

Soil microarthropods (Acari, Collembola) from beach and dune: characteristics and ecosystem context

Koehler, Hartmut, Munderloh, Elke & Hofmann, Sybilla

Institute of Ecology and Evolutionary Zoology, FB2, University of Bremen, POB 330440, D 28334 Bremen, Germany; Tel. +49 421 218 4179; Fax +49 421 218 4864; E-mail: GEFKEN@ZEN.UNI.BREMEN.DE

Abstract. Soil microarthropods (Acari, Collembola) were analyzed along transects from shore to brown dune in two sandy coastal sites of the North Sea (Jutland, Denmark, and Spiekeroog, East Frisian island, Germany). Predatory mites (Acari: Gamasina) and Collembola were determined to species. The Jutland and the Spiekeroog sites each yielded 22 Gamasina species, 10 of which are common to both areas. Collembola were identified from the Spiekeroog samples only (also 22 species).

Largest mite abundances were found in Jutland in primary dunes (419 tsd. ind./m²) and on Spiekeroog in old brown dunes (314 tsd. ind./m²). Compared to the mites, Collembola abundances are low, with maxima of 77 tsd. ind./m² in Jutland (yellow dune) and only 18 tsd. ind./m² on Spiekeroog (old yellow dune).

The communities of predatory mites (Gamasina) and Collembola along transects from shore inland to brown dune are quite specific. High similarities are found for the predatory mites between the specific dune sites of the two North Sea areas, particularly for yellow dune.

Additionally, preliminary data are presented for the southern Baltic Coast. The findings are discussed in a broader context. Arguments focus on conservation and biogenic dune stabilization.

Keywords: Biogenic sand stabilization; Conservation; Gamasina, Collembola.

Nomenclature: Gamasina after Karg (1971), Collembola after Gisin (1970).

Introduction

Coastal dunes have a very characteristic vegetation, depending on their distance from the sea and on their age (Ellenberg 1986). Especially the very young fore-dunes and yellow dunes are highly dynamic areas. From shore to old brown dune, the sandy character of the soil remains pretty much the same. However, pedological, biotic and abiotic factors change along this transect from sand with almost no structure and neutral or slightly alkaline pH, to podsollic acid brown earth. This well definable sequence is of great interest for ecologists in

order to study the distribution of plants and animals (e.g. van Heerdt & Mörzer-Bruyns 1960; Heyken 1965; Isermann & Cordes 1992; Jungerius 1990; Rose 1988; Willis 1989). However, information on the distribution of soil meso- and microfauna along this gradient is limited (Bigot 1961; Bussau 1990; Luxton 1990; Petersen 1965; Poinot 1966; Willmann 1953).

In a recent paper (Koehler et al. in press), the distribution of predatory mites (Acari: Gamasina) to sites from tidal line to brown dune in Jutland (Denmark) was compared to findings from similar sites on Spiekeroog (East Frisian Island). Distinct communities could be identified along the transects. Particularly for yellow dunes, the communities of Jutland and Spiekeroog are very similar. There is weak evidence for the correlation of occurrences of Gamasina species with growth forms of plants (Koehler et al. 1992).

The current paper gives a synopsis of the findings for Gamasina and presents new data on springtails (Insecta: Collembola) from the Spiekeroog transect. It focusses on the description of the distribution of these soil microarthropods in dune sites of Spiekeroog, and on a comparison of Gamasina communities from Spiekeroog, Jutland and the southern coast of the Baltic Sea. In an integrated view of the dunes as an ecosystem, biogenic sand stabilization is addressed, as well as problems of conservation and of risk assessment of climatic change on dune stability.

Sites, Material and Methods

Spiekeroog (Table 1)

Spiekeroog is an island within the Wadden Sea, off the coast of Lower Saxony (Germany). Six dune sites, primary dune, young and old yellow dune, grey dune, young and old brown dune were sampled in September 1990. To compare the findings with those from Jutland, data from young and old yellow and brown dune, respectively, are combined. A short portrait of the island is given by Gerlach (1990). 1-m² plots with typical vegeta-

Table 1. Site characteristics.

	Spiekeroog			Jutland			Baltic	
							west	east
Climate								
Average yr. precipitation (mm)	670			670			500	650
Average yr. temperature (°C)	8.5			8.5			8	7
Dunes	white	grey	brown	white	grey	brown		
Age (1)	30	50	90-240					
Bulk density (2)	138	109	83	142	136	115		
Water content (3)				6.4	7.2	16.5		
Pore volume (4)	48.1	58.7	48.8	45.1	48.8	56.8		
Organic C (5)				0.03	1	2.9		
pH (6)	7.3	5.9	3.3	6.3	3.6	3.3		

(1) years after Sindowsky (1973).

(2) dry wt. soil in g/100 cm³, average for 0-12 cm depth.

(3) %, at day of sampling.

(4) %, calculated from dry weight by the formula of Hartge (1978).

(5) %, organic carbon was determined by incineration.

(6) in CaCl₂.

tion from north-facing slopes of the dunes were selected (Munderloh & Hofmann 1992): primary dune: *Agropyron junceum*; yellow dune: *Ammophila arenaria*, *Sonchus arvensis*, *Festuca rubra* s.l.; grey dune: *Empetrum nigrum*, *Festuca rubra* s.l., *Lotus corniculatus*, *Galium mollugo*; brown dune: *Empetrum nigrum*, *Polypodium vulgare*.

Jutland (Table 1)

The research area is situated on the dunes of the westcoast of southern Denmark (Jutland), near Houstrup, north of Esbjerg. Six sites were selected in September 1988, from tidal line to brown dune. Dune sites faced west to north-west. Samples from yellow, grey and brown dune were taken from 1-m² sample plots with typical vegetation: tidal line: almost no debris; beach: unvegetated; primary dune: *Agropyron junceum*; yellow dune: *Ammophila arenaria*, *Elymus arenarius*, *Sonchus arvensis*; grey dune: *Ammophila arenaria*, *Cladonia* spp., *Hieracium umbellatum*, *Corynephorus canescens*; brown dune: *Empetrum nigrum*, *Calluna vulgaris*, *Polypodium vulgare*, *Salix repens*.

Baltic Coast

Qualitative sampling was performed along the southern Baltic Coast, in July 1992: Boiensdorfer Werder (Salzhaff, Germany; *Zostera debris*), dunes of Wolinski and Slowinski National Park (Poland) and August 1993: along the coast of Latvia (Melecis & Koehler msr.).

Soil samples

Soil samples were taken with a soil corer from 0-4, 4-8, 8-12 cm (surface 25 cm², volume 100 cm³).

Jutland: three soil cores each were taken from tidal line and beach and eight from each dune site (September 1988).

Spiekeroog: 10 soil cores were taken randomly from 1-m² plots from each site (September 1990).

Baltic Coast: no soil corer was used. From each site, a minimum of 300 cm³ soil was filled in plastic bags for transportation to the field-lab.

Extraction and determination of soil microarthropods

Dynamic extraction was used (Macfadyen-canister-type apparatus; Jutland: 5 days; Spiekeroog, Latvian coast: 10 days). Temperatures were raised every 12 (24) hr to reach 60 °C on upper soil surface. Some samples from the Baltic Coast were extracted with a portable apparatus within 48 hr.

When large amounts of sand were encountered in the collecting canister, mesofauna was recovered by repeated swivelling of the fluid followed by decantation until no animals were found any more. Subsamples of sand were finally checked for remaining fauna.

Soil microarthropods were counted with a binocular to group level. Gamasina species were determined microscopically mainly after Karg (1971). Collembola mainly after Gisin (1970).

Table 2. Soil microarthropods from the soil of coastal and dune sites (Jutland *Jut*, Spiekeroog *Spiek*) and other grasslands.

	Collembola		Acari		Gamasina	
	Jutland	Spiekeroog	Jutland	Spiekeroog	Jutland	Spiekeroog
Tidal line	6		4		2	
Beach	22		40		2	
Primary dune	47	4	419	1	5	0.3
White dune	77	3/18 ¹	318	106/96 ²	4	2/2 ³
Grey dune	33	16	189	132	5	12
Brown dune	9	6/15 ³	33	250/314 ³	1	2/4 ³
	Collembola		Acari		Gamasina	
REC80 ^{1,2}	190		250		20	
Pasture ^{1,2}	15		40		3	
Meadow ^{1,2}	40		150		4	
Ley ^{1,2}	80		190		10	

individuals in thousands/m², rounded measures

REC80: successional regularly mown grassland site.

¹ = Spiekeroog; abundances of young/old sites.

^{2,3} = Sites in the vicinity of Bremen, northern Germany.

Results

Microarthropods

The colonization of the sand of the two North Sea sites by soil microarthropods is considerable and compares well to that of other soils (Table 2). Trends of abundances varied, however: in Jutland, largest numbers of microarthropods were extracted from the sand of primary dunes and on Spiekeroog from old brown dunes.

In primary and yellow dunes, the majority of soil microarthropods tends to colonize depths below 4 cm, whereas in grey and brown dunes the upper layer (0-4 cm) is preferred.

Collembola were more abundant in Jutland than on Spiekeroog; on both sites, however, much inferior to the mites, which occurred in comparable quantities. Symphypleona are found in both areas, but only in grey and brown dune sites.

Considerable numbers of Protura were extracted from yellow and grey dune soil (5 - 6 tsd. inds./m²).

Gamasina were abundant in primary, yellow and grey dunes of Jutland. On Spiekeroog, highest abundances of these predators were found in the soil of grey dunes.

Collembola (Spiekeroog)

The Collembola from the Spiekeroog sites belong to 22 species. Eight dominant species (relative abundance > 10%) have a share of almost 85% of all individuals (Fig. 1, Table 3). The highest species number (13 species) was encountered in grey dunes. The small euedaphic species *Mesaphorura macrochaeta* dominated the

Collembola community with the exception of grey dunes. The occurrence of other species is more restricted to a specific dune type.

The Collembola community of primary and yellow dune sites is characterized by *Xenylla maritima*, *Anurida maritima* and *Willemia scandinavica*. Also, some individuals of *Isotoma thermophila* were found in primary dunes only. This species is known from the literature from beach and yellow dune (Franz 1975; Petersen 1965; Strenzke 1955). Being a xerophilous species (Fjellberg 1980; Gisin 1943; Joosse & Verhoeff 1987; Schaller 1951), *Xenylla maritima* was dominant also in grey dunes. It is reported from dune sands by several authors (Agrell 1934; Krogerus 1932; Mallow et al. 1984; Petersen 1965).

The Collembola community of grey and brown dunes is dominated by *Entomobrya nivalis*, *Isotoma notabilis*, two Symphypleona species (*Sminthurides pumilis*, *Neelus minimus*) and *Anurida pygmaea*. *Entomobrya nivalis*, a species occurring in dry habitats (Fjellberg 1980), is characteristic particularly of grey and young brown dunes. Symphypleona and *Anurida pygmaea* are known from soils rich in organic material as well as from grey and brown dunes (Doppelreiter 1979; Hagvar 1982; Petersen 1965; Pozo 1986; Tamm 1986).

Gamasina (Spiekeroog, Jutland, Baltic Coast)

From the samples collected, a total of 43 species was identified (Table 3). The Gamasina communities of Spiekeroog and Jutland comprise 22 species each, 10 of which are common to both sites.

The highest diversity with 16 species was encountered in the grey dune of Spiekeroog, followed by yel-

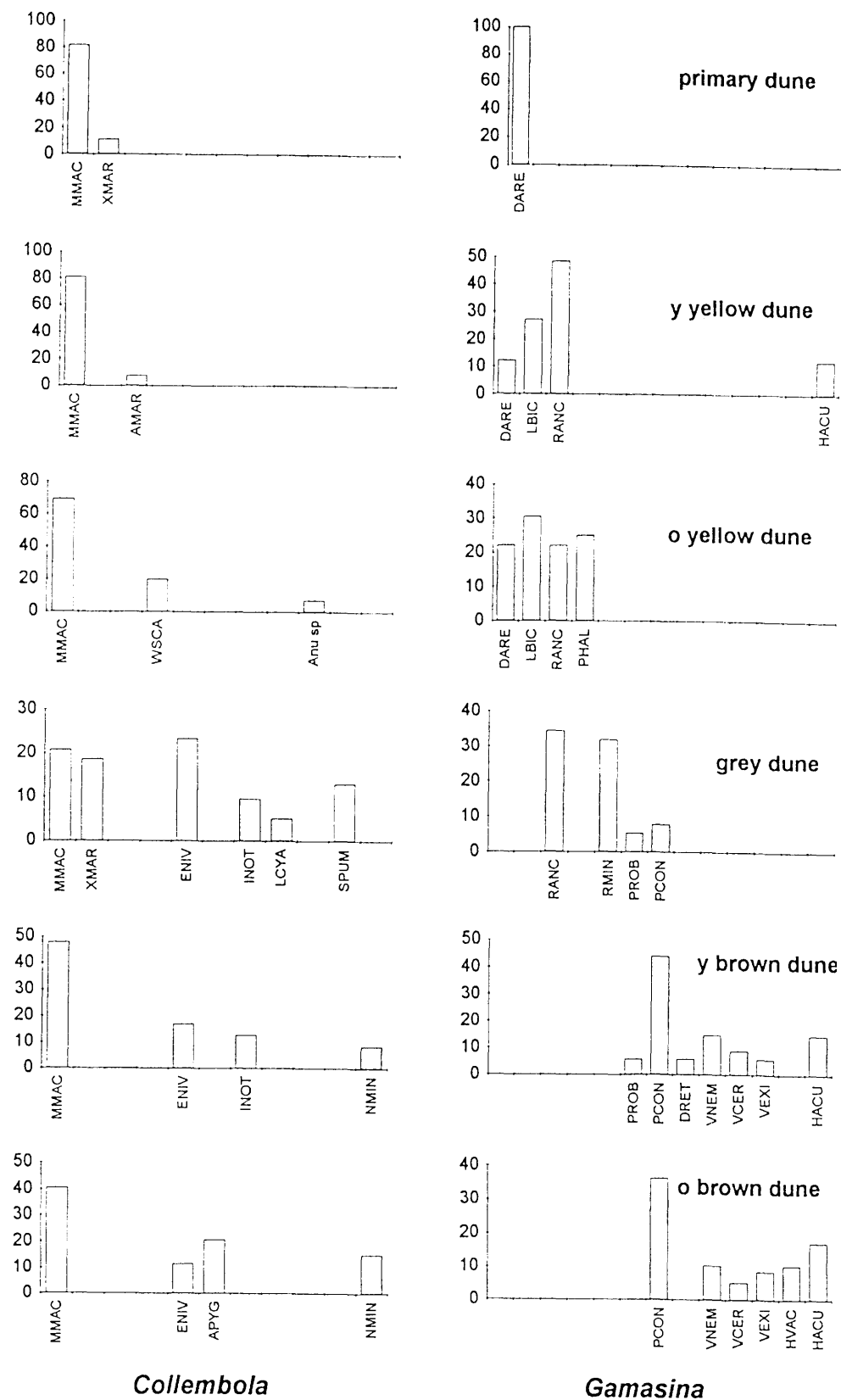


Fig. 1. Relative abundances (percentage, 0-12 cm depth; only species with more than 5% abundance are included) of Collembola and Gamasina species from six dune sites along a transect from primary to brown dune, Spiekeroog. For species code see Tables 3 and 4.

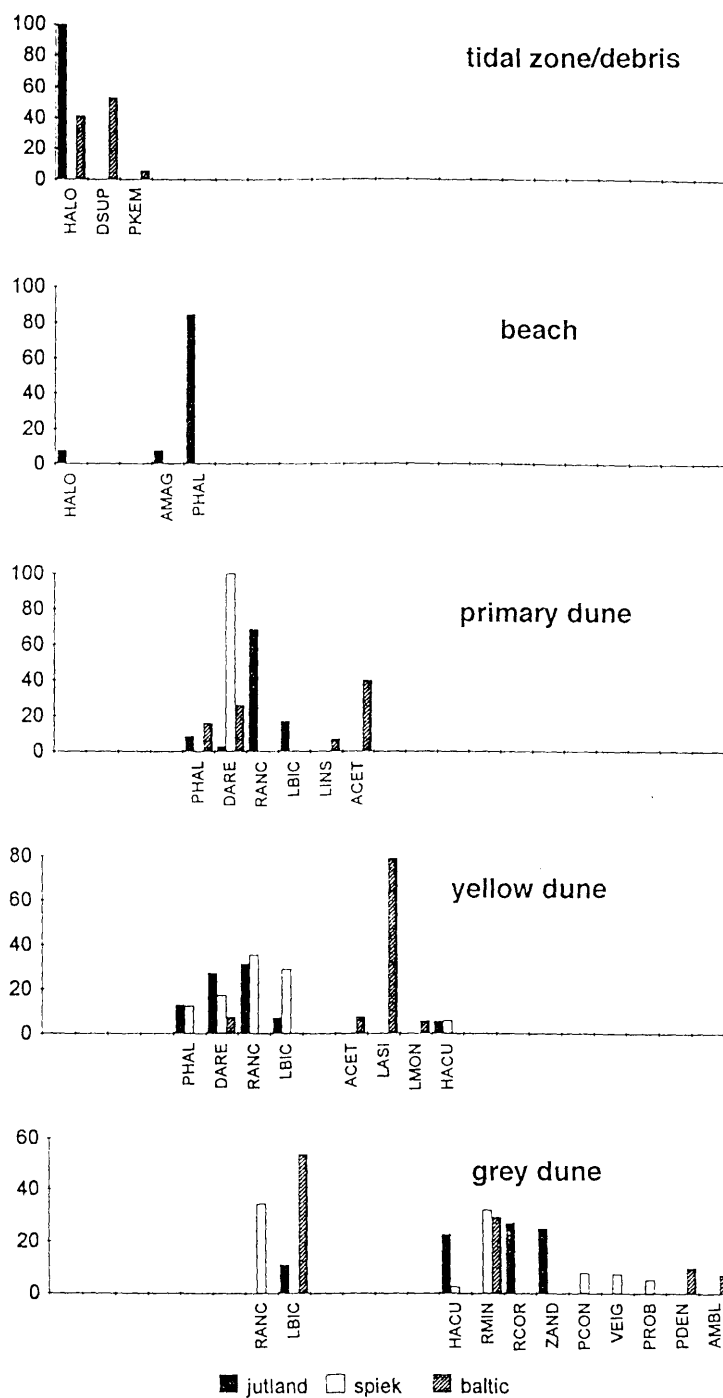


Fig. 2. Distribution of Gamasina to coastal habitats: jutland = Jutland (Denmark), spiek = Spiekeroog (Germany), baltic = southern Baltic Coast. Relative abundances in percentage, only species with more than 5% abundance are included; for species code see Table 4.

low dune in Jutland and brown dune on Spiekeroog with 12 species each. From the Baltic Coast, 13 species have been identified up till now; many more are expected, since the material examined is still relatively small.

The delimitation of the Gamasina taxocenoses along the Spiekeroog transect is still clearer than that of the Collembola (Fig. 1). There is an increase in diversity from primary to old yellow dune with typical species.

Grey dune is inhabited by a transition community, having species in common both with the more coastal habitats and with brown dune. Brown dune is inhabited by a taxocenosis dominated by surface dwelling *Veigaia* species. As may be expected, high similarities are found between young and old sites of the same dune type.

The taxocenoses in Jutland are well defined as well,

Table 3. Collembola from Spiekeroog (ind. in tsd./m², 0-12 cm depth).

Species	Code	Primary	y-white	o-white	Grey	y-brown	o-brown
<i>Anurida maritima</i> (Guerin-Menneville 1836)	AMAR		0.20				
<i>Anurophorus</i> spec.	Anu sp	0.04	0.12	1.20	0.32		
<i>Anurida pygmaea</i> (Börner 1901)	APYG			0.08	0.16		3.04
<i>Entomobrya nivalis</i> (Linné 1758)	ENIV		0.04	0.04	3.60	0.96	1.68
<i>Isotoma notabilis</i> Schäffer 1896	INOT				1.48	0.72	
<i>Lepidocyrtus cyaneus</i> Tullberg 1871	L.CYA				0.80		
<i>Mesaphorura macrochaeta</i> (Rusek 1976)	MMAC	2.64	2.20	11.80	3.20	2.72	5.92
<i>Neelus minimus</i> Willem 1900	NMIN					0.48	2.20
<i>Sminthurides pumilis</i> (Krausbauer 1898)	SPUM				2.00		0.12
<i>Willemia scandinavica</i> Stach 1949	WSCA		0.12	3.40			
<i>Xenylla maritima</i> Tullberg 1869	XMAR	0.36			2.88	0.04	
<i>Dicyrtoma fusca</i> (Lucas 1842)						0.20	
<i>Folsomia quadrioculata</i> Tullberg 1871					0.56	0.12	
<i>Friesea</i> species			0.04				
<i>Isotoma thermophila</i> (Axelson 1900)		0.08					
<i>Isotoma viridis</i> Bourlet 1839					0.04		
<i>Neanura muscorum</i> (Templeton 1835)					0.16	0.20	0.48
<i>Orchesella cincta</i> (Linné 1758)						0.16	0.44
<i>Proisotoma subminuta</i> Denis 1931		0.12		0.44			
<i>Sminthurus viridis</i> (Linné 1758)					0.04	0.08	0.08
<i>Tullbergia affinis</i> Börner 1902				0.04			
<i>Willemia anophthalma</i> Börner 1901					0.20		0.68
undetermined		0.28	0.08	1.12	0.16	0.76	0.68
Total individuals		3.52	2.80	18.12	15.60	6.44	15.32

Code only for species with relative abundance > 5 %.

which is documented by rather low indices of similarity between consecutive sites along the transect (Koehler et al. in press).

The distribution of Gamasina species in specific coastal sites from three geographic areas (Spiekeroog, Jutland, southern Baltic Coast) is shown in Fig. 2, leaving out grey and brown dunes, which have their own peculiarities. The major occurrence of *Halolaelaps* species is restricted to tidal zone and beach as that of *Dissololncha superbus* to debris. Also, *Parasitus halophilus* is dominant only in sites close to the sea, but not in frequently submerged sand. Species from the euedaphic family Rhodacaridae, particularly *Rhodacarus ancorae*, dominate the Gamasina fauna in primary, yellow and on Spiekeroog also in grey dunes. *Leiioseius bicolor*, a drought resistant species (Karg 1971), is important in yellow and grey dune soils. According to the information given by Karg (1971), most species were found in their typical habitats, particularly those living close to the sea.

Discussion

There are some short comings to the data presented. The investigations are short-term studies with a limited sample size. Characterization of dunes as primary, yellow,

low, etc. dunes may be an insufficient habitat description to achieve similar settings for a comparison of different geographic areas. Soil development, exposition of sites and vegetation must be observed in detail and should not differ between two sites to be compared, as it is for the exposition of the respective dunes with slopes facing west in Jutland and north on Spiekeroog.

On the other hand, our data allow the deduction of hypotheses on the distribution of soil microarthropods to the dunes for mainly two reasons:

1. The samples yielded a plentiful and diverse microarthropod community from the dune sand.
2. For comparison of sites being geographically far apart, beach and dune offer a maximum of comparability because of relatively high geomorphogenetic, pedologic, mesoclimatic and floristic similarity.

The communities from the sites along the transects are specific, both for Collembola and Gamasina. There are more species of Collembola with less restricted ecological requirements than of Gamasina. This fact is reflected in the similarities of the communities along the transects from sea to brown dunes, which are high for Collembola and low for Gamasina.

The highest species numbers were found both for Collembola and Gamasina in grey dunes, which may be explained by its intermediate location between early successional, dynamic yellow dune and older, stabilized

Table 4. Gamasina from Spiekeroog (S), Jutland (J) and the Baltic Coast (B).

Species	Code	Tidal/beach	Primary	Yellow	Grey	Brown
<i>Arctoseius cetratus</i> (Sellnick 1940)	ACET			B, (J)		
<i>Antennoseius magniscutum</i> (Weis-Fogh 1947)	AMAG	J			J	
<i>Amblyseius similifloridanus</i> (Hirschmann 1962)	AMBL				J	
<i>A. aurescens</i> Athias-Henriot 1961	AMBL			J		
<i>A. formanensis</i> Karg 1970	AMBL					
<i>A. obtusus</i> (C.L.Koch 1839)	AMBL				S	
<i>A. okanagensis</i> (Chant 1957)	AMBL				B	
<i>A. umbraticus</i> (Chant 1956)	AMBL	B				
<i>Dendrolaelaps arenarius</i> Karg 1971	DARE		J, S	J, S		
<i>Dissolonychus superbus</i> (Hull 1918)	DSUP	B				
<i>Hypoaspis aculeifer</i> (Can. 1938)	HACU			J, S	J, S	S
<i>Halolaelaps</i> spec.	HALO	J, B	B			
<i>Lasioseius</i> nov. spec.	LASI			B		
<i>Leioseius bicolor</i> (Berlese 1918)	LBIC		J	J, S	J, S, B	
<i>L. insignis</i> Hirschmann 1963	LINS		B			
<i>L. montandus</i> Hirschmann 1963	LMON			B		
<i>Pergamasus comus</i> Karg 1971	PCON			J	J, S, B	J, S
<i>Pseudoparasitus dentatus</i> (Halbert 1930)	PDEN				J	
<i>Parasitus halophilus</i> (Sellnick 1957)	PHAL	J	J	J, S		
<i>P. kemperi</i> Oudemans 1902	PKEM	B				
<i>Pergamasus robustus</i> (Oudemans 1902)	PROB				S	S
<i>Rhodacarus ancorae</i> Karg 1971	RANC		J	J, S	S	J
<i>R. coronatus</i> Berlese 1921	RCOR			J	J	J
<i>R. minimus</i> (Karg 1961)	RMIN				S, B	
<i>Veigaia cerva</i> (Kramer 1976)	VEIG				S	S
<i>V. exigua</i> (Berlese 1917)	VEIG				S	J, S
<i>V. nemorensis</i> (C.L.Koch 1839)	VEIG				S	J, S
<i>Zercon andrei</i> (Sellnick 1958)	ZAND				J	
<i>Asca aphidioides</i> (Linné 1758)					S	
<i>A. bicornis</i> (Can. et Franz 1887)					S	
<i>Blattisocius tarsalis</i> (Berlese 1918)				J		
<i>Dendrol. septentrionalis</i> (Sellnick 1958)				J		
<i>Dendroseius reticulatus</i> Sheals 1956						S
<i>Hypoaspis cuneifer</i> (Michael 1891)						S
<i>H. vacua</i> (Michael 1891)					J, S, B	S
<i>Leioseius minusculus</i> Berlese 1905				J		
<i>Pergamasus quisquiliarum</i> (G.&R.Can. 1882)						J
<i>P. septentrionalis</i> (Oudemans 1902)					S	S
<i>P. vagabundus</i> Karg 1968						S
<i>Prozercon trågardi</i> (Halbert 1923)				J	J, S	J
<i>Rhodacarellus silesiacus</i> Willmann 1935					S	
<i>Sejus necorniger</i> (Oudemans 1903)			J			
<i>Veigaia kochi</i> (Trågardi 1901)						S

Code only for species from tidal zone to grey dune with relative abundance > 5%.

brown dune. Here, an increase of habitat heterogeneity and a relative minimum of unfavourable abiotic conditions (like influence of salt and low habitat stability in foredunes and high acidity in brown dune) may allow for a high diversity.

Considering the low values of plant cover, plant species richness and organic C, it is surprising to find in young dunes a relatively diverse and abundant soil microarthropod community. This is indicative of the existence of a complex soil ecosystem, the interactions within which are responsible for biogenic sand stabili-

zation. Furthermore, evidence from the literature supports the following hypotheses on the existence and on some functions of the (partial) ecosystem of dune sand.

Judged from the low carbon quantities, there is little food for soil organisms. Airborne foams from surf and blown sand with adhering microorganisms from the intertidal may provide highly nutritious organic input to bacteria and plants (Fay & Jeffrey 1992; Wilson 1959). Especially in the more humid season, green algae and blue cyanobacteria grow on the sand surface (Pluis & de Winder 1990). On the one hand, they contribute to sand

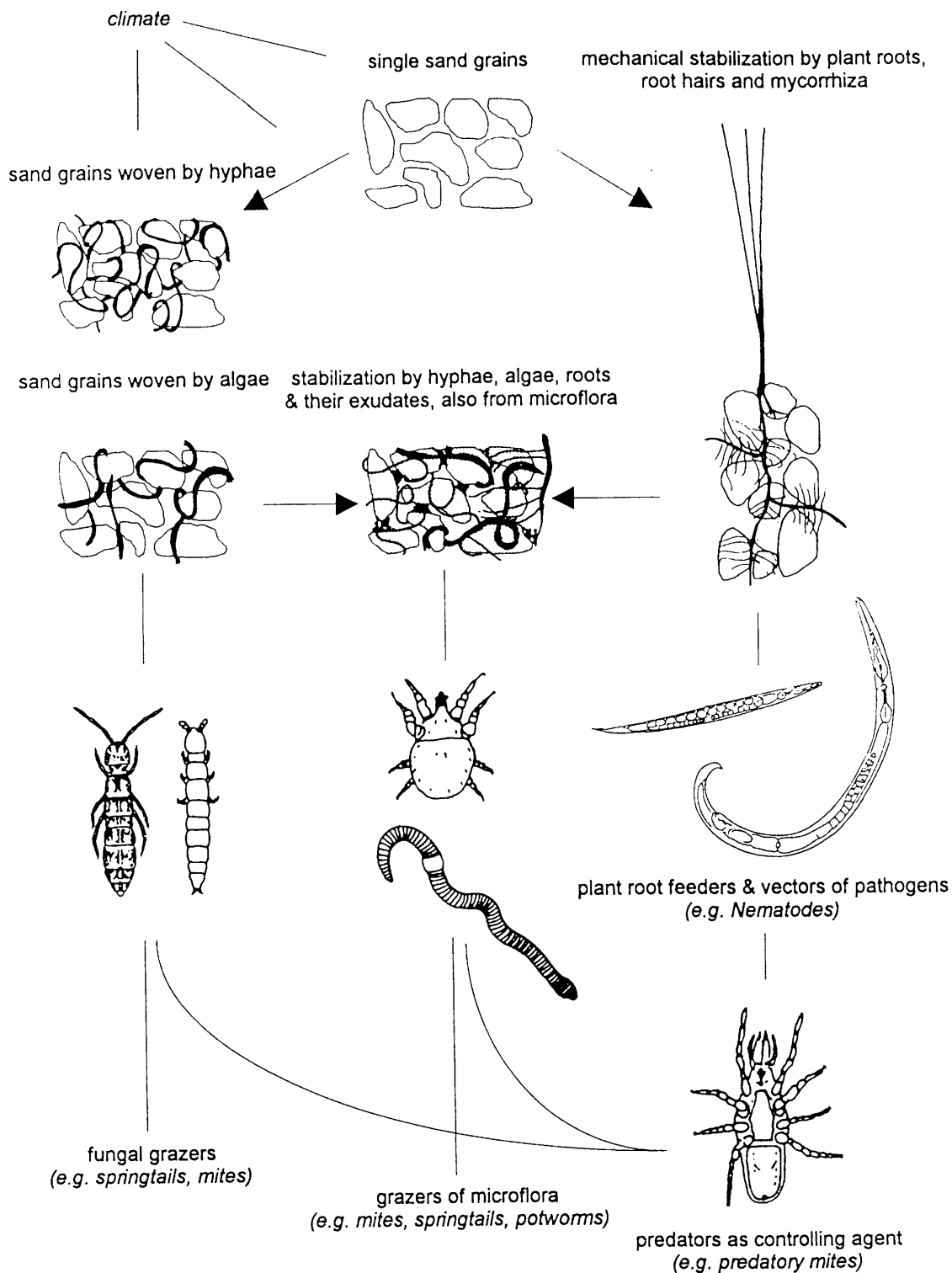


Fig. 3. Ecological interactions, leading to biogenic sand stabilization in coastal dunes.

stabilization by enmeshment and slimes, on the other hand they are food for surface-living arthropods and when buried by overblowing sand also for euedaphic

soil mesofauna. This grazing may stimulate algal activity, which has also been reported for grazing of fungal hyphae (Coleman 1985; Hart 1985; McGonigle & Fitter

1988). Exudates from roots of pioneer plants in primary dunes may trigger a whole sequence of reactions of soil animals and interactions as has been described by Clarholm (1985) from laboratory experiments: Root exudates stimulate microbial activity causing an increase of CO_2 . This attracts Protozoa and Nematodes. Nematodes are potentially harmful to *Ammophila* (van der Putten et al. 1990), leading to its degradation. Other interactions may follow: bacterial and fungal feeding Nematodes and Collembola are potential prey for predaceous mites (Karg 1971).

In nutrient deficient yellow dune, mycorrhiza is very important for nutrient cycling (Read 1989). Mycorrhiza are a favourite food of Protura, which belong to the soil mesofauna, and are quite abundant in young dune soils. Thus they are interacting with mycorrhizal dune plants, having an indirect effect on their dune stabilizing features.

Soil microflora spores are taken up by soil mesofauna with their feeding activities, but they are not digested. By defecation, soil mesofauna is an important vector of microflora dispersal, which is of particular importance in dynamic habitats, such as primary and yellow dune.

The evidence sketched so far, gives some ideas on the role soil biota play in the stabilization of dune sands and dune formation, which are summarized as follows (Fig. 3): Bacterial and algal slimes serve as a glue between single grains. Algal, fungal and mycorrhizal filaments provide mechanical stabilization and plant roots hold together sand grains both by exudates and root hairs (Koske & Polson 1984; Pluis & de Winder 1990; Rose 1988). Grazers of microflora, fungi and algae like potworms (Enchytraeidae) mites or Collembola, and predators like Gamasina, may influence and control this system.

Our findings on abundance and specific species composition of soil mesofauna taxocenoses confirm the value of dunes as unique habitats. The study is a small step towards an ecosystem understanding, which is not only relevant for nature conservation, but also for coastal conservation: with their sand stabilizing potential, soil biota contribute to coastal resilience. This has to be quantified in future research to assess the risk of a reduction of this stabilizing potential due to pollution or climatic change.

Our (for some areas preliminary) results show, that high abundance and diversity is found over an extended geographic transect, crossing climatic zones. Detailed analyses of the communities of this transect are under way (Handelmann & Heldt in prep.) to elaborate the possibilities of a predictive assessment of effects of climatic change.

Acknowledgements. Part of the study was supported by the University of Bremen within the twin programs with Gdansk and Riga. The support of the Polish National Park Authorities, particularly the enthusiasm of Dr. Rabski (Slowinski National Park) and that of the University of Riga, particularly of Dr. Balodis and Dr. Melecis and their group, is greatly acknowledged.

References

- Agrell, J. 1934. Studien über die Verteilung von Collembolen auf Triebssandböden. *Entomol. Tidskr.* 55: 181-249.
- Bigot, L. 1961. Essai d'écologie quantitative sur les invertébrés de la Sansaure Camarguaise. *Cent. reg. Doc. ped. Aix*: 1-140.
- Bussau, C. 1990. Nematoden aus Küstendünen, Schleswig Holstein, Dänemark. *Zool. Anz.* 225: 161-188.
- Clarholm, M. 1985. Possible roles for roots, bacteria, protozoa and fungi in supplying nitrogen to plants. In: Fitter, A.H. (ed.) *Ecological interactions in soil*, pp. 355-365. Blackwell, Oxford.
- Coleman, D.C. 1985. Through a ped darkly: an ecological assessment of root-soil-microbial-faunal interactions. In: Fitter, A.H. (ed.) *Ecological interactions in soil*, pp. 1-21. Blackwell, Oxford.
- Doppelreiter, H. 1979. Untersuchungen über Artenspektrum, Verteilung und Biozidempfindlichkeit von Collembolen im Fichtenwaldboden. 1. Artenspektrum und Verteilung, 2. Biozidempfindlichkeit. *Z. ang. Ent.* 88: 113-124, 453-470.
- Ellenberg, H. 1986. *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*. 4th ed., pp. 490-509. Ulmer, Stuttgart.
- Fay, P.J. & Jeffrey, D.W. 1992. The foreshore as a nitrogen source for marram grass. In: Carter, R.W.G., Curtis, T.G.F. & Sheehy-Skeffington, M.J. (eds.) *Coastal Dunes*, pp. 177-188. Balkema, Rotterdam, Brookfield.
- Fjellberg, A. 1980. *Identification keys to Norwegian Collembola*. Norsk Entomologisk Forening, Ås.
- Franz, H. 1975. *Die Bodenmesofauna der Erde in bioökologischer Betrachtung*. Teil 1, Steiner Verlag, Wiesbaden.
- Gerlach, A. 1990. Spiekeroog - a short portrait of an island. *Eurodunes* 2: 65-68.
- Gisin, H. 1943. Ökologie und Lebensgemeinschaften der Collembolen im Schweizer Exkursionsgebiet Basels. *Rev. Suisse Zool.* 50: 131-224.
- Gisin, H. 1970. Die Collembolenfauna Europas. *Mus. Hist. Nat. Genf.*
- Hagvar, S. 1982. Collembola in Norwegian coniferous forest soils. 1. Relations to plant communities and soil fertility. *Pedobiologia* 24: 255-296.
- Hart, D.D. 1985. Grazing insects mediate algal interactions in stream benthic communities. *Oikos* 44: 40-46.
- Hartge, K.H. 1978. *Einführung in die Bodenphysik*. Enke, Stuttgart.
- Heyken, A. 1965. Vegetationstypen der Küstendünen an der östlichen und südlichen Nordsee. In: Raabe, E.-W. (ed.) *Mitt. d. AG f. Floristik in Schl.-Holst. und Hamburg*, p. 13.

- Isermann, M. & Cordes, H. 1992. Changes in dune vegetation on Spiekeroog (East Friesian Islands) over a 30 year period. In: Carter, R.W.G., Curtis, T.G.F. & Sheehy-Skeffington, M.J. (eds.) *Coastal Dunes*, pp. 201-209. Balkema, Rotterdam, Brookfield.
- Joosse, E.N.G. & Verhoeff, H.A. 1983. Developments in ecophysiological research on soil invertebrates. *Adv. in Ecol. Res.* 16: 175-234.
- Jungerius, P.D. 1990. The characteristics of dune soils. *Catena Suppl.* 18: 155-162.
- Karg, W. 1971. Die freilebenden Gamasina (Gamasides), Raubmilben. In: Dahl, M. & Peus, F. (eds.) *Die Tierwelt Deutschlands*, Vol. 59, pp. 1-475. Fischer, Jena.
- Koehler, H. 1992. The use of soil mesofauna for the judgement of chemical impact on ecosystems. *Agric., Ecosyst. & Envir.* 40: 193-205.
- Koehler, H., E., Munderloh & Hofmann, S. In press. The terrestrial mites of sand dunes from two sites of the North-Sea Coast, with special reference to the Gamasina. *Proceedings EURAAC-Congress Krynica (Poland) 1992*.
- Koehler, H., Hofmann, S. & Munderloh, E. 1992. The soil mesofauna of white-, grey- and brown-dune sites in Jutland (Denmark) with special reference to the Gamasina (Acari, Parasitiformes). In: Carter, R.W.G., Curtis, T.G.F. & Sheehy-Skeffington, M.J. (eds.) *Coastal Dunes*, pp. 273-281. Balkema, Rotterdam, Brookfield.
- Koske, R.E. & Polson, W.R. 1984. Are VA mycorrhizae required for sand dune stabilization? *BioScience* 34: 420-424.
- Krogerus, R. 1932. Ökologie und Verbreitung der Arthropoden der Triebsandgebiete an den Küsten Finnlands. *Acta Zool. Fennici* 12.
- Luxton, M. 1990. The marine littoral mites of the New Zealand region. *J. R. Soc. New Zealand* 20: 367-418.
- McGonigle, T.P. & Fitter, A.H. 1988. Ecological consequences of arthropod grazing on VA mycorrhizal fungi. *Proc. R. Soc. Edinburgh* 94B: 25-32.
- Mallow, B., Ludwig, D. & Crossley, D.A. 1984. Microarthropod community structure in a coastal dune ecosystem on Jekyll Island, Georgia. *Pedobiologia* 27: 365-376.
- Munderloh, E. & Hofmann, S. 1992. *Synasien der Bodenmesofauna in Dünen unterschiedlichen Sukzessionsalters der Insel Spiekeroog (Ostfriesland)*. Diplomarbeit Univ. Bremen, FB2.
- Petersen, H. 1965. The Collembola of the Hansted Reserve, Thy, North Jütland. *Entomol. Medd.* 30: 313-395.
- Pluis, J.L.A. & de Winder, B. 1990. Natural stabilization. *Catena Suppl.* 18: 195-208.
- Poinsot, N. 1966. Etude écologique des Collembolés des dunes de Beynes (Haute Camargue). *Rev. Ecol. Biol. Sol* 3: 483-493.
- Pozo, J. 1986. Ecological factors affecting Collembola populations. Ordination of communities. *Rev. Ecol. Biol. Sol* 23: 299-311.
- Read, D.J. 1989. Mycorrhizas and nutrient cycling in sand dune ecosystems. *Proc. R. Soc. Edinburgh*, 96B: 89-110.
- Rose, S.L. 1988. Above and belowground community development in a maritime sand dune ecosystem. *Plant Soil* 109: 215-226.
- Schaller, F. 1951. Zur Ökologie der Collembolen des Mainzer Sandes. *Zool. Jb. (Syst.)* 79: 449-513.
- Sindowsky, K.-J. 1973. Das ostfriesische Küstengebiet: Inseln, Wattenmeer und Marschen. *Sammlg. Geolog. Führer* 57: 1-162.
- Strenzke, K. 1955. Verbreitung und Systematik der Collembolen der deutschen Nord- und Ostseeküste. *Veröff. Inst. Meeresforsch. Bremerhaven* 3: 46-65.
- Tamm, J.C. 1986. Fünfjährige Collembolensukzession auf einem verbrannten Kiefernwaldboden in Niedersachsen. *Pedobiologia* 29: 113-127.
- van der Putten, W.H., Maas, P.W.Th., van Gulik, W.J.M. & Brinkman, H. 1990. Characterization of soil organisms involved in the degeneration of *Ammophila arenaria*. *Soil Biol. Biochem.* 22: 845-852.
- van Heerdt, P.F. & Mörzer-Bruyns, M.F. 1960. A biocenological investigation of a yellow dune region of Terschelling. *Entomol. Tijdschr.* 103: 225-275.
- Willis, A.J. 1989. Coastal sand dunes as biological systems. *Proc. R. Soc. Edinburgh*, 96 B: 17-36.
- Willmann, C. 1953. Die Milbenfauna der Nordseeinsel Wangerooge. *Veröff. Inst. Meeresforsch. Bremerhaven* 1: 139-186.
- Wilson, A.T. 1959. Surface of the ocean as a source of airborne nitrogenous material and other plant nutrients. *Nature* 184: 99-101.

Received 20 March 1995;

Revision received 1 June 1995;

Accepted 27 July 1995.