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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

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Abstract. The ground beetles and spiders of two salt marshes at the German North and Baltic Sea coast were investigated by pitfall traps in 1997 and 1998. While the sites at the North Sea coast are tidal salt marshes, the salt marshes at the Baltic Sea are not influenced by tides. Pitfall traps were installed in a gradient from 20 to 150 cm above MHT (mean high tide: 157 cm + NN, NN: 500 cm above 0 at Amsterdam gauge) at the North Sea coast or NN at the Baltic Sea coast at six or seven sampling elevations, each with five replicates. Conductivity, water content, organic substance, frequency or duration of floodings, sand content and pH of the soil were determined. The flooding regime is the major factor controlling the zonation of invertebrates. Two and three invertebrate assemblages at the North and Baltic Sea, respectively, were distinguished. These corresponded well with the vegetational zones. The border between the two zones was at 60–80 cm above MHT at the North Sea. The three zones at the Baltic Sea extended between 20 and 30 cm, 40 to 80 cm and 100 to 150 cm above NN. The elevation of the mean abundance of species above MHT or NN was calculated. A tide simulation experiment resulted in a shifting population and in an increasing activity under a tidal regime as predicted for the global climate change conditions in 2050. From the actual elevation of the mean abundance, the habitat size of salt marsh species was calculated for a moderate and worse scenario of global climate change. Habitat reduction becomes highest for species of the lower salt marsh zone. Under worse conditions the gradiental length of habitat will only amount to a maximum of 20 m at the slopes of the dikes.

Introduction

According to current climatic models, the natural greenhouse effect of the atmosphere will be augmented by the anthropogenic input of CO_2, CH_2 and N_2O gases (Seiler and Hahn 1998). The global climatic change will increase the temperature by approximately 1 or 2 °C during the next 50 years (Graßl 1993), melting icesheets and glaciers and resulting in a sea level rise between 20 and 30 cm by 2050 (Sterr 1998a, b).

Many species of salt marshes are restricted to that habitat due to their physiological requirements or competition. The tides or inundations and the salt water mainly influence the distribution of the species, contributing to a distinct zonation not only in the plant community but also in invertebrate assemblages (Irmler and Heydemann 1986; Odum 1988; Adam 1990; Andresen et al. 1990; Meyer et al. 1995). The elevated sea level in connection with an increasing storm intensity will initiate a shift of the species to higher elevations of the salt marshes. As nearly all salt marshes of western and middle Europe are bordered by dikes, the evasion area is restricted for the species (Heydemann 1979a). Thus, populations of the salt marsh species face the dilemma between increased inundation by the increasing sea level and the lack of space to retreat. Predicting the reaction of the salt marsh community to climate change is also important, because many salt marshes in Europe are presently endangered and therefore protected in the Wadden Sea National Park or in nature reserves at the Baltic Sea.

In order to predict the impact of the rising sea level on the invertebrates of salt marshes, detailed investigations on the vertical distribution of the species in the salt marsh gradient and their behaviour on increasing inundation frequency are necessary. Thus the following questions are considered in the present study: (1) To what extent are the species of the salt marshes restricted to specific zones? (2) Do differences between the coastal salt marshes at the North and the Baltic Sea exist? (3) How do species react to an increasing inundation frequency? (4) Is it possible to predict the size of the habitat area for the species under the impact of an increasing sea level?

Materials and methods

Description of the investigated sites

The salt marshes investigated were located at the Wadden Sea of the eastern North Sea coast near Friedrichskoog and at the western Baltic Sea coast near Howacht (both Schleswig-Holstein, northern Germany) (Figure 1). Climatic characteristics of the two sites are as follows: mean yearly temperature is 8.4 °C at Howacht and 8.5 °C at Friedrichskoog, annual precipitation is 745 mm at Howacht and 1012 mm at Friedrichskoog. During the investigation period between April and November, the mean temperature was 12.1 °C in 1998 and 13.6 °C in 1997. Yearly precipitation was higher in 1998 with 749 mm (Howacht) and 849 mm (Friedrichskoog) than in 1997 with 628 mm at both sites. While the Friedrichkoog salt marsh at the North Sea is flooded by a tidal regime, at the Baltic Sea no tides occur. Thus, Howacht salt marsh was irregularly flooded during eastern storms almost in winter time.

The vegetation of the Friedrichskoog salt marsh was characterised by a zonation: a lower *Puccinellietum maritimae* between 0 and 60 cm above mean high tide (MHT varies along the North Sea coast. According to the official tide tables of Friedrichskoog gauge, in 1997 and 1998 it was 157 cm + NN, NN: 500 cm above 0 at Amsterdam gauge), and a *Festuca rubra* community between 80 and 130 cm above MHT. A Molinio-Arrhenateretea community existed in the upper zone higher than 130 cm above MHT, which is typical for fresh grassland with low salt water influence. At Howacht, the *P. maritimae* extended between 0 and 30 cm above NN,

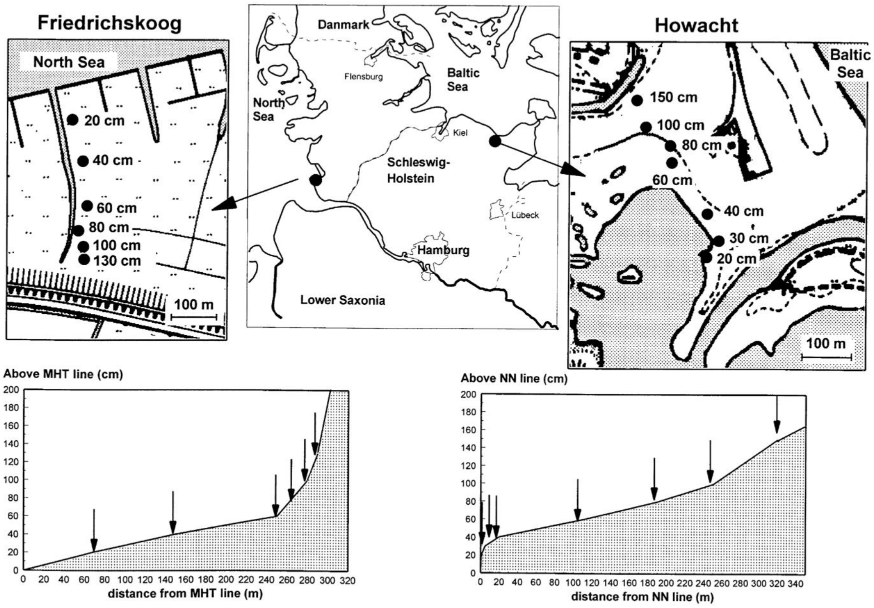

Figure 1. Map of the Friedrichskoog salt marsh at the North Sea and the Howacht salt marsh at the Baltic Sea (sampling elevations marked by points) and the transect of the slope above MHT or NN line with sampling elevations marked by arrows.

a *Juncetum geradii* between 40 and 80 cm above NN and a *Festuco-Galietum* veri (Onno 1933) in the uppermost zone between 100 and 150 cm.

The soils at Friedrichskoog originated from calcareous marine and loamy sediments that become more sandy in the upper zones. At Howacht, the soils in the lower zone also originated from calcareous marine sediments, but a sedge peat developed that extended up to 60 cm above NN. The peat of the lowermost zone between 0 and 30 cm above NN contains a high content of sandy sediments. In the uppermost zone above 60 cm NN, a sandy soil developed from backshore dry sands and gravel pit with low nutrient content.

The overall gradient of measured environmental parameters is shown in Table 1. As the salt marsh of the North Sea at Friedrichskoog is mainly determined by the tides, the inundation frequency was calculated from the official tide tables of Friedrichskoog gauge, while the mean yearly inundation of Howacht marsh at the Baltic Sea was determined from the continuously measured sea level using a pressure sensor (DKlog 200, Driessen and Kern, Bad Bramstedt). The following parameters were determined in May, August and October of 1997 with three replicates at each sampling elevation. Salt content was determined as conductivity (WTW-Conductometer LF 191, Wissenschaftlich-Technische Werkstätten, Weilheim, Germany), pH in H_2O (WTW pH-Meter PMX 2000), water content as the difference between dry and fresh weight of 50 g soil, organic substance by heat

Table 1. Environmental parameters measured at the six or seven elevations of salt marshes, respectively, at Friedrichskoog and Howacht (SE in brackets).

Level (cm)	Conductivity (µS)	Water content (%)	Organic substance (%)	Inundation	Sand content (%)	pH
Friedrichskoog[a]						
20	1310 (911)	21 (5)	2.3	200 (25)	34.6	8.8 (0.2)
40	832 (336)	23 (1)	2.6	92 (3)	32.8	8.9 (0.3)
60	1140 (104)	25 (2)	2.9	52 (1)	35.6	8.7 (0.1)
80	995 (593)	21 (12)	3.3	27 (4)	34.3	8.9 (0.3)
100	902 (639)	26 (4)	5.0	16(2)	30.8	8.8 (0.1)
130	864 (660)	20 (3)	3.9	8 (4)	40.0	8.7 (0.3)
Howacht[b]						
20	4897 (1797)	56 (12)	10.1	214.2	38.9	8.0 (0.4)
30	5187 (2244)	62 (9)	22.9	158.4	34.6	7.7 (0.3)
40	7150 (3667)	70 (6)	44.7	125.4	5.7	7.1 (0.3)
60	2737 (287)	71 (5)	63.6	22.2	7.1	6.4 (0.2)
80	870 (350)	62 (6)	60.8	6.1	9.9	6.7 (0.2)
100	148 (5)	34 (7)	9.1	2.8	79.8	7.1 (0.4)
150	117 (43)	21 (7)	11.8	0.1	82.0	6.3 (0.1)

[a] North Sea: level above MHT; inundation: floodings per year. [b] Baltic Sea: level above NN; inundation: accumulated duration (days).

combustion at 450 °C, sand content by sieving after removing the organic substance by digestion with H_2O_2 (Scheffer 1992).

Experimental design and analyses

The research was performed between April 1 and October 31 in 1997 and 1998 at six and seven sampling elevations at Friedrichskoog and Howacht salt marshes (Figure 1). The sampling elevations were measured referring to both the MHT level at the Friedrichskoog salt marsh and NN at the Howacht salt marsh. At each elevation five replicate pitfall traps were installed with an opening of 17.6 cm circumference. The traps were filled with formaldehyde (4%) and a detergent liquid. Pitfall traps were sampled every second week. For traps at lower elevations a mechanism was built to prevent inflow of water into the trap during high tide. The construction for these traps was as follows: A seesaw was installed at the pitfall trap with an air-filled balloon at one side and a cover on the other side. During increasing tide the balloon was lifted by the water pressing the cover on the pitfall trap (Meyer et al. 1995).

In 1999 the behaviour of the two ground beetle species *Dicheirotrichus gustavii* and *Pogonus chalceus* was investigated in artificial salt marshes under different simulated tide conditions. The artificial salt marshes were constructed by putting original sods from the salt marsh into a 5 × 5 m basin. In total, three basins were filled with salt marsh sods. The three basins were situated on the campus of the University of Kiel. They had a sloping floor to guarantee a continuous inundation from the lower edge to the high edge of the basin. The upper edge was 50 cm higher than the lower edge. The three basins were situated around a central basin, which contained the salt water. Water inflow and outflow was regulated separately for each basin to control the time and the level of the inundation. The simulated tide conditions referred to three scenarios of sea level change in the year 2050:

- Scenario 1: no additional anthropogenic impact will cause an increase of the sea level to 15 cm plus 10 cm by higher tides;
- Scenario 2: a low additional anthropogenic impact will cause an increase of the sea level to 35 cm plus 20 cm by higher tides;
- Scenario 3: a high additional anthropogenic impact will cause an increase of the sea level to 55 cm plus 30 cm by higher tides.

According to official measurements of the gauge at Friedrichskoog, the tidal cycle is between three and four inundations per week at 20 cm above MHT, 1.2 and 1.7 floodings per week at 40 cm above MHT, 0.7 and 0.9 floodings per week at 60 cm above MHT. Within the artificial salt marshes the following tide conditions were observed referring to a site at about 60 cm above MHT.

basin 1: one inundation per week filling the basin to $\frac{1}{2}$ referring to conditions of scenario 1,

basin 2: two inundations per week filling the basin to $\frac{1}{2}$ and to $\frac{3}{4}$ referring to conditions of scenario 2, and

basin 3: three inundations per week filling the basin to $\frac{1}{2}$, $\frac{3}{4}$ and totally referring conditions of scenario 3.

Each basin was divided into five zones and three columns to differentiate 15 quadrants in each basin. The lowest zone with three quadrants was permanently flooded. The remaining terrestrial 12 quadrants were provided with pitfall traps. Thus, distance between pitfall traps was 1 m in the vertical and 1.25 m in the horizontal direction. These pitfall traps contained no conservation liquid and caught specimens were released to the basin for recatch. Sampling periods were in weekly intervals between June and September and pitfall traps were controlled every second day during sampling periods. In total, each basin was stocked with 108 and 84 individually marked beetles of *Pogonus* and *Dicheirotrichus*, respectively. To determine the direction of the migration, only those marked specimens were considered, which were caught at least two times. A specimen that was found in two vertically adjacent pitfall traps was supposed to use two zones. A specimen that was found in horizontally adjacent pitfall traps was supposed to use two columns. Thus, the migration in the vertical direction referred to the number of used zones, while for the horizontal direction the number of used columns was considered. The radius of activity was measured using the distance between pitfall traps of recaught individuals per time.

The elevation of the mean abundance in the flooding gradient was calculated for each species using the formula:

$$H_i = \sum_{i=20}^{150} n_i m_i / N \qquad \mathrm{SE} = \sqrt{\sum_{i=20}^{150} n_i (m_i - H_i)^2 / N}$$

n_i is the abundance of species i at elevation m_i, m_i is the elevation (cm) above MHT and N is the total abundance of species i in the whole gradient.

The actual zonation in the salt marsh was used to predict possible zonations under the different conditions of an increasing sea level. It is assumed from the Gaussian distribution that the main habitat is between the lower and upper standard error (SE) of the elevation of the mean abundance (H_i). The habitat extension for each species was derived from the real profile of the salt marsh at Friedrichskoog. In total, extension of this salt marsh between 0 cm MHT and the dike was 300 m (Figure 1). Detailed maps of contour lines in 20 cm steps were not available. Friedrichskoog salt marsh was chosen for the prediction, because the contour lines were nearly parallel to the dike line as a result of the artificial origin. At this salt marsh the habitat space along the slope therefore corresponds closely with the total habitat space in the salt marsh. Ascending slope in that area is between 0.2 and 0.27 cm m^{-1} between 20 and 80 cm above MHT and 3 to 4 cm m^{-1} between 80 and 130 cm above MHT. For the prediction of the habitat space under climatically changed conditions, no increase of the soil level by sedimentation was assumed, because no valid data exist to predict the sedimentation under an increased sea level condition for this area.

Statistical analyses were performed using the program Statistica (StatSoft 1996). Mean elevation of the species between the two salt marshes was compared by *t*-test, differences between the basins were tested by a one way ANOVA and a post-hoc analysis (Fishers's PLSD), abundance of zones was tested by Mann–Whitney *U*-test. Pearson correlation was used to analyse the relation between tide frequency and distribution of species. For the classification of the sites the dominance of each species at each sampling elevation was calculated and an unweighted average cluster analysis was performed with these data. Distance was adjusted to percent similarity. Canonical correspondence analyses (CCA) were performed using the program CANOCO for Windows to study the influence of environmental parameters on the assemblages.

The elevation above MHT or NN was used to analyse the influence of the floodings. Due to the tidal regime at Friedrichskoog salt marsh it was not possible to calculate the inundated period for each sampling elevation, as it was possible for the non-tidal Howacht salt marsh of the Baltic Sea. The number of tides exceeding each sampling elevation was calculated from the maximum levels of high tides at Friedrichskoog salt marsh, which were available from the official tide tables of Friedrichskoog guage.

Results

Composition of the community

Total species richness at Friedrichskoog salt marsh of the North Sea coast and Howacht salt marsh of the Baltic Sea coast was 82 species and 99 species of spiders; 65 species and 49 species of ground beetles, respectively. At Friedrichskoog,

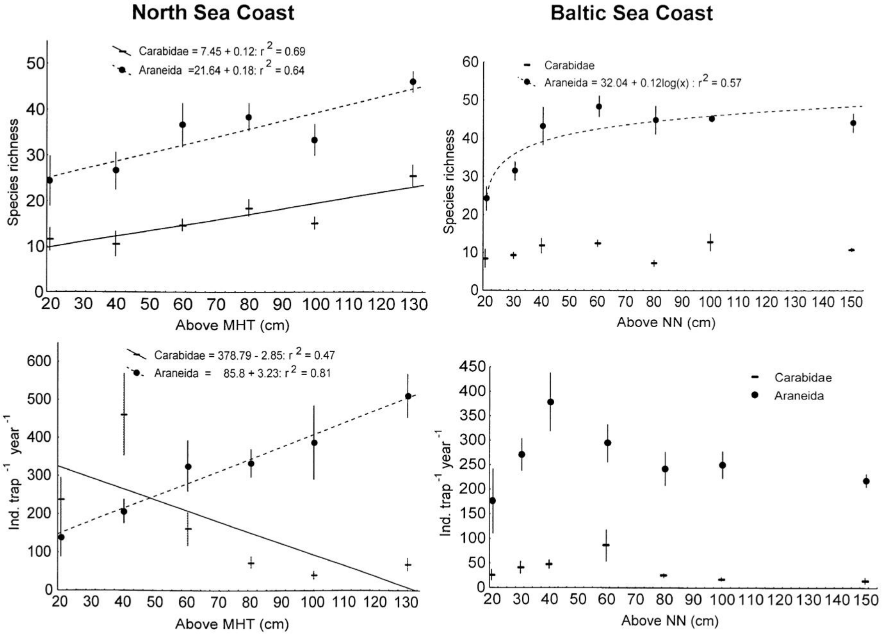

Figure 2. Gradiental analysis of species richness and abundance of Carabidae and Araneida in the two investigated salt marshes. Mean species richness (vertical bars indicate standard error) refers to the number of species in the five replicate pitfall traps for the 2 years at each sampling elevation. Only significant ($P < 0.05$) regression lines are shown.

species richness of spiders and ground beetles increased from lower elevation to higher elevations, whereas abundance increased in spiders, but decreased in ground beetles (Figure 2).

At the Howacht salt marsh of the Baltic Sea coast only the species richness of spiders was significantly correlated with the level above NN. Species richness of ground beetles was relatively constant, between 8 and 12 species per trap, and abundance fluctuated between 25 and 80 ind. trap^{-1} year^{-1} with highest abundance at 60 cm above sea level (Figure 2). Very low abundance was detected in elevations higher than 80 cm above NN. Spiders showed a significant increase of species richness between 20 and 40 cm above NN followed by a constant species richness in higher elevations with approximately 45 species per trap. Abundance of spiders was not significantly correlated with elevations. It was low near the coast line, increased to about 40 cm above NN and was constant in higher elevations with about 250 ind. trap^{-1}year^{-1}.

The cluster analyses with spiders and ground beetles showed the highest differences between the two coastal salt marshes (Figure 3). At the Friedrichskoog salt marsh two groups of sites were formed. The first group included the sites between 20 and 60 cm if ground beetles are considered or between 20 and 80 cm if spiders are considered. A second group included the sites between 80 and 130 cm in ground

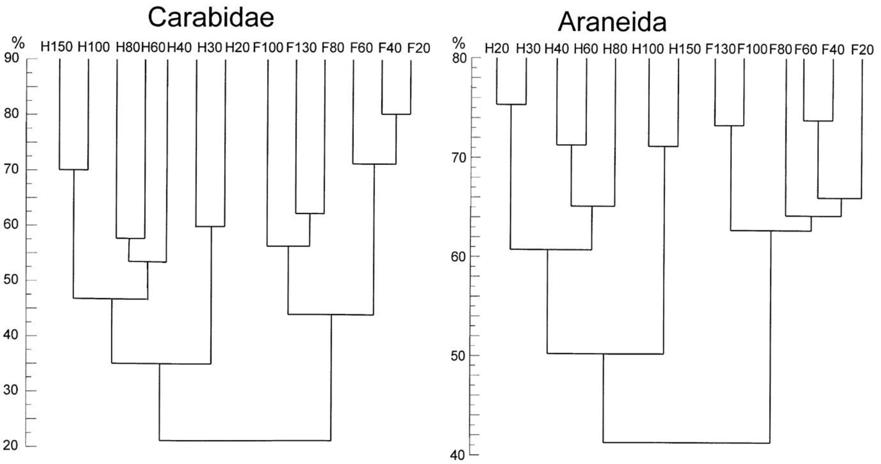

Figure 3. Unweighted-average cluster analysis of the ground beetles (Carabidae) and spiders (Araneida) from the German North Sea coast at Friedrichskoog (F) and the Baltic Sea coast at Howacht (H) (additional numbers indicate the level above MHT for Friedrichskoog or NN for Howacht).

beetles or between 100 and 130 cm in spiders. At the Howacht salt marsh of the Baltic Sea three groups were differentiated: sites at 20 and 30 cm for group 1, between 40 and 80 cm for group 2, and at 100 and 150 cm for group 3.

For the CCA the environmental variables were considered. ANOVA statistics showed no significant difference over the gradient of sand content, pH, water content, and organic substances at the Friedrichskoog salt marsh of the North Sea (Table 1). Also the slight differences of salt content between low elevations and high elevations were statistically not significant. Inundation frequency reflected the highest differences in the gradient. At the Howacht salt marsh of the Baltic Sea, pH was similar to Friedrichskoog salt marsh, demonstrating no gradiental change, whereas the soil greatly differed between the elevations. The peat soil between the 20 and 80 cm sampling level revealed two zones, one zone at the 20 and 30 cm sampling elevation with high sand content and a second zone between the 40 and 80 cm sampling elevation with low sand content. Mean water content was very similar in both zones. The salt content was very high in particular at the 30 and 40 cm sampling levels, caused by drying effects after salt water inundation. Salt water in that part of the Baltic Sea is usually 10‰, while North Sea salt water has 36‰. A third zone at the 100 and 150 cm sampling levels had a high sand content reflecting a moderate dry dune habitat. The accumulated duration of inundation also decreased significantly from low to high elevations.

In general, a high correlation was found between the level above MHT or NN and conductivity ($r = -0.62$, $P = 0.03$) and organic substance and sand content ($r = -0.61$, $P = 0.03$), respectively. Organic substance was therefore omitted in the CCA, while conductivity was kept due to the high difference between the North Sea coast at Friedrichskoog and the Baltic Sea coast at Howacht. Water content and pH of soil were also omitted due to the low differences in the gradient.

If ground beetles are considered, the three variables included in the model of CCA explained 42% of the variance between the sites. Elevation above MHT or NN was the major parameter explaining 17% of total variance. Both conductivity and sand content explained 16 and 9%, respectively. According to the Monte Carlo permutation test, the first variable was significant with $F = 2.2$ ($P = 0.02$).

The three variables explained 37% of the variance between the sites concerning the spider distribution. Conductivity was the major parameter with 18% explanation. Elevation above MHT or NN and sand content explained 11 and 8%, respectively. The first variable was not significant due to the results of the Monte Carlo permutation test.

Zonation of species

The distribution of ground beetle and spider species at the two coasts reflects the results of the cluster analysis (Tables 2 and 3). Among the species that were found with more than 10 specimens, eight ground beetle species (10% of species) and six spider species (5% of species) occurred only at one of the two coasts. Ground beetle species were also more restricted to single habitats than spiders. At Friedrichskoog salt marsh seven ground beetle species only occurred at the upper zone (100–130 cm above MHT), at Howacht salt marsh 15 ground beetle species were recorded in only one or two of the three zones. In contrast, at both Friedrichskoog and Howacht salt marsh only one and three spider species respectively were restricted to one or two zones.

Only few species were exclusively found in the lower salt marsh. At Friedrichskoog salt marsh no ground beetle species was exclusively found at the lower zone between 20 and 60 cm above MHT. According to the elevation of the mean abundance, *P. chalceus*, *D. gustavii*, *Walckenaeria kochi*, and *Baryphyma duffeyi* mainly occurred lower than 60 cm above MHT. At Howacht salt marsh more species were frequently found at lower elevations. For eight ground beetle species and 12 spider species an elevation of the mean abundance lower than 60 cm above NN was determined.

Distribution along the salt marsh gradient was also different between the two coasts. Six ground beetle species and four spider species occurred at higher elevations at Friedrichskoog salt marsh than at Howacht salt marsh. Thus, compared to the ground beetles, spiders showed in average a higher flexibility due to the zonation. On average, the SE of the mean elevation for ground beetles and spiders was 28, 30 and 35, 63 cm at Friedrichskoog and Howacht salt marsh, respectively.

The influence of the tidal regimes on the zonation of species was tested using the number of tides exceeding the six sampling elevations at Friedrichskoog salt marsh within the period from April to October (Table 4). Frequent high tides resulted in a shift of several species into higher zones. In particular, the ground beetles reacted positively to a higher tide regime. Zonation of the species *Bembidion minimum*, *Bembidion normannum* and *Dyschirius salinus* is positively correlated with tides exceeding the 20 and 40 cm level, although they predominately inhabited middle levels of the salt marsh at 60 and 70 cm above MHT. The following species were

Table 2. Abundance of carabid beetles (individuals trap^{-1} 10 days^{-1}) in the five separated assemblages at Friedrichskoog and Howacht salt marshes and corresponding elevation of the mean abundance (H_i).

	Friedrichskoog (North Sea)				Howacht (Baltic Sea)				
	Individuals per 10 days (cm above MHT)		H_i (cm above MHT)		Individuals per 10 days (cm above NN)			H_i (cm above NN)	
Species	20–60	80–130	Mean	SE	20–30	40–80	100–150	Mean	SE
Pogonus chalceus	**5.54**	0.63	44	23					
Bembidion normannum	**0.35**	0.18	64	35					
Dyschirius politus	0.19	0.25	67	33					
D. thoracicus	0.13	0.27	73	30					
Dicheirotrichus gustavii	**5.46**	1.13	47	20	0.43			30	8
*D. salinus**	0.48	0.40	71	35	0.20			20	0
*Agonum marginatum**	0.01	**0.13**	80	16	0.25			30	8
*Bembidion minimum**	0.76	0.60	63	34	**1.40**	0.46		33	14
*B. aeneum**	0.24	0.26	68	39	**0.35**	0.30		35	12
Pterostichus strenuus	0.04	0.08	73	37	0.01	**0.18**		52	16
*Amara communis**		0.25	110	24	0.02	0.01		55	25
Pterostichus vernalis		0.25	100	10	0.24	0.28	0.28	71	55
P. melanarius		0.20	105	25	0.03	0.08	0.04	71	42
Calathus fuscipes		0.20	105	25		0.12	0.33	100	32
A. lunicollis		0.30	110	14			0.20	100	0
*P. diligens**		0.20	130	0	0.08	0.11	0.04	64	53
A. spreta		0.27	130	0	0.04	0.03	**0.36**	97	53
B. varium					**0.52**	0.04		29	13
P. niger					0.06	**0.46**	0.12	63	48
A. infima							0.23	128	25
Masoreus wetterhallii							0.23	150	0
Clivina fossor	0.36	0.26	68	35	0.02	0.11	0.04	86	53
Loricera pilicornis	0.05	0.08	71	41	0.12	0.05	0.08	67	56
A. familiaris	0.02	0.03	78	48	0.02	0.04	0.13	77	39
D. globosus	0.10	**0.39**	81	35	0.51	**1.15**	0.22	59	38
Harpalus affinis	0.06	**0.22**	80	35	0.01	0.05	**0.23**	94	40
A. aenea	0.01	0.07	79	45	0.01	0.04	**0.17**	91	43
Pseudoophonus rufipes	0.04	**0.16**	73	36		0.01	0.06	103	37
Trechus quadristriatus	0.23	0.28	76	33		0.12	0.13	99	39
Calathus melanocephalus	0.01	**0.13**	94	25		0.09	**0.41**	109	35

*Difference H_i between the two coasts significant with $P < 0.05$ due to *t*-test; bold: abundance is significantly higher with $P < 0.05$ due to *U*-test.

Table 3. Abundance of spiders (individuals trap^{-1} 10 days^{-1}) in the five separated assemblages at Friedrichskoog and Howacht salt marshes and corresponding elevation of the mean abundance (H_i).

	Friedrichskoog (North Sea)				Howacht (Baltic Sea)				
	Individuals per 10 days (cm above MHT)		H_i (cm above MHT)		Individuals per 10 days (cm above NN)			H_i (cm above NN)	
Species	20–80	100–130	Mean	SE	20–30	40–60	80–150	Mean	SE
Baryphyma duffeyi	0.07	0.02	57	30					
Walckenaeria unicornis	0.03	0.06	73	40					
Erigone arctica	0.96	**1.88**	88	30					
Clubiona terrestris	0.11	0.20	93	30					
W. kochi	0.03		38	20	**0.45**	**0.96**	0.12	45	17
*E. longipalpis**	**2.17**	1.28	64	32	**0.47**	0.02	0.01	35	24
Argenna patula	**0.39**	0.24	64	34	0.33	0.28	0.11	70	49
Hypomma bituberculatum	0.25	0.15	64	38	0.10	0.10	0.15	83	50
*Pirata piraticus**	0.07	0.02	65	25	**0.74**	0.46		33	12
Pardosa purbeckensis	0.38	0.35	66	38	**3.18**	**3.67**	0.99	47	32
Silometopus reussi	0.06	0.11	70	40	0.17	0.23	**0.48**	83	62
Gongylidiellum vivum	0.19	0.20	70	36	0.27	**0.45**	0.28	57	47
Clubiona stagnatilis	0.07	0.08	71	36	0.02	0.10	0.04	72	43
Diplostyla concolor	0.04	0.05	72	44	0.06	0.08	0.11	71	59
Micrargus herbigradus	0.02	0.04	72	46	0.02	0.11	0.11	83	39
Araeoncus humilis	0.10	**0.24**	74	37	0.04	0.10	**0.25**	83	42
Oedothorax retusus	0.57	0.67	75	37	**1.27**	0.81	0.58	53	38
Silometopus ambiguus	0.35	0.39	75	38	0.17	0.04	0.01	57	46
Lepthyphantes tenuis	0.15	**0.29**	76	37	0.33	**0.43**	0.26	63	53
Pachygnatha degeeri	0.24	**0.41**	79	36	0.04	**0.31**	**0.38**	78	59
O. apicatus	0.19	0.26	79	38	**0.21**	0.10	0.11	66	56
Oedothorax fuscus	1.28	1.61	79	35	0.30	0.21	0.35	69	54
Allomengea scopigera	0.11	0.08	80	31	0.18	0.19	0.12	48	28
*Pardosa amentata**	0.11	0.16	80	38	0.06			25	5
Pachygnatha clercki	0.16	0.19	81	30	**0.45**	**0.56**	0.26	57	45
E. atra	0.41	**0.84**	81	39	**1.70**	0.90	1.33	70	62
P. pullata	0.05	**0.13**	82	31	0.06	**0.29**	**0.27**	70	51
*Leptorhoptrum robustum**	0.09	0.13	83	32	0.06	**0.21**	0.04	52	19
Dicymbium nigrum	0.28	**0.59**	84	36	0.04	**0.13**	0.23	77	39
Bathyphantes gracilis	0.40	**0.88**	87	34	0.62	0.62	0.66	67	53
Centromerita bicolor	0.05	0.04	87	29	0.45	0.65	0.62	65	45
Ozyptila westringi					0.08	**0.36**	0.12	58	27
W. monoceros						0.02	0.08	98	33

*Difference H_i between the two coasts significant with $P < 0.05$ due to *t*-test; bold: abundance is significantly higher with $P < 0.05$ due to *U*-test.

Table 4. Pearson correlation coefficients between the elevation of the mean abundance and tides exceeding different levels above MHT at Friedrichskoog salt marsh (only significant coefficients with $P < 0.05$ are listed).

	Percentage tides exceeding level (cm above MHT)					
Species	20	40	60	80	100	130
Pogonus chlaceus		0.36		0.42	0.45	
Bembidion minimum	0.53	0.55	0.48	0.49	0.52	0.53
B. normannum	0.46	0.52	0.54	0.50	0.53	
Dyschirius salinus	0.40	0.40			0.37	
Oedothorax retusus	0.54	0.53	0.45			

Table 5. Occurrence and migration of two ground beetles species in the experimental systems with different tidal regimes.

	Basin 3			Basin 2			Basin 1		
	N	Mean	SE	*N*	Mean	SE	*N*	Mean	SE
P. chalceus									
Used zone	61	2.8*	0.9*	62	1.9	0.7	63	2.0	0.8
Used number of zones	21	2.1	0.8	22	2.1	0.6	20	1.8	0.8
Used number of columns	23	2.0	0.8	22	2.2	0.8	22	2.0	0.8
Radius of migration (m day^{-1})	21	0.11*	0.11*	22	0.13*	0.14*	20	0.06	0.05
D. gustavii									
Used zone	48	3.6*	0.7*	18	3.1	0.6	22	3.0	0.5
Used number of zones	19	1.7	0.8	6	1.7	0.5	3	1.3	0.6
Used number of columns	19	2.1	0.7	6	2.2	0.4	3	2.0	1.0
Radius of migration (m day^{-1})	19	0.35	0.46	6	0.15	0.19	3	0.09	0.08

N – number of specimens included in the statistical analysis; * significant with $P < 0.05$ due to ANOVA.

also tested, but showed no correlation with the tidal regime: *D. gustavii*, *Bembidion aeneum*, and *Dyschirius thoracicus*. Zonation of spiders was not correlated with the tide regime, with the exception of *Oedothorax retusus*.

Behaviour in the experimental systems

The seasonal activity of the two investigated ground beetle species *P. chalceus* and *D. gustavii* in the experimental basins is similar to the seasonal activity in the field. *Dicheirotrichus gustavii* was mostly active in late summer from August to September, whereas *P. chalceus* showed two periods of activity in early summer and in late summer (Figure 4). Habitation of the four differentiated zones was analysed counting all individually marked beetles. As found in the field, *P. chlaceus* inhabited slightly lower zones than *D. gustavii* (Table 5). In basin 1 with low inundation regime, *P. chalceus* and *D. gustavii* were found on average at zones 2 and 3, respectively. The higher inundation regime in basin 3 resulted in a significant preference of a higher zone, whereas no difference was determined between basins 1 and 2.

In basins 2 and 3 the average number of used zones was 2.1 and 1.7 for *Pogonus*

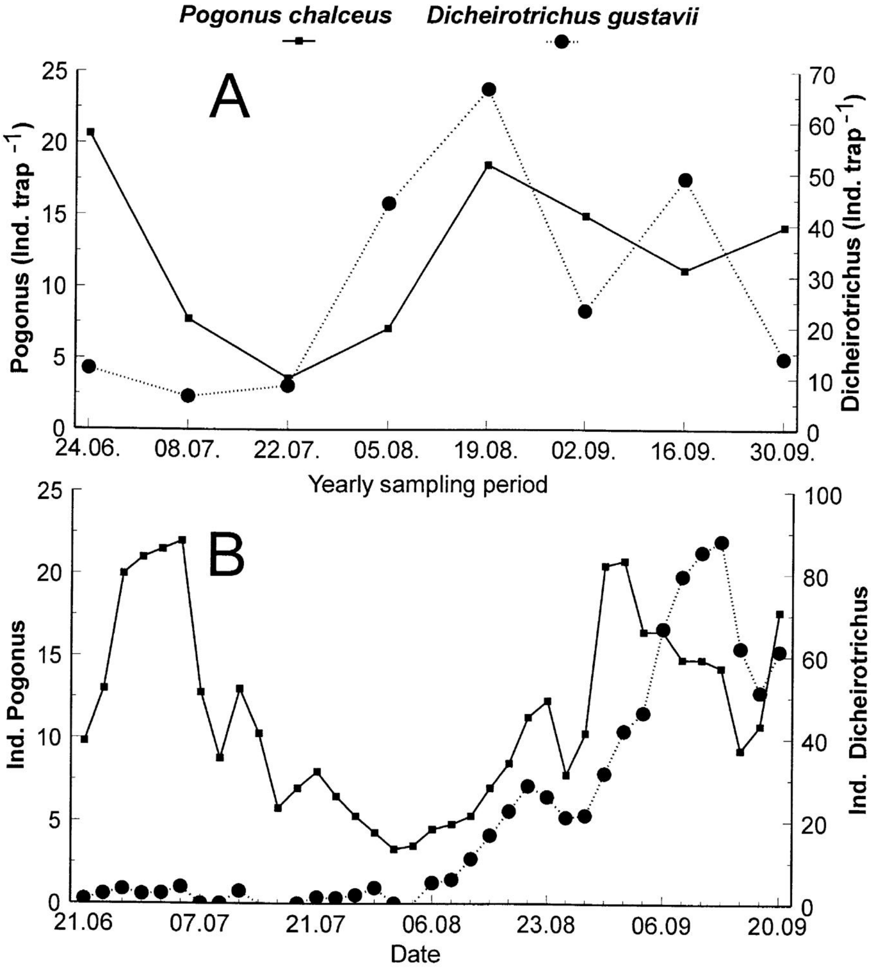

Figure 4. Seasonal dynamics of *P. chalceus* and *D. gustavii* in the Friedrichskoog salt marsh in 1997 and 1998 (A) and in the tidal experiment in 1999 (B).

and *Dicheirotrichus*, respectively (Table 5), whereas it was only 1.8 and 1.3 in basin 1, reflecting higher values for the migration in the vertical direction. However, the differences were not significant. Horizontal migration also shows no significant difference between the inundation regimes. The determination of the radius of activity resulted in a decreasing gradient from basin 3 with the high inundation regime to basin 1 with the low inundation regime. The difference was significant only for *P. chalceus.*

Predicted reaction on increasing sea level

At present, extension of the habitat at Friedrichskoog salt marsh of the North Sea

Table 6. Gradiental extension of habitat (m) at the investigated Friedrichskoog salt marsh of the North Sea coast for several species derived from the elevation of the mean abundance (H_i) and the standard error.

		Scenario		
Species	Actual	1	2	3
Pogonus chalceus	180	100	17	13
Dicheirotrichus gustavii	162	70	12	11
Bembidion minimum	173	67	18	18
B. normannum	174	68	19	19
Dyschirius politus	153	44	18	16
B. aeneum	176	72	21	20
Dyschirius salinus	147	38	19	18
D. thoracicus	116	30	17	14
Baryphyma duffeyi	178	76	17	15
Erigone longipalpis	160	53	19	17
Pardosa purbeckensis	168	76	20	19
Silometopus reussi	173	66	22	20
S. ambiguus	148	40	20	18
E. arctica	46	18	16	13

Actual – actual sea level; scenario 1 – 25 cm higher sea level; scenario 2 – 55 cm higher sea level; scenario 3 – 85 cm higher sea level.

totals between 180 and 116 m for species of the lower and middle levels of the salt marsh (Table 6). The zonation of *Erigone arctica*, a representative of the uppermost salt marsh, extends over a length of only 46 m. Under the varying described conditions of the different scenarios the habitat extension decreased to about 13–20 m independently from the actual extension. In particular the extension of the habitat for species of the lower salt marsh will decrease. The main effect will exist already between the actual conditions and scenario 1. The additional effect of scenarios 2 and 3 is negligible, because the habitats of the species under conditions of scenario 1 are situated already at the slope of the dike.

Discussion

In tidal salt marshes floodings and salinity affect a distinct zonation of plants and animals. MHT is the main dividing line between the regularly flooded low salt marsh and the irregularly flooded high marsh (Odum 1988). While zonation of plants is well studied (Beeftink 1977; Adam 1990), poor knowledge is available about animal zonation in the terrestrial salt marshes (Heydemann 1979b; Andresen et al. 1990). In this study only the high marsh is considered that is the main habitat for the terrestrial invertebrates and vascular plants.

At the North Sea coast, the vegetation above the MHT line is differentiated into two zones: a lower zone with the typical plant species *Puccinellia* ssp. and *Halimione portulacoides* and an upper zone with *Festuca rubra* and *Juncus gerardii* (Dijkema et al. 1990). Main factors are the tidal flooding and the soil aeration. The border between the two zones is about 50 cm above MHT. In his investigations on the plant communities of the Leybucht (northern Germany), Scherfose (1989) found a border between the *Puccinellion* community and lower *Armerion* community at 20–40 cm above MHT. Both Dijkema et al. (1990) and Scherfose (1989) published the border between the two zones at a number of 100 floodings year^{-1}.

Compared with the vegetation, the border between the two faunal assemblages at Friedrichskoog salt marsh of the North Sea is slightly higher for both ground beetles and spiders at 60 and 80 cm above MHT, respectively. At that level the number of floodings is between 50 and 30 floodings year^{-1}, similar to the number of floodings of the Leybucht at the same level. Further detailed investigations on the flooding gradient and the faunal composition of a North Sea salt marsh are not available. Weigmann (1973) studied the oribatid and collembolan fauna of salt marshes and found also the main differences in the composition of hemiedaphic species between the *Puccinellia* community and the lower *F. rubra* community. In his investigation the border between the two assemblages is likely between 25 and 50 cm above MHT. The number of floodings were between 254 or 194 for the lower assemblage and at least 66 or 112 for the upper assemblage. However, small differences were observed for the edaphic species, perhaps less influenced by the floodings due to their life in the aerated strata of the soil. Differences between three zones of salt marshes were also determined for gall midges (Meyer 1984), but data were insufficient to differentiate distinct assemblages. The zonation of the vegetation and the faunal communities are also influenced by the grazing regime (Bakker and Ruyter 1981; Irmler and Heydemann 1986; Kiehl 1997). The upper assemblage successively shifted to lower MHT levels during a succession of abandoned salt marsh (Andresen et al. 1990).

The vegetation of the salt marshes of both the Baltic Sea and the North Sea coast is characterised by a similar composition (Dijkema 1990). In the Baltic Sea salt marsh, the lower zone is dominated by *Puccinellia maritima* and found its upper border at 25 cm above NN; the upper zone is dominated by *J. gerardii* and *F. rubra* occurring between 25 and 45 cm above NN (Jeschke 1987). Due to the faunal zonation of the Howacht salt marsh of the Baltic Sea, only two assemblages may be associated to salt marshes, because the uppermost assemblage at a level higher than 60 or 80 cm above NN was on sites with dune-like environmental conditions. Corresponding well with the vegetational zones, the border between the two faunal assemblages at Howacht salt marsh (Baltic Sea) lies between 30 and 40 cm above NN for ground beetles and spiders. Schaefer (1970) also found the main differences for several faunal groups of a Baltic Sea salt marsh between the *Puccinellia* type and the *J. gerardii* type.

In correspondence with the present study, a distinct decrease of species richness with decreasing elevation was also found by other investigations on the faunal composition of the salt marshes (Schaefer 1970; Weigmann 1973). Due to our results, a linear decrease with decreasing elevation occurred in the Friedrichskoog salt marsh of the North Sea, whereas in the Howacht salt marsh of the Baltic Sea species richness decreased only in spiders at elevations lower than 40 cm NN. The low species richness of the *Puccinellion* community at the Baltic Sea coast is referred to a loss of species of the *J. gerardii* community (Schaefer 1970). In our study, the *Puccinellion* community also included exclusive species occurring only at that low level. In particular, these species were also found in the Friedrichskoog salt marsh of the North Sea, where they occupied a wider range of elevation. In contrast to the investigations of Schaefer (1970), the *J. gerardii* zone was transitional including species of the lower and upper elevations, e.g. *B. minimum* and *Calathus fuscipes*.

It can be assumed from the correspondence analysis or the correlation between the elevation of the mean abundance and the floodings that the flooding regime plays the major role for the occurrence of animal species. Salinity may be additionally important. That is also shown by the occurrence of exclusively coastal and non-exclusively coastal species at the low elevations of the Baltic Sea coast. Up to an elevation of 80 cm above NN, salinity at Howacht salt marsh of the Baltic Sea is higher than or equal to that of the Friedrichskoog salt marsh of the North Sea. In spite of the salinity conditions at that elevation, many coastal species, e.g. *D. gustavii*, occurred at lower elevations in Howacht salt marsh than in Friedrichskoog salt marsh. Non-coastal species occurring at low levels originate from fresh grassland, e.g. *Loricera pilicornis* and *Pterostichus strenuus*, indicating wet soil conditions (Lindroth 1945; Klieber et al. 1995; Irmler 1999; Turin 2000). They colonised the salt marsh due to the moist soil conditions and did not exceed a mean lower level of 70 cm MHT at the North Sea or NN at the Baltic Sea. Therefore, the high species richness in higher levels of the salt marshes is mostly referred to the higher number of species developing in the fresh grassland behind the dikes or in the dunes. Only few species are restricted to the environmental conditions of the high levels of salt marshes. Among both ground beetles and spiders typical coastal species, e.g. *D. salinus* (Lindroth 1945; Turin 2000) or *Silometopus ambiguus* (Locket and Millidge 1953; Reinke and Irmler 1994), are mainly distributed in the middle salt marshes at about 70 cm above MHT or NN. Only *E. arctica* can be regarded as a characteristic species of the high salt marsh.

In addition to the normal tidal regime of the North Sea, extreme heavy floodings also influence the occurrence and abundance of the species (Främbs 1997). Species are drifted to higher levels and abundance is reduced. Retreat into deeper strata of the soil plays an important role against the catastrophic impact of tides or inundations. Only few species seem to be adapted to the tidal rhythm, e.g. *D. gustavii*, which can adapt its circadian rhythm to the shifting tidal rhythm (Foster 1983). Furthermore, flight ability exists in several species. The development of wings in populations of the ground beetle *P. chalceus* depends on the age of salt marshes (Desender 1985). Colonisation occurs by flying beetles, but during several generations beetles lose their flight ability by selecting specimens with poor functional flight muscles or small wing size. Regular migrations induced by the floodings seem not to be developed, because they were never observed in the existing literature. However, populations are shifting as a result of the flooding regime. The average abundance of the spider *Erigone longipalpis* shifted between different levels of the salt marsh corresponding to the MHT levels of the respective year (Irmler and Heydemann 1985) or also within a year (Reinke et al. 2000). Variance between years or within one year did not exceed 30 cm. It could be shown in the tide simulation experiment that also species, which retreat into the soil in correspondence to the flooding events, e.g. *D. gustavii*, react on the increasing level or frequency of the floodings by a shift to higher levels. It is obvious from this tide simulation experiment that both species *P. chalceus* and *D. gustavii* can react with higher activity on the increasing level or frequency of floodings. Thus, it can be assumed that even species with poor flight behaviour are able to retreat actively to higher levels of the salt marsh. However, the experiments in the basins with an experimental tide regime also indicate that the species maintained their zonal occurrence to a high extent. This means that in a scenario with a moderate sea level increase (in basin 2) species stay in their usual zone and react on the higher tides by an increased activity. This may have an effect on the energetic balance of the species and may lead to a higher food supply.

It is obvious that under the conditions of an increasing sea level the size of the habitat for the salt marsh species depends on the sedimentation processes or the growing of the peat soil at the North and Baltic Sea, respectively. The sedimentation in the North Sea is highly dependent on the local conditions. According to Sterr (1998a, b) erosion may even predominate, in particular at sandy coasts, and predictions are not available for distinct coastal areas. At the Baltic Sea coast, the increasing sea level may partly be compensated by the growing peat soil (Müller-Motzfeld 1994).

At the North Sea coast, the habitat will be diminished up to a stripe of 20–25 m along the dikes, if the sedimentation is lower than the increase of the sea level. In particular the habitat for the species of the lower salt marsh will decrease to a high extent. Nevertheless, the habitat reduction of high salt marsh species is very important, because they actually suffer under the loss of their habitat by diking in this century. The small size of the habitat of *E. arctica* is mostly related to the loss of high salt marsh zones in the past. However, many species of the high salt marsh are also found in salty grassland behind the dikes, e.g. *E. arctica* and *S. ambiguus* (Reinke and Irmler 1994). These species occurred in new polders behind the dike only for a few years and disappeared after about 5 or 6 years of succession (Heydemann 1967; Meijer 1980). This is also due to halobiontic or halophilic ground beetle species (Verschoor and Krebs 1995).

It is also possible that competition will play a more important role among salt marsh species, in particular if a higher food supply is required due to the higher activity for a moderate sea level increase. It is known that the exclusive occurrence of several species in salt marshes is the result of competition with species of fresh grassland (Bethge 1973). If the habitat of the salt marsh species will be reduced by an increasing sea level, the competition among salt marsh species might increase. It is not likely that species become extinct under these conditions, but decreasing habitat space will effect abundance. We may not predict the critical population for the different species, but the future danger of local extinction will be much higher, in particular regarding the frequent heavy floodings at the coast.

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