Faun.-Ökol.Mitt. 9, 131- 148 Kiel, 2010

The spider fauna of Baltic Sea coast habitats

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Summary

The spider fauna of six habitat types at the Baltic Sea coast were investigated in 2009: wooded cliffs, woodless cliffs, lagoons, sandy beaches, gravel-beaches, and primary dunes. According to the ordination analysis the six habitat types are clearly characterised by typical compositions of their spider fauna and by their environmental conditions. The main factors with regard to the spider assemblages were: soil moisture, tree cover, and soil pH. Analyses of the sand - gravel gradient resulted in typical species for different mixtures of the material. *Pardosa agricola* was mainly found on gravel-beaches, *Arctosa cinerea* in intermediate stages, and *Philodromus fallax* and *Arctosa perita* on sandy beaches. Lagoons provided no specific spider assemblages compared to mainland reeds. The spider assemblage of wooded cliffs was characterised by species of woods with high soil pH and in woodless cliffs spiders of early succession stages dominated. Overall, sandy beaches and primary dunes combined high species richness with the highest number of endangered species. On gravel pit beaches a low species richness was found, but several typical species occurred.

Keywords: Spiders, Baltic Sea, coast, beach, cliffs

Zusammenfassung

Die Spinnenfauna von Küstenhabitaten der Ostsee

Die Spinnenfauna von sechs Habitattypen der Ostseeküste wurde im Jahr 2009 untersucht. Diese waren bewaldete und unbewaldete Steilküsten, Küstenlagunen, Sandstrände und Kiesstrände sowie die Primärdünen Zone. Die sechs Habitattypen lassen sich sowohl aufgrund ihrer Spinnengemeinschaften als auch aufgrund ihrer Umweltfaktoren klar unterscheiden. Die wichtigsten Faktoren für die Zusammensetzung der Spinnengemeinschaften waren die Bodenfeuchte, die Waldbedeckung und der pH-Wert des Bodens. Die Analysen zur Verteilung von Arten im Sand - Kies Gradienten der Strände ergaben, dass *Pardosa agricola* die Kiesstrände, *Arctosa cinerea* mittlere Zustände zwischen Sand und Kies und *Philodromus fallax* sowie *Arctosa perita* Sandstrände bevorzugten. Die Spinnenfauna an Strandlagunen unterschied sich kaum von Ufern der Binnenland Röhrichte. Die Fauna der bewaldeten Steilküsten enthielt typische Arten basenreicher Wälder, die unbewaldeten Steilküsten Arten von frühen Sukzessionsstadien. Insgesamt enthielten Sandstrände und Primärdünen sowohl viele Arten als auch die meisten gefährdeten Arten. Auf Kiesstränden wurden zwar wenige Arten nachgewiesen, doch kamen dort mehrere typische Arten vor.

Schlüsselwörter: Spinnen, Ostsee, Küste, Strand, Steilufer

Introduction

Although our knowledge of the spider fauna of costal habitats in northern Germany highly increased in the last 50 years, several specific habitats particularly of the Baltic Sea coast have never been studied. First information about the spider fauna of the Baltic Sea coast were given by BOCHMANN (1941) and KNÜLLE (1952, 1953). Later, most investigations were restricted to salt marshes of the North Sea (HEYDEMANN 1960, IRMLER & HEYDEMANN 1985, 1986, ANDRESEN et al. 1990, MEYER et al. 1997, FINCH et al. 2007). A more comprehensive study refers to the island of Norderney, which includes dunes, dune fens and wooded habitats (SCHULTZ 1995). Information on other coastal habitats than salt marshes can be found in general studies that include also so far unpublished records (REINKE & IRMLER 1994, FRÜND et al. 1994, FINCH 2008). Nevertheless, as a consequence of lacking studies, no information is available for sandy beaches, gravel-beaches, wooded and woodless cliffs, and lagoons. This lack of information must be highly criticised, because these habitats are included in the list of endangered habitats in the Fauna-Flora-Habitat (FFH) directive of the European Union (EU), where, in particular, coastal lagoons are listed in a priority class (RIECKEN et al. 2006).

Concerning to the FFH directive, endangered habitats have to be monitored according to their unchanging status. As precondition to notice changes, the starting faunal compositions must be known. The present investigation thus aims to describe the spider composition of highly endangered habitats of the Baltic Sea coast, e.g. sandy or gravel pit beaches, wooded or woodless cliffs and coastal lagoons. In this respect, the main aim of this study is to answer questions concerning species richness and restriction of species to the habitats. Additionally, the environmental conditions were investigated, which may be responsible for the occurrence of spiders. In particular, the conditions on beaches in the sand – gravel gradient were focused to explain the distribution of spiders.

Study site and methods

The investigation was performed in 2009, from April, 9th to August, 20th at nine locations along the Baltic Sea coast in Schleswig-Holstein, northern Germany (Fig. 1). At these 9 locations, different sites were selected that represent the following habitat types: woodless and wooded cliffs, sandy and gravel pit beaches, primary dunes, and lagoons (Tab. 1). Spiders were recorded by means of pitfall traps. At least 4 replicate pitfall traps at each site should be gained at each sampling interval. To compensate losses of traps by tourist disturbance, the number of pitfall traps was enhanced up to 8 traps at individual sites with regard to the loss likelihood. Table 1 shows the maximum number of pitfall traps at the different sites. For the final calculation only 4 replicates were used for each site. Pitfall traps with an opening of 5.6 cm diameter were filled with 10 % vinegar and a detergent liquid and covered by a transparent shelter against direct precipitation.

In total, 3 to 5 replicates of habitat types were achieved. To compare the environmental conditions between the habitat types, the following environmental parameters were determined: soil moisture by difference between wet weight and dry weight of soil as mean of 11 sampling intervals, pH in deionised water using a WTW pH-Meter, organic matter after combustion of a dried soil sample, sand content by sieving using a 0.063 mm sieve after oxidising the organic matter by H_2O_2, and gravel content by sieving a larger soil sample in the field, finer silt and clay material was derived by subtracting (SCHLICHTING et al. 1995).

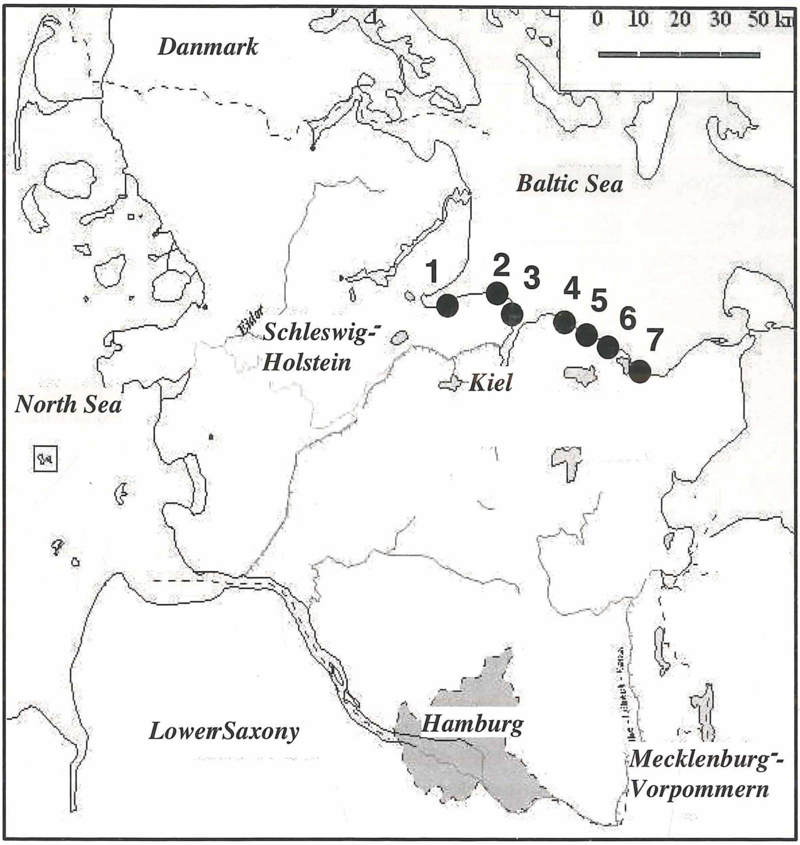

Fig. 1: Investigated locations at the Baltic Sea coast: Lindhöft (1), Dänisch-Nienhof (2), Stohl (3) Stakendorf and Hohenfelde (4), Hubertsberg (5), Behrensdorf and Lippe (6), Weißenhaus (7).

The statistical analysis was performed using the program PAST (HAMMER et al. 2001). Data were tested according to parametric or non-parametric distribution using the Kolmogorov-Smirnov test. Differences between two habitats were tested by U-test or t-test., correlations by Pearson correlation. For the calculation of rarefaction species richness a restriction to 50 specimens was defined. Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) was executed using the program CANOCO (TER BRAAK & SMILAUER 1998). According to TER BRAAK (1987) a distinct ordination of assemblages can be expected at eigenvalues higher than 0.5. Monte Carlo Permutation test was performed to find the significance of environmental factors. The normally distributed data of environmental factors of assemblages and species richness were compared using ANOVA with subsequent LSD post hoc test using the program STATISTICA (STATSOFT 2004)

In the beach habitats, sand and gravel contents were closely correlated: sand content = 97 + 0.96 * gravel content ($r = 0.99$; $p < 0.001$). The sand – gravel gradient was subdivided into the following three classes: gravel: > 70 % gravel and < 30 % sand; medium: 10 – 60

% gravel and 40 - 90 % sand, sand: > 90 % sand and < 10 % gravel. For the woodless cliffs moisture conditions were subdivided into the classes: moist: > 8%, intermediate: 7 - 8 %, and dry: < 7%. To analyse the abundance in these gradients, Kruskal-Wallis ANOVA was used with subsequent U-test and Bonferroni correction using the program STATISTICA .

The nomenclature of species refers to the World Spider Catalog Version 10.0 (PLATNICK 2000). The Red List status for the country of Schleswig-Holstein was derived from REINKE et al. (1998); the Red List status for Germany derived from PLATEN et al. (1998).

Table 1: Habitats at the investigated locations with number of replicate pitfall traps and abbreviations of locations and habitats; Tk Nr. number of the referring TK map.

Location/Habitat (abbreviation)	TK Nr.	Lagoon (L)	Sandy beach (SB)	Gravel beach (GB)	Primary dune (PD)	woodless cliff (WL)	Wooded cliff (WC)
Behrensdorf (KB)	1629	4	6	.	.	.	.
Dänisch-Nienhof (DN)	1526	.	.	4	.	4	4
Hubertsberg (HB)	1629	.	.	6	.	4	.
Hohenfelde (HF)	1628	4	8	.	4	.	.
Lippe (KB)	1629	.	4	.	4	.	.
Lindhöft (LH)	1525	.	6	.	.	.	4
Stakendorf (SD)	1528	4	6	.	4	.	.
Stohl (ST)	1526	.	.	6	.	4	.
Weißenhaus (WH)	1630	.	6	8	4	4	4

Results

Species composition

A total of 4425 spider specimens were identified to 149 species. Species richness at the individual locations ranged between 28 to 72 species, but different numbers of habitats and pitfall traps have to be taken into account (Tab. 2). Some species that have been rarely found in the past, e.g. *Arctosa cinerea,* seem to cover a wider distribution on Baltic Sea beaches than supposed before. It was found at all locations with the exception of those where only coarse gravel-beaches were studied. Some more species, in particular from beaches, are of national importance, because they are included in the German Red List of spiders, e.g. *Sitticus distinguendus, Tibellus maritimus, Trachyzelotes pedestris,* and *Trichopterna cito.* Records of *Pardosa agricola* and *Malthonia campestris* provide important information, since the distribution and ecological demands of both species are scarcely known. In particular *Malthonia campestris* was rarely found in Germany. Here it occurred on a gravel-beach at Hubertsberg. According to the Red List of Schleswig-Holstein two species, i.e. *Arctosa cinerea* and *Sitticus distinguendus,* are extremely endangered (RL 1), 5 species are endangered (RL 2), and 18 species are moderately endangered (RL 3).

Table 2: Abundance of species per pitfall trap per 125 days at 8 locations (for sites per location see table 1; the sites of location Lippe are included in location Behrensdorf).

Art	Behrens-dorf	Dänisch-Nienhof	Hohen-felde	Huberts-berg	Lind-hof	Staken-dorf	Stohl	Weißen-haus
Agyneta cauta	.	0.25	.	.	.	.	.	.
Agyneta conigera	.	.	.	.	0.25	.	.	.
Allomengea vidua	1.75	.	.	.	.	.	.	.
Alopecosa fabrilis	.	.	.	.	.	0.20	.	.
Alopecosa pulverulenta	1.25	.	2.50	1.03	0.25	0.25	.	0.33
Apostenus fuscus	.	.	.	.	.	.	.	0.50
Araeoncus crassiceps	.	.	0.14	7.10	.	0.67	.	5.45
Araeoncus humilis	.	0.25	.	.	.	0.17	.	0.17
Arctosa cinerea	6.83	.	1.02	0.45	0.25	3.47	.	0.75
Arctosa perita	6.83	.	2.40	.	1.15	1.57	.	7.33
Bathyphantes approximatus	15.33	.	1.33	0.33.	.	5.17	.	.
Bathyphantes gracilis	11.08	0.50	11.89	0.50	0.25	6.03	0.25	1.45
Bathyphantes nigrinus	.	.	.	0.33	.	.	.	.
Bathyphantes parvulus	1.42	0.25	1.67	.	.	.	.	.
Ceratinella scabrosa	.	0.75	.	.	1.08	.	.	.
Clubiona frisia	3.00	.	.	.	.	.	.	0.67
Clubiona neglecta	.	.	0.25	.	.	.	.	.
Clubiona phragmitis	1.00	.	0.58	.	.	.	.	.
Clubiona reclusa	.	.	.	.	0.25	.	0.25	.
Clubiona stagnatilis	0.25	.	.	.	.	.	.	.
Clubiona subtilis	.	.	.	.	.	.	.	1.00
Clubiona terrestris	0.25	.	.	.	.	.	.	0.25
Coelotes terrestris	.	0.50	.	.	.	.	.	1.00
Dicymbium nigrum	.	0.25	0.58	0.25	.	.	.	0.38
Dicymbium tibiale	0.25	.	.	.	.	.	.	.
Diplocephalus cristatus	0.25	3.00	.	1.25	.	0.25	1.00	3.23
Diplocephalus latifrons	.	.	.	.	1.67	.	.	0.75
Diplocephalus permixtus	0.50	.	.	.	.	.	.	.
Diplocephalus picinus	0.25	1.00	.	.	0.25	.	.	2.05
Diplostyla concolor	23.25	6.75	7.67	6.60	1.08	23.83	6.50	9.52
Dismodicus bifrons	.	0.25	0.25	.	.	.	.	.
Donacochara speciosa	.	.	0.25	.	.	.	.	.
Drassodes cupreus	1.17	.	.	.	.	.	.	.
Drassodes pubescens	.	.	.	.	.	0.25	.	.
Drassylus lutetianus	1.92	.	1.50	0.25	.	1.33	.	.
Drassylus praeficus	.	.	.	.	.	0.50	.	.
Drassylus pusillus	.	.	0.50	.	.	0.67	.	0.75
Drepanotylus uncatus	.	.	1.00	.	.	.	.	.
Enoplognatha mordax	0.25	.	.	.	.	.	.	.

Art	Behrens-dorf	Dänisch-Nienhof	Hohen-felde	Huberts-berg	Lind-hof	Staken-dorf	Stohl	Weißen-haus
Enoplognatha ovata	.	.	.	0.33	.	.	.	.
Erigone arctica	20.17	0.25	0.84	4.78	18.75	36.25	37.25	6.19
Erigone atra	4.67	1.00	3.40	1.15	1.75	6.55	1.00	9.97
Erigone dentipalpis	1.42	.	.	0.45	0.75	1.03	0.20	5.92
Erigone longipalpis	.	.	.	.	1.50	0.17	.	.
Erigonella hiemalis	.	0.25	.	.	.	0.25	0.25	.
Ero furcata	.	.	.	.	.	.	.	0.25
Euophrys herbigrada	.	.	0.25	.	.	.	.	.
Gnathonarium dentatum	1.83	.	7.17	.	.	0.25	.	.
Gonatium rubellum	.	.	.	.	.	.	.	0.25
Gongylidiellum latebricola	.	.	.	.	.	0.25	.	.
Gongylidiellum murcidum	.	.	.	.	.	0.25	.	.
Hahnia nava	.	.	0.33	.	0.25	.	.	.
Hahnia pusilla	.	1.25	.	.	.	.	.	.
Hypomma bituberculatum	0.25	.	1.00	.	.	0.50	.	.
Hypomma fulvum	0.25	.	.	.	.	0.20	.	.
Kaestneria dorsalis	1.25	.	.	.	.	.	.	.
Kaestneria pullata	0.25	.	.	.	.	0.17	.	.
Larinioides cornutus	0.25	.	.	.	.	.	.	.
Lepthyphantes minutus	.	.	.	.	.	0.25	.	.
Linyphia hortensis	.	0.50	.	.	.	.	.	2.00
Lophomma punctatum	.	.	.	.	.	0.50	.	.
Malthonica campestris	.	.	.	1.00	.	.	.	.
Maso sundevalli	.	0.50	.	0.25	1.20	.	.	2.75
Meioneta affinis	.	0.25	.	.	.	.	.	.
Meioneta saxatilis	.	0.25	.	0.53	.	.	.	.
Micaria pulicaria	0.50	.	.	.	.	.	.	.
Micrargus herbigradus	0.50	.	.	0.25	0.25	0.50	.	0.25
Micrargus subaequalis	.	0.25	.	.	0.25	.	0.33	.
Microlinyphia pusilla	0.50	.	.	.	.	0.25	.	.
Microneta viaria	.	.	.	.	0.75	.	.	1.25
Minyriolus pusillus	.	.	.	.	0.25	.	.	.
Neottiura bimaculatum	.	.	0.14	.	.	.	.	.
Neriene montana	.	0.25	.	.	.	.	.	.
Neriene peltata	.	.	.	.	0.25	.	.	.
Neriene radiata	.	.	.	.	.	0.25	.	.
Nuctena umbratica	0.25	.	.	.	.	.	.	.
Oedothorax apicatus	20.00	1.50	5.47	5.60	6.95	12.72	7.43	14.57
Oedothorax fuscus	4.42	.	1.81	.	1.50	7.43	.	1.70
Oedothorax gibbosus	.	.	.	.	.	0.83	.	.
Oedothorax retusus	1.50	.	31.67	.	.	0.17	.	2.13

Art	Behrens-dorf	Dänisch-Nienhof	Hohen-felde	Huberts-berg	Lind-hof	Staken-dorf	Stohl	Weißen-haus
Ozyptila praticola	.	0.25	.	.	.	.	.	.
Ozyptila trux	0.25	0.25	.	.	.	0.25	.	.
Pachygnatha clercki	6.67	.	2.00	.	0.25	3.50	.	0.75
Pachygnatha degeeri	.	0.25	0.58	0.45	.	.	0.33	0.25
Pachygnatha listeri	.	.	.	.	.	.	0.45	.
Palliduphantes pallidus	0.25	.	.	0.58	0.50	.	.	2.97
Pardosa agrestis	0.33	.	.	0.60	.	.	0.50	.
Pardosa agricola	36.33	18.75	6.09	33.20	.	1.77	8.83	33.29
Pardosa amentata	0.25	0.25	0.13	0.53	1.00	3.75	0.50	0.58
Pardosa hortensis	.	.	.	.	.	.	.	0.25
Pardosa lugubris	.	.	.	.	.	0.33	.	1.15
Pardosa monticola	0.50	.	.	.	.	0.33	0.17	.
Pardosa nigriceps	.	.	.	.	.	.	0.33	.
Pardosa prativaga	35.50	.	8.00	.	0.50	5.75	0.25	.
Pardosa pullata	.	.	.	.	.	0.50	.	0.25
Pelecopsis parallela	0.75	0.25	4.23	.	0.75	0.42	.	2.08
Philodromus fallax	8.25	.	0.25	.	.	.	.	0.50
Phlegra fasciata	.	.	0.25	.	.	.	.	.
Phrurolithus festivus	3.25	6.00	0.25	.	0.25	.	8.20	0.70
Phrurolithus minimus	0.50	.	.	0.25	.	0.25	0.20	0.25
Pirata piraticus	48.75	.	7.42	.	.	17.87	.	.
Pisaura mirabilis	0.50	.	.	.	.	.	.	.
Pocadicnemis juncea	1.75	0.50	0.14	0.75	0.70	0.75	.	1.67
Porrhomma campbelli	0.17	.	0.52	.	.	0.50	.	.
Porrhomma microphthalmum	1.00	.	5.10	.	0.25	1.70	.	0.17
Porrhomma pallidum	0.25	.	.	.	.	.	.	.
Prinerigone vagans	0.42	.	.	.	.	.	.	.
Robertus lividus	.	.	.	0.20	0.25	0.50	.	0.42
Saaristoa abnormis	.	0.25	.	.	.	.	.	.
Savignya frontata	1.50	.	2.08	.	.	.	.	.
Scotina gracilipes	.	.	.	.	.	.	.	0.25
Scotophaeus scutulatus	.	0.50	.	.	.	.	.	.
Segestria senoculata	.	.	.	.	0.33	.	.	.
Sitticus distinguendus	1.00	.	0.33	.	.	0.25	.	0.50
Steatoda castanea	.	.	0.25	.	.	.	.	.
Stemonyphantes lineatus	0.25	.	0.67	1.50	.	0.25	1.50	0.50
Styloctetor stativus	.	.	.	.	.	.	.	0.50
Tallusia experta	.	.	1.00	.	.	0.33	.	.
Tegenaria atrica	.	.	.	0.25	.	.	.	.
Tenuiphantes cristatus	0.25	.	.	.	.	.	.	.
Tenuiphantes flavipes	0.67	0.25	.	.	.	.	0.25	0.50

Art	Behrens-dorf	Dänisch-Nienhof	Hohen-felde	Huberts-berg	Lind-hof	Staken-dorf	Stohl	Weißen-haus
Tenuiphantes tenebricola	0.75	1.50	.	0.25	0.25	0.45	0.25	2.38
Tenuiphantes tenuis	3.42	4.75	3.71	4.50	2.25	3.00	1.67	10.75
Tenuiphantes zimmermanni	0.25	3.25	0.42	1.25	1.33		0.25	6.77
Tetragnatha extensa	.	0.25	.	.	.	.	.	.
Tibellus maritimus	.	.	.	.	.	.	.	1.20
Tibellus oblongus	.	.	0.25	.	.	.	.	.
Trachyzelotes pedestris	.	.	.	.	.	.	.	0.25
Trichopterna cito	.	.	.	.	.	.	.	0.58
Trochosa ruricola	4.17	0.25	5.06	.	0.50	11.20	2.12	0.67
Troxochrus scabriculus	1.25	.	.	.	0.50	1.25	.	7.20
Walckenaeria atrotibialis	1.75	2.50	.	.	0.25	.	.	.
Walckenaeria corniculans	.	.	.	.	.	.	.	0.75
Walckenaeria cuspidata	.	0.25	.	.	.	0.50	.	.
Walckenaeria dysderoides	.	0.50	.	.	0.58	.	.	.
Walckenaeria furcillata	.	.	.	.	.	.	.	0.25
Walckenaeria incisa	0.25	.	.	.	.	.	.	.
Walckenaeria obtusa	.	.	.	.	.	.	.	0.25
Walckenaeria unicornis	0.75	.	.	.	.	0.50	0.25	.
Walckenaeria vigilax	0.75	.	.	.	.	.	.	.
Xerolycosa miniata	.	.	1.50	.	.	.	.	0.17
Xysticus cristatus	1.25	2.00	3.21	.	.	0.17	0.75	1.50
Xysticus kochi	.	.	19.81	.	.	0.45	.	0.17
Xysticus ulmi	0.25	.	.	.	.	.	.	.
Zelotes electus	.	.	2.17	.	.	.	.	0.33
Zelotes latreillei	.	.	.	.	1.00	.	.	.
Zelotes longipes	0.25	.	.	.	.	0.25	.	.
Zora spinimana	.	.	.	.	.	0.25	.	0.75
Zygiella atrica	0.33	.	0.39	.	.	.	.	.
Total species richness	72	42	53	32	41	62	28	65

Species assemblages

According to the Detrended Correspondence Analysis and the Cluster Analysis 6 assemblages were differentiated (Fig. 2), which mainly correspond with the selected habitat types. The eigenvalue of 0.73 of the 1st axis indicates sufficient ordination distinctness. Only in the group of sandy beaches one site was originally placed to the gravel beaches. The first axis seem to represent the gradient from the wooded habitat to the open bare sand habitats, as the wooded cliffs were ordered to the right side and the sandy beaches to the left side. Due to the Cluster Analysis, the main gap between the habitat types is found between the beach habitats including the primary dune zone and the remaining habitats of cliffs and lagoons. Percent similarity was only 10 % between these two groups, whereas at least about 20 % was exhibited within these two groups. According to the Canonical Correspondence Analysis 3 environmental parameters, e.g. soil moisture (F =

3.9, $p = 0.005$), tree cover ($F = 3.6$, $p = 0.005$), and soil pH ($F = 1.8$, $p = 0.03$) showed significant influences on the species composition of the assemblages. This indicates that the first axis in the Detrended Correspondence Analysis represents not only a vegetation cover gradient, but also a soil moisture gradient. Content of organic matter and sand content were without significant influence on the variance of the species distribution.

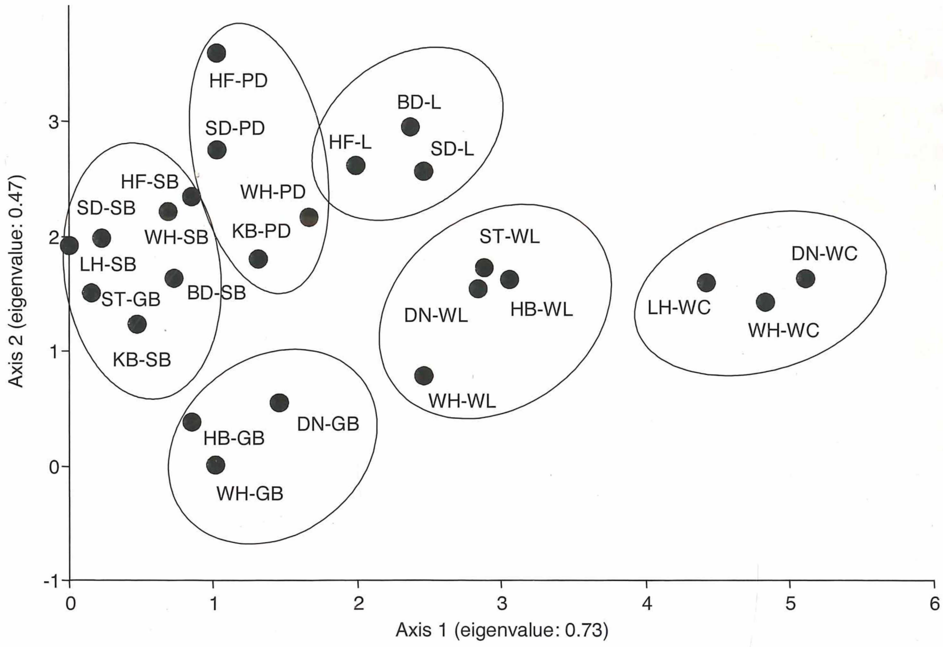

Fig. 2: Result of the Detrended Correspondence Analysis showing the six differentiated habitat types; abbreviations see table 1.

All habitat types are characterised by a specific combination of environmental parameters (Tab. 3). Beside the wood vegetation, the wooded cliffs are characterised by medium high soil moisture and the highest organic content in the soil that is even higher than in the lagoon habitat. The lagoon habitat is differentiated from all other habitats by the extremely high soil moisture. On average, organic matter is nearly as high as in the wooded cliffs, but sand content is similarly high as in the sandy beaches. Compared to the wooded cliff, the woodless cliff exhibited a significantly lower soil moisture and organic content in the soil. The three beach habitats are indicated by the low soil moisture. The dune habitat provided the highest sand content combined with a low content of gravel, which is significantly higher in the sandy beaches.

Table 3: Environmental parameters and dominance of species of the six differentiated assemblages (different underlines indicate different homogenous groups due to the results of ANOVA for environmental parameters and Kruskal-Wallis ANOVA for species, only species with a dominance > 1 in one habitat are included).

Art	Wood cliff	Woodless cliff	Lagoon	Sandy Beach	Prim. Dune	Gravel beach
Soil moisture (%)	18±3.0	8±1.1	31±5.9	1±0.5	1±0.5	1±0.6
Wood	yes	no	no	no	No	No
Sand content (%)	36±6	46±3	51±16	78±29	92±9	23±20
Gravel pit content (%)	5±2	8±2	20±20	19±30	8±8	77±20
Soil pH	7.4±0.1	7.9±0.2	7.5±0.2	7.3±0.2	7.2±0.1	7.9±0.3
Organic content of soil (%)	6.6±2.6	1.1±0.1	5.6±0.9	0.2±0.2	1.4±2.2	0.3±0.1
Tenuiphantes zimmermanni	15.9	2.2	.	0.3	0.5	1.7
Diplocephalus picinus	6.0	.	0.1	.	.	.
Tenuiphantes tenebricola	5.7	0.7	0.1	0.3	0.6	.
Walckenaeria atrotibialis	6.4	.	0.4	.	.	.
Palliduphantes pallidus	5.1	0.9	.	0.1	0.2	.
Linyphia hortensis	3.4	0.2	.	.	.	0.3
Coelotes terrestris	2.3	0.2	.	.	.	.
Ceratinella scabrosa	4.7	.	.	.	.	.
Diplocephalus latifrons	4.5	0.6	.	.	.	.
Microneta viaria	3.9	.	.	.	.	.
Maso sundevalli	3.9	0.3	.	0.1	1.9	.
Hahnia pusilla	2.9	.	.	.	.	.
Pardosa lugubris	1.7	.	0.1	.	.	.
Walckenaeria dysderoides	1.6	0.7	.	.	.	.
Scotophaeus scutulatus	1.1	.	.	.	.	.
Tenuiphantes tenuis	8.8	13.3	1.6	1.6	5.6	1.4
Diplostyla concolor	7.1	25.4	17.3	0.3	0.6	2.6
Phrurolithus festivus	.	16.2	0.1	0.7	2.1	0.3
Diplocephalus cristatus	0.6	6.4	0.1	0.2	.	2.0
Stemonyphantes lineatus	.	4.0	.	0.2	0.5	.
Xysticus cristatus	.	3.7	.	0.9	2.4	.
Pirata piraticus	.	.	19.3	0.7	1.1	.
Pardosa prativaga	.	0.3	12.7	0.4	0.7	.
Bathyphantes approximatus	.	0.4	5.9	.	.	.
Gnathonarium dentatum	.	.	3.2	.	.	.
Pachygnatha clercki	.	0.2	3.1	0.5	1.0	.
Oedothorax retusus	.	.	12.0	0.6	0.7	.
Trochosa ruricola	.	1.1	5.4	1.8	2.6	0.3
Drassylus lutetianus	.	.	1.5	.	0.2	0.2
Savignya frontata	.	.	1.1	0.1	.	.
Bathyphantes gracilis	.	0.6	5.4	2.8	2.6	0.7

Art	Wood cliff	Woodless cliff	Lagoon	Sandy Beach	Prim. Dune	Gravel beach
Pardosa amentata	0.4	0.4	1.3	1.1	.	0.4
Erigone arctica	.	0.3	.	30.0	0.2	3.3
Oedothorax apicatus	.	0.5	0.2	16.8	4.8	5.0
Oedothorax fuscus	.	.	0.1	4.2	0.4	.
Porrhomma microphthalmum	.	.	0.4	2.4	0.6	.
Arctosa cinerea	.	.	.	2.3	1.9	1.1
Philodromus fallax	.	.	.	1.9	0.9	.
Arctosa perita	.	.	.	2.4	9.9	0.6
Erigone atra	0.7	0.9	0.4	5.3	5.7	1.4
Erigone dentipalpis	.	0.3	.	2.0	1.9	0.1
Pelecopsis parallela	.	.	0.1	0.9	3.9	0.3
Pocadicnemis juncea	.	0.3	0.2	0.8	2.2	0.6
Zelotes electus	.	.	.	.	1.8	.
Xysticus kochi	.	.	.	1.5	12.1	.
Troxochrus scabriculus	0.7	0.4	0.7	0.4	4.8	.
Clubiona frisia	.	.	.	0.3	2.3	.
Sitticus distinguendus	.	.	.	0.2	1.4	.
Alopecosa pulverulenta	.	0.7	0.6	0.2	1.3	0.3
Xerolycosa miniata	.	.	.	0.1	1.1	.
Pardosa agricola	.	8.8	0.1	10.7	9.5	66.7
Araeoncus crassiceps	.	2.1	.	0.2	.	7.4

Most of the six differentiated habitat types show also significantly different dominances of individual spider species. Exceptions are the woodless cliffs and the sandy beaches. In the wooded cliffs, *T. zimmermanni, D. picinus,* and *T. tenebricola* exhibited significantly higher dominances than in the remaining habitats. A set of further 12 species can be regarded to characterise the wooded cliffs. Both *T. tenuis* and *D. concolor* occurred in similarly high abundances in the wooded and woodless cliffs and in these two habitats and additionally at the lagoons, respectively. *P. festivus* showed highest dominance in the woodless cliffs, but variance was too high to reflect significant results compared to the other habitats. Five species were found at significantly higher numbers in lagoons than in all other habitats. These are: *P. piraticus, P. prativaga, B. approximates, G. dentatum,* and *Pachygnatha clerki. E. arctica, O. apicatus,* and *O. fuscus* were the characteristic species of sandy beaches including the two beaches with larger amounts of gravel. In particular, *E. arctica* accounts for 30 % of all spiders in that habitat. Further 3 species are mainly found here and in the adjacent primary dune zone. These two adjacent zones are connected by the occurrence of *A. perita* that exclusively inhabited the sandy habitats of the beach and the primary dunes. Whereas the dune habitat was indicated by a significant high dominance of *P. parallela,* the gravel pit beaches were mainly inhabited by *P. agricola* that account for more than 60 % of all spiders in that habitat.

Species richness

The analysis of species richness using number of species per trap and rarefaction species richness had the following results (Tab. 4). Gravel-beaches exhibit the lowest species richness according to both indicators. This low status of species richness is also significant according to ANOVA and LSD post hoc test. Primary dunes are the most species-rich habitat that is also supported by the significance in species richness trap^{-1} and rarefaction species richness. The remaining habitats are placed between these two habitats in different order for either species richness trap^{-1} or rarefaction species richness. Wooded cliffs show a high rarefaction species richness, but low species richness per trap. The highest number of endangered species is also found in primary dunes. Overall, beach habitats show higher numbers of endangered species than cliffs or lagoons.

Table 4: Species richness indicators of the 6 habitat types; rarefaction species richness refers to 50 specimens; different exponents indicate significant differences due to ANOVA and Fisher LSD-test; RL species: species richness of endangered species according to the Red List of Schleswig-Holstein.

	Species richness trap^{-1}			Rarefaction species (50)			RL species
	Mean	SD	Conf. (95 %)	Mean	SD	Conf. (95 %)	
Lagoons	^{c}16.3	3.1	2.0	^{ba}13.6	1.1	2.7	4
Wooded cliff	^{ab}9.2	2.9	1.8	^{cb}18.2	1.0	2.5	2
Woodless cliff	^{a}7.6	2.4	1.3	^{b}14.3	2.5	4.0	1
Gravel-beach	^{a}6.4	2.4	1.6	^{a}8.9	1.9	4.6	4
Primary dune	^{c}16.4	3.3	2.1	^{c}19.6	1.2	2.9	14
Sandy beach	^{b}11.1	4.5	1.6	^{b}13.8	4.1	3.4	11

Gradient analysis in the beach-dune habitat complex

One aim of the study was to find differences in the gradient between sand and gravel-beaches (Fig. 3). Five species with high abundance were selected that seem to prefer different parts of this habitat complex. *Pardosa agricola,* occurred in a variety of coastal habitats with significant dominance in the gravel pit assemblage (Table 3). This preference is supported by the gradient analysis. The species prefers the gravel pit habitat in significant higher abundances than the other two beach habitat conditions ($H = 12.5$, $p = 0.002$, $n = 40$). Abundance successively decreases, if gravel content decreases. On sandy beaches the abundance was at least 4 to 5 times lower than on gravel-beaches. This was also true if the sandy primary dunes are compared with the sandy beaches. Abundance on the primary dunes was as low as on the sandy beaches ($F = 2.2$, $p = 1.4$, $n = 36$). *Erigone arctica* occurred in all beach habitats in high abundance with highest dominance in the sandy beach assemblage (Table 3). According to the gradient analysis, abundance was highest in beaches with medium gravel content, but without statistical significance ($H = 5.4$, $p = 0.1$, $n = 40$). However, the comparison between sandy beaches and dunes shows that *E. arctica* prefers the beach habitat and avoids the higher elevated zone of primary dunes ($F = 7.0$, $p = 0.01$, $n = 36$). In contrast to *E. arctica,* the higher abundance of *Arctosa cinerea* in the beaches with medium gravel content was significant compared to sandy beaches and gravel-beaches ($H = 6.9$ $p = 0.03$, $n = 40$). The negative effect of sandy soils is supported by the low abundance in primary dunes, where sandy soils dominated. It exhibited low abundances with no significant differences between the two sandy habitats ($F = 0.14$, $p = 0.71$, $n = 36$).

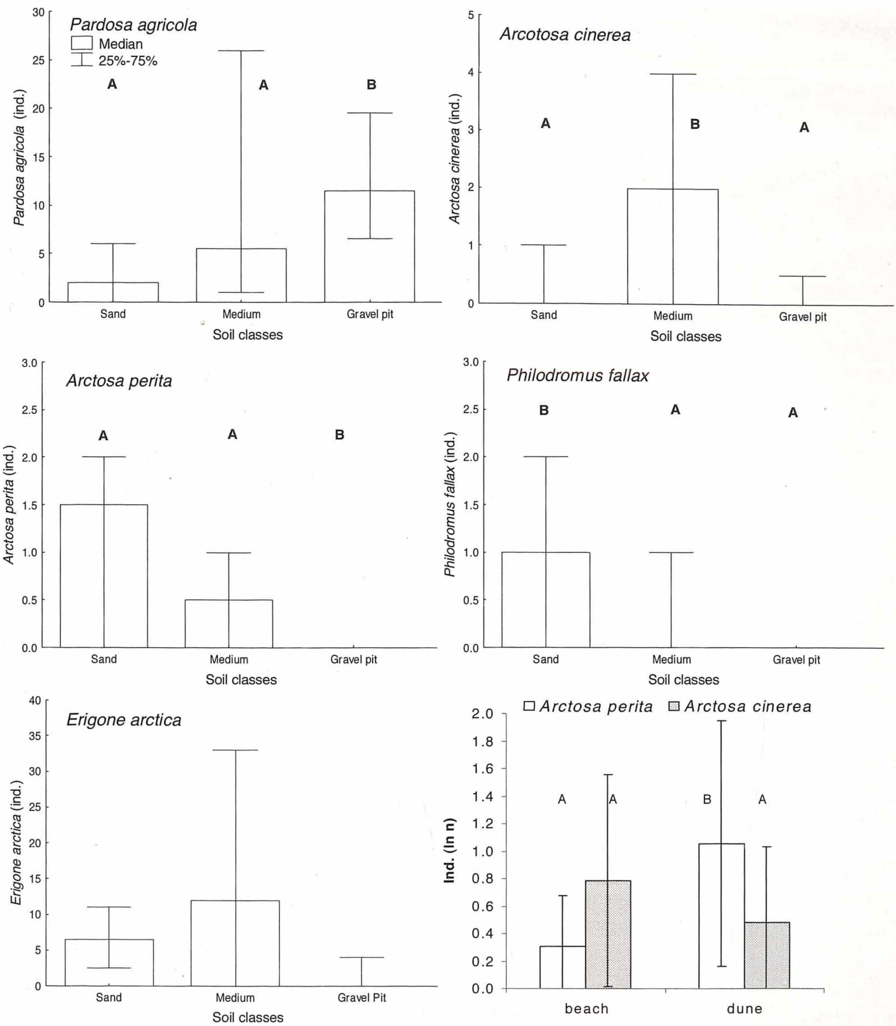

Fig. 3: Abundance of five species in the sand-gravel pit gradient of beaches and differences in the abundance between sandy beach and primary dune in *A. perita* and *A. cinerea*; different characters indicate significant differences between the compared fractions.

Regarding the five selected species, i.e. *A. perita* and *Philodromus fallax*, preferred the sandy beaches. Both species were absent only in gravel-beaches (*A. perita*: H = 15.7, p = 0.0004; *P. fallax*: H = 11.2, p = 0.004, n = 40). Whereas abundances of *A. perita* showed no differences between sandy beaches and intermediate beaches, abundance of *P. fallax* was represented with significantly higher abundance in sandy beaches than in intermediate beaches. No difference was found between sandy beaches and primary dunes in *P. fallax* (F = 0.5, p = 0.48, n = 36), but *A. perita* was significantly higher abundant in primary dunes than in sandy beaches (F = 4.3, p = 0.02, n = 36).

It was also tried to find impacts of soil conditions to the typical six species of the woodless cliffs (Table 3). For this analysis the occurrence of species at different relationships between sand and finer silt and clay material was analysed. However, no influence was found. Another analysis was made using moisture conditions at woodless cliffs, but only *Phrurolithus festivus* provided significant results (Fig. 4). This species was nearly absent under moist conditions, but more or less equally abundant under dry and intermediate conditions ($H = 12.1$, $p = 0.002$, $n = 16$).

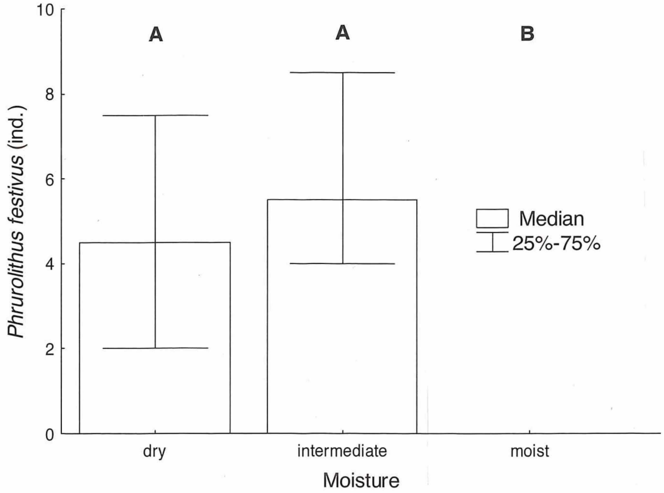

Fig. 4: Abundance of *Phrurolithus festivus* in the moisture gradient of woodless cliffs; different characters indicate significant differences between the compared fractions.

Discussion

In contrast to the North Sea coasts, very few information is available on the ecology of the spider fauna of the Baltic Sea coasts. BOCHMANN (1941) was the first, who studied different dunes at the North and Baltic Sea coast. He already mentioned the different habitats of *A. cinerea* and *A. perita*, as well as the restriction of *P. fallax* to beaches. His observations to the dune preference of *A. perita* and the beach preference of *A. cineraea* are supported by the present study. In his studies of coasts and banks, KNÜLLE (1952, 1953) included a higher number of habitats and gave a rough characterisation of their spider fauna. Concerning the Baltic Sea coasts, he described the restriction of *P. agricola* to the beach zone. Later, SCHAEFER (1970) investigated the terrestrial fauna of coastal dunes and salt marshes. He stressed the fact that out of the 97 spider species most species only used one habitat type. The similarity was lowest between salt marshes and dunes or dry grassland and only slightly higher between dunes and dry grasslands. According to his investigations salt marshes are characterised by the high dominance of *Pardosa purbeckensis*, *Pirata piraticus*, and *Oedothorax fuscus*. In dunes, the widely distributed species *Oedothorax retusus*, *Bathyphantes gracilis*, and *Centromerita bicolor* were the most frequent species. His results on salt marshes were supported by later investigations of REINKE et al. (2000), who found *Pardosa purbeckensis*, *Oedothorax retusus* and *Erigone atra* as most frequent species. In his investigations at different locations from the southeast to the north of Schleswig-Holstein, HOERSCHELMANN (1990) found a varying composition of assemblages in similar habitats. Comparing these studies, the different niches of the *Pardosa* species were conspicuous with *P. purbeckensis* in salt marshes, *P. agricola* on beaches, *P. pullata* at lagoons, *P. monticola* in dry grassland, and *P. nirgiceps* in coastal heath.

Our results of other coastal habitats supported the fact that great differences in the composition of spider assemblages can be found even in short distant habitats. Overall, soil moisture was the main environmental factor for the separation of spider assemblages. The high importance of moisture for the occurrence of spiders in coastal habitats was also found in investigations on a dune island in the North Sea (SCHULTZ & PLAISIER 1995). HOERSCHELMANN (1990), too, found moisture as one of the most important parameters at the Baltic Sea coast, which was distinctly more important than salinity. He also stressed the importance of the changing climate in the west-east gradient.

In our investigation, sandy beaches and primary dunes that seem to have very similar environmental conditions can be clearly divided by the composition of their spider assemblages. Our study on environmental parameters exhibited significant differences in the gravel-content and soil pH, which may be the reason for the different occurrence of species. Subsequent changes from low elevated sites to higher elevated sites were observed in salt marshes of the Baltic Sea coast (REINKE et al. 2000), although the gradient is more distinctly developed at the North Sea coast (IRMLER et al. 2002, FINCH et al. 2007). The different frequencies of flooding events were discussed to be responsible for the changes in the salt marsh gradient. The decreasing flooding events on sandy areas of the coast are also the reason for the changes in the soil composition, e.g. gravel is more frequent in low elevated sites than in higher elevated sites, because the heavy gravel material is deposited near the sea line. Input of calcareous material decreased from low elevated sites to higher elevated sites, which is obvious by the decreasing pH from sandy beach to primary dunes. Thus, several environmental gradients may be responsible for the differences of the species composition between sandy beaches and primary dunes.

The impact of floods also determines the sand - gravel gradient on beaches. Beaches with 100 % gravel content are located at sites that are extremely exposed to the sea. The clear differences in the assemblage composition and the changing abundance of individual species in the sand - gravel gradient face the importance of the soil conditions even on similarly high elevations to the sea. Our investigations show that gravel sites are very poor in spider species. Nevertheless, a few species seem to prefer such extreme sites, e.g. *Pardosa agricola*. The extremely endangered *Malthonica campestris* was found only on one gravel site, but was too rare to analyse its ecological preferences. The also endangered *Arctosa cinerea* seems to prefer intermediate conditions concerning the gravel content.

According to the composition of the spider assemblages the investigated lagoons seem to contain no species of salty habitats. Typical species of salt marshes, e.g. *Pardosa purbeckensis*, have not been found (IRMLER et al. 2002, REINKE et al. 2000). These findings are in accordance with the results of HOERSCHELMANN (1990), who also found no species of salty habitats at lagoons, although one of them had contact to the Baltic Sea. In contrast to the results of HOERSCHELMANN (1990), who found *Pirata piraticus* and *Pardosa pullata* to be most common at lagoons, the most abundant species in our study were *P. piraticus* and *Pardosa prativaga*. The high dominance of *Oedothorax retusus* and the occurrence of *Pocadicnemis juncea*, only, refer to moist coast-near habitats. The absence of spider species of the similarly moist salt marshes may be referred to the specific situation of the lagoons, which were located behind the dune zone without connection to the sea. It can be supposed that the influence of salt water is very low and may be the reason for the loss of typical salt marsh species.

Specific environmental conditions are provided by the woodless cliffs. However, it seems that only very few spider species are adapted to such conditions. Abundant species, e.g. *Tenuiphantes tenuis* and *Diplostyla concolor* are found in a great variety of habitats. Only *Phrurolithus festivus* may be favoured by specific conditions of woodless cliffs, but its ecological demands are unknown. In former investigations in Schleswig-Holstein, the species was found in a variety of habitats with highest number of records from bogs (REINKE & IRMLER 1994). Our present findings at the Baltic Sea coast are supported by the investigation of SCHULTZ (1995) on the island of Norderney. SCHULTZ (1995) described the ecological demands of the species as follows: soil surface of fresh to dry, open habitats with high inclination. Thus, *Phrurolithus festivus* seem to be a pioneer species of early succession sites with low vegetation cover as they are represented by the woodless cliffs.

It was expected that the wooded cliffs are characterized by species that are rarely found in the woods of the mainland, because the high soil pH with values higher than 7 is significantly different from normally acid woods in greater distance from the coast. Indeed, the wooded cliffs are mainly characterised by the high dominance of *Tenuiphantes zimmermanni*, which was found in a mean dominance of nearly 16 %, there, but in acid woods of the mainland in dominances lower than 2 % (IRMLER & HEYDEMANN 1988). The high dominance of *Diplocephalus picinus* can be also referred to the high soil pH. In the comparison of woods in Schleswig-Holstein, the species was found in high abundance only in beech woods with high soil pH, whereas it was nearly absent in acid woods. The high influence of the soil on the spider assemblages was already stressed by IRMLER & HEYDEMANN (1988), who also found that the soil pH influences the abundance of soil spiders.

Finally the value of spider species and assemblages for the evaluation of coastal habitats under conservational aspects should be discussed. FINCH & SCHULTZ (1997) introduced a classification system to define typical species for individual coastal habitats. According to their data dunes had the highest numbers of typical or very typical species. Our investigations support this evaluation. Primary dunes had the highest species richness per trap and also the highest rarefaction species richness, which means that diversity must be higher than in all other investigated habitats. This high importance of primary dunes is highlighted by the highest number of endangered species. Sandy beaches seem to have also a high importance in this respect, because high species richness per trap, high rarefaction species richness, and a high number of endangered species were found in this habitat. According to spider species, the high status of primary dunes in the Red List of German habitats seems to be justifiable (RIECKEN et al. 2006). The high classification of lagoons in the Red List of German habitats can not be supported by the spider fauna. In spite of the high species richness per trap, rarefaction species richness reached only an intermediate status and number of endangered species was also low. Moreover, no specific species have been found, which may be restricted to coastal lagoons. A more detailed attention should be focused on gravel-beaches, although species richness and the number of endangered species are low. However, several species seem to be typical for this habitat, in particular, the rarely found *Malthonia campestris*. *Pardosa agricola*, too, has its main habitat on such gravel-beaches. The importance of gravel-beaches in Germany is emphasised by the restriction to the Baltic Sea coast, whereas sandy beaches are also found at the North Sea coast.

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