).

22.4.6 Germany: North Sea Coast

Studies with more general aspects that also include salt marsh carabid beetles and spiders from the North Sea Coast (East Frisian Islands, Finch 2008: Aranea; Plaisier and Stumpe 2008: Carabidae) and from the Baltic Sea Coast (Schultz 2002: Carabidae; Dormann et al. 2010: Carabidae) include the following investigations:

Hauener Hooge (Ley Bay, Lower Saxony) was established in 1956 as an 80 ha summer polder in the Ley Bay. Dahl and Heckenroth (1978) delivered a landscape ecology report on vegetation and avifauna. Wilkens et al. (1983) studied the fauna of the Wadden Sea (Makro-endofauna, epifauna, fishes) as well as birds and terrestrial taxa by diverse methods and published data on epigaeic invertebrates, in particular, on spiders. Andresen et al. (1990) studied the long-term development using carabids and spiders. The dynamic processes in the Ley Bay resulted in problems for shipping traffic and in consequence in a plan to embank the whole bay. The upcoming environmental consciousness led to the conservation of the largely intact habitats of the Ley Bay and to the construction of the 'Leybuchthörn' with a new sluice. The history of embankments of the former 'Leybucht' is excellently documented in Meyer (2001).

The summer dike of Hauener Hooge was partly removed in October 1994 as compensation for coastal protection actions. In consequence, the summer polder was opened to floods. Götting (2001) studied carabid beetles, amphipods, and some spider taxa (Lycosidae, Tetragnathidae) in the period 1995–1997 and in 1999. The first results indicated a rapid change in the arthropod communities by the increased seawater influence. "The abundance of the salt marsh amphipod *Orchestia gammarellus* increased considerably [. . .]', spider assemblages shifted to more hygrophilous species. Halophilic carabid species, such as *Bembidion minimum* and *B. aeneum*, decreased in numbers, while the number of some halobiontic species increased moderately (*Pogonus chalceus* and *Dyschirius salinus*). The salt marsh species *Pardosa purbeckensis* was the most abundant spider species with a strong decrease in the last study year, a phenomenon that also occurred in other species.

The faunal change towards a salt marsh community started already in the first year after opening the summer dike, but this depends on diverse abiotic factors and "is rarely predictable without reference data" (Götting 2001). Unfortunately, data from the same sites with identical taxa before the opening of the summer dike is not available. The data of Wilkens et al. (1983) indicates that a high potential exists that other specific salt marsh species shall colonise this site. Arens (2005) stated that the measurement was successful and no further measures were needed.

Langeoog summer polder (NLWKN 2005): 2 years after the removal of the old summer dike, Niedringhaus et al. (2008) studied spiders (Araneae), ground beetles (Carabidae), bugs (Heteroptera), and cicadas (Auchenorrhyncha) in 2005/2006. Pitfall traps were exposed in parts of the former summer polder and behind the new established summer dike. A total of 74 species were found in front of the new summer dike: 30 spiders, 11 carabid beetles, 18 bugs, and 15 cicadas. A total of 44 species were characterised as species specialised on or preferring salt marshes. A large part of characteristic species colonised the area after re-embankment and occurred in stable populations. In particular, bugs and cicadas displayed high densities. An increase in species richness was assumed for spiders and ground beetles.

Tegeler Plate (Weser estuary): 2 years after the breaches were performed, the halophilic or halobiontic salt marsh species *Bembidion aeneum, B. iricolor, B. minimium, Dyschirius obscurus,* and *Amara convexiuscula* had colonised this oligohalinic site (Tesch 2003; Bremenports 2014).

Wursten Coast: Berensch-/Spieka-Neufeld (Främbs et al. 2000; Wilkens and Parzefall 1979; see Chap. 23).

Neuwerk: Fründ (1996) studied the spider and carabid beetle fauna of the foreland of Neuwerk Island before the opening of the summer polder in the south-east. Only the halobiontic *Pardosa purbeckensis* was found at all sites. The halophilic *Erigone longipalpis* was also found in high numbers, but it was absent or had low numbers at sites, where *P. purbeckensis* was abundant. There were remarkable differences in the distribution pattern of halophilic and halobiontic species considering the different regions of the foreland. The total number of carabid beetles was low, whereas four halobiontic and two halophilic species displayed no clear pattern.

Elbe estuary: The paper by Gürlich (1999) includes carabid data on the de-embankment sites of Zollenspieker, Hahnöfer Binnenelbe, and Hetlingen.

Beltringharder Koog: This new embankment included a Regulated Tidal Exchange (RTE) open to the Wadden Sea at Lüttmoor sluice. In 1994, a reinforcement against the flood dynamics was established. Between 1988 and 1996, the following groups were studied (Schmidt and Abraham 1997): vegetation, birds, water taxa, molluscs, and terrestrial arthropds (Staphylinidae, Saldidae, Syrphidae, Proctotrupidae, Symphyta, specialised endophagous insects, a Pteromalid parasitoid, Aculeata, some Curculionidae, Diptera, carabid beetles, and spiders). Among spiders, the halobiontic *Pardosa purbeckensis* and the halophilic *Enoplognatha mordax* strongly decreased in subsequent years due to reduced flooding and salt content in the soil. Among carabid beetles sampled between 1988 and 1996, the abundance of the halobiontic species *Pogonus chalceus* increased strongly except for a drop in 1994, whereas the abundance of *Bembidion minimum*, which was most abundant at the beginning, decreased fast but reached a steady state on a low level afterwards. The abundance of *Dicheirotrichus gustavii* also decreased remarkably on the RTE sites.

Overall, the quick changes in habitat quality and conditions by desalination and the natural flood regime caused drastic changes in the composition of the fauna with a loss of salt marsh species on many sites. In contrast to most spider species, some halophilic and halobiontic carabid beetle species revealed clearly increased numbers in the study period, but others also showed declining numbers. The great majority of the remaining species is represented by euryoecious species.

22.4.7 Germany: Baltic Sea Coast

Stakendorf (Schleswig-Holstein): The nature conservation area at Smoel was established in 1990; the former dike was removed to compensate dike enhancements at other places. The 50 ha area includes mainly lagoons and foredunes.

Karrendorfer Wiesen: (#67 in Wolters 2006), see Chap. 24.

Polder Ziesetal: After a natural breach in 1995, the dike was fully removed in 1999. The former polder was flooded depending on changes of the water level in the Baltic Sea. In 2000 and 2001, Grünwald (2002) studied the carabid beetles. More details are found in Bury et al. (2003) and Fock et al. (2002). The saline species occurred in the centre of the area and along the coastline (Grünwald 2002) with low numbers as a consequence of the low salt content in the Baltic Sea (7–10%, Grünwald 2002) and the fact that the study was performed immediately after the total removal of the dike. In the successive years, two of the three halophilic or halobiontic species showed declining abundances. The same effect occurred also for the halotolerant *Bembidion transparens*. 29 abundant and euryoecious species developed differently, 20 species showed increasing numbers (12 more than twice as much), only seven species revealed a decreasing number including three with half as much. No carabid data exists about the situation in the polder before the breach (Grünwald 2002).

References

ABPmer White Papers (2011) Case study on the Beltringharder Koog Regulated Tidal Exchange Scheme (Germany). http://www.abpmer.net/omreg/

Andresen H, Bakker JP, Brongers M, Heydemann B, Irmler U (1990) Long-term changes of salt marsh communities by cattle grazing. Vegetation 89:137–148

Arens S (2005) Beweissicherung Küstenschutz Leybucht–Vegetationsentwicklung in der Leybucht 1995–2004. Berichte des NLWKN, Betriebsstelle Brake-Oldenburg, p 108

Armstrong S (2011) Managed realignment cross Western Europe–progress over the first two decades. OMReg downloads

Assmann T, Terlutter H (1999) Die längszonale Gliederung der Laufkäferfauna der Ems – Laufkäfer in Auen. Angewandte Carabidologie Suppl 1:33–40

Atkinson PW, Crooks S, Grant A, Rehfisch MM (2001) The success of creation and restoration schemes in producing intertidal habitat suitable for waterbirds. English Nature research report 425. English Nature, Peterborough

Bonn A, Hagen K, Wohlgemuth-von Reiche D (2002) The significance of flood regimes for carabid beetle and spider communities in riparian habitats–a comparison of three major rivers in Germany. River Res Appl 18:43–64

Bremenports (2014) Geschäftsbericht. bremenports GmbH & Co. KG, Bremen

Bruns HA (1997) 10 Jahre Beltrinharder Koog. Wattenmeer International 1:16–18

Bury M, Czyz H, Fock T, Grünwald M, Hergarden K, Köhler M, Niedzwiecki E, Protasowicki M, Repasi D, Trzaskos M, Vettter L, Walter J, Zander B (2003) Deichrückbau und Salzgrasland an der südlichen Ostseeküste, vol 20. Reihe A, Schriftenreihe der Fachhochschule Neubrandenburg

Castelijns H, van Kerkhoven W, Maebe J (1997) Vogels Van Het Sieperdaschor: Over Een Niet Voorziene Dijkdoorbraak En De Onverwacht Gunstige Gevolgen Die Dat Voor Vogels Had. Natuurbeschermingsvereniging de Steltkluut in samenwerking met het, RIKZ ed. Terneuzen en Middelburg

Charlier RH, Chaineux MCP, Morcos S (2005) Panorama of the history of coastal protection. J Coast Res 21:79–111

Dahl H-J, Heckenroth H (1978) Landespflegerisches Gutachten zu geplanten Deichbaumaßnahmen in der Leybucht. Naturschutz und Landespflege in Niedersachsen 7:1–17

De Leeuw C, Meijer ML (2002) Proefgebieden herstel zoet-zout overgangen in Noord Nederland. werkdocument concept. RIKZ, Haren. http://www.zoetzout.nl

Deboeuf C, Herrier JL (2002) The restoration of mudflats, saltmarshes and dunes on the eastern bank of the Yzer-rivermouth, Nieuwpoort. In: Veloso-Gomes F, Taveira-Pinto F, das Neves L (eds) Littoral 2002, 6th International symposium. A multi-disciplinary symposium on Coastal Zone research, Eurocoast & EUCC–The Coastal Union, pp 201–202

DEFRA/Environmental Agency (2002) Managed realignment review project report. www.salmon-trout.org/pdf/Defra_(2008).pdf

Desender K, Maelfait J-P (1999) Diversity and conservation of terrestrial arthropods in tidal marshes along the River Schelde: a gradient analysis. Biol Conserv 87:221–229

Desender K, Baert L, Malfait J-P (2006) Evaluation of recent nature development measures in the river IJzer estuary and long-term ground beetle and spider monitoring (Coleoptera, Carabidae;

Araneida). Bulletin de l'institut royal des sciences naturelles de Belgique, entomologie 76:103–122

Desender K, Maelfait J-P, Baert L (2007) Ground beetles as 'early warning-indicators' in restored salt marshes and dune slacks. In: Isermann M, Kiel K (eds) Restoration of coastal ecosystems, Coastline reports, vol 7, pp 25–39

Doody JP (2008) Saltmarsh conservation, management and restoration. In: Coastal systems and continental margins 12. Springer, Dordrecht

Dormann W, Mißkampf R, Kamer N, Mossakowski D (2010) Die Dynamik der Diversität der Tierarten und Zönosen in einer sich wandelnden Umwelt unter besonderer Berücksichtigung von Dispersionsprozessen. Westliche Boddenlandschaft. In: Schickhoff U, Seiberling S (eds) Entwicklung der Biodiversität in Salzgrasländern der Vorpommerschen Boddenlandschaft. Bundesamt für Naturschutz, Bonn, Bad Godesberg, p 102

Eertmann RHM, Kornman BA, Stikvoort E, Verbeek H (2002) Restoration of the Sieperda Tidal Marsh in the Scheldt Estuary, The Netherlands. Restor Ecol 10:438–449

English Nature (1992) Historical study of sites of natural sea wall failure in Essex. English Nature Research report 15:30 pp, 51 maps

English Nature; Environment Agency DEFRA; LIFE, and NERC (Natural Environment Research Council) (2003) Coastal habitat restoration, towards good practice. http://www.english-nature.org.uk/livingwiththesea/project_details/good_practice_guide/Home.htm. Accessed 1 Jan 2006

Esteves LS (2014) Managed realignment: a viable long-term coastal management strategy? Springer, Dordrecht

Evans PR (1997) Improving the accuracy of predicting the local effects of habitat loss on shorebirds: lessons from the Tees and Orwell estuary studies. In: Goss-Custard JD, Rufino R, Luis A (eds) Effect of habitat loss and change on waterbirds. HMSO, London

Evans PR, Ward RM, Bone M (2001) Seal Sands northwest enclosure intertidal habitat re-creation: invertebrate recolonisation and use by waterfowl and shorebirds, 1997–2000. Final report to INCA projects and English Nature. Department of Biological Sciences, University of Durham

Eyre MD, Luff ML (2005) The distribution of Epigeal beetle (Coleoptera) assemblages on the North-East England Coast. J Coast Res 21:982–990

Finch OD (2008) Die Webspinnen, Weberknechte und Pseudoskorpione der Ostfriesischen Inseln. In: Niedringhaus R, Haeseler V, Janiesch P (eds) Die Flora und Fauna der Ostfriesischen Inseln, vol 11. Schriftenreihe Nationalpark Niedersächsisches Wattenmeer, Wilhelmshaven, pp 103–112

Fock T, Hergarden K, Repasi D (eds) (2002) Salt grasslands and coastal meadows in the Baltic region. Proceedings of the 1st conference. Neubrandenburg. Reihe A, 18

Främbs H, Kinder M, Hielen B, Böhme B, Günther C-P, Rachor E, Cordes H, Mossakowski D (2000) Renaturierung salzbeeinflußter Lebensräume der Nordseeküste. Abschlußbericht des Salzwiesenprojektes Wurster Küste (1991-1999), im Auftrag des BMU, der BfN und der Projekt-Trägergemeinschaft. 298 p + Anhang

Fründ H-C (1996) Laufkäfer- und Spinnenfauna ausgewählter Flächen des Vorlandes der Insel Neuwerk im Nationalpark Hamburgisches Wattenmeer. Unpublished report, p. 16

Goeldner-Gianella L (2007a) Perceptions and attitudes toward De-polderisation in Europe: a comparison of five opinion surveys in France and the UK. J Coast Res 23:1218–1230

Goeldner-Gianella L (2007b) Dépoldériser en Europe occidentale. Annales de Geographie 656: 339–360

Götting E (2001) Development of salt marsh arthropod fauna after opening a summer polder. Senckenberg Marit 31:333–340

Grünwald M (2002) Carabid beetles as indicators of salt grasslands: the example of polder "Ziesetal". In: Fock T, Hergarden K, Repasi D (eds) Salt grasslands and coastal meadows in the Baltic region. Proceedings of the 1st conference, FH Brandenburg. Reihe A, 18, pp 101–113

Gürlich S (1999) Die Laufkäferfauna der Tideelbe. Angewandte Carabidologie Suppl 1:3–32

Haeck J (1971) The immigration and settlement of Carabid beetles in the new Ijsselmeer-Polders. Miscellaeneous papers. Landbouwhogeschool, Wageningen 8:33–51

Hagge A, Thiel H, Peters CP, Lüdemann KL (1998) Hydrobiologische Untersuchungen im Beltringharder Koog und in den vorgelagerten Wattgebieten. In: Abschlussbericht 1987–1997–Teil 3: Salzwasserlagune. Universität Hamburg, Hamburg

Hendrickx F, Maelfait J-P, Muylaert W, Hoffmann M (1998) Spider distribution patterns along the tidal River Scheldt (Belgium). In Selden PA (ed) Proceedings of the 17th European colloquium of arachnology, Edinburgh 1997, pp 285–291

Herrier J-L, Van Nieuwenhuyse H, Deboeuf C, Deruyter S, Leten M (2005) Sledgehammers, cranes and bulldozers: restoring dunes and marshes by removing buildings and soil. In Herrier J-L, Mees J, Salman A, Seys J, Van Nieuwenhuyse H, Dobbelaere I (eds) Proceedings 'dunes and estuaries 2005'–international conference on nature restoration practices in European coastal habitats, Koksijde, Belgium, 19–23 September 2005. VLIZ Special Publication 19:14 + 685, pp 79–94

Heydemann B (1960) Die biozönotische Entwicklung vom Vorland zum Koog. Vergleichend-ökologische Untersuchungen an der Nordseeküste. I. Spinnen (Araneae). Abhandlungen der math.-nat. Klasse der Akademie der Wissenschaften und Literatur Mainz 11:744–913

Heydemann B (1962) Die biozönotische Entwicklung vom Vorland zum Koog. Vergleichend-ökologische Untersuchungen an der Nordseeküste. II. Käfer (Coleoptera). Abhandlungen der math.-nat. Klasse der Akademie der Wissenschaften und Literatur Mainz 11:765–964

Heydemann B (1967) Die biologische Grenze Land–Meer im Bereich der Salzwiesen. Steiner, Wiesbaden

Heydemann B (1981) Ökologische Leitsätze zur Frage der Eindeichungen im Wattenmeer Nordwesteuropas. Nordfriesland–Zeitschrift für Kultur, Politik, Wirtschaft 15:9–27

Irmler U, Heydemann B (1986) Die ökologische Problematik der Beweidung von Salzwiesen an der niedersächsischen Küste - am Beispiel der Leybucht. Naturschutz u. Landschaftspflege Niedersachsen 11:1–115

Meijer J (1971) Immigration of arthropods into the new Lauwerszee Polder. Miscellaneous Papers Landbouwhogeschool, Wageningen 8:53–64

Meijer J (1973) Die Besiedlung des neuen Lauwerszee polders durch Laufkäfer (Carabidae) und Spinnen (Araneae). Faunistisch-ökologische Mitteilungen 4:169–184

Meijer J (1974) A comparative study of the immigration of carabids (Coleoptera, Carabidae) into a new polder. Oecologia 16:185–208

Meijer J (1980) The development of some elements of the arthropod fauna of a new polder. Oecologia 45:220–235

Meyer C (2001) Beweissicherung Küstenschutz Leybucht. Morphologisch-sedimentologische Untersuchungen (Abschlussbericht), Dienstbericht Forschungsstelle Küste 6/2001, p 17

Müller CD (1960) Fauna und Sediment in der Leybucht. Jahresbericht 1959 Forschungsstelle für Insel–und Küstenschutz. Norderney 11:39–178

Niedringhaus R, Lieckweg T, Freund H (2008) Besiedlung einer Salzwiese durch Arthropoden nach einer Rückdeichung. Faunistische Untersuchungen im Langeooger Sommerpolder im Jahr 2006, p 23. http://cdl.niedersachsen.de/blob/images/C52494635_L20.pdf

NLWKN (2005) Renaturierung Langeooger Sommerpolder. www.nlwkn.niedersachsen.de/live/live.php?navigation_id=8438&article_id=39166&_psmand=26

OMreg (2021) A database of completed coastal habitat creation schemes and other adaptation projects. https://www.omreg.net

Pétillon J, Garbutt A (2008) Success of managed realignment for the restoration of salt-marsh biodiversity: preliminary results on ground-active spiders. J Arachnol 36:388–393

Pétillon J, Georges A, Canard A, Lefeuvre J-C, Bakker JP, Ysnel F (2008) Influence of abiotic factors on spider and ground beetle communities in different salt-marsh systems. Basic and Applied Ecology 9:743–751

Plaisier F, Stumpe C (2008) Zur Besiedlung der Ostfriesischen Inseln durch Sandlaufkäfer und Laufkäfer. In: Niedringhaus R, Haeseler V, Janiesch P (eds) Die Flora und Fauna der Ostfriesischen Inseln. Schriftenreihe Nationalpark Niedersächsisches Wattenmeer, vol 11, pp 197–208

Reading CJ, Paramour OAJ, Garbutt RA, Barratt DR, Chesher T, Cox R, Gradwell M, Hughes R, Myhill DG, Rothery P, Whitelaw RIA, Gray AJ (2000) Managed realignment at Tollesbury and Saltram. Annual report for 1999. Unpublished report. Centre for Ecology & Hydrology, Dorset

Rupp-Armstrong S, Nicholls RJ (2007) Coastal and estuarine retreat: a comparison of the application of managed realignment in England and Germany. J Coast Res 23:1418–1430

Schmidt S, Abraham R (1997) Untersuchungen zu den Wirbellosen im Beltringharder Koog. Abschlussbericht für die Untersuchungsperiode 1988–1996, Hamburg, unpublished, p 143

Schultz R (2002) Ground beetles (Coleoptera: Carabidae) as bioindicators for the revitalization of saline-grasslands on the Baltic Sea coast. In Fock T, Hergarden K, Repasi D (eds) Salt grasslands and coastal meadows in the Baltic region. Proceedings of the 1st conference. FH Brandenburg, Neubrandenburg, pp 114–132

Seiberling S, Stock M, Thapa PP (2009) Renaturierung von Salzgrasländern bzw. Salzwiesen der Küsten. In: Zerbe S, Wiegleb G (eds) Renaturierung von Ökosystemen in Mitteleuropa. Spektrum Akademischer Verlag, Heidelberg, pp 183–208

Simenstad CA (2002) Special issue: dike/levee breach restoration of coastal marshes. Restor Ecol 10:431–605

Terlutter H (1999) Die Carabidenfauna der unteren Ems zwischen Hebrum und Emden. Laufkäfer in Auen. Angewandte Carabidologie, Suppl. 1:41–53

Tesch A (2003) Tegeler Plate–Ausdeichung eines Sommerpolders in der Brackwasserzone der Weser: Planung und erste Erfahrungen. Bremer Beiträge für Naturkunde und Naturschutz 6:65–74

Turin H (2000) De Nederlandse loopkevers, verspreiding en oecologie (Coleoptera: Carabidae). Nederlandse Fauna 3. Nationaal Natuurhistorisch Museum Naturalis, Leiden, 666 pp

Turin H, Alders K, Den BPJ, Van Essen S, Heijerman T, Laane W, Penterman E (1991) Ecological characterization of carabid species (Coleoptera: Carabidae) in the Netherlands from thirty years of pitfall sampling. Tijdschrift voor Entomologie 134:279–304

Turin H, Kotze DJ, Müller-Kroehling S, Saska P, Spence J, Heijerman T (2022) Ecology and conservation of the dutch ground beetle fauna – lessons from 66 years of pitfall trapping. Wageningen Academic Publishers, p 452

Van Duin WE, Esselink P, Bos D, Klaver R, Verweij G, van Leeuwen P-W (2007) Proefverkweldering Noard-Fryslân Bûtendyks. Evaluatie kwelderherstel 2000-2005. Report Alterra/IMARES-Texel, Den Burg/report 2006-045, Bureau Koeman en Bijkerk, Haren. A & W-report 840 Altenburg & Wymenga, Veenwouden, 115 pp + App

Van Oevelen D, Van den Bergh E, Ysebaert T, Meire P (2000) Literatuuronderzoek naar–estuariene herstelmaatregelen. Rapport Instituut voor Natuurbehoud IN.R.4, Brussel

Van Wingerden WKRE (1973) Dynamik einer population von *Erigone arctica* white (Araneae, Micryphantidae). Prozesse der Natalität Faunistisch-ökologische Mitteilungen 4:207–222

Wilkens H, Parzefall J (1979) Landschaftsökologische Analyse und Wertung des Sommerkoogs von Spieka-Neufeld/Berensch-Arensch. Gutachten im Auftrag des Wasserwirtschaftsamtes in Stade, p. 38

Wilkens H, Andres H-G, Faubel A, Gillandt L, Hartwig E, Hüppop O, Martens J, Schulz K (1983) Ökologische Analyse der Leybucht. Arbeiten aus der Forschungsstelle Norderney 8:1–144 (+19 p. Anlagen)

Wolfram C, Hörcher U, Kraus U, Lorenzen D, Neuhaus R, Dierssen K (1998) Die Vegetation des Beltringharder Kooges 1987-1998 (Nordfriesland). Mitteilungen der Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg 58:1–220

Wolters M (2006) Restoration of salt marshes. Proefschrift Rijkuniversiteit Groningen. Van Denderen, Groningen

Wolters M, Garbutt A, Bakker JP (2005) Salt-marsh restoration: evaluating the success of deembankments in north-West Europe. Biol Conserv 123:249–268

Salt Marsh Restoration in a Summer Polder at the Wursten Coast

23

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Abstract

The value of summer polders for the conservation of halobiontic salt marsh species was investigated along a salt marsh coast in Lower Saxony and compared with adjacent salt marshes open to the sea. In this study the vegetation was considered as well as different parts of the fauna. The results revealed that the summer polder was low successful to preserve the halobiontic community. The main inhibiting factor was the small diameter of a sluice installed in the summer dike that prevents a near-natural flooding regime. There was either too much or too less water in the summer polder to give at least suboptimal conditions for halobiontic species. Two solutions were recommended to achieve an effective tidal regime in the summer polder: (1) a bigger opening in the summer time or (2) a complete removing of the summer dike which is equal to de-embankment conditions.

23.1 Introduction

Along the North Sea Coast of Lower Saxony and Schleswig-Holstein, high dikes protect the marsh of the mainland against floods. High elevated cliff coasts produced by the Saale glacier period only exist near Husum and at the northern part of the

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Author "Brigitte Hielen" has died before the publication of this book.

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Wursten Coast, south of Cuxhaven. In the past, salt marshes in front of the sea dikes were embanked with additional lower summer dikes at many locations of Lower Saxony. Consequently, salt marshes, between the sea dike and the summer dike, the so-called summer polders, were rarely flooded, mainly by heavy storm surges in winter. Therefore, the influence of salt water is lower in the polder than in salt marshes open to the sea in front of sea dikes and the former upper salt marshes were transformed into fertile agricultural grasslands.

The salt marsh project ‘Wurster Küste’ (Wursten Coast) aimed to restore salt marsh assemblages in the summer polder and the adjoining areas by opening the summer dike by a sluice in the summer dike, which should reconnect a former tidal creek, the ‘Ententief’, to the tidal dynamics. The changes resulting from the sluice effects should explain to which extent salt water input influences the polder area. The results should serve to develop concepts for future management to preserve the salt-preferring vegetation and fauna. In particular, rare coastal plant and animal communities should be promoted in the polder area. This realignment was classified as a Regulated Tidal Entrance (RTE) (Wolters 2006; OMReg 2016).

The needed diameter of the sluice tube for the necessary inflow of salt water was politically not enforceable.

23.2 Area and Methods

23.2.1 Description of the History and Present Status of the Sites

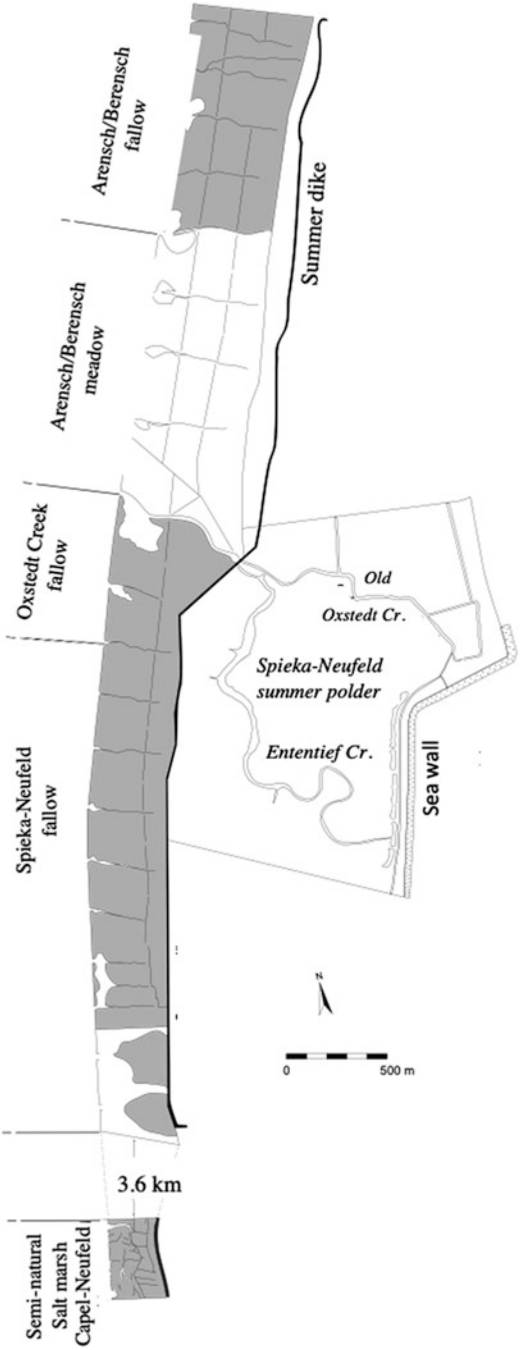
The project area at the Wursten Coast is situated southwest of Cuxhaven. Both northern and southern parts of the area border on coastal dunes in front of Saalian moraines at the eastern mainland and a high sea wall, respectively. The maximum distance between the sea wall and the summer dike is 1.5 km. On its western side, the project area is open to the Wadden Sea.

The project area included three parts (Fig. 23.1): (i) the Spieka-Neufeld summer polder of about 280 ha (Fig. 23.2), (ii) the adjacent salt marsh in front of the separating low summer dike, and (iii) a salt marsh near Cappel-Neufeld with a coastline of 300 m, 5.0 km south of the new ‘Ententief sluice’ as a reference for a semi-natural area.

The grassland of the summer polder grew under natural conditions for centuries until it was diked from 1855 to 1870 (Köster 1917). Since 1900, mesohaline and species-rich grassland with relicts of salt marsh vegetation survived within the drained former tidal inlets. With the beginning of the 1950s, agricultural use was moderately intensified in one part of the polder; in another part a strong intensification was established, including melioration, mineral fertilisation, soil break, and surface levelling, which induced species-poor grasslands (Kinder 2002).

Just before the beginning of the project, the summer polder grassland was mainly used as pasture for cattle and horses. In 1992, the status quo of the fauna and vegetation was analysed, and in 1993, the present agricultural management was established. In 1995, the former tidal inlet ‘Ententief’ was reconnected to tides by the

Fig. 23.1 Wursten Coast Project area



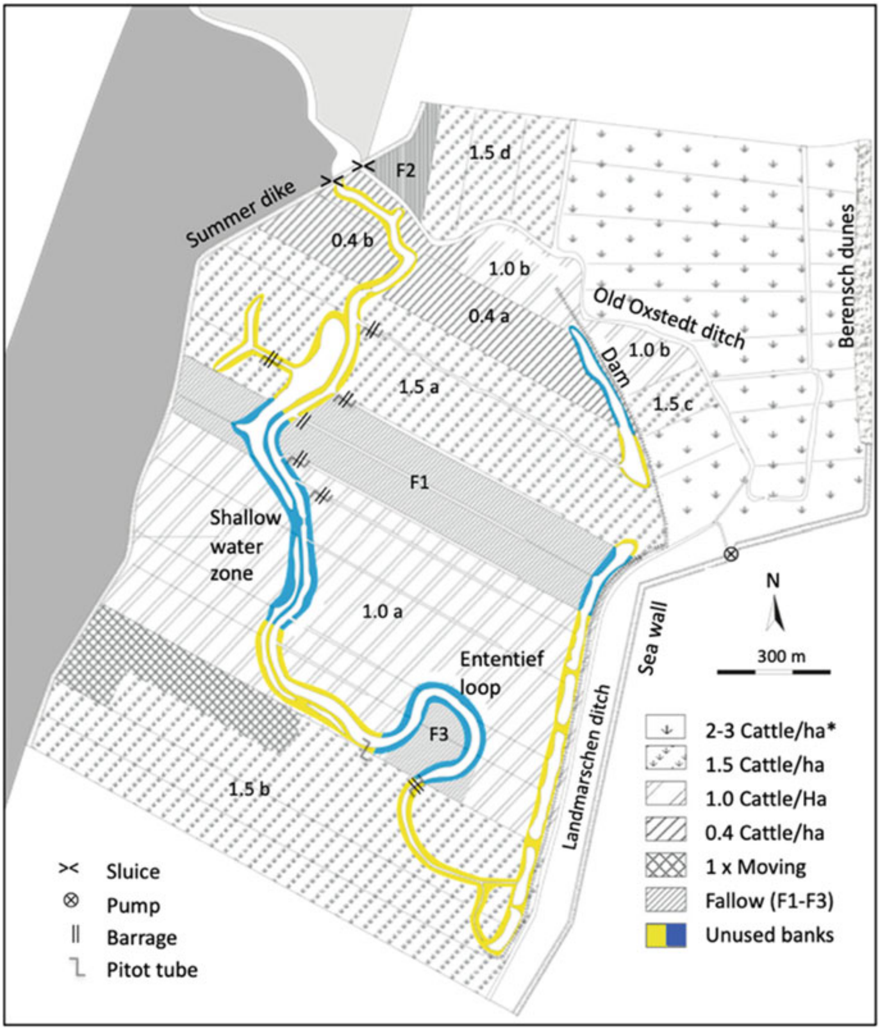


Fig. 23.2 The Spieka-Neufeld summer polder at Wursten coast. The indicated management measures were introduced in 1992. In 1995, the former tidal inlet ('Ententief') was reconnected to the tides by a new built sluice. *: Some parts were also used as meadows for mowing

sluice and allows flooding by seawater. Additionally, existing ditches were excavated mechanically to NN level and a shallow water zone was created, mainly at the west side of the 'Ententief' (Fig. 23.2).

At the beginning of the project, the salt marsh and large parts of the polder grassland resembled a short cut golf lawn (Dierssen et al. 1988) due to intense grazing with up to seven sheep/ha or three cattle/ha, respectively (Böhme et al. 1999). After the start of the project, the foreland was used as meadow (Arensch/

Berensch) and in the part north of the sluice as fallow–Fallow Oxstedt Creek and Fallow Spieka-Neufeld south of the Oxstedt Creek sluice.

The influence of the opening of the summer dike was studied by monitoring the development of the vegetation and selected animal groups, i.e. carabid beetles, spiders, true bugs, selected aquatic and marine organisms, and birds. Fenced experimental plots were installed in the salt marsh in front of the summer dike to prevent sheep from grazing and to initiate a succession of natural salt marsh communities. Sheep grazing ended completely in 1996 in large parts of the salt marsh area.

The sluice pipe has a diameter of 1.3 m and its bottom was levelled to NN, which allows an inflow of up to 40,000 m^3 of seawater passing through the sluice gate at each tide.

In the Spieka-Neufeld polder, areas with various intensities of cattle grazing (2 x 0.4, 3 x 1.0, 3 x 1.5, and 1 x 1.5–3.0 cattle/ha), a meadow, and three fallow areas were established (Fig. 23.2).

In contrast to the Spieka-Neufeld salt marsh, the Cappel-Neufeld salt marsh had been heavily drained in the past. In spite of cattle grazing, a semi-natural grassland was partly maintained in the area. The different structure of the Cappel-Neufeld salt marsh and that at the Spieka-Neufeld summer polder is demonstrated by aerial photographs in Chap. 4 (Fig. 4.9).

The foreland salt marsh and the summer polder grassland mainly differ in the flooding frequency and salinity. Average flooding per year is 420 times, 171 times, and 58 times at an elevation of −10 cm MHW, +1.8 MHW, and at +2.1 m, respectively. During the period from 1991 to 1999, the summer polder was partly or completely flooded six times by severe storm surges, which resulted in a temporarily increase in salt content of the soils (Fig. 23.3) (Kinder et al. 2002).

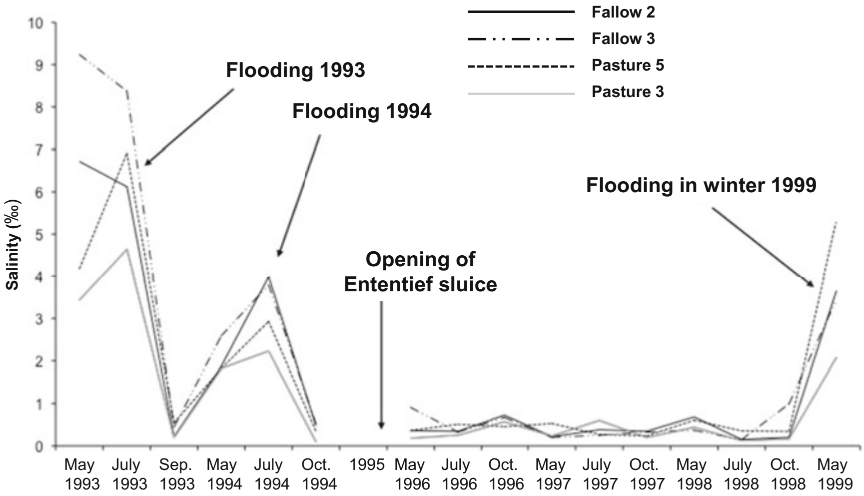


Fig. 23.3 Salinity dynamics of the summer polder soil after the impact of heavy storm surges (according to Kinder et al. 2002; Hassenstein 1998; Albersmeyer 1998)

23.2.2 Survey of the Terrestrial Fauna

From 1991 to 1999, carabid beetles, true bugs, and spiders were collected at 40 sampling sites for a period of 6-months each year (April to September) (for details, see Främbs et al. 2002, Tables 4.4 and 4.5). Soil dwelling groups of Carabidae, Heteroptera, and Araneae were sampled with Barber traps (four per sampling site). At plots in the tidal zone, floating traps were used (Främbs and Stahl 1997). Araneae and Heteroptera of the vegetation layer were collected by standardised scoop net sampling, d-vac sucking, and photo-eclectors. Hand sampling was performed at watersides. In total, the collected material included 139 species of Carabid beetles (179,724 specimens), 77 species of Heteroptera (14,367 specimens), and 170 species of Araneae (252,492 specimens).

23.3 Results

23.3.1 Flora and Vegetation of the Summer Polder

After the implementation of the sluice, halophyte vegetation was established on pioneer sites of the salt marsh zone along the banks of 'Ententief' and connected ditches up to 20 cm above MHW (Puccinellietum maritimae, Salicornietum brachystachyae). A total of 18 halophytes were found. Extensively grazed banks offer optimal light conditions for flood resistant halophytes, which are adapted to grazing. Tall plants of brackish reeds (Bolboschoenetum maritimi) and stands of *Elymus athericus* cover banks without grazing. High differences were found between the new established pioneer sites and the older banks of the 'Ententief' and adjacent ditches. In spite of the higher salt contents, these 'Ententief' stands were not colonised by halophytes.

Soil salt content increased by the daily floods and caused the vegetation changes along the 'Ententief' and connected ditches. Unexpectedly, the influence of floods was not higher than before in most areas of the polder that received their low salt content only by floods of storm surges. In this area, the development of vegetation altered only as a consequence of the changed intensity of agricultural use (Fig. 23.4).

Extensification produced an enormous expansion of the fallow area that now covers 90% of the area. The majority of coast-specific species, in particular those of the upper salt marsh, benefit from grazing intensities between 1.0–2.0 cattle/ha, which generate small-scale diverse mosaic patterns of high- and low-growing vegetation (Figs. 23.5 versus 23.6).

The following plant species became problematic in the salt marsh of the foreland and in the summer polder: *Spartina anglica* is widely spread at the Wursten Coast and locally even dominant. Before the extensification, it was restricted to the Wadden Sea and to some margins of the ditches in the foreland. Few specimens existed along the 'Ententief' of the polder. Although no remarkable changes were found within the project period, dispersal is likely along the lower zone of the 'Ententief' and in the implemented flat-water zone. *Elymus athericus* and its hybrids

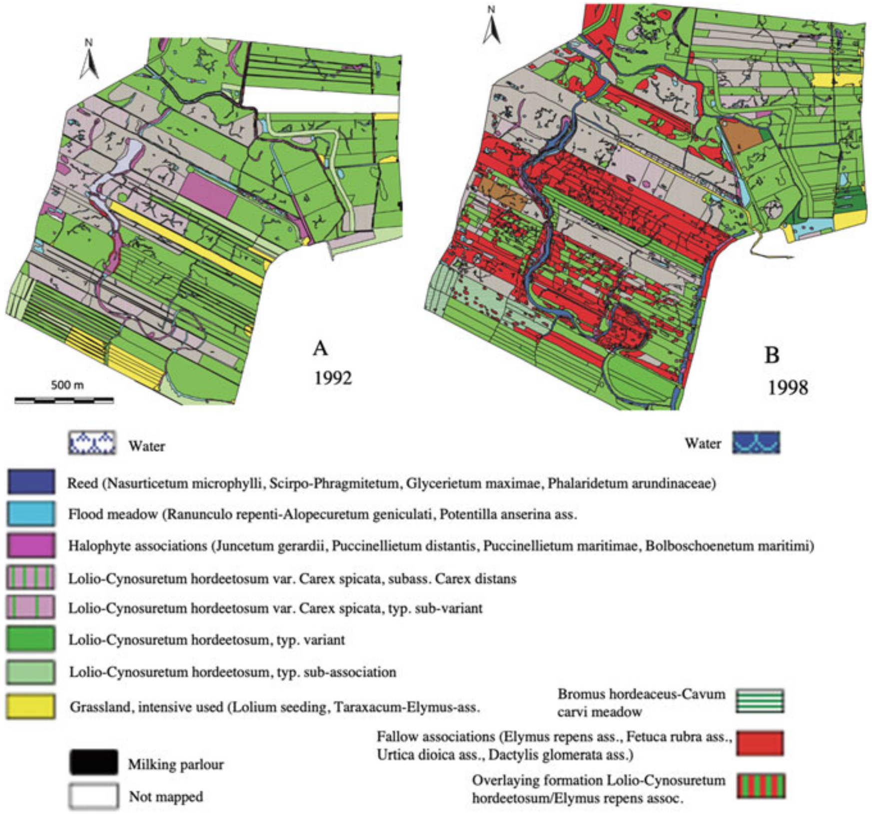
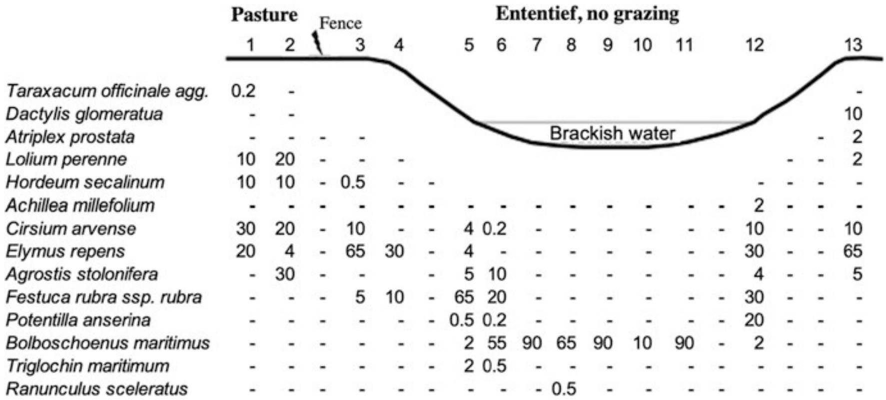


Fig. 23.4 Vegetation of the Spieka-Neufeld summer polder (**a**) in 1992 and (**b**) in1998. The summer dike borders to the west. Original: M. Kinder



	1	2		3	4		5	6	7	8	9	10	11		12			13
Taraxacum officinale agg.	0.2	-																-
Dactylis glomeratua	-	-																10
Atriplex prostata	-	-	-	-													-	2
Lolium perenne	10	20	-	-	-											-	-	2
Hordeum secalinum	10	10	-	0.5	-	-									-	-	-	-
Achillea millefolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Cirsium arvense	30	20	-	10	-	-	4	0.2	-	-	-	-	-	-	10	-	-	10
Elymus repens	20	4	-	65	30	-	4	-	-	-	-	-	-	-	30	-	-	65
Agrostis stolonifera	-	30	-	-		-	5	10	-	-	-	-	-	-	4	-	-	5
Festuca rubra ssp. rubra	-	-	-	5	10	-	65	20	-	-	-	-	-	-	30	-	-	-
Potentilla anserina	-	-	-	-	-	-	0.5	0.2	-	-	-	-	-	-	20	-	-	-
Bolboschoenus maritimus	-	-	-	-	-	-	2	55	90	65	90	10	90	-	2	-	-	-
Triglochin maritimum	-	-	-	-	-	-	2	0.5	-	-	-	-	-	-	-	-	-	-
Ranunculus sceleratus	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-

Fig. 23.5 ‘Ententief’ vegetation before connection to tidal influence. 1–13: Vegetation survey along a 50 m transect. Modified according to Kinder et al. (2002)

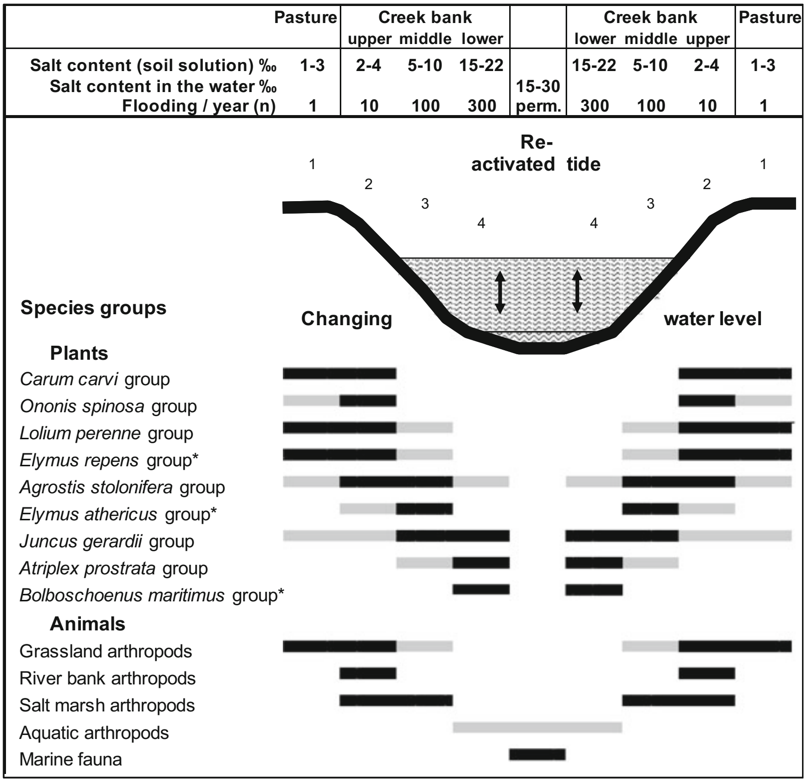


Fig. 23.6 Ecological groups of vegetation and fauna at the central ‘Ententief’ Creek after connection to tides of the North Sea. *Black* main, *grey* side occurrence, *: dominant under extensivation. Modified according to Kinder et al. (2002)

are a major problem after the extensification of salt marshes (Bakker 1993). Sea couch was found more frequently in the salt marshes north of Spieka-Neufeld than in the semi-natural, un-grazed area at Cappel-Neufeld. After extensification, the species dispersed over a wide area and colonised the lower zones with higher flood rates in the foreland. It firstly colonised the summer polder after flood influence. *E. athericus* grew in rich stands in the abandoned central ‘Ententief’ region. A future increase of cover is expected at stands with low density.

While *S. anglica* and *E. athericus* may cause the expected problems in the salt marshes of the foreland the development of the following species will affect plant biodiversity in the summer polder. Reed (*Phragmites communis*) had not colonised the area after abandonment, obviously, because it could not penetrate the established populations of *Bolboschoenus maritimus* along the ‘Ententief Creek’ within the study period (Fig. 23.4). Besides reed, *Elymus repens* and *Cirsium arvense* will moderately benefit from the reduced agricultural and the low tidal influences.

23.3.2 Terrestrial Arthropods

The changes in the hydrological regime and the vegetation structure that mainly depend on the grazing regime were the key factors for the changes in the arthropod fauna. Considering elevation and intensity of agricultural use, indicator species of Carabidae, Heteroptera, and Araneae were combined to groups with respect to their occurrence in different foreland or summer polder habitats (Table 23.1).

Terrestrial arthropods are affected by the tidal flooding of salt marshes in two ways: (1) Regular tides cause a permanent soil wetness and salt content that are needed by the assemblages of the lower salt marsh. (2) Storm surges affect the salt marsh species immediately and partly with fatal effects for the local assemblages as found in the first years of the project. Storm surges washed out a high number of hibernating arthropods and transported them to the Geest margin (Främbs 1997) or the open sea, which was found for all three studied taxa in the foreland area with sheep grazing. However, it was markedly reduced for spiders and carabid beetles at sites with high and dense vegetation (Främbs 2002a).

The three studied taxa reacted differently on the fallow succession. After 3 years of foreland abandonment, the abundance of Heteroptera decreased or became even extinct, in particular species preferring banks. The same trend existed for carabid beetles for a longer period, while spiders reacted nearly indifferently.

In the summer polder, populations of salt marsh indicator species, i.e. *Dicheirotrichus gustavii*, *Pogonus chalceus*, *Bembidion minimum*, *B. normannum*, *Halosalda lateralis*, *Erigone longipalpis*, and *Pardosa purbeckensis*, greatly increased, mainly along the banks of those ditches that were connected to the tidal water regime. These species were already present in the summer polder before opening the new sluice, but benefited from the expansion of banks with low and sparse vegetation after the tidal influence. Later, the arthropod populations decreased again with subsequently up growing vegetation.

In the summer polder, the moderate reduction of agricultural use induced a high increase of the abundance of hygrophilic arthropods, in particular, after 3 to 4 years. Salt marsh species showed a similar development after the reduction of grazing intensity at the banks of ditches and in the wet mesophilic grassland.

23.3.3 Aquatic (Limnic) Arthropods

Aquatic Heteroptera, water beetles, dragonfly larvae, and the water spider *Argyroneta aquatica* were collected at sampling sites in 'Ententief' Creek, ditches, pools, and limnic creeks. A total of 74 species were found with 26 species indifferent to salt (not listed in Table 23.2), 38 salt tolerant species, 10 characteristic brackish-water species (Table 23.2), three halobiontic species, and seven halophilic species.

The distribution of these species in 'Ententief' Creek and in ditches reflects a gradient of decreasing tidal dynamics and salt content. In the mixo-haline 'Ententief', a salt gradient was revealed from the summer dike sluice to the main dike. Salt concentration decreased from polyhaline (30‰) to β-mesohaline

Table 23.1 Distribution of coastal specific arthropods at Wursten Coast after the implementation of measures. The reaction of species towards their probable zonal distribution in natural salt marshes is indicated. Zonation according to vegetation. Combined from Främbs (2002a) and Kinder et al. (2002), modified. *Aran* Araneae, *Car* Carabidae, *Het* Heteroptera, *FL* Foreland, *SP* Summer polder

Eulittoral	Foreland	Summer polder			Zone
Wadden	Salt	River bank	Grassland		
Sea	Marsh	Wetted	Wet	Wet-fresh	
		Under salt influence		(Salt infl.)	
Cillenus lateralis (Car)					A
	Praestigia duffeyi (Aran)				B
	Pogonus chalceus (Car), *Pogonus luridipennis* (Car), *Dicheirotrichus gustavii* (Car), *Dyschirius chalceus* (Car), *Dyschirius salinus* (Car), *Chiloxanthus pilosus* (Het), *Saldula palustris* (Het), *Conostethus salinus* (Het), *Orthotylus moncreaffi* (Het)				C1
	Europiella decolor (Het)				C2
	Bembidion minimum (Car), *Bembidion normannum* (Car), *Halosalda lateralis* (Het)				C3
		Saldula pilosella (Het)			D1
		Bembidion iricolor (Car), *Amara convexiuscula* Car)			D2
		Bembidion aeneum (Car), *Salda littoralis* (Het), *Ozyptila westringi* (Aran)			D3
		Silometopus reussi (Aran)			D4
	Erigone longipalpis (Aran), *Erigone arctica* (Aran)				E1
	Pardosa agrestis purbeckensis (Aran), *Argenna patula* (Aran), *Silometopus ambiguus* (Aran), *Enoplognatha mordax* (Aran)				E2
	Leptorhoptrum robustum (Aran), *Robertus arundineti* (Aran)				E3

Zone A–E: Potential occurrence of species expected for a natural salt marsh zonation
A. Upper Eulittoral (Spartinietum); preference for flooding
B. Lower most salt marsh (Spartinietum-Puccinellietum); likely preference for flooding
C. Lower salt marsh (Puccinellietum to lower Festucetum); flooding tolerance,
  C1 Poorly vegetated or grazed salt marsh (FL) and river banks (SP)
  C2 Unused salt marsh (FL) and river banks (SP) with Artemisia maritima
  C3 lower flooding tolerance
D: Upper salt marsh and upper Festucetum up to salty grassland; no flooding tolerance
  D1 Poorly vegetated or grazed river banks (SP)
  D2 Indifferent
  D3 Poorly vegetated or grazed banks and grassland (SP)
  D4 Banks and grassland out of use (SP)
E: No preference of a particular level (Puccinellietum to salt grassland); flooding tolerance
  E1 Poorly vegetated or grazed salt marshes (FL), banks and grassland (SP)
  E2 unused salt marsh (FL) and poorly vegetated or grazed banks and grassland (SP)
  E3 Unused salt marsh (FL), banks and grassland (SP)

Table 23.2 Colonisation of water habitats by indicative aquatic arthropods before and after the implementation of the hydrological measures in the Spieka-Neufeld summer polder in 1995. Creeks = Arenscher and Alter Oxstedter Bach, xx habitat with main occurrence, x habitat with secondary occurrence, –: no occurrence; *Brack.* Brackish; *St.top*: Stenotopic; *RL*: Red list, *LS* Lower Saxony, *D* Germany. *Perm.* permanent, *w.* water, Modified according to Främbs (2002b)

		Ententief				Ditches		Pools		Creeks		Species (n)				
		Sea: near		Sea: far				Near geest				Σ	Brackish	St. top	RL LS	RL D
Species group		B	A	B	A	B	A	B	A	B	A					
1	Perm., calm w. 5–30‰	x	x	x	xx	x	xx	x	x	x	x	4	3	2	–	1
2	Perm., calm w. 3–18‰	x	–	x	xx	x	x	x	x	–	–	5	1	2	–	–
3	Perm. itches/pools 3—10‰	x	–	x	–	xx	xx	x	x	x	x	17	4	7	3	2
4	Permanent pools 3—5‰	–	–	–	–	–	–	xx	xx	–	–	18	2	7	4	7
5	Limnic floating w. <0.5‰	–	–	–	–	–	–	–	–	xx	xx	4	–	–	–	–

1. Heteroptera: *Sigara stagnalis* (Leach), *Sigara lateralis* (Leach), *Sigara striata* (Linnaeus), *Paracorixa concinna* (Fieber)

2. Heteroptera: *Notonecta viridis* Delcourt, *Notonecta glauca* Linnaeus Odonata, larvae *Enallagma cyathigerum* Charpentier, *Aeshna mixta* Latreille

Coleoptera: *Enochrus bicolor* (Fabricius)

3. Heteroptera: Gerris *lacustris* (Linnaeus), *Corixa affinis* (Leach)

Coleoptera: *Helophorus brevipalpis* Bedel, *Helophorus aquaticus* (Linnaeus), *Ochthebius marinus* (Paykull), Ochthebius *dilatatus* Stephens, *Coelambus parallelogrammus* (Ahrens), *Agabus conspersus* (Marsham), *Helophorus flavipes* Fabricius, *Rhantus suturalis* (MacLeay), *Agabus bipustulatus* (L.), *Anacaena limbata* (Fabricius), *Ochthebius minimus* (Fabricius), *Hydrobius fuscipes* (L.), *Cercyon marinus* Thomson, Hydroporus planus (Fabricius), *Helophorus grandis* Illiger

4. Heteroptera: *Gerris thoracicus* Schummel, *Sigara semistriata* (Fieber), *Corixa punctata* (Illiger), *Hesperocorixa linnaei* (Fieber), *Callicorixa praeusta* (Fieber), *Cymatia bonsdorffii* (C. Sahlb.)

Odonata, larvae: *Ischnura elegans* (Vander Linden), *Sympetrum vulgatum* (L.), *Lestes barbarus* (Fab.), *Lestes sponsa* (Hansemann), *Lestes virens* (Charpentier), *Aeshna grandis* (L.)

Araneae *Argyroneta aquatica* (Clerck)

Coleoptera *Coelambus impressopunctatus* (Schaller), *Noterus clavicornis* (De Geer), *Haliplus apicalis* Thomson, *Laccophilus minutus* (L.), *Gyrinus caspius* Ménétriés

5. Heteroptera *Sigara falleni* (Fieber)

Coleoptera *Hydroporus palustris* (Linnaeus), *Laccobius minutus* (Linnaeus), *Potamonectes depressus* (Fabricius) conditions (5‰). Some perennial pools at the eastern part of the polder had a low salt content (3–5‰, α-oligohaline). They get salt input only when the polder was flooded by storm surges. Additionally, two limnic watercourses exist in the summer polder (Arensch Creek and Old Oxstedt Creek) with constantly low salinity (<0,5‰). (Details in Främbs 2002b).

23.3.4 Zoobenthos

The marine species colonised the ‘Ententief’ Creek and the connected ditches immediately after the opening of the sluice. Fish, shrimps, and the characteristic benthic species reached rapidly high population densities, particularly in the lower course of the ‘Ententief’ Creek. Because of their salt tolerance, they could also settle in the upper ‘Ententief’. Colonisation by the marine benthic fauna displayed strong fluctuations. Its succession was interrupted by cold winters (1995/96/97) and drying up of some creek banks as a result of constant easterly winds. The marine fauna at the lower course of the creek was very similar to that in front of the summer dike.

After the connection to the tidal regime, 18 brackish-water species were found in the waterbodies of the summer polder in 1996 (Table 23.3). At first glance, this increase might be interpreted as a positive development concerning species diversity (Hassenstein 1998). However, Hassenstein also stated that the succession was not finished. The data of 1998 corroborated this hypothesis: seven species did not occur furthermore; three species were only found rarely at single stations. Only *Manayunkia aestuarina* (Polychaeta) showed an increase in the ‘Ententief’ Creek.

The decrease of most species may be associated with the high salt content at the ‘Ententief’ stations under research. The α-mesohaline to polyhaline conditions for zoobenthos differed from the brackish-water (oligohaline to b-mesohaline) condition that is preferred by these species.

The missing freshwater inflow from the inland was the main reason that prevented brackish-water species from a colonisation of the summer polder. This inflow was cut by a dam between the polder area and the Old Oxsted Creek.

Full lists of species sampled in the project can be found in Främbs et al. (2002). Results considering the vegetation of the foreland are documented in Kinder et al. (2002) and the birds in Hielen (2002).

23.4 Conclusions

In the Wursten Coast Project, a regeneration of salt marsh vegetation and fauna in the Spieka-Neufeld polder was intended by reconnecting the polder to the tides of the sea through installation of a new sluice in the summer dike. The establishment of the sluice had only success in a small part of the polder area along the ‘Ententief’ Creek, the ditches, and an area lowered in level besides the creek.

Table 23.3 Brackish-water species of the project area. Modified and rearranged from Böhme et al. (2002). Estuaries: number of Estuaries in the German Bay with record of the species. *M* Mollusc, *A* Annelid, *C* Crustacean, *F* Fish; * Threatened species of Red List (Binot et al. 1998); +: Main occurrence, (+): Species that occur only occasionally or sporadically, –: Species not studied

		Foreland		Summer polder					Estuaries
	Study site	Oxst.	Oxst.	Oxst.	Ententief			Arensch	
		tidew.	creek	ceek				creek	
	Connection to tide	–	–	Before	Before	After	After	After	–
	Study year	<1996	1996	1996	1964	1996	1998	1998	N
M	*Potamopyrgus antipodarum*	.	(+)	+	+	(+)	.	.	9
M	*Assiminea grayana**	(+)	.	.	.	.	.	.	5
M	*Alderia modesta**	.	.	.	.	(+)	.	.	4
M	*Limapontia depressa**	.	.	.	.	(+)	.	.	–
A	*Streblospio benedicti**	+	(+)	.	.	+	(+)	+	3
A	*Marenzelleria sp.*	.	(+)	.	.	+	(+)	+	–
A	*Manayunkia aestuarina*	+	(+)	.	.	(+)	+	.	6
A	*Paranais litoralis*	+	.	+	+	+	–	–	12
A	*Nais elinguis*	.	.	+	+	+	–	–	–
A	*Tubifex costatus*	+	+	.	.	.	–	–	11
A	*Monopylephorus irroratus*	.	.	+	.	.	.	.	3
C	*Palaemon longirostris*	.	(+)	.	.	+	.	.	–
C	*Palaemonetes varians*	.	(+)	.	+	+	(+)	.	–
C	*Eriocheir sinensis*	.	(+)	.	.	(+)	.	.	–
C	*Neomysis integer*	.	+	.	+	+	.	.	–
C	*Gammarus duebeni*	–	.	–	+	+	–	–	3
C	*Gammarus zaddachi*	–	.	–	.	+	–	–	3
C	*Gammarus salinus*	–	(+)	–	+	(+)	–	–	2
C	*Gammarus tigrinus*	.	.	+	+	+	–	–	–
C	*Lekanesphaera rugicauda*	.	+	.	.	+	.	.	3

(continued)

Table 23.3 (continued)

		Foreland		Summer polder					
		Oxst.	Oxst.	Oxst.				Arensch	
	Study site	tidew.	creek	ceek	Ententief			creek	Estuaries
F	*Pomatoschistus microps*	.	(+)	+	.	+	+	–	–
	Number of species	>5	12	>6	8	18	>5	>2	16

Overall, the sluice had no effect on the tidal high-water level in the polder area. The surface remained permanently up to 65 cm below the adjacent Wadden Sea surface, which is explained by the small dimension of the sluice. The inflow of seawater was too low and the drainage during ebb tide too effective.

Two alternatives offer solutions to achieve an effective tidal regime in the summer polder: (1) a bigger opening in the summer dike or (2) the dike has to be completely removed.

A dam prevents freshwater inflow from the mainland that deteriorates the conditions for the endangered brackish-water animals. In consequence, in 1998, brackish water conditions (α-oligohaline to β-mesohaline) were established only in small parts of the area.

References

Albersmeyer J (1998) Die Einwanderung mariner Makrofauna in die Gewässer eines Sommerpolders an der Wurster Küste nach deren Wiederanbindung an das marine System. Diploma thesis, Universität Bremen

Bakker JP (1993) Strategies for grazing management on salt marshes. Kluver, Dordrecht, p 400

Binot M, Bless R, Boye P, Gruttke H, Pretscher H (1998) Rote Liste gefährdeter Tiere Deutschlands. Schriftenreihe für Landespflege und Naturschutz 55. Bonn, Bundesamt für Naturschutz

Böhme B, Främbs H, Hielen B, Kinder M (1999) Salt marsh project 'Wurster Küste': regeneration of coastal grassland and salt marshes. Senckenbergiana maritima Suppl 29:37–42

Böhme B, Günther C-P, Rachor E (2002) Aquatische Fauna. Zoobenthos: Weichtiere, Ringelwürmer, Krebstiere. In: Främbs H et al (eds) Renaturierung salzbeeinflusster Lebensräume der Nordseeküste. Salzwiesenprojekt Wurster Küste, vol 68. BfN-Skripten, Bonn, pp 195–218

Dierssen K, von Glahn H, Härdtle W, Höfer H, Mierwald U, Schrautzer J, Wolf A (1988) Rote Liste der Pflanzengesellschaften Schleswig-Holsteins. Schriftenreihe des Landesamtes für Naturschutz und Landschaftspflege Schleswig-Holsteins 6. Kiel Landesamt für Naturschuthz und Landschaftspflege Schlewsig-Holstein

Främbs H (1997) Auswirkungen von Sturmfluten auf die Laufkäfer (Col. Carabidae) der Nordseeküste. Arbeitsberichte Landschaftsökologie Münster 18:47–61

Främbs H (2002a) Terrestrische Arthropoden: Landwanzen, Laufkäfer, Webspinnen. In: Främbs H et al (eds) Renaturierung salzbeeinflusster Lebensräume der Nordseeküste. Salzwiesenprojekt Wurster Küste, vol 68. BfN-Skripten, Bonn, pp 129–181

Främbs H (2002b) Aquatische Fauna. Limnische Arthropoden: Wasserwanzen, Wasserkäfer, Libellen, Spinnen. In: Främbs H et al (eds) Renaturierung salzbeeinflusster Lebensräume der Nordseeküste. Salzwiesenprojekt Wurster Küste, vol 68. BfN-Skripten, Bonn, pp 184–194

Främbs H, Stahl R (1997) Eine aufschwimmende Bodenfalle zur Erfassung epigäischer Arthropoden in überflutungsgefährdeten Lebensräumen. Arbeitsberichte Landschaftsökologie Münster 18:287–289

Främbs H, Kinder M, Hielen B, Böhme B, Günther C-P, Rachor E, Cordes H, Mossakowski D (2002) Renaturierung salzbeeinflusster Lebensräume der Nordseeküste. Salzwiesenprojekt Wurster Küste, vol 68. BfN-Skripten, Bonn, p 325

Hassenstein W (1998) Auswirkungen der Wiederanbindung der Gewässer eines Sommerpolders an das marine System auf die genuine Brackwasserfauna. Diploma thesis, Universität Bremen

Hielen B (2002) Vögel. In: Främbs H, Kinder M, Hielen B et al (eds) Renaturierung salzbeeinflusster Lebensräume der Nordseeküste. Salzwiesenprojekt Wurster Küste, vol 68. BfN-Skripten, Bonn, pp 219–270

Kinder M (2002) Vegetation. In: Främbs H, Kinder M, Hielen B et al (eds) Renaturierung salzbeeinflusster Lebensräume der Nordseeküste. Salzwiesenprojekt Wurster Küste, vol 68. BfN-Skripten, Bonn, pp 89–128

Kinder M, Främbs H, Hielen B, Mossakowski D (2002) Regeneration von Salzwiesen in einem Sommergroden an der Nordseeküste: E+E-Vorhaben “Salzwiesenprojekt Wurster Küste”. Natur und Landschaft 78:343–353

Köster A (1917) Die Erbauung der Cappel-Neufelder Sommerdeiche. Jahrbuch Männer vom Morgenstern 17:69–91

OMReg (2016) ABPmer’s Query database: Online Marine Registry OMReg. http://www.abpmer.net/omreg/index.php

Wolters M (2006) Restoration of salt marshes. Proefschrift Rijkuniversiteit Groningen. Van Denderen, Groningen

Estimated Future Effects of the Sea Level Rise Exemplified by the Wursten Coast

24

Wolfgang Dormann

Abstract

A model considering the scenarios with the future sea level increase and the surface levelling of the Wursten coast (Lower Saxony) should monitor the changes expected for the salt marsh fauna and the fauna in a summer polder. Additionally, different sedimentation conditions were considered. According to the simulation *Erigone longipalpis* and *Bembidion normannum* will benefit from the increasing MHW in this part of the coast depending on the sedimentation rate. In the summer polder, the situation is much more complicate. In the summer polder, results showed that only under de-embankment conditions regeneration of specialised halobiontic species can be expected.

24.1 Introduction

The future rising sea level and the effect of storm surges will reduce the area of foreland salt marshes, in particular, of the upper salt marsh. Regarding the function of summer polders under future conditions, the low height of embankments against the sea favours the settlement of salt marsh arthropods.

It was already demonstrated in the past that salt marsh species are able to colonise new emerging habitats (Topp 1988; Götting 2001). These results were supported by our investigations at the Ententief Creek of the Spieka/Neufeld summer polder (Chap. 23; Främbs et al. 2002), where a mosaic of marine, brackish, and terrestrial habitats was established after the instalment of a new sluice. Subsequent to the opening of the new sluice, some specialised coastal species settled there, e.g. the

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endangered specialist carabid beetles *Bembidion iricolor*. The following analysis will simulate the reaction of specialist species presently living in summer polders. The simulations are performed for the Wursten Coast.

24.2 Methods and Data for a Simple Model

The reaction of species on the future sea level rise in the foreland was estimated for two areas: (1) the Oxstedt Fallow in front of the Spieka/Neufeld summer polder at Wursten Coast and (2) the summer polder itself. For Oxstedt Fallow, a simple model was implemented using the elevation data based on fine levelling of R. Kesel (Främbs et al. 2002), data on erosion and sedimentation observed after the strong storm surge ‘Kerstin’ in January 2000, and the data of vegetation and fauna.

Oxstedt Fallow: A digital elevation model was calculated applying the software ArcView (ESRI). Three scenarios were selected with both a sea level rise and increase of half tidal range (according to the official scenarios; see Chap. 2):

$$\mathrm{M20}: 15 + 10/2, \mathrm{M45}: 35 + 20/2, \text{and } \mathrm{M70}: 55 + 30/2\ \mathrm{cm}.$$

The symmetric MHW-curve at Wursten Coast allows us to calculate the values from the sum of the sea level rise plus half the tidal range. The three scenarios with sea level rise and tide range were complemented by three sedimentation scenarios:

S0: Sedimentation remains as it presently exists until 2050
S1: Sedimentation with a medium rate of 1.2 cm $\mathrm{yr.}^{-1}$ as typical for island salt marshes and
S2: High sedimentation rate of 2.4 cm $\mathrm{yr.}^{-1}$ that is characteristic for mainland salt marshes

Thus, a total of 3 x 3 = 9 scenarios were analysed.

The following aspects were taken into account in the calculation of the scenarios: For a medium-term period, a negative sediment balance of the Wadden Sea with a decreasing sedimentation rate in salt marshes was assumed (Fleming, written comm.). The changing sedimentation rates along the salt meadow elevation gradient were also considered (Eysink 1987). Additionally, the erosion data from 1997 to 2000 were integrated using an idealised and highly simplified approach (Chap. 19 and Fig. 21.6). The measured area losses in that period were extrapolated for the simulation period and integrated into the simulation by shortening the respective transect in the central area according to the coastal squeeze effect (Doody 2004).

Simulation runs were done in 50 iteration steps in combination with the annually rising sea level (log50 of the rise in 2050).

Summer polder: A digital elevation model was generated on the basis of the levelling data of R. Kesel (Kinder 2000), which covers an area of 200 ha with 13,000 levelling points. Therefore, the levelling was refined by interpolation of intermediate data. The interpolated data was corrected using aerial photographs, topographical maps, and own records of the terrain, which made it possible to minimise mistakes and to integrate minimum water levels at depressions and pigging systems. Additionally, the same use of ArcView application and the same scenarios and rates of sedimentation were used as for the foreland. The following models were simulated:

BS: Basic situation for 1998.
DP: Sluice and summer dike (SD) persist or SD heightened in order to continue agricultural use.
R50: Removal of summer dike in 2050.
R00: Removal of summer dike in 2000.

The calculations for R00 were done with the same instructions as that for the foreland. The situation of the variants DP and R50 was more complex because the minimum height of 3.43 m above NN of the summer dike prevents a normal tide effect and the 1.3 m diameter of the sluice allows only a restricted water inflow (Kinder 2000). For these two treatments, the following additional hydrographic data was used:

- Average spring-tide curve of Cuxhaven gauge 1998 (BSH 1997).
- Daily high-water data of Spieka/Neufeld gauge of 1998 (NLWKN 1999).
- Flow velocity depending on water level and inflow capacity at the summer polder sluice (STAWA 1996).
- Evaluation of data from the summer polder gauges 'Bypas' and 'Ententiefschleife' (flooding frequency, height, and duration; selected elevations compared with gauge Spieka/Neufeld) (Kinder 2000).

The water dynamics within the summer polder differ from that of the foreland due to the restricted diameter of the sluice. For the polder, the MHW value (+1.30 m above NN) of Kinder (2000) was used under consideration of the lower height of tides: the MHW value of the gauge at the sluice is approximately 8 cm higher than that at Ententief (Kinder 2000). MHW zones considering the effect of corrected data are graphed in Fig. 24.4 (BSc, DPc).

The suitable area for two spiders and two carabid beetles was calculated using the zonation index with the standard deviation as limits for the suitable area.

24.3 Results and Discussion

24.3.1 Foreland Salt Marsh Area

A compact transect was selected for the prediction of the sea level rise effect in order to focus on the results of the scenarios without distraction by the shape of the area (Fig. 24.1). Using the results of the nine scenarios of the predicted sea level rise and the changed sedimentation, changes in the elevation morphology can be derived (Fig. 24.2a). All scenarios reveal an area reduction of the lower zones located in the

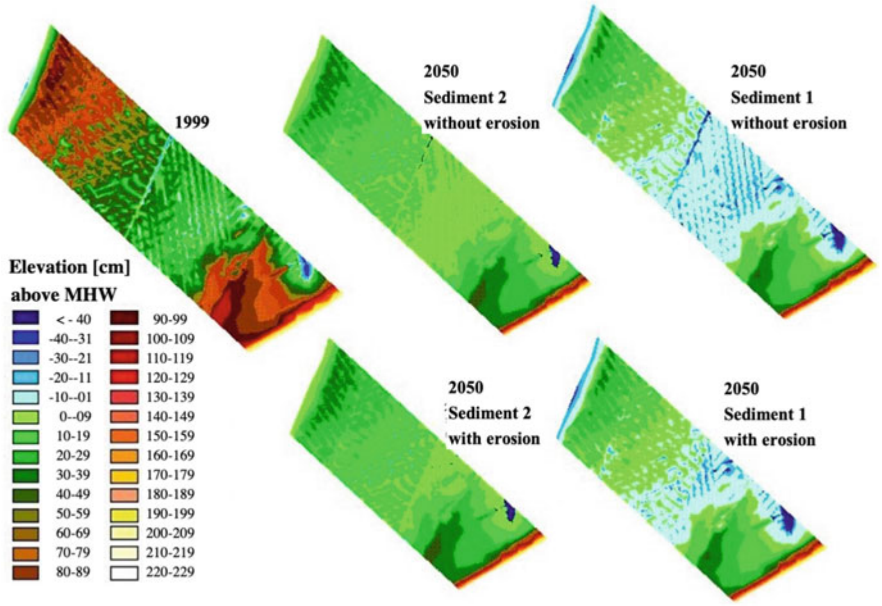

Fig. 24.1 Simulation of potential changes at Oxstedt Fallow until 2050. Calculated for a 100 m transect, a sea level rise of +55 cm and a + 30 cm increase of tidal range (M70). Upper left side of the transects borders the Wadden Sea, down-right the summer dike

centre of the transects, in particular, the range of −10 to +0.90 cm MHW. The total area of the transect reduced from 3.4 ha at the beginning in 1999 to 2.7 ha in 2050.

These changes directly affect the suitable living area for arthropod species that prefer specific salt and inundation conditions. The area alterations were used to estimate the future available space for salt grassland arthropods (Fig. 24.2a). This estimation concerns characteristic spider and carabid species of the lower and upper salt marsh. The future extent of the single species habitat was calculated using the zonation index and the changed suitable elevation zones. The results shown in Fig. 24.2b reflect the simulations for a 100 m broad transect of Oxstedt Fallow for four characteristic spider and carabid species: *Erigone longipalpis*, *Silometopus ambiguous*, *Bembidion normannum*, and *Bembidion minimum*.

The prediction of scenarios with sedimentation surplus differs significantly from scenarios without sedimentation surplus. The four analysed species can use smaller parts of their habitat areas if no sedimentation is assumed (see Chap. 14). In the simulation, both species of the lower salt marsh (*Erigone longipalpis* and *Bembidion normannum*) benefit from increasing MHW (M20, M45) in combination with sedimentation surplus (S1, S2) due to the increasing area of the low elevated zones. In contrast, the species of the upper salt marsh (*Silometopus ambiguous* and *Bembidion minimum*) cover less area—with some exceptions (M20-S1 and M20-S2). Integration of erosion has no effect on these tendencies. The spider

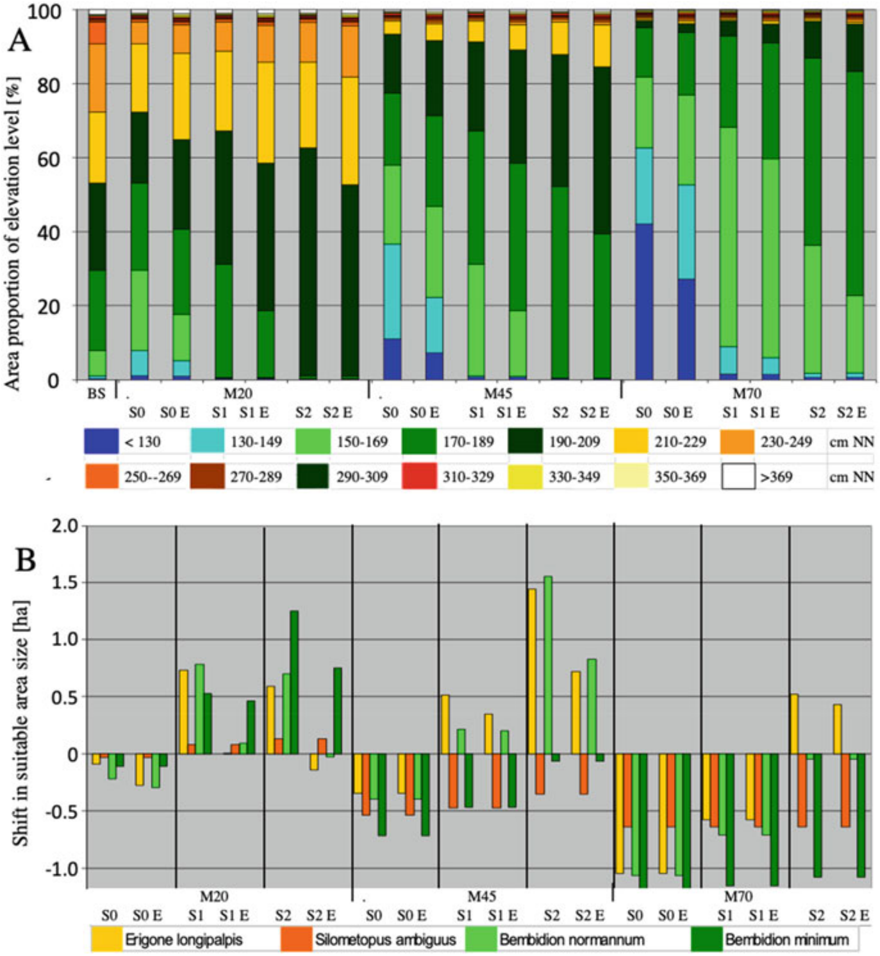

Fig. 24.2 (**a**) Simulation of area proportion of elevation levels for a 100 m transect at Oxstedt Fallow, the area of which changed from 3.4 ha (BS: Basic situation) to 2.7 ha in 2050. MHW level numbers indicate the lower limit of a 20 cm interval. (**b**) Area shifts of habitats suitable for four characteristic salt marsh species. Column BS in (**a**) represents the basic situation; other columns represent the simulation result of different scenarios for 2050. Column pairs reveal results of scenarios without or with erosion (E), respectively. Letters below indicate the model (M): increase of MHW; *S* scenario with sedimentation

Erigone longipalpis is the only species with a possible positive reaction in the scenario with an MHW increase of +70 cm.

For two effects, increasing abundances were predicted. On the one hand, the living area increased for species of the lower salt marshes in unlikely scenarios with a combination of low or mean increase of the sea level and no sedimentation surplus. On the other hand, the abundance of upper salt marsh species increases in the scenarios with low sea level rise (M20). However, most scenarios reflect degrading conditions with increasing problems for species that are already threatened today by decreasing habitat ranges.

24.3.2 Summer Polder Salt Marsh

24.3.2.1 Changes in Elevations and Spatial Conditions

The simulation was also applied to the situation of the summer polder at Spieka-Neufeld (Fig. 24.3). The present situation in the summer polder is characterised by wide areas with suitable elevation for the fauna of upper salt marshes. However, the flooding frequency is low due to the restricted diameter of the sluice and the closed valve of the sluice in summer to protect grazing cattle and horses (see Chap. 23). According to the elevations calculated in the scenarios, approximately 5–10% of the polder area are potential habitats for species of salt marshes and banks (Främbs et al. 2002).

When the summer dike persists up to 2050 (Fig. 24.3b: DP), the number of overflows will increase to 11 times per year. If agricultural use will continue in the future, the summer dike must be heightened. In the scenario with continuing existence of the summer dike, sedimentation will decrease and MHW will be significantly lower than in the foreland. The upper salt marshes will cover only 1–2% of the area, but 30–40% of the area in the central and south-eastern parts will be at MHW level or lower. The rising sea level in the future will cause higher floods in the foreland with the effect of an increasing risk for erosion and breach of the summer dike during storm surges. This event of an eroded summer dike was simulated in the 2050 scenario (Fig. 24.3c: R50). According to the results of this scenario, 80–90% of the polder area will suffer under long-term inundation and deterioration of terrestrial arthropod habitats.

Both dike persistence and dike removal in 2050 pose problems. If the summer dike will persist, the following problems will prevail: (i) the risk of an uncontrollable breach of the summer dike and (ii) an insufficient increase of the polder because of lacking sedimentation. Connecting the polder to the full influence of tides may be an alternative strategy, which means to cut-off the summer dike as early as possible. This scenario was simulated in R00 starting in 2000 (Fig. 24.3d).

If the polder is opened for sediments brought by flooding, the sedimentation rate (2.4 cm per year used in this simulation) is not sufficient to enlarge areas of upper salt marshes. However, it should be considered that sedimentation will happen accidently with local deviations, in particular, at locations exposed to floods. For example, higher sedimentation rates may occur in the western part of the summer polder during storm surges.

24.3.2.2 Shifts in Areas Suitable for Salt Marsh Arthropods

In the summer polder, the spider *Erigone longipalpis* and the carabid beetle *Bembidion normannum* will benefit from a sea level rise (Fig. 24.4c). However, the increase depends on the sedimentation rates. A higher sedimentation rate will

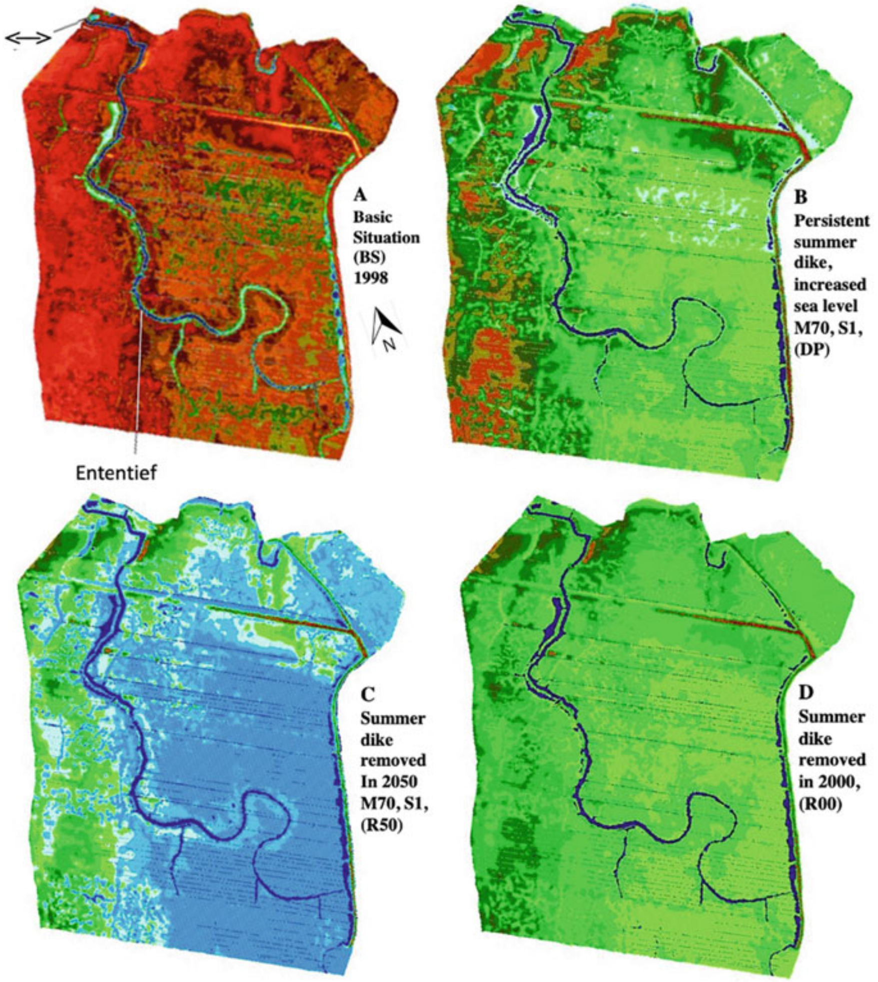

Fig. 24.3 Elevation models of the summer polder Spieka-Neufeld. (**a**) BS: Basic situation in 1999, (**b**–**d**): Scenario M70, (**b**) DP: Summer dike persistent and heightened, (**c**) R50: Summer dike cut-off in 2050, (**d**) R00: Summer dike removal in 2000,: Sluice. Colours indicate elevation levels as in Fig. 24.1

increase their abundance, whereas a strong sea level rise combined with low sedimentation will have a contrary effect.

In contrast to the promotion of the two lower salt marsh species, nearly all simulations predict habitat losses for the spider *Silometopus ambiguus* and the carabid beetle *Bembidion minimum* of the upper salt marsh, except scenario M20 with a low sea level rise. In this scenario, minor changes are predicted for *Silometopus ambiguus* and even remarkable area increases for *Bembidion minimum.*

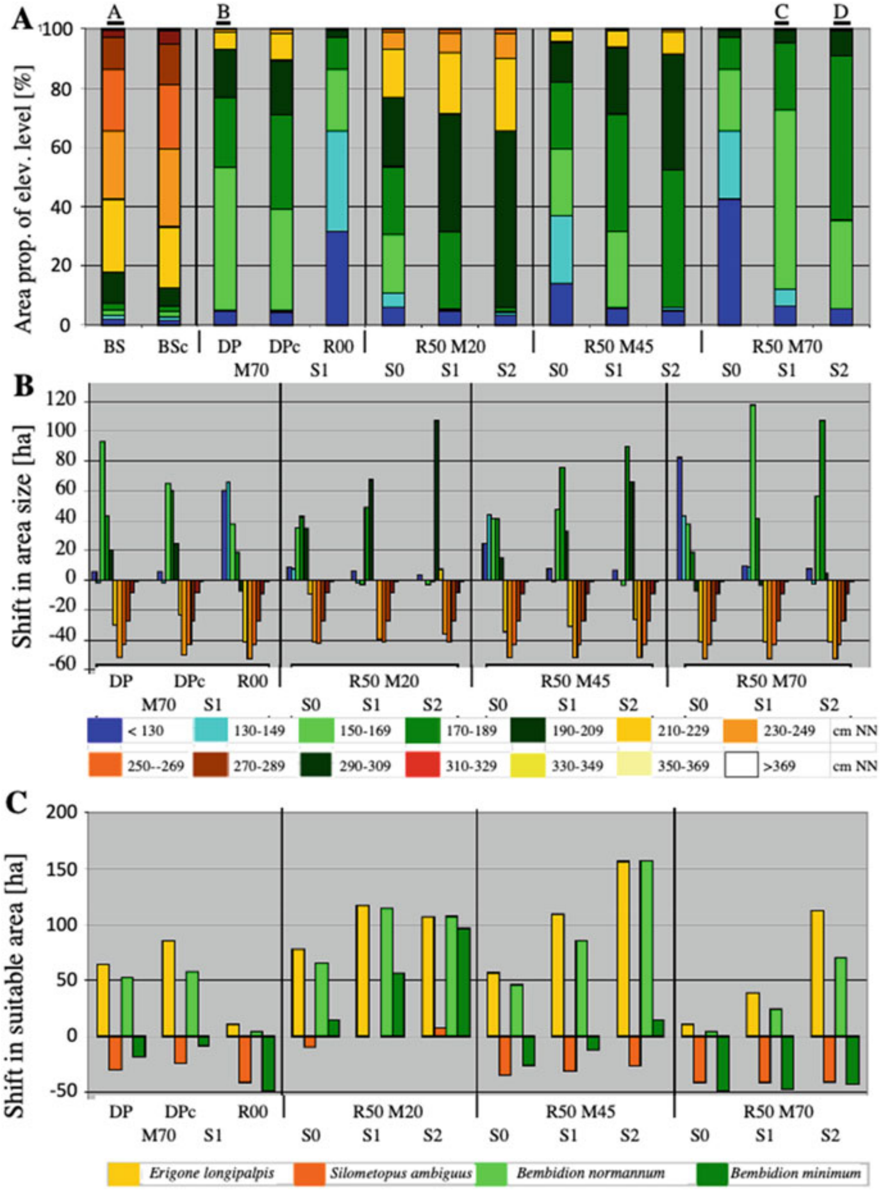

Fig. 24.4 Area proportions of elevation levels in the summer polder Spieka-Neufeld. (**a**) Absolute changes in area extent, (**b**) and potential balance of habitats suitable for four specific salt marsh arthropods. (**c**) *DP* Dike permanent, *DPc* DP with corrected MHW, R00: Dike removal in 2000, R50: Dike removal in 2050, *M* Climate scenario (Temperature + 20, +45, +70 °C), *S* Sedimentation (S0: no, S1: 1.2, S2: 2.4 cm/a), *A–D*: Corresponding graphs in Fig. 24.3

24.4 Conclusions

The simulation results and the findings of de-embankment measures (see Chap. 23) demonstrate that salt marshes can be regenerated in summer polders in a relatively short period. Stenoecious and highly specialised species were able to successfully colonise the new habitats within a few years.

Medium-term maintenance of a summer dike would run the risk of losing the regeneration potential for the development of a salt marsh, because summer dikes could not be preserved for a long time. The elevation in front of the summer dike will rise by increasing sedimentation, while the elevation of the polder area will not change its height. Over a long time, the risk of an accidental break will increase.

Simulations that are more detailed have to be performed, i.e., with the inclusion of agricultural use, which has a high impact on the fauna. Additionally, the summer polder function as a bulwark against raising rising sea level in order to protect the sea wall has to be rechecked.

References

BSH (Bundesamt für Seeschifffahrt und Hydrographie) (1997) Gezeitentafeln für das Jahr 1998. Europäische Gewässer, Hamburg

Doody JP (2004) 'Coastal squeeze'–an historical perspective. J Coast Conserv 10:129–138

Eysink WD (1987) Gaswinning op Ameland-Oost, effecten von de bodemdaling. Rep Delft Hydr Lab 114:1–53

Främbs H, Kinder M, Hielen B, Böhme B, Günther C-P, Rachor E, Cordes H, Mossakowski D (2002) Renaturierung salzbeeinflußter Lebensräume der Nordseeküste. Abschlußbericht des Salzwiesenprojektes Wurster Küste (1991–1999), im Auftrag des BMU, der BfN und der Projekt-Trägergemeinschaft

Götting E (2001) Development of salt marsh arthropod fauna after opening a summer polder. Senckenberg Marit 31:333–340

Kinder M (2000): Standortfaktoren. In: Främbs H., Kinder M., Hielen B., Böhme B, Günther C-P, Rachor E, Cordes H, Mossakowski D Renaturierung salzbeeinflußter Lebensräume der Nordseeküste. Abschlußbericht des Salzwiesenprojektes Wurster Küste (1991–1999), im Auftrag des BMU, der BfN und der Projekt-Trägergemeinschaft

NLWKN (Niedersächsischer Landesbetrieb für Wasserwirtschaft Küsten- und Naturschutz) (1999) Written communication

STAWA (Staatliches Amt für Wasser und Abfall Stade) (1996) Zusätzliche hydraulische Untersuchungen und Auswertungen zum Betrieb des Nebensieles (Bypass) im Zuge des Ententiefs. Unveröff. Gutachten, Stade

Topp W (1988) Besiedlung einer neu entstandenen Insel durch Laufkäfer (Col., Carabidae). Zoologische Jahrbücher. Abteilung für Systematik, Ökologie, und Geographie der Tiere 115: 329–361

Restoration of Salt Meadows at the Baltic Sea Coast: The De-Embankment Experiment at Karrendorf Meadows

25

Stefan Seiberling, Roland Schultz, and Gerd Müller-Motzfeld

Abstract

The de-embankment of the Karrendorf Meadows located at the Baltic Sea in north-eastern Germany was studied for vegetation and faunal changes. Embankment of the coastal area was established 150 years ago, de-embankment started in 1993. The development of the de-embanked area was compared with a second area (Koser Meadow) that was never embanked. The results revealed that vegetation zones will shift upward if no natural or man-made barriers exist to prevent a landward movement of coastal grassland. Thus, brackish plant species will benefit from de-embankment under rising sea levels. Similar processes were observed for the brackish fauna. Within a few years after de-embankment, the dominance structure of the carabid assemblage of the de-embanked area adjusted to that of the two foreland salt grassland sites.

Author "Gerd Müller-Motzfeld" has died before the publication of this book.

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25.1 Introduction

The impact of climate change and especially of sea level rise on the vegetation of Atlantic and North Sea salt marshes has already been studied in several research projects (e.g. (Dijkema 1992); (Mulder 1993); (Orson et al. 1985, 1998)). For the Baltic Sea, only a few studies are available on Danish salt marshes and coastal brackish meadows (Vestergaard 1997, 2001).

Therefore, research efforts are also needed to investigate the eastern coastal brackish meadows of the Western Pomeranian ‘Bodden’ (Sect. 25.1). In contrast to the tidal North Sea Coast with euhaline and polyhaline conditions, the ecosystems of the Baltic Sea Coast are subject to non-tidal brackish inundations (Chap. 6). For this reason, the Western Pomeranian coastal brackish meadows differ from the Atlantic and Danish salt marshes in sequence of zones and composition (Chap. 14). The mainly cattle-grazed, coastal brackish meadows replace reeds (*Phragmites australis, Bolboschoenus maritimus, Schoenoplectus tabernaemontani*) as natural vegetation of the sheltered ‘Bodden’ coasts. Furthermore, grazing leads to a compaction of the upper soil-layer and the development of coastal salt-grassland peat soils (Jeschke 1987) that consist of alternating mineral and organic layers a few decimetres above the mean water level (MWL).

The peninsula ‘Karrendorfer Wiesen’ (Karrendorf Meadows) in the Greifswalder Bodden (Fig. 25.1) has been used for cattle grazing for centuries. Consequently, it developed into an irregularly inundated salt grassland that is typical for the Baltic Sea Coast and can be distinguished by its different genesis from North Sea salt marshes. Cattle grazing was the reason for its open character and the development of the stable, mineral rich coastal inundation peat soil, protected against erosion (Chap. 3).

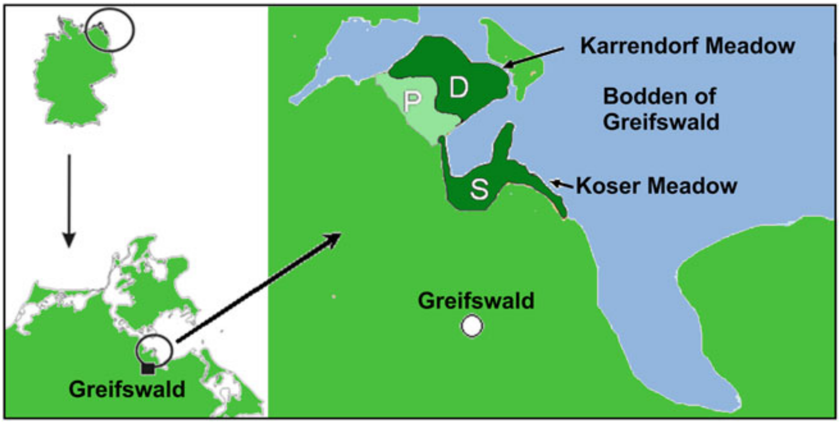

Fig. 25.1 Study locations at the ‘Greifswalder Bodden’. *D* De-embankment of Karrendorf Meadows, *P* polder, *S* Coastal brackish meadow (Kooser Meadows); *Left* Map: D-Sat4 (Buhl Data Service GmbH)

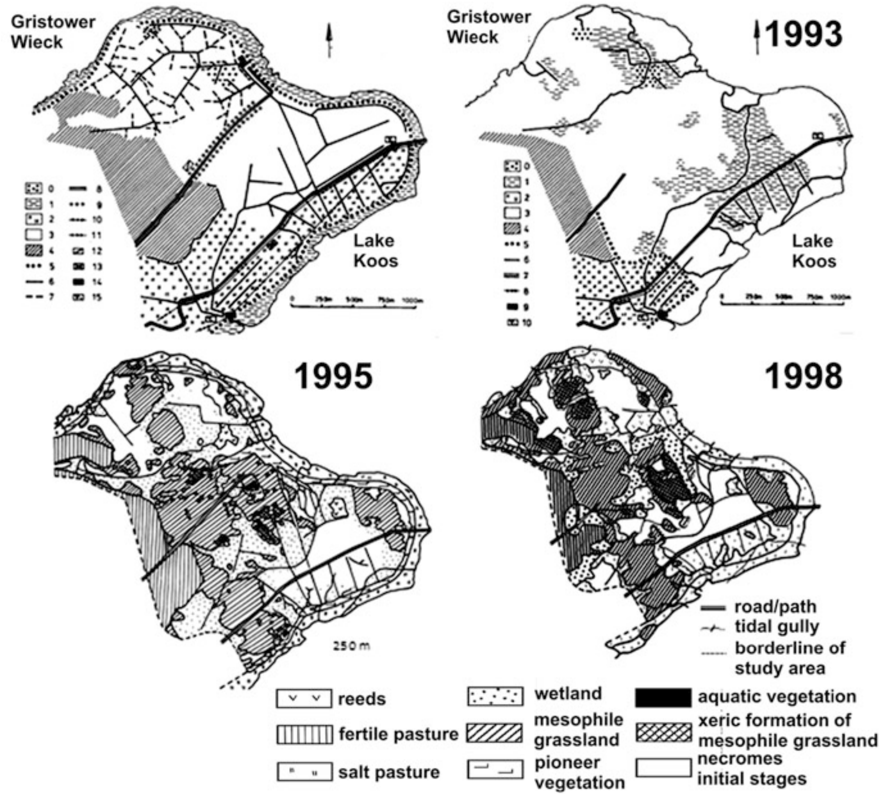

Fig. 25.2 Karrendorf Meadows before (left) and after de-embankment in 1993 (Holz et al. 1996), 1995 and 1998. Left: 0: reeds, 1: salt pan, 2: intensive pasture, 3: intensive meadow, 4: field, 5: dike, 6: creek, 7: run-off ditch, 8: road, 9: windbreak, 10: overhead line, 11: telephone cable, 12: silo, 13: milking house, 14: pumping station, 15: transformer. Right: 0: reeds, 1: foreland, 2: extensive pasture, 3: meadow (flooded), 4: field, 5: dike, 6: creek, 7: road, 8: telephone cable, 9: pumping station, 10: transformer

About 150 years ago, the studied area was embanked. After the embankment, a period of drainage, peat mineralisation, soil cultivation, and intensive agricultural use followed (Müller-Motzfeld and Holz 1996) (Figs. 25.1 and 25.2). In December 1993, the outer dike of the Karrendorf Meadows was removed and the material was used to fill up former drainage ditches. Water elevators were removed, too. Grazing of the area was reduced to one cattle/ha. Old creeks, which could be identified from an aerial photo of 1936, were opened again to re-establish a functioning creek system and a natural flooding situation. Preliminary results were already published (Holz et al. 1996).

This research is regarded as a field experiment to study the consequences of climate change-related sea level rise on salt grassland. Since no extended beaches or dunes exist in the Karrendorf study area, it can be used to predict the sea level rise with increasing floods on salt grassland at the Baltic Sea Coast.

Answers to the following questions are expected: (i) How do complex biogeocenoses react to inundations by brackish water? (ii) Can degraded coastal inundation peatland be restored? (iii) Can salt grassland exposed to inundation grow at the same rate as sea level rises? (iv) What is the time-space dimension of these processes? (v) What are the consequences for the coastal zone management of the inundation area with respect to coastal and nature protection?

25.2 Effects on Plants and Vegetation

The influence of changing submergence periods (frequency and duration of flooding) on species and vegetation of coastal meadows was studied using two different methods. The de-embankment of the Karrendorf Meadows, a 360 ha polder 10 km north of Greifswald (Mecklenburg-Vorpommern, Germany), was carried out in 1993. From 1993 to 2000, data on vegetation and site conditions of that area were collected and compared with the nearby coastal brackish meadow Kooser Meadows which were never diked (Fig. 20.1).

The ‘space’ for ‘time’ approach was selected to study the re-establishment of characteristic vegetation in formerly poldered freshwater grassland. The comparison with the coastal brackish meadow is also appropriate to evaluate the succession after the re-introduction of brackish inundation and to predict its future development.

25.2.1 Predictions of Climate and Sea Level Change

The predictions of climate change with relevance to the southern Baltic Sea Coast concerning temperature, precipitation, wind, and sea level are as follows: temperature is expected to increase between 0.8 and 2.6 K within the following 50 years {Houghton et al. 2001 1229 /id}). This has an impact on oceans due to thermal expansion of the water body and an increased melting rate of both arctic and continental ice shields and permafrost soils {Houghton et al. 2001 1229 /id}). For the global sea level rise, a wide range of values is assumed according to various models (Chap. 2). The IPCC scenarios predict a sea level rise for the next 100 years, ranging from both a low estimate and a high estimate of 0.19 m–0.83 m and 0.06 m–0.34 m, respectively, until 2050 {Houghton et al. 2001 1229/id}).

Storch et al. (1998) developed a local scenario for the eastern German Baltic Sea Coast, based on the ECHAM4/OPYC3-model (Röckner et al. 1998) and on the IS92a Emissions Scenario with a yearly CO_2-growth rate of 0.85%. According to that model, the annual precipitation increases by 9% until 2050 related to the period from 1961 to 1990. Increases in spring (+22%), autumn (+15%), and winter (+11%) are combined with drier summers (−6%). The annual temperature is predicted to increase by 2.5 K with a rise above average values in spring and winter. Until 2050, the regional wind speed will increase by 3.6% resp. 6.6%, especially in autumn and

Table 25.1 Wind-driven changes in seasonal inundation frequency for the year 2050 in percent for the period between 1961 and 1990 (Storch et al. 1998). Local impacts without consideration of the global sea level rise

	Elevation above MWL (cm)				
	0	10	20	40	60
Winter (DJF)	0.27	0.31	0.33	0.16	0.19
Spring (MAM)	0.32	0.56	0.88	0.69	0.09
Summer (JJA)	0.18	0.44	1.19	2.19	1.16
Autumn (SON)	0.12	−0.07	−0.13	−0.51	−0.16
Yearly average	0.19	0.23	0.25	0.02	0.08

winter, and decrease by 4% in summer. Beckmann and Tetzlaff (1999) predict an increase in slight storm surges between 1–1.2 m NN. The local scenario also allows predictions of wind-driven local modifications of the submergence period (Table 25.1).

The global contribution of about 20 cm (IPCC mid estimate) has to be added in the model if the impact on the vegetation is regarded. According to the local scenario, the inundation frequency will increase depending on months and elevations. In summer, particularly in June, an increase of the inundation frequency is expected. In May, inundations will be more frequent than the yearly average. An opposite development is predicted for autumn with a decreasing submergence period for elevations higher than 10 cm above MWL. Compared to the global sea level rise, the local modifications of the submergence period are of little relevance (Vestergaard 2001). However, they have an impact on the inter-seasonal distribution pattern of inundation frequencies.

With regard to the vegetation of coastal brackish meadows, the predicted increase in air temperature and changes in precipitation patterns may cause modifications in soil salinity, especially in summer. This may shift competitive relationships among plant species because species tolerating higher salinity and lower ground water levels may benefit from the future conditions. Low rainfall and high summer temperatures indirectly impact the vegetation by promoting soil development processes, such as vertical shrinkage of some centimetres and a higher flooding frequency (Beeftink 1987). This effect is counteracted by the increase in inundation frequency in spring and early summer, while the autumnal decrease has an aggravating impact. As no studies have been made on the impact of submergence periods, precipitation, and temperature on peat soils of the Baltic Sea Coast, these assumptions can only be qualitative.

25.2.2 Environmental Preconditions

The ‘Bodden’ were formed during the Litorina-transgression (7000–5700 BP) when the postglacial sea level rise flooded moraine depressions and created shallow lagoons such as the ‘Greifswalder Bodden’ southeast of the Island of Rügen and the ‘Darss-Zingst Bodden Chain’. Corresponding to the retardation of the transgression, sheltered coastal zones were covered by the so-called coastal transgression mires (Jeschke 1987) forming peat under the influence of brackish backwater situations.

The impact of rising sea levels on coastal brackish grassland depends on the relation between eustatic sea level change and isostatic land movements. Furthermore, accretion of the surface, depending on organic and mineral sedimentation and compaction of the soil, modifies the effective sea level rise. For the Greifswald coast, an isostatic uplift of about 10 mm/century was determined (Kolp 1979). According to Jeschke (1996), the sea level rise of 3–4 mmpy during the main stage of the Litorina-transgression was too fast for coastal adjustment processes. For the sheltered inner coasts of Western Pomerania, a subsidence of less than 2 mmpy allows the development of coastal brackish grassland-peat with both a maximum and a mean accretion rate of 1.9 mmpy and 1 mmpy since 1872, respectively (Janke and Lampe 1996). In the westerly Wismar Bay, a yearly transgression of 2–3 mm occurs which is too high for peat formation; the result is coastal brackish grassland on mineral soil (Jeschke 1983). Soil compaction allows peat formation up to a few decimetres above MWL (Jeschke 1987). In consideration of this data, the effective sea level rise will amount to about 15 cm for the next 50 years: including an assumed 20 cm eustatic sea level rise (IPCC mid estimate), 0.6 cm isostatic uplift (Kolp 1979), and 5 cm accretion (Janke and Lampe 1996). The unpredictable magnitude of the vertical shrinkage of the soil is not taken into account.

25.2.3 Conclusions from De-Embankment Effects

If an effective sea level rise of 15 cm in the course of the next 50 years is assumed, the species have to move towards higher levels in a corresponding height. The following question has to be answered: Will the present sequence of zones just be found 15 cm higher in 2050 or will the species shift result in new species compositions with respect to the single species movement capacities?

In 2000, 7 years after de-embankment, the impact of the re-established brackish flooding regime differs among the vegetation zones. At the de-embankment site, the seaward edge of freshwater communities (*Lolio-Cynosuretum*) was situated 100 cm above MWL, whereas it was found 40 cm above MWL in the embanked polder. On the coastal grassland, the freshwater communities were restricted to elevations higher than 80 cm above MWL. Therefore, a further adaptation of the saltwater–freshwater transition zone is not to be expected, because the re-establishment of brackish inundation can be regarded as an abrupt sea level rise of about 60 cm within 1 year.

In contrast to the saltwater–freshwater transition zone, the *Juncetum gerardi* Nordhagen 1923 as the typical coastal brackish grassland vegetation has not completely re-colonised its characteristic elevation.

On the species level, characteristic freshwater species of the polder display different rates of upward movement as a reaction to brackish flooding

Table 25.2 Lowest elevation of occurrence and dominance of selected freshwater grassland species for polder, de-embankment site, and salt grassland. Transects range from 0 cm to 120 cm above MWL, and 40 cm–120 cm above MWL for the de-embankment site, respectively, with steps of 20 cm

	Lowest occurrence (cm MWL)			Lowest occurrence cover >25% (cm MWL)		
Species	Polder	De-embankment	Coastal grassland	Polder	De-embankment	Coastal grassland
Agrostis stolonifera	0	40	0	0	40	0
Elytrigia repens	20	40	40	20	60	40
Holcus lanatus	0	60	40	20	80	–
Dactylis glomerata	20	180	20	40	–	100
Agrostis capillaris	40	100	80	100	100	80

(Table 25.2). *Elytrigia repens* showed the slightest reactions with an upward shift of 20 cm, whereas the upward shift of *Dactylis glomerata* was 100 cm. *Holcus lanatus* and *Agrostis capillaris* reacted intermediately. In the polder transect, *Agrostis stolonifera* revealed its lowest occurrence at MWL which corresponds to a minimum upward movement of 40 cm. The seaward border of *Elytrigia repens* in the coastal brackish grassland was equal to the de-embankment site. *Agrostis stolonifera* also occupies lower elevations. The occurrence of the other species lies between that of the de-embankment and the coastal brackish grassland. They were all found beyond the salt-impacted zones.

In contrast to the levels of the vegetation zones, an even shift in the sequence of zones was not found in the transition zone between coastal brackish grassland and freshwater grassland on the species level. This is due to different tolerances against flooding and salinity, which is also true for the lowest elevation of species dominance, defined as a mean cover of more than 25%. The reaction of *Elytrigia repens* (+40 cm) and *Agrostis stolonifera* (+40 cm) was low compared to *Holcus lanatus*, showing an upward shift of 60 cm. In the de-embanked area, the dominant stands of *Agrostis capillaris* were located beyond the impact of brackish water flooding, whereas *Dactylis glomerata* dominates from 100 cm above MWL upwards. The elevations of dominant species were approximately equal on de-embankment sites and coastal brackish grassland. Consequently, no further shift is to be expected.

A comparison between the three types of sites reveals characteristic differences in species composition. The highest species diversity is found in the polder vegetation (Fig. 25.3), which is mainly due to the higher number of (11–15) species. In both the brackish and the de-embankment grassland, 5–13 and 5–8 species were found, respectively. Highest species numbers were found at 120 cm above MWL in the polder and at both 60 and 80 cm above MWL and at 100 cm above MWL in the brackish grassland and the de-embankment site, respectively. Obviously, an

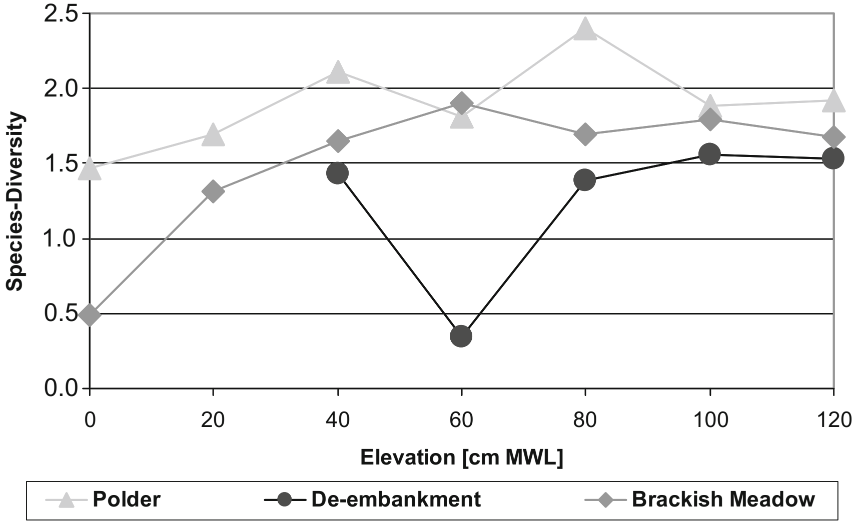

Fig. 25.3 Plant species diversity (Shannon–Weaver) for different elevations of polder, de-embankment site, and coastal brackish meadow based on three records for each site and elevation

increasing stress-related selection occurs with decreasing elevation. In the polder, the ground water level is the main stressor, while for the other sites, salinity and inundation are limiting factors. With increasing elevation, the competition of dominating species is of increasing importance for species richness. The importance of increasing competition with increasing elevation is clearly displayed in the brackish grassland, where the number of species decreased from 13 to 10 species between 80 and 120 cm above MWL. This reduction corresponded with the dominance of *Elytrigia repens* and *Dactylis glomerata*. The same situation was found after de-embankment at an elevation of 60 cm above MWL. *Elytrigia repens* and *Agrostis stolonifera* were the co-dominating species, while all other freshwater grassland species were extinct and the characteristic brackish species were not yet present. At the elevations higher than 60 cm, species diversity resembled that of the coastal grassland. The herbs *Anthriscus sylvestris, Daucus carota, Cerastium holosteoides,* and *Stellaria graminea* and the grasses *Agrostis stolonifera, Dactylis glomerata,* and *Festuca pratensis* were absent under re-established brackish flooding except the slightly salt tolerant *Plantago media* and *Trifolium fragiferum*.

The de-embankment obviously causes a ‘replacement’ and not a ‘movement’ of vegetation due to its abrupt occurrence. For a continuous effective sea level rise of 15 cm over 50 years, the predominant type of succession should be an upward movement.

25.2.4 Conclusions from Species-Amplitudes of Elevation, Salinity, and Groundwater

The submergence period is the most important ecological factor for the sequence of zones in salt marshes (Beeftink 1979). Inundation frequency and inundation periods show a negative exponential correlation with elevation. The species are distributed along the elevation gradient depending on their competitiveness.

To define elevation levels characterised by groups of species with differing inundation- and salinity-tolerance, the vegetation at the de-embankment site and the coastal brackish grassland was recorded and elevation determined. Subsequently, vegetation records and species were classified according to their occurrence above MWL.

When exposed to a sea level rise, the different grassland species showed individual reactions. Especially at the seaward edge of coastal brackish grassland, species will be extinct if their physiological inundation tolerance is exceeded (Van Diggelen 1991). In this zone, interspecific competition is less important than in the central parts of the coastal brackish grassland and the transition zone between salt water and fresh water. Stressed and weakened by increasing inundation, species have to move upwards for a successful competition. In this case, they have to compete with species of higher zones. The option to move upwards is restricted when the increased flooding has no effect on the competitive ability. The upward movement is successful, if the resistance of species in the upper grassland against invasion by upward-moving species decreases.

Another important factor is grazing: by trampling and feeding, the more or less dense grassland sward is damaged which generates low competitive patches, which provided for the establishment of upward-moving species. Under this aspect, maintained grazing of coastal brackish meadows is of special importance.

Regarding the vegetation, five species groups characterised five elevation levels ranging from below 10 cm above MWL (level 1) to above vegetation-effective inundation (level 5). The species groups show different elevation amplitudes and, thereby, submergence periods (Table 25.3).

Group 1: species tolerate long periods of water logging and even submergence, being competitive only under such stressful conditions, e.g. *Salicornia europaea* agg. At higher elevations, they only occur in low-competition patches. Dispersed by seeds, *Puccinellia distans* populates open mudflats in the de-embanked depressions. In contrast to *Salicornia europaea* agg., it also spreads vegetatively after establishment. *Salicornia europaea* has a lower inundation tolerance compared to *Puccinellia distans* (Van Diggelen 1991).

Group 2: species have a high dispersal ability. They are also highly stress-tolerant and populate the whole zone under saltwater influence. *Chenopodium album* and *Spergularia salina* are pioneer species with high seed dispersal potential. *Spergularia salina* facilitates the colonisation of highly saline mud flats by shading which reduces transpiration-induced salinity peaks (Bertness and Hacker 1994). Without grazing, *Phragmites australis* is highly competitive even in

Table 25.3 Elevation levels of coastal brackish grassland with tolerated amplitudes of characterising species groups. Scale of competitiveness: high (black), low (grey), none (white)

		Elevation levels				
n=31		1	5	13	3	9
cm NN		< 10	10-30	30-80	80-90	>90
Species groups	1	■	▒			
	2	▒	■	■	■	
	3			■	■	■
	4				■	■
	5				▒	■

(1) *Puccinellia distans subsp. distans, Salicornia europaea* agg.; (2) *Aster tripolium, Atriplex prostrata, Bolboschoenus maritimus, Chenopodium album, Glaux maritima, Juncus gerardii, Phragmites australis* subsp. *australis, Plantago major* subsp. *winteri, Plantago maritima subsp. maritima, Potentilla anserina, Spergularia salina, Triglochin maritimum*; (3) *Achillea millefolium* subsp. *millefolium, Centaurea jacea, Centaurium littorale* subsp. *littorale, Cerastium holosteoides, Cirsium arvense, Elytrigia repens* agg.*, Leontodon autumnalis subsp. autumnalis, Lolium perenne, Lotus tenuis, Ranunculus acris* subsp. *acris, Trifolium fragiferum, Trifolium repens* subsp. *repens*; (4) *Alopecurus geniculatus, Cynosurus cristatus, Dactylis glomerata subsp. glomerata, Holcus lanatus, Juncus bufonius, Juncus effusus, Plantago lanceolata, Poa pratensis subsp. pratensis, Rumex crispus, Stellaria graminea, Trifolium pratense* subsp. *maritimum*; (5) *Agrostis capillaris* subsp. *tenuis, Deschampsia cespitosa, Juncus ranarius, Rumex acetosa, Rumex acetosella, Stellaria media.*

elevated zones. In pastures, it is widely replaced by *Agrostis stolonifera* with similar amplitude of tolerating elevation, salinity, and inundation. *Phragmites australis* or *Bolboschoenus maritimus* only dominate in long-lasting submerged shallow depressions. The cessation of grazing after de-embankment facilitates the colonisation of bare mud flats by taller species, which results in dominant stands of *Agrostis stolonifera*, impeding the establishment of coastal brackish grassland species of group 3.

Group 3: species reveal higher landward amplitude. They are less flooding-tolerant than those of group 1 and 2. They characterise higher zones of coastal brackish grassland along the southern Baltic Sea Coast. The taxonomic status of *Elytrigia repens*, *Leontodon autumnalis*, and *Trifolium repens* is unresolved because they are typical freshwater grassland species with adaptations to salinity and flooding. Without grazing, *Elytrigia repens* tolerates re-established brackish flooding even at an elevation of 10 cm above MWL for at least 7 years.

Group 4: species have a low tolerance against salinity and are competitive merely in the highest parts of the coastal brackish grassland. *Holcus lanatus* and *Poa pratensis* are able to survive brackish inundation at a height of 60 cm above MWL for at least 7 years.

Group 5: species are intolerant against salinity and partly against flooding. They are characteristic for the seaward edge of freshwater grasslands. Exclusively,

> *Deschampsia cespitosa* is able to survive short periods of freshwater submergence but is excluded by saltwater influence. After de-embankment, it seems to be resistant to brackish inundation at an elevation of 60 cm above MWL for several years, whereas *Agrostis capillaris* is limited to zones beyond 100 cm above MWL.

If decreasing precipitation is assumed for the eastern part of the German Baltic Sea Coast, soil salinity will likely increase due to lower leaching. This process is enhanced by lower brackish flooding frequencies in autumn. Thus, species with a high tolerance for salinity and summer drought periods will benefit. Under these conditions, and according to their amplitudes of salinity and soil water level (Seiberling, unpublished data), characteristic species of the higher coastal brackish meadows, such as *Lotus tenuis, Festuca rubra, Plantago major* subsp. *winteri, Leontodon autumnalis, Trifolium fragiferum*, and the pioneer species *Spergularia salina* will gain a competitive advantage and might expand landward. *Juncus gerardii* and *Agrostis stolonifera* as characteristic species of coastal brackish grassland are also promoted. Freshwater species with a similarly high salt tolerance (*Achillea millefolium, Poa pratensis, Trifolium repens, Elytrigia repens, Holcus lanatus*, *Cirsium arvense*) will tolerate a further increase in salinity. Similarly, a high yearly minimum of soil water levels characterises the habitat of *Salicornia europaea* and *Aster tripolium*. Therefore, they will be disadvantaged by falling soil water levels and especially by summer and autumn droughts.

25.2.5 Consequences on the Species Level

Salicornia europaea and *Puccinellia distans* remain exiguous at the seaward edge because submergence will last too long. The survival of these species only seems to be possible in depressions below MWL and isolated from regular flooding and longer periods of emergence.

An upward expansion will be likely for species of group 3 that are weakened at the present elevation of 30–45 cm above MWL (Table 25.4). Consequently, the

Table 25.4 Elevation-shifts in coastal grassland vegetation following an effective sea level rise of 15 cm. Changes relative to present elevation and distribution (Table 7.3–b3); *black* expansion, *dark grey* unchanged, *light grey* decline, *white* disappearance

MWL (cm)		0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110
Species groups	1	□	□	□	▩	▩	▩	▩	■	■	■													
	2	░	░	░	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩	■	■	■	
	3								░	░	░	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩
	4																		□	□	□	▩	▩	▩
	5																		□	□	□	▩	▩	▩

expansion of group 1 species will depend on the availability of low-competition patches provided by mechanical disturbance.

The species of group 2 will hardly change their zonal distribution. Like species of group 1, the majority is constricted to conditions of low competition rather than being able to successfully invade zones above 70 cm above MHW.

Under grazing, *Agrostis stolonifera* will be able to compete with freshwater grassland species at the seaward edge of freshwater communities. Without grazing, *Phragmites australis* will also be able to stretch landward. *Agrostis stolonifera* will have the strongest inhibiting impact on upward-moving populations due to its extraordinary tolerance of submergence.

The upward shift is inhibited by species of group 3 and 4, especially by *Elytrigia repens, Poa pratensis*, and *Holcus lanatus*. Additionally, grazing of the transition zone between salt- and freshwater grasslands, in particular, is of crucial importance to provide space for expansion of coastal brackish grassland species and to avoid dominant stands of a few grasses.

For the seaward edge of their distribution, species of group 3 have to face the same threats concerning submergence as species of group 2. The landward edge of their expansion is too high to be primarily influenced by the rising sea level.

The freshwater species of group 5 will also be displaced at the seaward edge. The landward distribution is not influenced by changing hydro periods.

The results show that there is a serious threat of a squeeze of elevation amplitudes for coastal brackish grassland species and halophytic pioneers resulting from competitive exclusion or from abiotic conditions exceeding physiological niche limits. The maintenance of an adapted grazing regime for coastal brackish meadows is crucial for a facilitation of landward expansion of coastal brackish grassland species. ‘Adapted grazing’ in this context means, intensive enough to provide patches of low competition to permit the establishment of halophytes.

Due to their tolerance of increased salinity and decreasing soil moisture resulting from higher evapotranspiration in the future and lower precipitation in the summer, certain coastal brackish grassland species will have competitive advantages over freshwater species, leading to an upward movement. However, especially freshwater species that tend to form dominant stands and to retard an upward shift of halophytes will be slightly weakened.

25.2.6 Consequences on the Vegetation Level

If no natural or man-made barriers exist to prevent a landward movement of coastal grassland, vegetation zones will shift upward. The degree of this shift will depend on the rate of the sea level rise and on flooding tolerance. According to the results of the de-embankment studies and the transplantation experiments of Folkowski et al. (2000), the impact of the sea level rise will be less serious for vegetation on the whole than for single species. With decreasing adaptation to flooding of a coastal grassland vegetation type, the effect of rising sea levels will increase (Beeftink 1979). Due to the exponential decrease of flooding with rising elevation above

MHW, the impact of flooding is stronger for the lower salt grassland. However, the reaction of low salt grassland vegetation is less sensitive to changes in flooding than for the high salt grassland or the freshwater grassland vegetation. Reeds (*Astero tripolii-Phragmitetum australis* Jeschke 1968; Krisch 1974) will not suffer under increased submergence periods at the seaward edge, while a landward expansion will be enhanced. This can be mainly ascribed to less frequent grazing due to a higher submergence period with less favourable conditions for cattle.

25.3 Effects on Spiders and Carabid Beetles

Studies on the epigeal fauna of the Karrendorf Meadows started already 1 year before the de-embankment by the installation of three groups of pitfall traps at different elevations and exposures.

In contrast to the vegetation, halotolerant and halobiontic carabids had already dispersed over the whole inundation area in the first year after de-embankment. In the second year, the carabid fauna of the formerly embanked area corresponded quantitatively and qualitatively with that at the same elevation levels of the former pre-dike area (Fig. 25.4). Spiders showed a similar development within 5 years (Fig. 25.5). Corresponding to the establishment of plant associations, carabid (Fig. 25.6) and spider assemblages became more differentiated.

The composition of carabids and spiders changed from intensive grassland assemblages to salt grassland assemblages. Correspondingly, catch numbers and

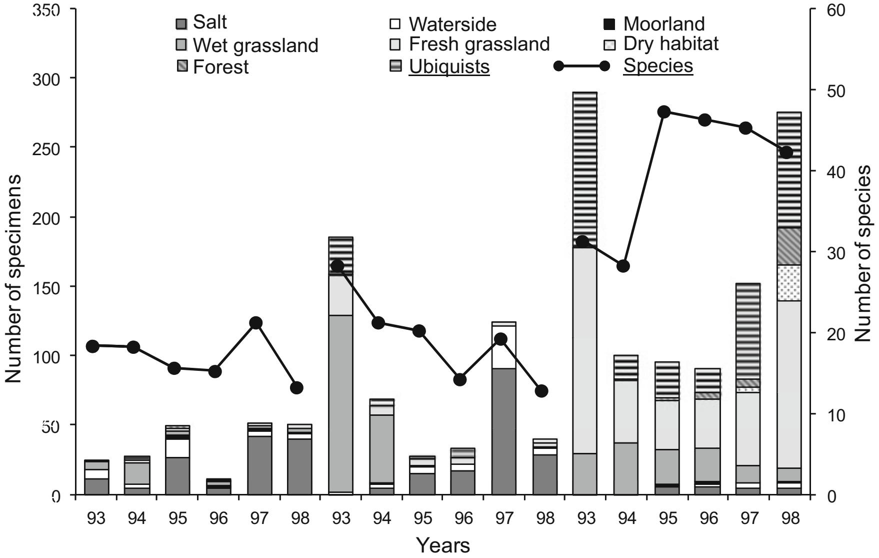

Fig. 25.4 Species number and numbers of specimens trapped in different habitat preference types of carabids at three selected sites of the Karrendorf Meadows 1993–1998

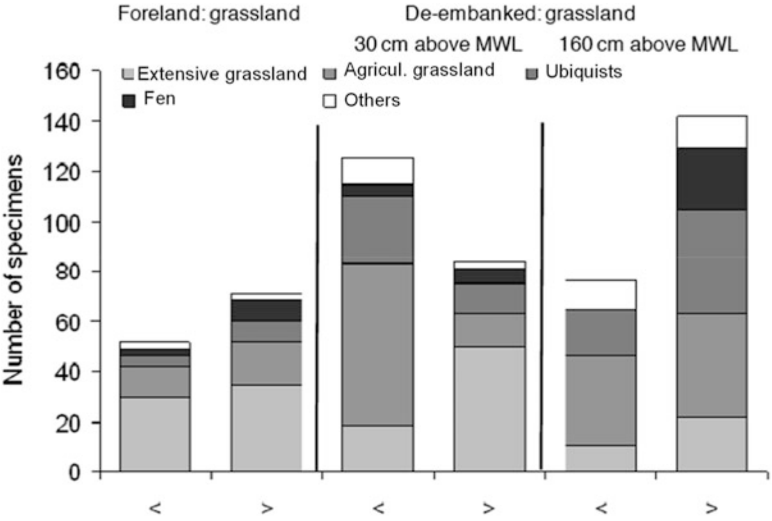

Fig. 25.5 Numbers of spider specimens of different habitat preference types trapped at three selected sites of the Karrendorf Meadows 1993–1998: < before de-embankment; > after de-embankment

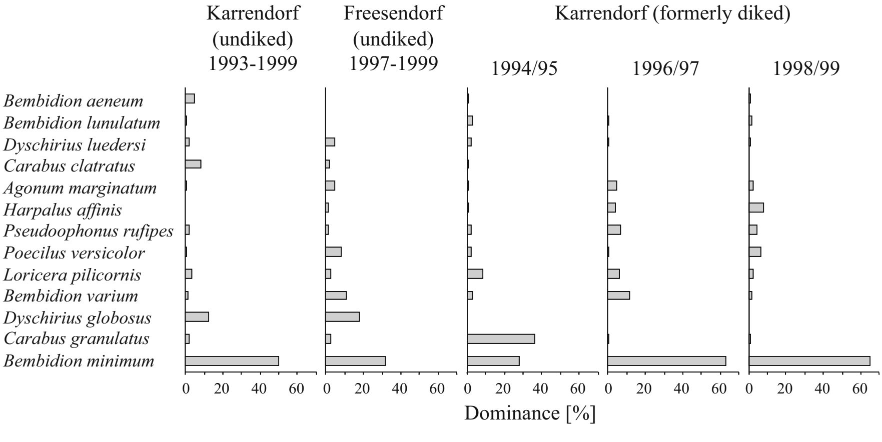

Fig. 25.6 Development of the most common carabid species on the de-embanked sites (30 cm MWL) of the Karrendorf Meadows in comparison with those of two never diked inundation grasslands at the same elevation

biomass decreased. The number of ubiquitous and xerophilous grassland species decreased, whereas the numbers of the typical species of salt grassland increased. Presently, the low lying and often-flooded areas were characterised by halobiotic and halophilic 'salt species' and by halotolerant species of shores and wet habitats. Typical species among both carabids and spiders were *Bembidion minimum* and

Table 25.5 Carabid dominance and species numbers of salt species on the Karrendorf Meadows 1997–1998 (pitfall catches)

	Elevation above MWL (cm)			
Species	30	50	70	Mean
Bembidion minimum	79.1	58.0	58.9	65.3
Bembidion lunulatum	0.7	1.7	0.4	0.9
Bembidion aeneum	0.2	2.2	1.5	1.3
Dyschirius salinus	–	0.1	–	0.1
Amara convexiuscula	–	0.1	0.1	0.1
Bembidion transparens	0.2	–	–	0.1
Dominance of salt pref. Species	80.1	62.1	60.9	67.8
Species number of salt pref. Species	4	5	4	

Erigone longipalpis, respectively. They occurred in highest dominances in the inundation areas.

At inundation sites, numbers of specimens were lower for carabids than for spiders, but species richness was equal in both groups. The assemblage consisted of some typical species of saline habitats, shores, bogs, and wetlands. The dominant species among carabids was *Bembidion minimum*, which represented 65–80% of carabids at the inundation area up to 70 cm MHW. Additionally, *Dyschirius salinus* and *Bembidion aeneum* occurred, which are typical species of saline habitats (Table 25.5).

The total number of epigeal species of the whole de-embanked area increased, because species of saline habitats immigrated to the lower elevated area and species that are sensitive to inundation or brackish water survived on the non-flooded sites.

Within a few years, the dominance structure of the carabid assemblage of the de-embanked area adjusted to that of the two foreland salt grassland sites (Fig. 25.6). The dominance of *Bembidion minimum* was even higher in the de-embanked site, since this species was the first that invaded into the new inundation area and could built up higher dominances than in the never embanked foreland.

In sum, plant associations showed a patchiness pattern due to different grazing intensities and both inundation frequency and duration. The faunal assemblages revealed a parallel development of a more diverse pattern than before the de-embankment.

References

Beckmann B-R, Tetzlaff G (1999) Veränderungen in der Häufigkeit von Sturmhochwassern an der Ostseeküste Mecklenburg-Vorpommerns und deren mögliche Ursachen. Die Küste 61:73–88

Beeftink WG (1979) The structure of salt marsh communities in relation to environmental disturbances. In: Jefferies RL, Davy AJ (eds) Ecological processes in coastal environments. Blackwell, Oxford, pp 77–94

Beeftink WG (1987) Vegetation responses to changes in tidal inundation of salt marshes. In: Andel JV, Bakker JP, Snaydon RW (eds) Disturbance in grasslands. Causes, effects and processes. Dr. W. Junk, Dordrecht, pp 97–117

Bertness MD, Hacker SD (1994) Physical stress and positive associations among marsh plants. Am Nat 144:363–372

Dijkema KS (1992) Sea level rise and management of salt marshes. Wadden Sea Newsletter 2:7–10

Folkowski A, Seiberling S, Ostendorp W, Bernhardt K-G (2000) Vegetationsdynamik, Populationsstruktur und Pflanzenfitness von Salzgrünlandstandorten an der Boddenküste Mecklenburg-Vorpommerns. Abschlussbericht Förderkennzeichen FP EMAU 27:97

Holz R, Herrmann C, Müller-Motzfeld G (1996) Vom Polder zum Ausdeichungsgebiet: Das Projekt Karrendorfer Wiesen und die Zukunft der Küstenüberflutungsgebiete in Mecklenburg-Vorpommern. Natur und Naturschutz in Mecklenburg-Vorpommern 32:3–27

Houghton JT, Ding Y, Griggs DJ, Noguer M et al (2001) Climate change 2001: the scientific basis. Contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Janke W, Lampe R (1996) Relief, Morphogenese und Stratigraphie der Karrendorfer Wiesen. Natur und Naturschutz in Mecklenburg-Vorpommern 32:28–42

Jeschke L (1983) Landeskulturelle Probleme des Salzgraslandes an der Küste. Naturschutzarbeit i Mecklenburg-Vorpommern 26:5–12

Jeschke L (1987) Vegetationsdynamik des Salzgraslandes im Bereich der Ostseeküste der DDR unter dem Einfluß des Menschen. Hercynia NF 24:321–328

Jeschke L (1996) Entwicklungsgeschichte der Bodden. Bodden, vol 3, pp 3–18

Kolp O (1979) Eustatische und isostatische Veränderungen des südlichen Ostseeraumes im Holozän. Petermanns Geogr Mitt 3:177–187

Mulder JPM (1993) Effects of increasing sea level rise on the geomorphology and ecological functioning of the Wadden Sea. Wadden Sea Newsletter 1:3–5

Müller-Motzfeld G, Holz R (1996) Die Karrendorfer Wiesen 1994–Bisherige Ergebnisse der wissenschaftlich-begleitenden Untersuchungen im Überblick. Natur und Naturschutz in Mecklenburg-Vorpommern 32:141–146

Orson RA, Panageotou W, Letherman SP (1985) Response of tidal salt marshes of the U.S. Atlantic and Gulf coasts to rising sea levels. J Coast Res 1:29–37

Orson RA, Warren RS, Niering WA (1998) Interpreting Sea level rise and rates of vertical marsh accretion in southern New England tidal salt marsh. Estuar Coast Shelf Sci 47:419–429

Röckner E, Bengtsson L, Feichtner J, Lelieveld J, Rodhe H (1998) Transient climate change simulations with a coupled atmosphere-ocean GCM including the tropospheric Sulphur cycle. MPI Report No 266, Max-Planck-Institute for Meteorology, Hamburg

Storch HV, Schnur R, Zorita E (1998) Szenarien und Beratung. Anwenderorientierte Szenarien für den norddeutschen Küstenbereich, Geesthacht

Van Diggelen J (1991) Effect of inundation stress on salt marsh halophytes. In: Rozema J, Verkleij JAC (eds) Ecological responses to environmental stresses. Kluwer Academic Publishers, Dordrecht, pp 62–73

Vestergaard P (1997) Possible impact of sea-level rise on some habitat types at the Baltic coast of Denmark. J Coast Conserv 3:103–112

Vestergaard P (2001) Impacts of climate change and sea level rise to Danish near shore ecosystems. In: Jørgensen AM, Halsnæs K, Fenger J (eds) Climate change research. Danish Contributions, Copenhagen, pp 256–262

Part V

Synthesis and Conclusions

Expert System: Plants

26

Detlev Metzing

Abstract

In the expert system, the coastal plant species and their relevant traits are listed. Occurrence at the North Sea and the Baltic Sea was considered for the two coasts. In total, 67 plant species were considered. Additionally, biological and ecological traits of these plants with a predicted regressive or progressive change of distribution ranges were listed.

26.1 Introduction

It is well-known that plant distribution depends on climate conditions (Walter and Breckle 1991). Taking the model predictions of climate change into consideration, the distribution areas of coastal plants will undergo large-scaled changes (dimension $>10^5$–10^6 m) (Metzing 2005). Modelling in Chap. 10 shows the potential impacts of direction, distance, and time on the shift of distribution ranges. However, an inherent attribute of ecological systems is the inertia to react on changed conditions (IPCC 2002). Therefore, the real alteration of distribution patterns will be species-specific depending on the particular response time of the single species (Huntley 1991; Webb 1992). We can distinguish progressive (immigration) and regressive (extinction and emigration) development with respect to distribution area changes. The speed of progressive shifts depends on the migration rates, whereas regression is regulated by persistence (Jackson and Overpeck 2000; Kirilenko and Solomon 1998).

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Table 26.1 Relevant traits for persistence of plant species

Persistence	High	Low
Genetic variability	High	Low
Lifespan	Long (many years until reproductive maturity)	Short
Temperature sensitivity	Only in one phase of life cycle (e.g. germination or period of establishment)	During (nearly) the whole life cycle
Reproduction	Vegetative reproduction possible	Only sexual reproduction
Seed bank	Long term	Missing

Table 26.2 Relevant traits for dispersal rates of plant species

Dispersal rate	High	Low
Reproduction rate	High	Low
Begin of reproductive stage	Short	Late (many years until reproductive maturity)
Diaspores	Mobile (e.g. anemochorous, ornithochorous, hydrochorous)	Largely immobile (autochorous)
Ecological amplitude	Euryoecious	Stenoecious
Dormancy	Missing or short, high variability of duration	Long, low variability

Persistence is the ability of a species to remain in an area with unfavourable conditions that lead to an interruption of the life cycle (e.g. if temperature conditions do not allow fructification or germination). Table 26.1 presents a survey of traits relevant for persistence.

Perennial species have a higher degree of persistence if temperature is the critical factor for germination or establishment. Consequently, regressive shifts of distribution boundaries will be retarded, depending on the lifespan of individuals. In the salt marshes, the majority of species is perennial, so that a certain persistence can be assumed here (Adam 2002). For example, trees are able to persist under suboptimal conditions for a long time (Franklin et al. 1992). However, in coastal habitats they play no decisive role. At progressive range margins, the dispersal or migration capacity of species determines whether they can keep pace with the shift in climatic gradients. Here, euryoecious species with high reproduction rates and mobile diaspores will have advantages (Nathan 2001) (Table 26.2). Species with a long life-span, such as trees, react with a considerable delay (Iverson et al. 2004; Malcolm et al. 2002; Webb 1992).

Plant species with wind-dispersed diaspores or with diaspores transported by birds can reach new habitats faster than species with heavy diaspores and without special dispersal modes (Bonn and Poschlod 1998). The dispersal of fruits or seed bundles and vegetative fragments by water is a suitable strategy of many coastal plants to colonise new areas (Packham and Willis 1997).

In general, colonisation is a long-lasting process because dispersing diaspores will not always establish themselves successfully (Melillo et al. 1996). Thus, Jackson and Overpeck (2000) stated that most species show a delayed response on shifts of climatic gradients—also in the case of species with progressive distribution boundaries. Additionally, the type of distribution boundaries influences the speed of range shifts. It can be assumed that shifts of physiologically limited range boundaries cause a faster reaction of the species than that of competition-related distribution limits.

Specific traits that cause a high dispersal rate may also induce higher persistence and vice versa, e.g. species with a graded germination strategy (a high variability in the dormancy period and the establishment of a seed bank) have advantages at the progressive distribution boundaries. Founder populations of these species built up in beneficial years will not become extinct immediately after unfavourable periods, because they can establish new populations from the seed bank (Savidge 1970). Furthermore, at regressive distribution boundaries, species with a seed bank can compensate years with extreme weather conditions better than species with seeds that all germinate in the first year.

Dispersal and persistence capacities could not be included in our modelling because quantitative studies on these aspects are hardly available. These attributes are insufficiently known for most species. However, biological and ecological traits included in Table 26.3 enable us to estimate potential range shifts for those species that could have a progressive or regressive development of their distribution ranges (Chap. 10 and Metzing 2005).

Table 26.3 Biological and ecological traits of plants with a predicted regressive or progressive change of distribution ranges at the German coasts

	Ecological traits							Distribution	Ecological preferences							Red list			
Taxon	LO	VR	LP	LF	ST	PO	DI		ZO	T	K	N	HE	S	CH	NS	WW	NW	WO
Plant taxa with a predicted progressive change of distribution range within the German coastal area (acc. to Metzing 2005)																			
Alopecurus arundinaceus	p	vs	d	H G	cs	w	a z-ep	m/mo-b·(k) +litEURAS	mepnb				o-m	Ha					
Arnica montana	p	vs	d	H G	csr	e	a z-ep	sm/mo-temp/ demo·subozEUR	epn	4	4	2	o-m	X		2	0	2	
Artemisia campestris	p		e	C	c	a e	a z-ep	m-temp·(subk)EUR-WAS	mepnb	6	5	2	b-p	X		V	0	P	
Atriplex calotheca	a		d	T	cs	w a e	hy	temp·litEUR	pn	6	x	8	o-m	X	x				0
Atriplex glabriuscula	a		d	T	cs	a e	hy a	temp-b·litEUR +OAM	pnb	6	4	9	o-m	X	x	R	P	1	2
Atriplex longipes	a		d	T	s	w	hy	temp·litEUR		6	?	8	a-o	Ha	x			1	
Bassia hirsuta	a		d	T	Sr	w	hy	sm-temp·subk +litEUR-WAS	epn	6	6	5	c-p	Ha	x			1	1
Blysmus rufus	p	vs	d	G	csr	w	hy z-ep o	austr/moAM+m/ mo-b·k+litEUR-SIB +AM	umepnb	6	x	4	o-m	Ha	x	2	2	1	1
×*Calammophila baltica*	p	vs	w	G	cs	w	hy	ntemp·litEUR		6	3	2	o-m	X	x				
Cochlearia danica	a-b (p)		w	T H	sr	e a	hy z-ep a	temp·ozlitEUR	pnba	6	3	5	o-m	Ha	(x)				3
Crambe maritima	p		w	H	cs	e a	a hy	sm + temp·litEUR	epn	6	x	8	o-m	X	x	R	0		2
Empetrum nigrum	p		e	W	csr	w e (apo syr) a	z-en o	sm/mo-b·(oz)CIRCPOL	enb	x	3	2	o	X					
Euphrasia micrantha	a		d	T hp	r	a e	s z-ep my?	temp-b·ozEUR	pnb	5	2	1	o-m	X			2	1	
Festuca polesica	p		d	H	cs	w	a z-ep	temp·subkEUR	pn	7	6	2	o-m	X					
Galium sterneri	p	v	d	H	csr	e	my?	ntemp-b·euozEUR		5	2	1	o-m	X				1	

Genista germanica	p		w	W	cs	e (hym)	au	sm/mo-temp·subozEUR	epn	5	4	2	o-m	X				0	
Gentianella campestris subsp. *baltica*	a		d	T	csr	e (apo lep) a	a	temp·ozEUR	pn	6?	4	?	o-m	X		0	1	0	
Gentianella campestris subsp. *campestris*	b		w	H	csr	e (lep apo) a	a s z-en	sm/mo-b·ozEUR	epnb	x	2	2	o-m	Hg					
Gentianella uliginosa	a		d	H	csr	e	a	temp·subozEUR	pn	6	2	2	o-m	Hg		0	1		
Juncus balticus	p	vs	w	G	cs	w	a z-ep	temp-b·ozlitEUR	pnb	4	2	2	o-m	Hg		0	1		0
Lathyrus japonicus	p	vs	w	H G	cs	e	au	sm-b·subozlitCIRCPOL	epnb	6	4	3	o-m	X	x	R	2		3
Leymus arenarius	p	vs	w	G	c	w	hy	sm-arct·litEUR	epnba	6	x	6	o-b	X	x				
Linnaea borealis	p		e	W	csr	e (syr)	z-ep my?	sm/mo--arct·(subk)CIRCPOL	epnba	x	5	2	o-b	Hg		1			
Liparis loeselii	p	vs	d	G H	csr	a	a	sm-temp·subozEUR-SIB+OAM+(WAM)	epn	6	4	2	o-m	Hg		2	1		
Listera cordata	p	vs	d	G	csr	e (dip hym) a	a	sm/mo-arct-(oz)CIRCPOL	epnba	4	3	2	o-m	Hg				0	
Melilotus dentatus	(a-) b		d	T H	csr	e (apo) a?	s au	m-temp·(k)EUR-WAS	mepn	6	7	5	m-c	Ha		0			1
Myosotis stricta	a		w	T	sr	a e (hym dip)	z-ep	m-b·(subk)EUR-WAS	mepnb	6	5	2	o-m	X		V			
Odontites litoralis	a		d	T hp	sr	e (apo) a	a s hy	temp·subozlitEUR	pn	6	?	4	m-b	Ha	x	1	1		3
Petasites spurius	p	vs	d	G	c	e a	a z-ep h	sm-temp·subk +litEUR-WAS	epn	6	6	5	o-m	X		1			P
Polygonum oxyspermum	a	vs	d		sr	w	hy z-ep my?	temp·subozlitEUR +(OAM)					o-c	X					1

(continued)

Table 26.3 (continued)

	Ecological traits							Distribution	Ecological preferences							Red list			
Taxon	LO	VR	LP	LF	ST	PO	DI		ZO	T	K	N	HE	S	CH	NS	WW	NW	WO
subsp. *oxyspermum*																			
Polygonum oxysp. subsp. *raii*	a (-b?)				sr	w a e	my?	sm-arct·ozlitEUR	pn	6?	4	8		X				1	
Potamogeton filiformis	p	vs	w	A		w h	hy z-ep	m/mo-arct·(suboz)CIRCPOL	mepnba	4	5	3		Hd		0			
Puccinellia capillaris	p		w	H	s	w	hy a z-ep	temp-b·ozlitEUR	pnb	6	?	4	o-m	Ha	x	R	P		?
Pyrola minor	p	vs	w	H C	s	e? a	a	sm/mo-arctCIRCPOL	epnba	x	x	2	o-b	Hg		3	3	3	
Pyrola rotundifolia	p	vs	w	H	s	e a	a o	trop/moOAS-m/mo-arct·(suboz)CIRCPOL	rmepnba	x	5	3	o-b	Hg		R [3]	2	1	
Plant taxa with a predicted regressive change of distribution range within the German coastal area (acc. to Metzing 2005**)**																			
Rumex longifolius	p		w	H	c	w	my? a	sm/mo-arctCIRCPOL		6	?	8	m-b						
Salix daphnoides	p		d	P N	c	e	a	sm/mo-b·subozEUR	epnb	x	4	4	o-m	X		u			
Salix hastata	p		d	N W	c	e	a	sm/alp-arct·(k)EURAS	epnba	3	7	4	o	Hg				P	
Salix pentandra	p		d	N P	c	e	a h	sm/mo-b·(k)EURAS	epnb	5	7	4	o-m	Hg		3			
Stellaria crassifolia	p	vo	w	H	csr	a e	my	sm/mo-arct·(k)CIRCPOL	epnba	5	7	3	a-o	Ha					
Vaccinium uliginosum	p		d	W	cs	e (hym dip)	z-en o	sm/mo-arct·(subk)CIRCPOL	epnba	x	5	3	o-m	Hg		3			
Vaccinium vitis-idaea	p	v	e	W	cs	e (apo)	z-en o	sm/mo·arct (subk)CIRCPOL	epnba	x	5	1	o-m	X		2		1	

Atriplex portulacoides	p	vo	e	C	cs	w	hy	m-temp·litEUR		6	x	7	o-m	Ha	x			2	
Beta vulgaris maritima	a-p				cs	w	hy	m-temp·subk +litEUR-WAS		6	4	9	o-p	Ha X	x	R			
Brassica oleracea	a-p		w	C	cr	e (apo) w a	hy a au h s	m-temp·ozlitEUR	mepn	7	2	8	c-p	X					
Calystegia soldanella	p	vs	d	H	cs	e	hy z-ep a au	austr+m-temp·ozlitCIRCPOL	epnb	6	2	5	o-b	X	x	1	1	1	
Carex trinervis	p	vs	w	G H	csr	w	my?	sm-temp·euoz litEUR		6	1	2	o-m	Hg	x	2	2	0	
Cerastium diffusum	a		w	T	r	a e	z-ep z-en	m-temp·ozlitEUR	mepn	6	2	2	m-p	Hg X	x	3	p	P	
Crithmum maritimum	p			H			hy	mtemp·litEUR +AFR						X		n. D.			
Cynodon dactylon	p	vs vo	d	G H	cs	w	a z-ep h	austr-stemp·(oz)CIRCPOL	uromep	7	3	5	m-p	X		u			
Erica cinerea	p	v	e	W	cs	e (apo dip)	a my?	sm-b·euozEUR		6	1	1	a-o	X					
Galium mollugo	p		d	H	c	e (dip) a	z-ep z-en	sm-tempEUR	mepnb	6	3		o-c	X					
Genista anglica	p		e	W	cs	e	au	m/mo-temp·euozEUR	mepn	5	1	2	o-m	X		0			
Glaucium flavum	b-p		d	T H	csr	e	a my? z-ep	m-temp·subk +litEUR+WAS	mepn	6	6	7	c	X	x	R			
Hordeum marinum	a		d	T	cs	w	hy	m-temp·subk +litEUR-WAS		6	4	5	o-p	Ha	x	0	0	0	
Ilex aquifolium	p		e	P	c	e	z-en h	m/mo-temp·ozEUR	epn	5	2	5	o-m	X					
Juncus anceps	p	vs	w	H	cs	w	hy	m-temp·euoz-litEUR		6	1	4	o-m	Ha Hg				2	

(continued)

Table 26.3 (continued)

	Ecological traits							Distribution	Ecological preferences							Red list			
Taxon	LO	VR	LP	LF	ST	PO	DI		ZO	T	K	N	HE	S	CH	NS	WW	NW	WO
Juncus maritimus	p	vs	d	G	cs	w	a z-ep	austrCIRCPOL-strop-temp·(oz)EUR-WAS	uromepn	7	3	6	o-m	Ha	x			P	P
Juncus pygmaeus	a		d	T	r	a w		m-stemp·euozEUR		7	1	2	o-m	Hg	x			1	
Koeleria arenaria	p	vs	w	H	cs	w	a	temp·euozlitEUR	epn	6	1	3	o-m	X		V	3		
Limonium vulgare	p	v	w	H	sr	e a	hy	m-temp·litEUR	mepn	6	3	5	bc-p	Ha	x	V	2		3
Oenanthe lachenalii	p		d	H	cs	e h	hy	m-temp·oz+litEUR	mepn	7	2	7	o-m	Ha		3	2	1	2
Trifolium ornithopodioides	a		d (w?)	T	r	e (apo)	z-en	sm-temp·ozEUR		6	2	?	o-m					P	
Tuberaria guttata	a		d	T	sr	a (c) e?	z-ep	m-temp·(oz-lit)EUR	mepn	7	2	1	o-m	X		R	1		
Ulex europaeus	p	vs	w	N	c	e (apo)	au my	sm-temp·euozEUR	pn	6	1	2	o-m	X		3	2	2	

LO Longevity (acc. to Jäger and Werner 2002; Senghas and Seybold 2000); *a* annual (incl. Winter annual), *b* biennial, *p* perennial

VR Vegetative reproduction (acc. to Jäger and Werner 2002); *v* vegetative reproduction, vs vegetative reproduction subterranean (stolons, root shoots, and rhizomes), *vo* vegetative reproduction over ground (runners, decumbent, and creeping shoots)

LP Leaf persistency (acc. to Ellenberg 1992; Jäger and Werner 2002); *e* evergreen, *w* hibernating green, *d* deciduous

LF Life form (acc. to Ellenberg 1992; Jäger and Werner 2002); *A* hydrophyte, *C* herbaceous chamaephyte, *G* geophyte, *H* hemicryptophyte, *N* nanophanerophyte, *T* therophyte, *W* wooden chamaephyte, *hp* hemi-parasite

ST Strategy type (acc. to Frank and Klotz 1990; Klotz et al. 2002); *c* competitor, *s* stress tolerator, *r* ruderal, cr, cs, and sr combinations

PO Pollination (acc. to Frank and Klotz 1990; Jäger and Werner 2002; Klotz et al. 2002); *a* autogamous, *c* cleistogamous, *e* entomogamous, hym pollinated by Hymenoptera, *syr* by Syrphidae, *apo* by Apoidea, *lep* by Lepidoptera, *dip* by Diptera, *w* anemogram, *h* hydrogamous

DI Dispersal (acc. to Bouman et al. 2000; van Dieren 1934; Jäger and Werner 2002; Klotz et al. 2002; Leege 1937; Müller-Schneider 1986; Packham and Willis 1997; Rumsey in Preston et al. 2002); *a* anemochorous, *my* myrmecochorous, *h* hemerochorous, *au* autochorous, *s* semachorous, *hy* hydrochorous, *z-ep* epizoochorous, *z-en* endozoochorous, *z* zoochorous, *o* ornithochorous

Distribution (acc. to Schubert and Vent 1986); *AFR* Africa, *ALP* Alps, *alp* alpine, *AM* America, *antarct*. Antarctic, *arct* arctic, *AS* Asia, *atl*. Atlantic, *AUST* Australia, *austr* austral, *b* boreal, *CIRCPOL* circumpolar, *demo* demontan, *euoz*. Euoceanic, *EUR* Europe, *k* continental, *lit* littoral, *m* meridional, *M* Central, *med*. Mediterranean, *mo* montane, *ntemp* northern temperate, *O* east-, *S* south-, oz. oceanic, *SIB* Siberian, sub sub-, *temp* temperate, *trop* tropical, *VORDAS* Middle East, *W* western

ZO Floristic zone (acc. to Frank and Klotz 1990); *u* austral/Antarctic, *r* tropical, *o* subtropical, *m* meridional, *e* submeridional, *p* southern temperate, *n* northern temperate, *b* boreal, *a* arctic

T Temperature figure (acc. to Ellenberg 1992): 3 indicator of cool conditions, 5 fairly warm cond., 7 warmth indicat. (4 and 6: intermed. values)

C Continentality figure (acc. to Ellenberg 1992): 1 extreme oceanic, in Central Europe only in a few outposts, 2 oceanic, mainly in the West, including western Central Europe, 3 between 2 and 4, in most parts of Central Europe, 4 sub oceanic, mainly in Central Europe, but spreading eastwards, 5 intermediate, weakly sub oceanic to weakly sub continental, 6 sub continental, mainly in the east of Central Europe and adjoining parts of Eastern Europe, 7 between 6 and 8, 8 continental, spreading into Central Europe from the east only exceptionally

N Nitrogen figure (acc. to Ellenberg 1992); 1 indicator of sites extremely poor in available nitrogen, 3 indicator of sites more or less poor in available nitrogen, 5 indicator of intermediate nitrogen availability, 7 plant often found in places rich in available nitrogen, 9 indicator of extremely rich situations

He Hemerobic levels (acc. to Frank and Klotz 1990; Klotz et al. 2002): *a* ahemerobic, *o* oligohemerobic, *m* mesohemerobic, *b* β-euhemerobic, *c* α-euhemerobic, *p* polyhemerobic, *t* metahemerobic

S Series (acc. to Hobohm 1993; Metzing 2005; Pott 1995; Westhoff 1947; Westhoff et al. 1993); *Ha* halo-, *Hd* hydro-, *Hg* hygro-, *X* xero-series

CH Fixation to coastal habitats: x only in coastal habitats (partly in inland salt biotopes, too)

Endangered: *RL* Red List, *NS* Lower Saxony–coastal region (acc. to Garve 2004), *WW* Lower Saxony Wadden Sea (acc. to von Der Ende 1995), *NW* Wadden Sea of Schleswig-Holstein and Hamburg (acc. to von Der Ende 1995), *WO* Baltic Sea coast of Schleswig-Holstein (acc. to Berg et al. 1996), *SO* Baltic Sea coast of Mecklenburg-Western Pomerania (acc. to Berg et al. 1996), 0 extinct or missing, 1 critically endangered, 2 endangered, 3 vulnerable, *D* data deficient, *G* assumingly endangered, *n. d.* no data, *P* potentially threatened, *R* extremely rare, *u* unsteady occurrence, *V* forewarn list,? present, but status unknown.–(Data partly completed by own assessments)

References

Adam P (2002) Salt marshes in a time of change. Environ Conserv 29:39–61

Berg C, Henker H, Mierwald U (1996) Rote Liste und Artenliste der Gefäßpflanzen des deutschen Küstenbereichs der Ostsee. Schriftenreihe für Landschaftspflege und Naturschutz 48:29–39

Bonn S, Poschlod P (1998) Ausbreitungsbiologie der Pflanzen Mitteleuropas. Quelle & Meyer, Wiesbaden

Bouman F, Boesewinkel D, Bregman R, Devente N, Oostermeijer G (2000) Verspreiding van zaden. KNNV Uitgeverij, Utrecht

Ellenberg H (1992) Zeigerwerte der Gefäßpflanzen (ohne *Rubus*). Ed. 2. Scripta Geobotanica 18:9–166

Frank D, Klotz S (1990) Biologisch-ökologische Daten zur Flora der DDR. Wissenschaftliche Beiträge der Martin-Luther-Universität Halle-Wittenberg 32(P41):1–167

Franklin JF, Swanson FJ, Harmon ME, Perry DA, Spies TA, Dale VH, McKee A, Ferrell WK, Means JE, Gregory SV, Lattin JD, Schowalter TD, Larsen D (1992) Effects of global climatic change on forests in northwestern North America. In: Peters RL, Lovejoy TE (eds) Global warming and biological diversity. Yale University Press, New Haven, CT, pp 244–257

Garve E (2004) Rote Liste und Florenliste der Farn- und Blütenpflanzen in Niedersachsen und Bremen. 5. Fassung, Stand 1.3.2004. Informationsdienst Naturschutz Niedersachsen 24:1–76

Hobohm C (1993) Die Pflanzengesellschaften von Norderney. Arbeiten aus der Forschungsstelle Küste 12:1–202

Huntley B (1991) How plants respond to climate change: migration rates, individualism and the consequences for plant communities. Ann Bot 67:15–22

Iverson LR, Schwartz MW, Prasad AM (2004) How fast and far might tree species migrate in the eastern United States due to climate change. Glob Ecol Biogeogr 13:209–219

Jackson ST, Overpeck JT (2000) Responses of plant populations and communities to environmental changes of the late quaternary. Paleobiology 26:194–220

Jäger EJ, Werner K (eds) (2002) Exkursionsflora von Deutschland. In: Gefäßpflanzen: Kritischer Band, vol 4, 9th edn. Spektrum Akademischer Verlag, Heidelberg

Kirilenko AP, Solomon AM (1998) Modelling dynamic vegetation response to rapid climate change using bioclimatic classification. Clim Chang 38:15–49

Klotz S, Kühn I, Durka W (2002) BIOLFLOR–eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenreihe für Vegetationskunde 38:1–334

Leege O (1937) Endozoische Samen-Verbreitung von Pflanzen mit fleischigen Früchten durch Vögel auf den Nordseeinseln. Abhandlungen herausgegeben vom Naturwissenschaftlichen Verein zu Bremen 30:262–284

Malcolm JR, Markham A, Neilson RP, Garaci M (2002) Estimated migration rates under scenarios of global climate change. J Biogeogr 29:835–849

Melillo JM, Prentice IC, Farquhar GD, Schulze E-D, Sala OE (1996) Terrestrial biotic responses to environmental change and feedbacks to climate. In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) Climate change 1995. The science of climate change. Cambridge University Press, Cambridge, pp 447–481

Metzing D (2005) Küstenflora und Klimawandel– der Einfluss der globalen Erwärmung auf die Gefäßpflanzenflora des deutschen Küstengebietes von Nord- und Ostsee. Dissertation. Carl von Ossietzky Universität, Oldenburg. http://oops.unioldenburg.de/138/2/metkue05.pdf

Müller-Schneider P (1986) Verbreitungsbiologie der Blütenpflanzen Graubündens. Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich 85:1–263

Nathan R (2001) Dispersal biogeography. In: Levin SA (ed) Encyclopedia of biodiversity, vol 2. Academic Press, San Diego [a. o.], pp 127–152

Packham JR, Willis AJ (1997) Ecology of dunes, salt marsh and shingle. Chapman & Hall, London

Pott R (1995) Die Pflanzengesellschaften Deutschlands, 2nd edn. Ulmer, Stuttgart

Preston CD, Pearman DA, Dines TD (eds) (2002) New atlas of the British flora. Oxford University Press, Oxford

Savidge JP (1970) Changes in plant distribution following changes in local climate. In: Perring F (ed) The flora of a changing Britain. E. W .Classey, Hampton, pp 25–31

Schubert R, Vent W (1986) Exkursionsflora für die Gebiete der DDR und der BRD. Kritischer Band. Volk und Wissen, Berlin

Senghas K, Seybold S (2000) Flora von Deutschland und angrenzender Länder, 91th edn. Quelle & Meyer, Wiebelsheim

Van Dieren JW (1934) Organogene Dünenbildung. M. Nijhoff, Den Haag

von Der Ende M (1995) Rote Liste der Farn- und Blütenpflanzen des deutschen Wattenmeerbereichs und Helgolands. Schriftenreihe für Landschaftspflege und Naturschutz 44:51–61

Walter H, Breckle S-W (1991) Ökologie der Erde–Geo-Biosphäre, vol 1–4. G. Fischer, Jena

Webb T III (1992) Past changes in vegetation and climate: lessons for the future. In: Peters RL, Lovejoy TE (eds) Global warming and biological diversity. Yale University Press, New Haven, CT, pp 59–75

Westhoff V (1947) The vegetation of dunes and salt marshes on the Dutch islands of Terschelling. Van der Horst, 's-Gravenhage, Vlieland and Texel

Westhoff V, Hobohm C, Schaminee JHJ (1993) Rote Liste der Pflanzengesellschaften des Naturraumes Wattenmeer unter Berücksichtigung der ungefährdeten Vegetationseinheiten. Tuexenia 13:109–140

Expert System: Spiders and Carabid Beetles 27

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Abstract

The expert system considers spiders and ground beetles in the study region with a total of 35 spider species and 37 ground beetle species. Distribution in Europe and along the North Sea coast and Baltic Sea coast is regarded separately. Traits, such as zonation, flooding tolerance, salt tolerance, etc., were noted.

27.1 Introduction

Climate change at the coasts may not only affect the zonation of species within the elevation gradient of salt marshes or a shift of the geographical distribution within the east–west gradient. It may also cause an immigration of new species from adjacent western or eastern areas or an extinction of northern distributed species within Central European regions. To analyse the geographical effects of the climate change on the species, already known ecological information was included to develop an expert system, from which probable consequences can be derived for future scenarios that consider sea level and temperature increases. Therefore, spider and ground beetle species were included in the list (Table 27.1, 27.2), which were

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Table 27.1 Ecological key factors and distributions of spiders, which enable us to estimate possible changes by climate change. Only those species were considered which are typical for salt marshes and saline coastal grassland and for which a response to climate change can be expected. For rare species with low recordings, preferences for specific ecological key factors were not calculated

Spiders (Araneae)	Geographic distribution											Distribution type	Elevation zone (above MHW at North Sea			
													North Sea			
	DK	NL	Bo	W	M	O	F	H	S	K	PL		l10%	-s	+s	u10%
A Species on salt marshes of the study sites																
Agyneta decora	+	+	0,2	+	+	0,1	+	2,0	0,5	+		atl [scand]	18	20	71	69
Allomengea scopigera	+	+	0,8	0,2	0,9	0,1	0,1	0,3	0,1	0,6	+	eurosib	20	24	184	216
Arctosa leopardus	+	+	2,6	0,1		0,1		+	0,1	+	+	eurosib	9	5	103	86
Argenna patula	+	+	1,4	2,3	0,2	1,3	1,1	0,6	+	+		atlmed	5	12	91	109
Ceratinella brevipes	+	+					+	0,1	+		+	eurosib		100	130	
Ceratinopsis stative	+	+	+	0,6	0,4		+	0,8	0,3	+	+	eurosib	34	25	121	110
Clubiona stagnatilis	+	+	0,1	0,1	0,1	+	0,1	0,1	0,1		+	eurosib	7	16	78	79
Enoplognatha mordax	+	+	+	0,1	+	0,4		0,1	0,1	+	+	atlmed	3	28	78	79
Erigone arctica maritima	+	+	+	+	+	+	49,3				+	circpol	26	52	118	115
Erigone longipalpis	+	+	0,4	1,3	4,0	15,0	63,5	1,3	8,3	43,3	+	atl	-10	4	90	95
Hypomma bituberculatum	+	+	+	0,2	+	1,0	0,3	0,1		+	+	eurosib	13	28	88	95
Tenuiphantes tenuis	+	+	0,2	0,3	0,9	0,1	0,9	4,0	0,1	0,1	+	eurosib	27	55	188	202
Leptorhoptrum robustum	+	+		+	0,1	5,7	0,2	0,2			+	eurosib [scand]	13	25	92	103
Oedothorax apicatus	+	+		0,1	0,4	0,1	0,8	0,2	+	2,6	+	eurosib	7	26	101	103
Oedothorax fuscus	+	+	+	0,4	1,6	24,9	41,5	1,4	1,7	11,6	+	eurosib	12	25	119	126
Oedothorax retusus	+	+	2,1	4,1	0,7	42,2	13,1	22,7	1,8	11,7	+	eurosib	26	42	180	190
Ozyptila westringi		+		0,5	0,2			0,6				atl ?	40	55	164	164
Pardosa purbeckensis	+	+	64,4	34,6	10,8	127,5	2,2	55,9	23,1	29,6	?	atl	6	9	99	96
Pirata piraticus	+	+	4,6	+		+	+	3,7	3,4	2,8	+	eurosib	13	2	128	184
Pocadicnemis juncea	+	+	0,1	0,9	0,6	0,1	0,1	0,7	0,1	+	+	euro	31	40	158	185
Porrhomma microphthalmos	+	+		+	+	0,1	0,4	0,1			+	euromed	-18	-5	86	98
Praestigia duffeyi	+	+	3,3	5,4	4,5	+	+					atl	6	8	54	65
Robertus heydemanni	+	?	(+)	(+)	(+)	+						atl ?				
Silometopus ambiguous	+	+			+	0,9	3,4	0,1	0,1	+		atl [scand]	-13	16	108	114
Silometopus elegans	+	+	0,5			(+)	(+)	+	+	+	+	euro				
Silometopus incurvatus	+	+	(+)	(+)	(+)	+			0,1	+	+	atl				
Silometopus reussi	+	+	0,4	0,9	0,1		0,1	6,2	0,1		+	atl [scand]	10	25	136	155
Troxochrus scabriculus	+	+		0,8	0,1	+	1,6	0,1		+	+	euro	32	42	98	108
Walckenaeria kochi	+	+	0,4	+	0,1	2,1	+	5,7		+	+	eurosib	7	14	126	130
Walckenaeria vigilax	+	+	0,2	1,5	0,3	0,3	0,2	1,4	+	0,2	+	euro	24	41	119	138
B Potentially immigrating species																
Arctosa fulvolineata												atlmed				
Erigone dentigera		+									+	eurosib				
Erigone psychrophile												bormont				
Hypselistes jacksoni	+	+										atl [scand]				
Satilatlas britteni	+	+										atl [scand]				

Geographical distribution: mean numbers (ind. · trap^{-1} · 100 days^{-1}) at the investigated regions of the German coasts: *Bo* Isle of Borkum, *W* Isle of Wangerooge, *M* Isle of Mellum, *O* Oxstedt, *F* Friedrichskoog, *H* Howacht, *S* Sundische Wiese, *K* Karrendorfer Wiese. Values between 0.05 ind. · trap^{-1} · 100 days^{-1} and 0.1 ind. · trap^{-1} · 100 days^{-1} were rounded up to 0.1 ind. · trap^{-1} · 100 days^{-1}, whereas lower values were indicated by '+'. Positive records from the investigated region, but with no records from this investigation, were indicated by '(+)'. Records from adjacent countries, i.e., DK for Denmark, NL for The Netherlands, PL for Poland, were listed with '+'
Type of distribution: *atl.* Atlantic, *atlbalt.* Atlanto-Baltic, *atlmed* Atlanto- Mediterranean, *bormont* Boreo-Montanic, *circpol.* Circum-Polaric, *euro.* European, *ceuro.* Central European, *eurotur* European-Turanic, *ceuropont* Central European-Pontic, *eurocasp.* European-Caspic, *euromed.* European-Mediterranean, *eurosib.* European-Sibiric, *eeurosib.* East European-Sibiric, *eurowsib.* European-West Sibiric, *pontomed.* Pontio-Mediterranean, scand. Scandinavian

(elevation in cm) or MWL at Baltic Sea)				Tot. Ind.	Flood	Salt pref.	Soil type pref.	Resp. to grazing	Body size (mm)		Hist. Pop. Development		Dispersion (Balloning)		Maturity period
Baltic Sea l10% %	-s	+s	u10%	n				.	min	max	Eas f	MV	Typ	Pot.	
31	47	125	141	553	1	1	U	gg	1.8	2.5	I		s	m	sten VII
15	23	99	105	564	1	1	U	ag	4.0	5.5	i		p	h	sten VIIb
				1774	2	1	U		6.5	9.5	c		p	m	sten VIIa-
15	35	102	96	1122	1	2	U, C	ag	2.5	3.2	i		y	m	sten VIIa-
25	44	124	125	32	1	1			1.3	1.8	c		s	h	sten VIIa-
60	68	135	150	393	1	1	S, U	gg	1.8	2.5	c		s	h	sten VIIa
29	50	144	155	79	1	1	U, C	ag	5.0	8.0	c		p	h	sten VII
				18	2	2	U	ag	3.0	4.5	c		p	l	sten VIIa
				9194	1	2	S, U	gg	2.5	3.6	d		y	vh	eu II
2	12	99	110	25387	1	2	U, TC	ag	2.4	3.5	c		y	vh	eu II
18	31	127	130	321	1	1	Indiff	ig	2.2	3.0	c		s	h	sten VII
17	28	117	137	1288	1	1	Indiff	gg	2.0	3.2	c		y	vh	eu II
26	33	71	72	1250	1	1	U, C	ig	3.0	4.8	c		s	h	eu II
29	44	145	156	825	1	1	Indiff	gg	2.0	3.3	c		y	vh	eu II
2	22	128	155	15891	1	1	Indiff	ig	1.8	2.9	c		y	vh	eu II
9	19	110	145	18585	2	1	Indiff	ig	2.0	3.0	c		y	vh	eu II
19	31	84	89	226	1	3	U	ag	2.6	4.8			p	l	sten VII
12	20	89	101	61403	2	3	U, C	ag	4.5	9.0	c		y	vh	sten VIIa-
<0	-6	80	85	2503	2	1	U	gg	4.0	9.0	c		s	h	sten VII
25	39	119	130	455	1	1	U, S		1.7	2.2			s	h	sten VII
15	26	118	121	124	1	1	U, C	gg	1.6	2.2	i		y	h	sten VIIa-
				1899	4	3	C	ag	2.2	3.0	i		s	m	sten VIIa
				4	1	3	U, C		2.3	2.5			p	l	sten VIIa-
16	25	107	116	853	1	3	U	gg	1.3	2.2	d		s	m	eu II
				82	1	1			1.0	1.6	c		y	m	sten VIIa-
25	18	124	119	16		3			1.3	1.7			s		
25	42	128	137	1486	1	1	U	gg	1.3	2.0	c		s	m	sten VIIa-
73	11	164	156	493	0	1	S, U		1.7	2.0	c		y	vh	sten VII
21	29	62	59	1630	2	1	U	ig	2.2	3.6	c		s	h	sten VIIa
9	13	97	93	622	2	1	U	gg	2.0	2.6	c		y	h	sten VII
						3			7.5	12.0			p		
						2			1.8	2.8			s		
						2			2.0	3.1			s		
						1			1.6	2.2			s		
						1			1.6	2.2			y		

Preferred zones within the salt marsh elevation: 110%: Elevation (cm) under which less than 10% of the total number was found, u10%: Elevation (cm) above which less than 10% of the total number was found, −s: Elevation (cm) of the lower standard error of the zonation index, +s: Elevation (cm) of the upper standard error of the zonation index

Tot. Ind.: Total number of specimens found in this investigation (columns B-K)

Flood: Estimated reaction to floods: 4: Only known from tidal habitats of the coasts, 3: Only known from habitats that were characterised by inundation, 2: More frequent in habitats with inundation than in those without inundation, 1: Equally frequent in habitats with inundation and in habitats without inundation, 0: Only known from habitats without inundation or very rare in habitats with inundation

(continued)

Table 27.1 (continued)

Salt habitat preference: 3: Only known from habits with salt influence, 3.3: Only known from polyhaline habitats, 3.2: Mainly found in mesohaline habitats, 3.1: Mainly found in oligohaline habitats, 2: in habitats with salt influence more frequent than in those without salt influence, 1: No difference in frequency between habitats with salt influence and those without salt influence

Soil type preference: S Mainly on sandy soils, *U* Mainly on silt soils, *C* Mainly on clay soils, *P* Mainly on peat soils, *H* humus soil, indiff without any obvious soil type preference

Body size (mm): In each case, the minimum (min.) and the maximum (max.) values are listed. Due to sexual dimorphism in spiders, the lower value mostly refers to the males, whereas the maximum value refers to females

Response to grazing: ag Preference for abandoned salt marshes, *gg* preference for grazed salt marshes, *ig* indifferent reaction to grazing

Historical development of the population: Estimation of the development of the population based on records since the middle of the nineteenth century: *d* Population decreased, *i* Population increased, *c* Population continued mainly on the same level, *ex* extinct; (): estimation is very uncertain, e.g. old records. Eastf: Population development on East Frisian Islands; MVP: Population development in Mecklenburg-Western Pomerania. Compared to spiders, database of ground beetle records for the East Frisian Islands is relatively good for individual time intervals. To estimate the population development of spiders before 1977, the data from the continental area of the Northeast German lowlands were integrated additionally to the data from the islands. As the older data on spiders and ground beetles are very vague, e.g., there are partly no records of abundance and different sampling methods were used, the estimation can be regarded as a very rough valuation, only

Dispersion: Referring to the type of dispersion, spiders were characterised by their potential of ballooning: *y* yes, ballooning is recorded, *s* ballooning is supposed, *p* potential of ballooning is not supposed, but ballooning is possible in juvenile spiders. *Maturity type or period:* the phenology of the spider species is described by the maturity or reproduction period that corresponds to the maximum of activity, if pitfall traps were used (maturity periods refer to Tretzel 1954 and Platen 1984)

Eu eurychronous maturity:

I main maturity period or period of copulation does not correspond with seasons; adult stages and different development stages were found together

II as I, but with distinct maximum activity in summer

IIa as I, but with maximum activity in spring

III as I, but with maximum activity in winter

III as I, but with maximum activity in fall

Dipl diplochronous maturity:

IV two seasonal maximum activities in spring and in fall; one maximum can be more distinct

V the two maximum activities are in summer and in winter

Sten stenochronous maturity

actually recorded from the coasts of the Netherlands or Poland. Additionally, several species were included, which were only recorded from inland salt habitats that may immigrate to coastal habitats. Nevertheless, the list focuses on species that occurred in salt grassland. Sandy or shingle beaches or cliff coasts are omitted, because the present detailed investigations only considered salt grassland.

To estimate the changes in the abundance of specific species at the different salt marshes of the German coasts, the mean numbers of individuals multiplied by· trap^{-1} and multiplied by 100 days^{-1} (mean number of individuals · trap^{-}1 · 100 days^{-1}) for the eight research areas are listed. The westernmost region included the area of the island of Borkum and the continental coast of Lower Saxony up to the island of

Mellum. The subsequent eastern North Sea coast includes the sites of the Oxstedt salt marshes up to the Wadden Sea coast of Schleswig-Holstein, followed by the western Baltic Sea coast in Schleswig-Holstein and the adjacent eastern Baltic Sea coast with the research areas in Mecklenburg-Western Pomerania. Using the records in the marginal areas of the German coasts, the abundance in the individual regions, and the geographical distribution, future climatic effects may be derived for the German coastal assemblages.

The following columns of the tables contain results of the environmental conditions derived from the presented investigations and from the knowledge of the scientists who participated. For these data, the specifically preferred elevation, the respective flood frequency preference, the presumed influence of salinity, and the soil type were estimated using data obtained in the current investigation. Furthermore, the response to grazing, derived from investigations of the research project ‘Ökosystemforschung Wattenmeer’ at the North Sea coast and comparable investigations in salt grasslands of the Baltic Sea, were also estimated.

The zonation index that indicates the width of an ecological niche in an elevation gradient was separately calculated for the North Sea and the Baltic Sea. It is presumed that a preferred zone extends between the lower standard error (−s) and the upper standard error (+s) of the zonation index. To estimate a total habitat extension, the lower and upper margins were listed which define the elevations in which less than 10% of the abundance was found, e.g., l10% means that only 10% of the abundance was found lower than this elevation and u10% is the respective upper elevation. The total abundance listed should give an idea about the database on which the zonation index was calculated.

For the estimation of the response to flood frequency, salt content, and soil type, the environmental conditions known from other studies (Meyer et al. 1997; Irmler et al. 2002; Irmler and Gürlich 2004) were included. Species were indicated by 0 term, which have been recorded from non-flooded habitats, only. An increasing affinity to floods is expressed in higher numbers up to 3. The last class (4) means that the species is only recorded from tidal habitats. In the same way, a preference for salt habitats is listed. For this environmental factor, the last class (3) (only recordings from salt habitats) is also divided into the subclasses 3.3 (polyhaline salt habitats), 3.2 (mesohaline salt habitats), and 3.1 (oligohaline salt habitats).

In contrast to species recorded by the project, detailed information on species known only from adjacent regions of the German coast are not available. For these species, given evaluations concerning flood, salt preference, etc., must be regarded as rough estimations by the experts of the research team. The same applies to species from southern inland salt habitats.

Grazing evidently represents the direct impact of humans on salt marshes. For this factor, only the general reaction to grazing was evaluated, whereas the different kinds of grazing were neglected. The evaluation of grazing effects is mainly based on the investigations in the salt marshes of Schleswig-Holstein (Reinke and Irmler 1994; Meyer et al. 1995) and in the Leybucht (Lower Saxony) (Irmler and Heydemann 1986; Andresen et al. 1990).

Table 27.2 Ecological key factors and distribution of carabid beetles, which enable us to estimate possible changes due to climate change (for explanations, see Table 27.1)

Ground beetles (Carabidae)	Geographic distribution											Distribution type	Elevation zone (above MHW at North Sea			
													North Sea			
	DK	NL	Bo	W	M	O	F	H	S	K	PL		l10%	-s	+s	u10%
A Species on salt marshes of the study sites																
Amara convexiuscula	+	+	0.1	0.5	0.1	+	+	(+)	(+)	+	+	eurocasp	20	31	155	183
Amara majuscula	+	+							+	+	+	eurosib				
Anisodactylus poeciloides	+	+							+	(+)	+	euromed				
Bembidion aeneum	+	+	0.2	+	0.2	2.8	0.4	1.3	(+)	0.5	+	atlbalt	18	39	104	108
Bembidion fumigatum	+	+				(+)	(+)	(+)	+	+	+	eurosib				
Bembidion iricolor	+	+	(+)	(+)	+							euromed				
Bembidion minimum	+	+	0.1	0.5	4.5	26	5.7	7.8	0.9	16	+	eurosib	19	23	112	93
Bembidion normannum	+	+	2.6	2.2	6.9	1	1.2				?	atlmed	7	16	120	135
Bembidion transparens	+							(+)	(+)	+	+	circpol				
Blemus discus	+	+	+	+	0.1	+	+	(+)	(+)	(+)	+	eurosib	5	19	62	62
Carabus clathratus	+	+	(+)	(+)					+	+	+	eurosib	70	77	150	160
Cillenus lateralis	+	+		0.1	3.8	+						atl	<5	-25	30	46
Dicheirotrichus gustavii	+	+	1.6	0.8	118	1.3	59	0.7	+		+	atlbalt	-18	-11	42	40
Dyschirius chalceus	+	+			+	0.1			(+)	(+)	+	eurotur				
Dyschirius globosus	+	+	26	18	20	0.1	2.5	19	1	1.2	+	eurosib	16	24	140	184
Dyschirius impunctipennis	+	+	+	(+)	(+)	(+)	(+)	(+)			+	eurosib				
Dyschirius obscurus	+	+	+	(+)	+	(+)	(+)	(+)	(+)	(+)	+	eurotur				
Dyschirius salinus	+	+	2	1.6	0.4	0.2	4	+	+	+	+	eurotur	10	21	89	100
Dyschirius thoracicus	+	+	(+)	(+)	0.9	(+)	1.8	(+)	(+)	(+)	+	eurosib	15	56	218	216
Masoreus wetterhallii	+	+	0.1	0.1	(+)			+	0.2	(+)	+	eurosib				
Omophron limbatum	+	+	+	(+)	(+)			(+)	(+)	(+)	+	eurosib				
Pogonus chalceus	+	+	4.3	2.4	40	1.6	63	(+)				pontomed	-8	-9	95	98
Pogonus luridipennis	+	+	(+)	(+)	+						+	eurocasp				
Stenolophus mixtus	+	+					+	+	+	+	+	eurosib				
B Potential immigrants from the region																
Acupalpus elegans	(+)	+					(+)				+	euromed				
Agonum monachum									(+)		?	pontomed				
Amara quenseli silvicola	+	+	?	?	?	?	(+)	(+)	(+)		+	eurosib				
Amara strenua	+	+				(+)	(+)				+	ceuro				
Bembidion ephippium	+	+	(+)	(+)	(+)	(+)	(+)				?	pontomed				
Bembidion maritimum	+	+	(+)	(+)	(+)	(+)	(+)					atl				
C Species potentially immigrating from inland salt habitats																
Amara strandi	?	?									?	ceuro				
Bembidion aspericolle											?	euro				
Dyschirius extensus												ceuropont				
D Species potentially migrating along coast																
Bembidion axillare		(+)										atlmed				
Dicheirotrichus obsoletus		+									?	atlmed				
Pogonus litoralis		+										euromed				
Tachys scutellaris		+										pontomed				

Specific attributes for carabid beetles: Dispersion: wing development reflecting the potential of dispersion: *b* brachypterous, *m* macropterous, *d* dimorph. The dispersion potential (Pot.) is evaluated by both the distribution and records in newly inhabited habitats. This mainly refers to observations on the island of Lütje Hörn that developed to the stage of a sand bank and where the settlement of species must be renewed by immigration in regular intervals: *vh* very high, *h* high, *m* medium, *l* low. Reproduction types: Autumn breeder: with larval hibernation (summer, fall, and winter reproduction with larvae in winter and partly with additional hibernation of adults); Spring breeder: with reproduction in spring and larvae in summer (hibernation of adults). Following Paarmann (1976), *Pogonus chalceus* is indicated as a Summer-breeder. They show one generation after the other due to the temperature conditions alone, without influence of day length. Other coastal species may belong to this type, but are hidden under spring breeders. +: development lasts several years, *: refers to Lindroth (1945)

(elevation in cm) or MWL at Baltic Sea)				Total Indiv.	Flood	Salt pref.	Soil pref.	Resp. to grazing	Body size		Hist. Pop. Development		Dispersion type		Breeder type
Baltic Sea									Min	Max.	E.Fr.	MVP	Type	Pot.	
l10%	-s	+s	u10%	n											
				82	1	2	S-U		10.0	13.0	C	c	m	h	A
				11	0	0	S		8.0	9.5		i	m	h	AS
				1	1	3			10.0	12.0		d	m		S*
19	19	94	98	928	2	3.1	U-C	ag	3.4	4.5	I	i	d	h	S
					2	2			3.5	4.1		i	m		S*
				7	1	3.1			4.5	5.5			m	i	S
10	12	78	77	10691	2	2	C-U	ig	2.5	2.9	C	c	m	h	S
				2380	4	3.2	C-U		2.5	3.4	I		m	h	S
				1	2	1			3.3	3.7		(i)	d		S*
				34	1	1			4.5	5.5	I	(i)	m		A
				24	1	1	C		20.0	36.0		i	D	vh	S
				779	4	2	S		3.5	4.5	C		D	h	S
14	22	38	37	34712	4	3.3	C-U	ig	5.0	7.5	C	c	M	h	A
				16	1	3.2	C-U		5.0	6.0	D	d	M	h	S
21	31	100	110	14149	1	1	H	ig	2.0	2.8	C	d	d	h	S
				2	1	2	C		4.0	5.0	C	ex	m	h	S*
				3	2	2	S		3.5	4.5	C	c	m	h	S
16	9	109	104	1259	1	3	C-U	ig	3.5	4.5	C	c	m	h	S
				420	2	1	S		3.5	4.5	C	c	m	h	S
10	67	168	57	54	0	1	S		4.7	7.8		c			A
				2	2	1	S		5.5	6.5	I	c	m	h	SA
				20214	4	3	C-U	ig	5.3	7.7	C		m	h	Su
				2	1	3.3	C-U		6.0	8.7	D		m	l	S
				6	2	1			5.0	6.0		i	m	h	S
					0	3			4.0	4.7			m	l	S
					3	3			6.5	8.8		(d)	m	l	S
					0	1			7.5	9.0	D	d	d		A
					0	1			8.0	10.0			m		S
					4	3			2.5	3.5	D		m	l	S
					4	1			3.5	4.1		i	m		S
					0	3			6.5	8.5			m	l	?
					0	3			2.0	2.6			m		?
					1	3			4.0	5.5			m		?
					?	3			2.5	3.0			m		S
					?	3			5.5	7.8			m		A
					?	3			7.0	8.0			?		S
					0	3			2.3	2.6			m		S

The last columns characterise the morphology and population ecology of species, referring to the body, dispersion potentials, and the population. This data should support an estimation of probable changes in the population dynamics, the immigration and the emigration potentials, in particular, in connection with observations in the eastern or western marginal regions.

References

Andresen H, Bakker JP, Brongers M, Heydemann B, Irmler U (1990) Long-term changes of salt marsh communities by cattle grazing. Vegetation 89:137–148

Irmler U, Gürlich S (2004) Die ökologische Einordnung der Laufkäfer (Coleoptera: Carabidae) in Schleswig-Holstein. Faun.–Ökol. Mitteilungen, Suppl 32:1–117

Irmler U, Heydemann B (1986) Die ökologische Problematik der Beweidung von Salzwiesen an der niedersächsischen Küste–am Beispiel der Leybucht. Naturschutz und Landschaftspflege Niedersachsen 11:1–115

Irmler U, Heller K, Meyer H, Reinke H-D (2002) Zonation of ground beetles (Coleoptera: Carabidae) and spiders (Araneida) in salt marshes at the north and the Baltic Sea and the impact of the predicted sea level increase. Biodivers Conserv 11:1129–1147

Lindroth CH (1945) Die fennoskandischen Carabidae, vol I. Göteborgs Kungl. Vetenskaps och Vitterhets-Samhälles Handlingar. Se. B, Göteborg

Meyer H, Fock H, Haase A, Reinke H-D, Tulowitzki I (1995) Structure of the invertebrate fauna in salt marshes of the Wadden Sea coast of Schleswig-Holstein influenced by sheep-grazing. Helgoländer Meeresuntersuchungen 49:563–589

Meyer H, Reinke H-D, Irmler U (1997) Die Wirbellosenfauna unterschiedlicher Salzwiesen an der Nordseeküste in Schleswig-Holstein und Niedersachsen. Faun-ökol Mitt 7:267–284

Paarmann W (1976) The annual periodicity of the polyvoltine ground beetle *Pogonus chalceus* marsh. (Col. Carabidae) and its control by environmental factors. Zool Anz 196:150–160

Platen R (1984) Ökologie, Faunistik und Gefährdungssituation der Spinnen (Araneae) und Weberknechte (Opiliones) in Berlin (West) mit dem Vorschlag einer roten Liste. Zool Beitr NF 28:445–487

Reinke H-D, Irmler U (1994) Die Spinnenfauna (Araneae) Schleswig-Holsteins am Boden und in der bodennahen Vegetation. Faunistisch-ökologische Mitteilungen, Suppl 17:1–148

Tretzel E (1954) Reife- und Fortpflanzungszeit bei Spinnen. Z Morph Ökol Tiere 42:634–691

Consequences of Climate Change for Biota of the Coastal Salt Marshes and Dunes: Synthesis, Final Conclusions, and Ideas of Compensation

28

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Abstract

In this chapter, the main results of the study are comprised and conclusions were made separately for the North Sea and the Baltic Sea coast. The integrated results regarded temperature and sea level changes and included soil processes and the biotic systems separated for vegetation and animal communities. Additionally, management impacts such as de-embankment or grazing are also considered. It could be shown that the complexity of the ecosystems and the uncertainness of the climate change predictions prevent concrete management proposals. An adapted monitoring of the coastal development on the local scale is needed as a consequence of the distinct local drift and sediment conditions at present and their future development.

Author “Gerhard Weidemann” has died before the publication of this book.

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28.1 Presumptions

The present book aims to close a gap of knowledge regarding the reaction of coastal biota under the conditions of the predicted climate change of Northern Germany. Research on climate change as a base for political activities concerns the reaction of a diverse number of ecosystem types, e.g., marine (e.g. Lozán et al. 2011) or lake ecosystems (e.g. George 2009), as well as agricultural (Fuhrer and Gregory 2014) or forest ecosystems (Freer-Smith 2009). Additionally, Schernewski et al. (2011) outline similar problems as in the present book for the Baltic Sea coast from a geographical point of view. The present book includes investigations made on the reaction of saline marshes and dunes, in particular the biological part of ecosystems, in the project: 'Effects of Climate Change on Biological Systems of Coasts', completed by additional investigations in the region. According to nature conservation research, the coastal ecosystems are one of the most sensitive systems regarding reactions to climate change, because in addition to temperature changes, severe effects are expected due to the sea level rise (Essl and Rabitsch 2013).

Beside temperature increases, a number of further factors are also associated with global climate changes, which are particularly relevant for coastal areas: the sea level rise itself, the increase of the tidal range, and the increasing number of storm floods. These factors directly affect the habitats of organisms of high-elevated areas by an increased input of saline water or an increasing duration of submersion depending on the local elevation conditions. Furthermore, sedimentation and erosion will change, which together with the named factors affect a physical–chemical alteration of the habitats and may implicate losses of the potential living area. The direct effect of submersion and increasing temperature triggers reactions depending on the specific physiological potential of species as well as the opportunities given under the realised niche of competition. Thus, changes are also expected on the level of populations, biocenoses, or assemblages as well as on the ecosystem functions and efficiencies.

The Northern German coasts exhibit various types of ecosystems differing in tidal regimes as well as sedimentation and erosion processes (Reise et al. 2010). In the present book, salt marshes and dunes were studied in detail, while cliff coasts and beaches were omitted. Salt marshes and dunes are heterogeneous ecosystems that are mainly controlled by the elevation above sea level and combined effects of salinity, moisture, and temperature as well as the development of different soils under differing conditions of sedimentation by the sea or wind transport. The study areas differ essentially between the North Sea and the Baltic Sea. The North Sea is characterised by pronounced tides, while tides are nearly absent in the Baltic Sea. The salt marshes at the North Sea coast are part of the Wadden Sea, which is singular in its large dimension worldwide (Reise 2021). The studied salt grassland is the more terrestrial part of the Wadden Sea (Reise 1985), while dunes developed at both coasts in the same way. This difference between both seas is accompanied by a decreasing gradient of salinity from west to east in the Baltic Sea (3.6% in the North Sea, 0.6% in the easternmost study area near Greifswald). Sea level fluctuations in the Baltic Sea are caused by storms and the resulting seiches and are non-periodic in contrast to the periodic tides at the North Sea coast.

For the estimation of the effects for specific regions of climate change, scenarios were used that predict sea level increases of 35–55 cm and tidal range increases of 20–30 cm in comparison to the actual conditions. Furthermore, a 10–15% increase in the number of storm flood events is expected and an increase of the mean annual temperature from 1.5 K to 2.5 K (Chap. 2). The conditions under these scenarios will impact the studied ecosystems differently: mainland versus island salt marshes and dunes, saline grassland of the North Sea versus those of the Baltic Sea.

28.2 Synthesis of the Project Results

To evaluate the reaction of salt marshes and saline grassland under the different scenarios, the changing sedimentation or development of peat (at the Baltic Sea) with the sea level rise is mainly responsible for the future conditions of these ecosystems. For the narrow East-Frisian Wadden Sea, a deficit or even loss of sedimentation is predicted (Bartholomä and Flemming 1995). Moreover, the sediment composition will change from fine sediments to coarser sediments at the foot of dikes. In contrast, sediment compensation for the coastal near Wadden Sea of Schleswig-Holstein might be possible. The process of sedimentation depends mainly on the formation of coasts and, therefore, on human impact by coastal management, e.g. the retreat of dikes towards the mainland or the safeguarding of summer polders to enlarge the area for tides (Reise 2015). The sedimentation is also influenced directly by grazing and trampling of cattle or sheep or indirectly by the changing vegetation with partial extreme differences, e.g. 2.3 cm year^{-1} under un-grazed conditions and 1.7 cm year^{-1} under grazed conditions in the Leybucht (Andresen et al. 1990). Regarding the used scenarios, the following results of the present project can be presented:

1. Reaction of plant and animal species to temperature increase:

   An eastward shift is expected for Atlantic plant species with eastern borders in the study area, e.g., *Crithmum maritimum* (Chap. 10); for some species, e.g., *Atriplex longipes*, a northern shift is supposed.

   Among the 223 plant species considered, 21–26 species have an increasing potential and 27–35 species have a decreasing potential for distribution. Depending on the predicted temperature increase, the modelled migration ranges between distances of at least 400–1000 km, which means that species' movement speed is 8–20 km year^{-1}. New combinations of plant species will develop unexpected responses to new competition.

   Predictions on the shifts of animal species are difficult; for single solitary bees a northern shift is probable, e.g., *Andrena cineraria*, with a speed of 7 km per year on average in the last 35 years (Chap. 12). An eastern shift of Atlantic bee species will not significantly affect the Central European bee fauna. For the North-Frisian bumble bee fauna, a constant emigration is observed.

For the Baltic Sea coast, an increase of transgradient continental species and of thermophilous southernly distributed species is observed in correspondence with the increasing temperature (Chap. 13). Species with a high salinity demand, e.g., *Bembidion minimum*, will distribute further eastwards.

An increase of continental agro-species seems to be more likely affected by their response to changed agricultural practices than to the changed climate.

2. Reaction of the soil system to temperature increase:
   In dunes, the grass *Calamophila baltica* exhibits higher growth under a moderate temperature increase with the consequence of increasing microbial biomass, nematode densities, and increasing development of soil aggregates (Chap. 17). Mesofaunal groups, such as Collembola and Gamasina, showed no effects. In salt marshes, an increased temperature enhances soil organism activity with an increasing redox potential and salt concentration after drying processes of the upper soil layer in summer.

   In lower soil layers, the redox potential will decrease (Chap. 16). The nutrient supply in salt marshes is controlled by the composition of the marine water; thus, no changes are expected because the higher primary production is compensated by an intensified mineralisation (Dahl and Dierssen 2000). The results concerning the N-supply are controversial. With regard to soil investigations, N-deficits will increase.

   Investigations on the vegetation let us assume that the turnover of the plant available N increases due to higher rates of mineralisation and denitrification. This leads to a higher primary production and salt tolerance, which impact the competition between plant species and change the species' composition.
3. Reaction of soils and organisms to the increasing sea level:
   The change of vegetation mainly depends on the local composition of plant species (Chaps. 10 and 14). On the local scale, vegetation change corresponds mainly with the inundation frequency and competition. Grazing conditions are a major factor controlling the vertical zonation. Prolonged inundation favours annual plant species and species with aerenchymas or lateral spreading capacity. Early succession stages benefit from heterogeneous patterns with high sedimentation or erosion areas with damaged vegetation. Species richness of saline grassland depends on the altitudinal expansion of the foreland (Chaps. 14 and 18).

   Zonation is developed at both the North Sea and the Baltic Sea. Zonation of assemblages shifts according to the overall flooding regime. On sites with few floods, low elevated assemblages expand to higher sites and vice versa.

   Seasonal dynamics varied corresponding to the local flooding frequencies. Seasonal migration is more expressed in species with high migration potential (flying ability). Spiders are more mobile than carabids and may react more flexibly to changed flooding regimes.

Several species react to a reduced living area with increasing activity and negative effects on energy balance (Chap. 20) with the danger of extinction.

28.3 Predictions for the Investigated Ecosystems

Our results exhibit that the future reaction of *salt marshes at the North Sea coast* under climate change conditions mainly depends on the sedimentation-erosion processes, provoking the question, whether the salt marsh can grow corresponding to the sea level rise or not? An example for a growing salt marsh is the site at Hedwigenkoog (Schleswig-Holstein), lying 380 m in front of the dike, elevated at 2.2 m above NN, and 20–30 cm above the elevation of the adjacent saline grassland. In front of this site, 10 km sandy intertidal mudflats have developed with a high sedimentation supply that is actually higher than the overall 20 cm per century. It can be supposed for this area that the sandy intertidal mudflats could be dislocated eastwards under the conditions of scenario 2 and sedimented up to 55–70 cm on the saline grassland. For this case, the surface of the saline grassland will keep pace with the increasing sea level and a de-embankment will not be needed. Moreover, it can be supposed that the sediments will be sandy-silty (carbon content 0.6–1.2% and calcareous at 4%). Under this assumption, an oxidised saline marsh will still exist in 50 years with similar nutrient reserves, water, and air capacity as today.

In contrast, the same process shall lead to dramatic problems when this up-growing happens in front of a summer dike. The opening of the summer polder at Wursten Coast demonstrates that such a restricted measure is insufficient to lead to an adequate grow up within the polder. Thus, a natural break of the summer dike is just a matter of time (Chaps. 23 and 25).

The higher temperature and increasing winter rainfall will enhance the activity of soil organisms and the water, matter, and air dynamics of the soil (Fig. 28.1). During summer, the upper soil layer will suffer under dry periods with the effect of an increasing redox potential and oxygen supply. Concurrently, the salinity will temporarily increase. As a result of the temperature increase, microbial activity and microbial carbon will increase in the soil, which will induce a reduction of the redox potential in the lower soil layer. As the nutrient supply in such salt grassland is controlled by the nutrient composition of the sea water, no higher primary production is expected because of the simultaneous increase of the mineralisation. With respect to the N-supply, either an increase of the N-deficit or a higher turnover of the plant available N is assumed due to higher mineralisation and denitrification rates (Dahl and Dierssen 2000). This process affects no increase of the primary production, but in some plant species of the saline grassland salt, tolerance might be enhanced. Both factors influence inter-specific competition and a change of the species composition.

In such salt grassland with a surplus of sedimentation, mainly the temperature and the rainfall as well as an increase of flooding events will impact the living conditions of species and the composition of the assemblages. Species that avoid moist conditions will benefit from summer dryness at the upper soil layer. As a consequence of the overall increase of the temperature, plant and arthropod species, which prefer dryness, will invade. A shift of single lower salt marsh species to higher elevations might be possible depending on the intensity and the frequency of these factors (Chaps. 14 and 18). Some arthropod species will react with higher activity

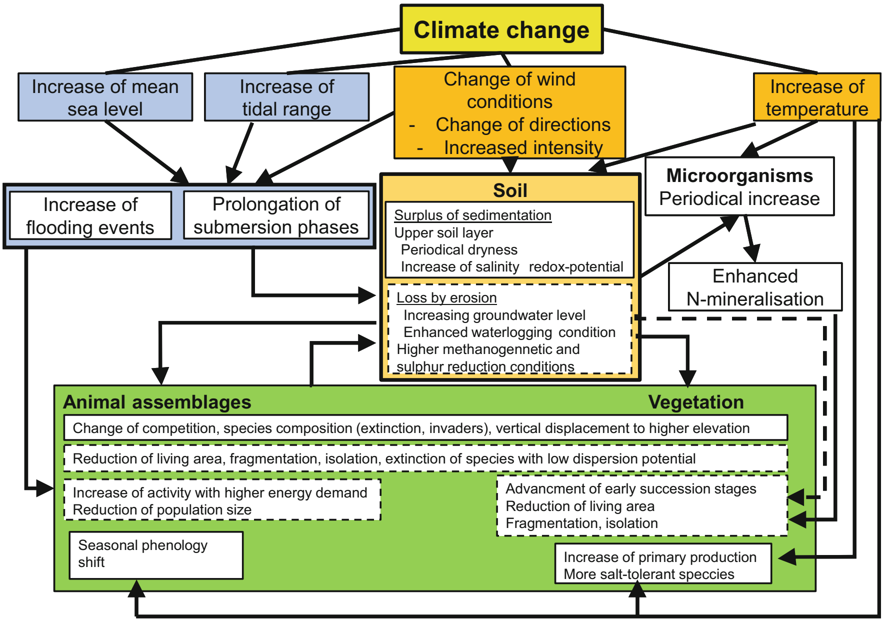

Fig. 28.1 Diagram of the effects of climate change conditions for salt marshes; solid lines indicate general impacts or those for saline grassland with sediment surplus; dotted lines for sites with sediment loss

followed by a higher energy demand and a decreasing population size under low prey supply conditions. They might become extinct in competition with better-adapted species.

Salt grassland without a surplus of sedimentation is expected at those locations of the North Sea coast, where at present low or no sedimentation exists (Fig. 28.1). Under the conditions of scenario 2 with a sea level increase of 55 cm, the groundwater table will increase for at least 55 cm. As a higher tidal range of approximately 30 cm is currently predicted, storm floods will occur more frequently and in longer periods with the consequence of still higher groundwater tables of approximately 70 cm. This is an effect of the moderate water flow in the lower soil layer of ca. 10 cm day^{-1}, which will lead to a retarded draining during low tides. With respect to this process in such salt grassland, conditions will exist that are found today in mudflat areas that are elevated ca. 70 cm lower. The number of flooding events of the floor at such sites will be not 70 times per year, but 500 times per year. The sites will suffer underwater logging conditions nearly the entire year, the redox-horizon will exist directly below the floor, and the plant assemblages will change dramatically to species of the poor glasswort vegetation. Overall, the water, matter, and redox-dynamics will develop to conditions as they are found today in mudflats. Because the soil temperature will be 2 K higher than today in mudflats, sulphur reduction and methane creation will still be more intensive.

A totally absent sedimentation will exist at only very few locations of the North Sea coast. They might be partly located between the East-Frisian islands and the mainland, but also at flood-exposed sites of the Wadden Sea of Schleswig-Holstein. A large part of the areas will double their sediment surplus from 20 cm to 40 cm century^{-1}. In this case, the oxidised salt grassland with a present Gr-horizon at ca. 100 cm below the floor will pass to normal salt grassland with an oxygen free horizon at ca. 20–30 cm below the floor. Under this presumption, the effects of the temperature increase will be less severe than under lower sedimentation conditions regarding the efficiency of soil organisms, because the higher temperature will be partly compensated by a lower oxygen supply.

Under the conditions with more frequent flooding events, the vegetation zone will shift to higher elevations. The species of the lower salt grassland will transfer to the upper salt grassland, in particular, if plant species of the upper salt grassland are impaired or extinct under the changed conditions. In contrast, the plant species of the upper salt grassland that are sensitive to the new conditions with more frequent flooding events, higher salinity, and mechanical stress will not be able to switch to higher elevations, because an upward displacement is mostly prevented by the dikes.

This is not only true for plant species, but also for many arthropod species. Several species of the lower salt grassland will react time-delayed, as shown by the experiments. Where dikes prevent a shift to higher elevated sites, extinction of species will occur at least locally without de-embankment or a shift of dikes further to the mainland. A shift of populations into the so-called sommergroden with low elevated dikes will diminish the effect when the summer dike is opened as seen by the investigation at the 'Wurster' coast.

However, stochastically occurring extreme events that affect accidently strong erosion or sedimentation are not considered. In the case of extreme erosion events, a total loss of the salt grassland or the development of open areas free for a new invasion of plant species may be the consequence. The latter development is supposed in the case of high sedimentation events, because the existing vegetation is lost and a new settlement of plants can start. These open areas will differ in their plant composition, because pioneer plants of the lower and upper salt grassland will invade (cf. Chap. 19).

The development of the salt grassland at the Wadden Sea side of islands will depend on feasibility, if the erosion on the backside of such islands is compensated by the sediment surplus on the seaside under the conditions of the increasing sea level. This will finally depend on the option of a shift of islands to the mainland or a stabilisation at their present locations (Bartholomä and Flemming 1995). Reise (2015, 2021) proposes a totally different land-use regime compared with the current one for large parts of the mainland adjacent to the Wadden Sea with human settlements surrounded by more marine or limnic elements in wide flat plains.

The soils of the *salt grassland at the Baltic Sea* of Mecklenburg-Vorpommern and Schleswig-Holstein differ distinctly from the salt marshes of the North Sea with respect to the soil type, soil structure, and soil development. A total of 75% of this habitat can be defined as coastal flooded fens that have developed by the changing non-periodic flooding events with inter-periods of dryness and silicate sedimentation

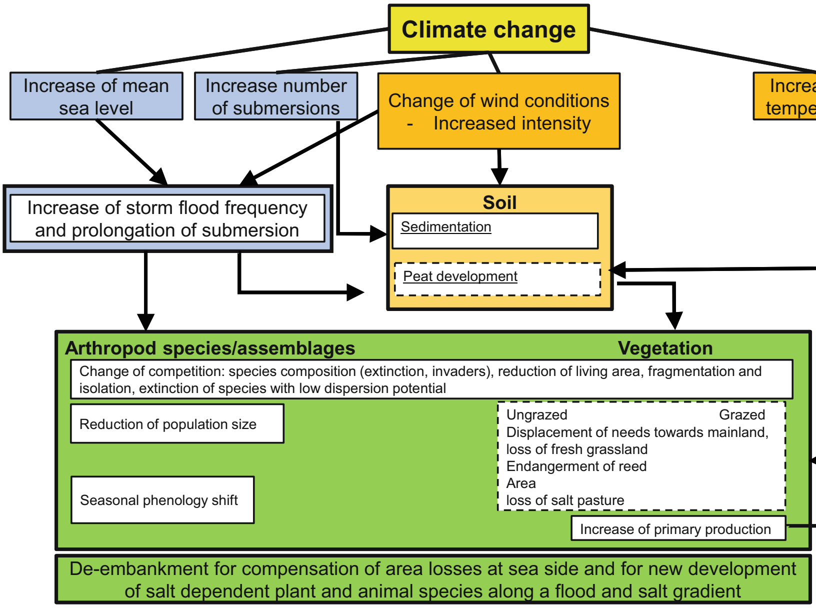

Fig. 28.2 Scenario of climate change dependent impacts on the brackish salt grassland of the Baltic Sea

(Jeschke 1995). The growth of these peat fens above the sea level mainly refers to the mineral sediments, while the peat development and the nutrient fixing are only partly involved. As a result of cattle grazing, the deposited minerals were fixed to the soil together with un-decomposed grass litter during water logging phases and developed mineral rich saline fens with ignition losses ranging from <40% to 60–80% (Janke and Lampe 1996).

If sedimentation and peat development grow correspondingly to the increase of the sea level, a vertical displacement of the salt grassland and reeds towards the dike is expected. In the case of narrow areas, the salt grassland is endangered by erosion. The changing flooding dynamics will affect the composition of the species assemblages in both vegetation and arthropods. The extent of the change depends on the grazing intensity (Fig. 28.2). If a lower sedimentation and peat development occurs, vegetation free depressions will develop or depressions will be sporadically covered by pioneer vegetation. Under the conditions of longer-lasting, non-flooded periods or sufficient sedimentation, a vegetation of brackish areas can develop upwards of 30–40 cm elevation. The composition of the vegetation and arthropod assemblages will depend on the heterogeneity of the elevation gradient and by the grazing intensity.

By de-embankment (Chaps. 22, 23, and 24), retention areas are made which facilitate a natural retreat of both vegetation and arthropod assemblages and a growth of the coastal fens corresponding to the increasing sea level. At present, the former salt grasslands located behind the dikes are elevated 20–40 cm below the salt grassland located in front of dikes due to sagging, peat mineralisation, and erosion (Holz et al. 1996). De-embankment will cause non-periodic dryness with increasing salinity and develop a halophilic brackish vegetation depending on the elevation relief and the number of flooding events. Grazing will produce a more homogeneous elevation gradient and a change of vegetation. Sedimentation will extend the brackish areas and change the zonation of the vegetation and arthropod assemblages. In particular, ground beetles will fast react on the changing conditions. Grazing by cattle is regarded as a key factor for the retention of salt grassland with a high peat growth and both stability and opening of the soil surface, because brackish reeds will prevail under un-grazed conditions.

Coastal dunes will react on the increase of temperature by an increasing productivity and biogenetic stabilisation of the sand on microscopic and macroscopic scales. In this ecosystem process, the increasing temperature and other climate factors, e.g., rainfall, will be involved. According to the climate scenario on the regional scale, a significant prolongation of the vegetation period and a higher microbial activity in the soil were expected. It is assumed that an enhanced decomposition rate, biogenetic stabilisation, and other processes of the soil genesis will occur, in particular, during the temperate and cool seasons without moisture deficits in the soil.

A future higher dryness in summer will not harm the development of xerophilous dune grasses such as *Ammophila arenaria* and *Calammophila baltica*, but it will concurrently decelerate the soil development processes and decrease the stability of sand aggregates. If this process will be combined with a higher endangerment for the coastal dunes by wind erosion cannot be estimated at present, because a decrease of the average wind speed in summer is also predicted. We assume that the climatic benefit for the vegetation, soil microorganisms, and other organisms involved in this process will predominantly generate an increase of the biogenic sand stabilisation.

From these results, we hypothesise that this process will promote the persistence and regeneration of coastal dunes. This is regarded as a positive aspect with respect to the conservation of coastal dunes. However, the contradictory prediction of increasing geomorphologic dynamics corresponding to the sea level increase as well as the increase of winter storms has to be considered. We presume that, on the one hand, the erosion of coasts will accelerate. On the other hand, the new development of dunes as a consequence of the higher sediment supply will increase when barrier islands are displaced towards the mainland.

The organisms of dunes prefer sandy and dry substrates and are resistant against sand cover. Thus, the predicted climate change will not lead to significant changes in the composition of the species assemblages. Only crowberry (*Empetrum nigrum*), a key species of tertiary dunes, will be replaced by heather (*Calluna vulgaris*), which, however, might significantly change the composition of the arthropod assemblages.

In spite of the increasing stability caused by the biogenic development of aggregates, we expect drastic losses of dune areas corresponding to the sea level increase. At the Baltic Sea coast, the bay bars might partly break and develop into an island coast.

28.4 Conclusions

From the integration of our results and under the presumptions of the deduced scenarios for the future development of the investigated coastal ecosystems, the following conclusions can be derived:

1. No direct negative impact is expected on organisms of salt marshes and dunes by single climate factors, because their changing dimension is in the range of their ecological potential. For several species, however, particularly among the ground beetles, a shift of their distributional area and an extinction of populations on a local scale will occur. The increase of extreme weather events, e.g., storm floods, can sporadically induce significant effects on populations of plant and animals with impacts on the composition and function of biocenoses.
2. Indirect effects are expected to be more serious, e.g., by the reduction of living space, which will harm not only single species, but also total biocenoses with all their ecological services on structure and function of the ecosystems.

   The preservation of salt marsh habitats with their specific flood and salt tolerant plant and animal species depends mainly on the facility to displace dikes towards the mainland by a well-timed de-embankment or opening of summer dikes as well as a compensation of the sea level increase by sediment surplus.
3. For dunes the same preconditions are working. In particular, young dunes are adapted to perturbation and able to regenerate quickly. In correspondence to salt marshes, the most important preconditions are the surplus of sediments and the area for displacement.

   The complexity of the investigated ecosystems and the uncertainness of the climate change speed in combination with variance of the natural sediment surplus on the local scale required for a corresponding growth of the marine littoral prevent simple proposals for solutions. The uncertainness of predictions about the future reactions of ecosystems are inevitable (Ekschmitt et al. 1996). Therefore, an adapted monitoring of the coastal development on the local scale is needed as a consequence of the distinct local drift and sediment conditions at present and their future development. Only regarding this successive process allows us to develop coastal management planning under consideration of socio-economic and nature conservation purposes.

References

Andresen H, Bakker JP, Brongers M, Heydemann B, Irmler U (1990) Long-term changes of salt marsh communities by cattle grazing. Vegetation 89:137–148

Bartholomä A, Flemming BW (1995) Zur Sedimentdynamik in den ostfriesischen Rückseitenwatten und den Veränderungen durch natürliche und anthropogene Einflüsse. Schriftenreihe der Schutzgemeinschaft Deutsche Nordseeküste 1:70–89

Dahl M, Dierssen K (2000) Bilanzierung von Stickstoffumsätzen in Salzmarschen der Nordsee in Abhängigkeit von sich änderndem Überflutungsgeschehen und ansteigenden Temperaturen. Forschungsbericht BMBF, Förderkennzeichen 01 LK 9611/0

Ekschmitt K, Breckling B, Matthes K (1996) Unsicherheit und Ungewissheit bei der Erfassung und Prognose von Ökosystementwicklungen. Verhandlungen der Gesellschaft f. Ökologie 26:495–900

Essl F, Rabitsch W (2013) Auswirkungen and Handlungsoptionen für den Naturschutz in Mitteleuropa. In: Biodiversität and Klimawandel. Springer Spektrum, Berlin, p 458

Freer-Smith P (2009) Forestry and climate change. CABI, Surrey, p 272

Fuhrer J, Gregory P (2014) Climate change impact and adaptation in agricultural systems. CABI, Reading, p. 298

George G (2009) The impact of climate change on European lakes. Springer Science & Business Media, Berlin, p 508

Holz R, Herrmann C, Müller-Motzfeld G (1996) Vom Polder zum Ausdeichungsgebiet: Das Projekt Karrendorfer Wiesen und die Zukunft der Küstenüberflutungsgebiete in Mecklenburg-Vorpommern. Natur und Naturschutz in Mecklenburg-Vorpommern 32:3–27

Janke W, Lampe R (1996) Relief, Morphogenese und Stratigraphie der Karrendorfer Wiesen. Natur und Naturschutz in Mecklenburg-Vorpommern 32:29–42

Jeschke L (1995) Salzgrasland und Röhrichte an der vorpommerschen Ostseeküste. In: Lamp J (ed) “Gemeinsam für die Ostsee”. Gesunde Küste–lebendes Meer, WWF Tagungsbericht, vol 9. Umweltstiftung WWF Deutschland, Stralsund, pp 185–199

Lozán JL, Graßl H, Karbe L, Reise K (2011) Warnsignale Klima: Die Meere. Hamburg, Wissenschaftliche Auswertungen, p 383

Reise K (1985) Tidal flat ecology. Springer, Heidelberg, p 194

Reise K (2015) Kurswechsel Küste. Was tun, wenn die Nordsee steigt? Wachholtz. Murmann Publishers, Kiel, p 199

Reise K (2021) Das Watt. Erlebt, erforscht und erzählt. Wunderwelt zwischen Land und Meer. Media Buchverlag, Hamburg

Reise K, Baptist M, Burbridge P, Dankers N, Fischer L, Burhard F, Oost AP, Smit C (2010) The Wadden Sea–a universally outstanding tidal wetland. Wadden Sea Ecosystem 29. Common Wadden Sea Secretariat, Wilhelmshaven, pp 7–24

Schernewski G, Hofstede J, Neumann T (2011) Global change and Baltic coastal zones. Springer, Dordrecht

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https://doi.org/10.1007/978-3-031-12539-3