SYSTEMATICS AND ECOLOGY OF DANISH SALT MARSH COMMUNITIES

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ABSTRACT. - A review of salt marsh communities and submerged saline communities in Denmark is presented. A total of 24 communities has been recognised from published accounts of Danish salt marsh vegetation along with own investigations. A floristical classification based on TWINSPAN analysis of 696 relevées has been performed. For each community the existing knowledge on ecology, succession and impacts of management are summarized.
KEY WORDS - Denmark, phytosociology, classification, salt marsh.

INTRODUCTION

Denmark is a pronounced coastal country with many marine habitats and thus plant communities. The status and distribution of Danish plant communities are mostly unknown, and the salt marsh communities are no exception to this lack of knowledge. As part of the project: "Indicators of Nature quality", a review of most Danish biotopes and their contents of plant communities is in progress. This paper is aiming at describing Danish salt marsh vegetation, relate this to the international system of plant communities and discuss the ecology and status of the obtained syntaxa.

SALT MARSH ECOLOGY

Salt marshes are usually defined as vegetation by herbs, grasses or low shrubs, which border saline water bodies (Adam, 1993). Salt marshes in Denmark develop on finer classes of texture (clay, silt, fine sand) at sheltered coasts, where the wave energy reaching the coastline is strongly reduced due to shallow water and/or protection behind islands.

In salt marshes there is a zonation of plant communities in response to different tidal periods of inundation. It extends from pioneer vegetation of the permanently waterlogged and unstable sand and mud to the drier, elevated and stable salt marsh

meadows or flats of the littoral fringe, where submergence only occurs during the highest tides of the year. According to the littoral-zone terminology defined by Du Rietz, the hydrolittoral zone is defined as the part of the coast situated between the lowest low water level and mean sea level; the geolittoral zone as the part situated between mean sea water level and the highest high water level; the epilittoral as the part situated above highest high water level (Tyler, 1969). The tidal flats in the Wadden Sea is situated between mean low water and mean high water i.e. in the transient zone between the hydro- and geolittoral zones. The true salt marsh is located on the geolittoral, while reed swamps are on both the hydro- and geolittoral. Particular high salt concentrations emerge by evaporation in depressions (salt pans), and the vegetation may be absent or sparse. On larger salt marshes tidal creeks may appear. Another important habitat is the driftlines, where different sorts of litter accumulate, creating the particular requirements of annual nitrophilous communities. To make the description of salt marsh communities as complete and informative as possible, we include all communities from sheltered coasts, e.g. submerged Seagrass beds.

THE VARIATION IN SALT MARSH COMMUNITIES IN DENMARK

The main environmental variables on Danish salt marshes vary considerably (Vestergaard, 1989). 1) The coast type geomorphology, including the texture of the substrate, varies from the Wadden Sea where the salt marsh communities are well developed and of good size, to very narrow salt marsh zones in the Inner Danish Waters, with less distinct plant communities. 2) The Danish Waters constitute a transitional zone in tidal amplitude between the Wadden Sea, where the springtide amplitude is approximately 200 cm and the Baltic Sea where it may be only a few cm (Svansson, 1975). 3) In the North Sea the sea water salt concentration is approximately 30‰, in the Inner Danish Waters it varies greatly, while in the Baltic Sea the salinity drops below 10‰. In addition to this overall picture local variations in salinity exist due to outlets of fresh water. 4) The geographical distribution of many coastal species depend upon climate factors. 5) Regarding the majority of the coastal species the actual distribution in Denmark largely seems to equal the potential distribution. For some species, however, the actual distribution seems to be smaller than the potential, e.g. *Spartina maritima*. 6) Human actions such as reclamation, agriculture, grazing, mowing and fertilisation have largely altered the structure, species composition and distribution of plant communities.

Methods

This study is based on relevant floristical data from published accounts of Danish salt marsh vegetation along with an independent field survey in different parts of Denmark (NERI 1996) (table 1). The field studies were carried out in the summer 1996 in 20 study areas. In each site 16 squares of each $1m^2$ were arranged along 4 transects and the abundance of every vascular plant species was estimated using van der Maarels scale, combining cover (Braun-Blanquet) and frequency: 1-4: <5% (1: rare, 2: few, 3: many, 4: numerous), 5: 5-12,5%, 6: 12,5-25%, 7: 25-50%, 8: 50-75%,

9: >75%. From the published studies data presenting only presence/absence were excluded from the classification. The relevés are distributed over most of Denmark (table 1), but certain regions, such as Northern Jutland is markedly underrepresented.

TABLE 1 - SOURCES AND LOCATION OF RELEVÉS USED IN THE CLASSIFICATION.

Source	Location	Numbers of relevés
Own investigations	All Denmark	300
Iversen (1936)	Skallingen, Hørup Hav, Ringkøbing Ford	99
Jessen (1968)	Vorsø	81
Beeftink (1959)	Skallingen	72
Mikkelsen (1949a)	Isefjorden	50
Iversen (1932)	Ringkøbing Fjord	20
Vestergaard et al. (1978)	Saltholm	19
Gravesen (1969)	Tipperne	14
Raunkiær(1910)	Fanø	9
Vestergaard (1987)	Baltic Sea	9
Vestergaard (1982)	Baltic Sea	8
Böcher (1946)	Ulvshale, Møn	6
Runge (1983)	Bornholm	5
Gravesen & Vestergaard (1986)	Køge Bugt	3
Grøntved (1929)	Amager Fælled	1
Total		696

The available data, in all 696 relevées and 262 species, were entered in the database programme Turboveg (Hennekens, 1995), and processed and analysed in the programme Megatab. For the actual classification of the data TWINSPAN was used, with cut-levels at 0, 18 38% and 68%. The synoptic tables were made using the Shake and Shifttab programs.

RESULTS

The numerical analysis resulted in 26 clusters, representing 12 salt marsh communities (table 2). In the descriptions of the validated communities, the cluster nr. (#) is indicated in brackets.

The basic unit in the descriptions is "community", using the Latin names of one or two of the most frequent species. Where there is an obvious phytosociological name for a community the internationally accepted syntaxonomical names have been included in the descriptions. Finally the documented communities have been arranged in a short synopsis in accordance with the higher phytosociological catagories of alliance, order and class (table 3).

For each community the physiognomy and floristic composition of the vegetation is given. This is followed by a description of the ecologogical conditions (e.g. climate, salinity, moisture, nutrient content and soil type), management demands, successional trends and impact from human activity (e.g. fertilization, eutrophication, drainage). Finally a preliminary estimate of the distribution of the 24 plant communities is given.

TABLE 2 - SYNOPTIC TABLE OF ANALYSED RELEVÉES. FOR EACH SPECIES THE CONSTANCE VALUE, E.I. THE PERCENTAGE OF RELEVÉS WHERE THE SPECIES OCCUR (E.G. 100^{70}) AND THE MEAN ABUNDANCE FOR ALL RELEVÉS IN THE CLUSTER (E.G. $100^{\mathbf{70}}$) IS INDICATED.

Cluster #	1	2	3	4	5	6	7	8	9	10	11	12	13
Number of relevées	6	10	28	41	9	4	65	58	75	23	38	129	82
Festuca rubra	100^{70}	40^{2}	.	15^{7}	.	5^{13}	35^{39}	12^{17}	100^{68}		97^{68}	68^{39}	78^{65}
Limonium vulgare	83^{26}	100^{29}	46^{4}	27^{15}	.	.	3^{64}	9^{32}	.	78^{6}	11^{20}	5^{5}	.
Artemisia maritima	83^{22}	60^{20}	.	.	.	.	3^{10}	12^{59}	.	48^{9}	8^{23}	12^{64}	.
Plantago maritima	83^{21}	100^{16}	4^{13}	63^{5}	.	.	57^{46}	98^{43}	11^{3}	91^{6}	71^{10}	72^{31}	57^{60}
Halimione portulacoide	67^{31}	100^{62}	50^{4}	42^{9}	.	.	2^{4}	.	.	70^{2}	.	.	.
Salicornia europaea	50^{4}	90^{2}	96^{10}	68^{6}	100^{88}	50^{24}	94^{73}	71^{37}	.	17^{2}	3^{4}	3^{8}	5^{13}
Puccinellia maritima	33^{2}	100^{7}	79^{31}	93^{58}	.	75^{75}	94^{79}	93^{56}	5^{57}	.	.	12^{27}	2^{25}
Suaeda maritima	.	70^{2}	68^{6}	29^{3}	22^{99}	.	91^{72}	36^{32}	.	9^{2}	3^{30}	10^{15}	1^{10}
Spartina x townsendii	.	.	54^{3}	.	.	.	.	.	.	.	.	.	.
Spergularia maritima	17^{3}	20^{3}	7^{2}	78^{3}	.	.	68^{53}	74^{21}	4^{2}	.	5^{2}	23^{15}	.
Aster tripolium	33^{11}	40^{4}	50^{5}	59^{9}	.	75^{36}	74^{65}	71^{45}	25^{16}	4^{2}	8^{7}	30^{34}	6^{29}
Triglochin maritimum	.	50^{2}	39^{5}	54^{5}	.	.	39^{37}	64^{32}	35^{20}	30^{2}	13^{4}	33^{22}	81^{38}
Puccinellia capillaris	.	.	.	.	67^{99}	.	2^{8}	.	3^{50}	.	.	.	.
Spergularia salina	17^{1}	.	.	.	67^{76}	75^{52}	11^{69}	2^{8}	4^{40}	.	.	2^{5}	.
Bolboschoenu maritimus	.	.	4^{15}	7^{3}	.	75^{83}	3^{99}	5^{5}	40^{23}	.	3^{38}	6^{37}	2^{23}
Juncus bufonius	.	.	.	2^{4}	44^{55}	75^{47}	.	.	3^{17}	.	.	.	2^{6}
Glaux maritima	33^{36}	.	4^{2}	10^{4}	.	25^{10}	26^{33}	91^{50}	33^{37}	.	32^{8}	78^{32}	63^{48}
Juncus gerardii	.	.	.	34^{20}	.	25^{30}	8^{11}	79^{52}	35^{42}	44^{5}	76^{8}	93^{51}	89^{61}
Agrostis stolonifera	17^{2}	.	.	2^{4}	44^{99}	50^{38}	5^{11}	40^{51}	85^{75}	61^{6}	95^{11}	77^{42}	92^{74}
Armeri mariti s. marit	.	.	.	2^{1}	.	.	.	.	1^{60}	70^{7}	.	2^{15}	4^{35}
Potentilla anserina	.	.	.	.	.	.	.	.	29^{47}	.	26^{3}	20^{26}	46^{39}
Elymus repens	.	.	.	.	.	.	2^{1}	9^{73}	1^{10}	.	11^{12}	23^{58}	2^{65}
Achillea millefolium	.	.	.	.	.	.	.	.	1^{6}	.	5^{12}	.	1^{6}
Phragmites australis	.	.	.	.	.	25^{99}	.	3^{99}	41^{56}	9^{2}	3^{3}	7^{52}	17^{40}
Festuca arundinacea	.	.	.	.	.	.	.	2^{5}	.	.	3^{8}	13^{11}	1^{70}
Iris spuria	.	.	.	.	.	.	.	.	.	.	.	.	.
Leontodon autumnalis	.	.	.	.	.	.	.		7^{46}	4^{2}	3^{4}	2^{3}	39^{40}
Armeria maritima	.	.	.	.	.	.	3^{19}	14^{44}	1^{60}	.	42^{9}	19^{24}	20^{60}
Bupleurum tenuissimum	.	.	.	.	.	.	.	.	.	.	3^{3}	.	.
Atriplex littoralis	.	.	.	.	11^{75}	.	14^{62}	14^{47}	3^{26}	.	.	8^{65}	.
Ruppia cirrhosa	.	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton pectinatus	.	.	.	.	.	.	.	.	.	.	.	.	.
Zostera marina	.	.	.	.	.	.	.	.	.	.	.	.	.
Ruppia maritima	.	.	.	.	.	.	.	.	.	.	.	.	.
Alopecurus geniculatus	.	.	.	.	.	.	.		12^{59}	.	3^{2}	0.8^{4}	7^{19}
Alopecurus pratensis	.	.	.	.	.	.	.	.	.	.	.	.	.
Astragalus danicus	.	.	.	.	.	.	.	.	.	.	.	.	.
Blysmus rufus	.	.	.	.	.	.	.	.	.	.	.	0.8^{68}	6^{45}
Cakile maritima	.	.	.	.	.	.	.	.	.	.	.	.	.
Cochlearia danica	.	.	.	.	.	.	2^{1}	.	1^{3}	.		3^{65}	1^{36}
Eleocharis uniglumis	.	.	.	.	.	25^{10}	.	.	37^{75}	.	.	0.8^{3}	16^{52}
Halimione pedunculata	.	.	.	2^{1}	.	.	26^{47}	14^{31}	.	.	3^{10}	3^{9}	1^{4}
Juncus articulatus	.	.	.	.	.	.	.	.	13^{37}	.	.	.	7^{23}
Juncus maritimus	.	.	.	.	.	.	.	.	3^{51}	.		0.8^{1}	.
Lepidium latifolium	.	.	.	.	.	.	.	.	1^{1}	.	.	.	.
Limonium humile	.	.	.	10^{5}	.	.	9^{99}	5^{35}	.	.	.	2^{32}	1^{60}
Odontites litoralis	.	.	.	.	.	.	.	3^{26}	1^{10}	.	.		21^{57}
Odontites verna	.	.	.	.	.	.	.	2^{4}	.	.	3^{2}	2^{2}	7^{26}
Ophioglossum vulgatum	.	.	.	.	.	.	.	.	.	.	.	.	6^{38}
Sagina maritima	.	.	.	.	.	.	.	.	.	35^{5}	.	2^{26}	5^{82}
Schoenoplect tabernaem	.	.	.	.	.	.	.	.	7^{14}	.	.	0.8^{2}	1^{4}
Spergula arvensis	.	.	.	.	.	.	.	.	3^{50}	.	.	.	.
Tetragonolob maritimus	.	.	.	.	.	.	.	.	.	.	.	.	1^{13}
Trifolium fragiferum	.	.	.	.	.	.	.	.	1^{1}	.	8^{3}	2^{11}	18^{45}
Triglochin palustre	.	.	.	.	.	25^{6}	.	2^{10}	27^{47}	.	3^{1}	.	9^{69}

1 = Artemisia maritima community
2 = Halimione portulacoides community
3 = Salicornia europaea community
4 = Puccinellia maritima community
5 = Salicornia europaea/Spergularia maritima-Puccinellia distans communities
6 = Scirpus maritimus community
7 = Puccinellia maritima community
8 = Puccinellia maritima community
9 = Phragmites australis-Scirpus maritima community
10 = Juncus gerardi community var. Festuca rubra littoralis
11 = Juncus gerardi community
12 = Juncus gerardi community
13 = Juncus gerardi community

TABLE 2 (CONTINUED). SYNOPTIC TABLE FOR ANALYSED RELEVÉES.

Cluster #	14	15	16	17	18	19	20	21	22	23	24	25	26
Number of relevées	44	3	3	3	11	1	9	17	19	9	3	2	4
Festuca rubra	91^{45}	67^{8}	100^{41}	67^{60}	18^{3}	.	89^{70}	82^{51}	11^{8}	11^{30}	.	.	.
Limonium vulgare	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia maritima	.	.	.	33^{15}	.	.	.	18^{16}	.	.	.	.	.
Plantago maritima	7^{27}	.	67^{15}	.	9^{2}	.	.	6^{10}	.	.	.	.	.
Halimione portulacoide	.	.	.	.	.	.	.	.	.	.	.	.	.
Salicornia europaea	.	.	.	.	.	.	.	.	.	.	.	.	.
Puccinellia maritima	2^{3}	.	.	.	.	.	.	.	.	.	.	.	.
Suaeda maritima	.	.	.	.	.	100^{10}	.	.	42^{30}	11^{10}	.	.	.
Spartina x townsendii	.	.	.	.	.	.	.	.	.	.	.	.	
Spergularia maritima	.	.	.	.	9^{8}	.	.	.	.	.	.	.	.
Aster tripolium	2^{3}	.	.	.	.	.	22^{35}	.	11^{60}	22^{50}	.	.	.
Triglochin maritimum	9^{9}	.	.	.	.	100^{30}	.	.	.	.	.	.	.
Puccinellia capillaris	.	.	.	.	.	.	.	.	.	.	.	.	.
Spergularia salina	.	.	.	.	.	.	.	.	5^{1}	.	.	.	.
Bolboschoenu maritimus	7^{3}	.	.	.	100^{53}	100^{99}	.	.	.	11^{1}	.	.	.
Juncus bufonius	.	.	.	.	.	.	.	.	.	.	.	.	.
Glaux maritima	9^{4}	33^{2}	.	.	.	.	11^{10}	.	11^{65}	.	.	.	.
Juncus gerardii	23^{10}	.	33^{10}	.	9^{8}	.	22^{45}	6^{10}	5^{30}	.	.	.	.
Agrostis stolonifera	84^{31}	.	.	67^{8}	9^{4}	.	89^{65}	6^{20}	5^{91}	.	.	.	.
Armeri mariti s. marit	2^{19}	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla anserina	84^{9}	67^{3}	67^{25}	.	.	.	78^{54}	47^{12}	37^{70}	11^{1}	.	.	.
Elymus repens	59^{19}	.	67^{70}	100^{58}	.	.	78^{79}	100^{68}	84^{90}	89^{96}	.	.	.
Achillea millefolium	9^{12}	100^{6}	67^{99}	100^{95}	.	.	.	29^{63}	.	.	.	.	.
Phragmites australis	.	67^{38}	.	.	.	.	11^{38}	12^{11}	11^{50}	44^{96}	.	.	.
Festuca arundinacea	32^{14}	.	100^{33}	100^{60}	.	.	56^{93}	59^{23}	.	.	.	.	.
Iris spuria	2^{99}	.	67^{90}	.	.	.	.	53^{73}	.	.	.	.	.
Leontodon autumnalis	43^{14}	.	67^{15}	100^{12}	.	.	.	24^{13}	.	.	.	.	.
Armeria maritima	14^{3}	.	.	100^{81}	.	.	.	.	.	.	.	.	.
Bupleurum tenuissimum	2^{4}	.	.	67^{18}	.	.	.	.	.	.	.	.	.
Atriplex littoralis	.	.	.	.	.	.	22^{35}	.	100^{97}	67^{64}	.	.	.
Ruppia cirrhosa	.	.	.	.	.	.	.	.	.	.	100^{88}	100^{98}	50^{83}
Potamogeton pectinatus	.	.	.	.	.	.	.	.	.	.	100^{67}	.	25^{6}
Zostera marina	.	.	.	.	.	.	.	.	.	.	.	100^{51}	.
Ruppia maritima	.	.	.	.	.	.	.	.	.	.	.	.	100^{81}
Alopecurus geniculatus	7^{36}	.	.	.	.	.	.	.	.	.	.	.	.
Alopecurus pratensis	.	.	.	.	.	.	.	6^{2}	.	.	.	.	.
Astragalus danicus	.	.	.	33^{15}	.	.	.	.	.	.	.	.	.
Blysmus rufus	.	.	.	.	.	.	.	.	.	.	.	.	.
Cakile maritima	.	.	.	.	.	.	.	.	5^{10}	.	.	.	.
Cochlearia danica	.	.	.	.	.	.	22^{25}	6^{10}	5^{30}	.	.	.	.
Eleocharis uniglumis	.	.	.	.	.	.	.	.	.	.	.	.	.
Halimione pedunculata	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus articulatus	2^{4}	.	.	.	.	.	.	.	.	.	.	.	.
Juncus maritimus	.	.	.	.	.	.	.	.	.	.	.	.	.
Lepidium latifolium	.	.	.	.	.	.	.	12^{95}	.	.	.	.	.
Limonium humile	.	.	.	.	.	.	.	.	.	.	.	.	.
Odontites litoralis	.	.	.	.	.	.	.	.	.	.	.	.	.
Odontites verna	.	.	.	.	.	.	.	.	.	.	.	.	.
Ophioglossum vulgatum	.	33^{13}	.	.	.	.	.	.	.	.	.	.	.
Sagina maritima	.	33^{1}.	.	.	.	.	.	.	.	.	.	.	.
Schoenoplect tabernaem	.	.	.	.	.	.	.	.	.	.	.	.	.
Spergula arvensis	.	.	.	.	.	.	.	.	.	.	.	.	.
Tetragonolob maritimus	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium fragiferum	25^{21}	.	.	.	.	.	.	.	.	.	.	.	.
Triglochin palustre	2^{8}	.	.	.	.	.	.	.	.	.	.	.	.

14 = Festuca rubra community
15 = Phragmites australis-Scirpus maritima community
16 = Festuca rubra/Elymus repens communities
17 = Epilittoral vegetation
18 = Scirpus maritimus community
19 = Scirpus maritimus community
20 = Potentilla anserina-Festuca arundinacea community
21 = Elymus repens community var. Lepidium latifolium
22 = Atriplex littoralis community (not included in the descriptions)
23 = Elymus repens community
24 = Ruppia maritima community
25 = Ruppia maritima community
26 = Ruppia maritima community

TABLE 3 - SYNOPSIS OF DANISH SALT MARSH COMMUNITIES.

Class: Zosteretea marinae Pignatti 1953
  Order: Zosteretalia marinae Beguinot 1941 em. R.Tx. et Oberdorfer 1958
    Alliance: Zosterion marinae Christiansen 1934
    *Association: Zosteretum marinae Christiansen 1934
    *Association: Zosteretum noltii Harmsen 1936

Class: Spartinetea maritimae R.Tx. 1961
  Order: Spartinetalia maritimae Conrad 1935
    Alliance: Spartinion maritimae Conrad 1952
    *Association: Spartinetum anglicae Corillon 1953

Class: Ruppietea maritimae J. Tüxen 1960
  Order: Ruppietalia maritimae J. Tüxen 1960
    Alliance: Ruppion maritimae Br.-Bl. 1931
    *Association: Ruppietum maritimae Iversen 1934

Class: Thero-Salicornietea Pign. 1953 em. R.Tx. in R.Tx. et Oberdorfer 1958
  Order: Thero-Salicornietalia Pign. 1953 emend. R.Tx. in R.Tx. et Oberdorfer 1958
    Alliance: Thero-Salicornion strictae Br.-Bl. 1933 em. R.Tx. 1950
    *Association: Salicornietum europeae Warming 1906
    *Association: Suaedetum maritimae (Conard 1935) Pignatti 1953

Class: Asteretea tripolii Westhoff et Beeftink apud Beeftink 1965
  Order: Glauco-Puccinellietalia Beeftink et Westhoff 1962
    Alliance: Puccinellion maritimae Christiansen 1927
    *Association: Spergulario-Puccinellietum distantis Feekes (1934) 1943
    *Association: Puccinellietum maritimae (Warming 1906) Christiansen 1927
    *Association: Halimionetum portulacoides Kuhnholtz-Lordat 1927
    Alliance: Armerion maritimae Br.-Bl. et De Leeuw 1936
    *Association: Juncetum gerardii Warming 1906
    *Community: Tetragonolobus maritimus
    *Association: Blysmetum rufi (G.E. et G. Du Rietz 1925) Gillner 1960
    *Association: Artemisietum maritimae Hocquette 1927
    *Association: Oenantho-Juncetum maritimi Fröde 1958
    *Association: Eleocharitetum uniglumis Nordhagen 1923
    Alliance: Silenion maritimae Malloch 1971
    *Community: Festuca rubra

Class: Plantaginetea majoris Tüxen et Preising in Tüxen 1950.
  Order:Agrostetalia stoloniferae Oberdorfer in Oberdorfer et al., 1967
    Alliance: Elymo-Rumicion crispi Nordhagen 1940.
    *Association: Elymetum repentis maritimum Nordhagen 1940
    *Community: Agrostis stolonifera-Triglochin palustre
    *Association: Potentillo-Festucetum arundinaceae Nordhagen 1940
    *Community: Agrostis stolonifera-Alopecurus geniculatus

Class: Phragmiteteo-Magnocaricetea Klika in Klika et Novák 1941
  Order: Phragmitetalia australis W. Koch 1926
    Alliance: Phragmition communis W. Koch 1926
    *Association: Phragmito-Scirpetum maritimi W. Koch 1926
    *Community: Scirpus maritimus

    *Community: Atriplici-Elymetum pungens

Class: Saginetea maritimae Wetshoff, van Leeuwen et Adriani 1962
  Order: Saginetalia maritimae Wetshoff, van Leeuwen et Adriani 1962
    Alliance: Saginion maritimae Wetshoff, van Leeuwen et Adriani 1962
    *Association: Sagino-Cochlearietum danicae R.Tx. et Gillner 1956

DESCRIPTION OF DANISH SALT MARSH COMMUNITIES

Zostera marina community

Zosteretum marinae

This community consists of rather dense stands of *Zostera marina* and occasionally *Z. angustifolia* and contains often the same species as the *Ruppia maritima* community.

Zostera marina is susceptible to tidal movements and occurs on sandy mud in the sub-littoral zone from the middle tidal reach to a depth of 5-15m (Iversen, 1932). It is sometimes found higher up on the flats in shallow depressions. According to Ostenfeld (1908, 1918) *Z. marina* appears along shores with a salt concentration between 7 and 30‰.

The *Zostera marina* community appears to be widespread in Denmark (e.g. Iversen 1932, 1936; Larsen, 1956; Petersen, 1982; Påhlsson, 1994). It has rarely been described quantitatively from Denmark and is not documented in the classification.

In Germany the *Zostera marina* community is declining because of waterpollution (Schubert *et al*. 1995).

Zostera nolti community

Zosteretum noltii

The *Zostera nolti* community is dominated by Zostera nolti, but *Ruppia*-species may also occur (Vestergaard & Vintner, 1985). Blue-green algae (Cyanophyta) such as *Microcoleus chtonoplastes* and *Lyngbya aestuarii*, are very important for the sedimentation in this community (Mikkelsen, 1969).

The *Zostera nolti* community is reported from shallow waters (often 20-50 cm depth), between the *Zostera marina* community, and the *Salicornia europaea*- or *Spartina maritima* communities. It may also appear in depressions near the transitionzone between the hydro- and geolittoral (Iversen, 1932). In the Wadden Sea, where the salt concentration is very high, *Zostera nolti* is more abundant than *Z. marina* (Mikkelsen, 1969).

This community is most prominent in the south-western Jutland and rare in the Baltic Sea, where the salinity is low (e.g. Iversen, 1932; Jessen, 1968; Petersen, 1982; Påhlsson, 1994).

The *Zostera nolti* community is declining in Germany because of water pollution (Pott, 1995) and the situation has been similar in Denmark.

Spartina maritima community

Spartinetum maritimae

The *Spartina maritima* community consists of a rather uniform pioneervegetation, dominated by the perennial *Spartina alterniflora* x *maritima (S. townsendii)* together with brown and green algae. *Spartina* creates vigorous ringshaped tussocks, that merge into large dense stands ousting other species on the tidal flats (Mikkelsen, 1969). Occasionally *Puccinellia maritima* can be found in the centre of larger *Spartina*-tussocks (Møller, 1963).

The *Spartina* community colonises the bare ground on low-lying, waterlogged mud, clay and sand in the lower geolittoral - earlier than the *Salicornia maritima* community. *Spartina* is more resistant to tidal erosion than other pioneer species on Danish salt marshes. At Skallingen Petersen (1982) found the *Spartina* community approximately 30 cm below and 15 cm above mean high water.

The *Spartina* community is very stable and competitive below the mean high

water line (Møller, 1963). When grazed the *Spartina* community is replaced by the *Puccinellia maritima* community, when the surface, in consequence of the land-reclamation, has been raised sufficiently. Otherwise it is invaded by reeds and is most often replaced by the *Scirpus maritimus* community or the *Phragmites australis-Scirpus maritimus* communities.

The community is not documented in our classification, but according to literature the main area of distribution is south-western Jutland with sporadic appearences in the Inner Danish Waters (e.g.Adsersen, 1974; Jensen, 1976; Petersen, 1982; Påhlsson, 1994).

The planting of Spartina began in 1931 for land reclamation purposes (Petersen, 1982), since then it has spread to the entire Danish Wadden Sea, where it is displacing *Zostera*- and *Salicornia* communities (Møller, 1963).

Ruppia maritima community

Ruppietum maritimae

The *Ruppia maritima* community is a species-poor vegetation consisting of the perennial *R. cirrhosa* (#24-25) and the annual *R. maritima* (#26). Near outlets of fresh water *Zannichellia palustris* and *Potamogeton pectinatus* may occur along with several other plant species and algae (#24) (Warming, 1906).

The vegetation occurs in the hydro- and sublittoral zones between the *Zostera marina* community and the pioneer communities or reed swamps, in depressions of the lower geolittoral zone and, locally, in brackish waters of coastal ponds and ditches which are only inundated by the highest tides, but where there is a strong influence of sea-spray (Rieley & Page, 1990). The *Ruppia maritima* community occurs on muddy or loamy sand (Warming, 1906) and may still appear at a salinity of 3‰ (Ostenfeld, 1918). The community is replaced by the *Zostera nolti* community at the Danish Wadden Sea (Mikkelsen,1969).

It is documented only from Ringkøbing Fjord, but probably has a much wider distribution in the inner Danish waters (e.g. Grüner, 1934; Iversen, 1932; 1936; Jessen, 1968; Larsen, 1956; Påhlsson, 1994; Warming, 1906).

The *Ruppia marina* community is rather susceptible to water pollution (Schubert *et al*., 1995).

It includes the association *Ruppietum chirrosa*.

Salicornia europaea community

Salicornietum europeae

Salicornia europaea, a small, annual succulent pioneer, dominates this community. The ground is covered by bluegreen algae and between the *Salicornia*-stems are numerous algae (Warming, 1906). The species composition depends upon the habitat and is here divided in one variant on tidal flats and another variant in depressions further up the geolittoral zone (salt pans), behind beach ridges and where the ground is bare due to cattle treading (Mikkelsen, 1949a; Petersen, 1982).

The *Salicornia* community on tidal flats is almost entirely consisting of *Salicornia europaea* occasionally with an element of *Spartina maritima*, *Ruppia maritima* and/or *Zostera nolti* (#3). It extends into the edge of the *Puccinellia maritima* community and in the upper parts several species from this community may appear e.g. *Puccinellia maritima, Aster tripolium, Suaeda maritima* and *Plantago maritima*. On the tidal flats *Salicornia europaea* is the first salt marsh pioneer and appears typically between 30 cm below mean high water and the mean high water line. This variation of the *Salicornia*

europaea community occurs where the salt concentration is very high.

The *Salicornia*-vegetation in salt pans covers rarely more than 50% of the ground and *Suaeda maritima* is often codominant along with *Halimione portulacoides, Spergularia marina, S. media, Puccinellia maritima, P. capillaris* and *Atriplex littoralis* (#5). In areas with large quantities of seaweed, *Bassia hirsuta* may be frequent (Vestergaard & Vintner, 1985). This variation forms a vegetation mosaic with the *Spergularia maritima-Puccinellia distans* community in depressions with lower salinity (Påhlsson, 1994), making a separation of the two communities difficult (#5). Although grazing has a positive effect on *Salicornia europaea* by reducing competitors and creating open space for seedlings, the cover of *Salicornia* increases immediately after the impact ceases, as a high proportion of seedlings are destroyed by trampling (Jensen, 1985). After some years, however, the competition from other species will gradually reduce the population of *Salicornia* and eventually cause its exclusion from the area. The species richness of heavily grazed lower salt marsh is rather low as the grazing animals disrupt the topsoil (Bakker *et al*., 1993).

The *Salicornia europaea* community is common and widespread (e.g. Beeftink, 1959; Gravesen, 1969; Grüner, 1934; Iversen, 1932, 1936; Jensen, 1976; Jessen, 1968; Mikkelsen, 1949a; NERI, 1996; Påhlsson, 1994; Raunkiær, 1910; Vestergaard *et al*. 1978; Warming, 1906), but only documented from a few salt marshes in this study (#3 & #5). The variant on tidal flats though does not appear in the Inner Danish Waters.

Many authors divide the *Salicornia europaea* community into several distinct communities (e.g. Gillner, 1960).

Suaeda maritima community

Suaedetum maritimae

The *Suaeda maritima* community is dominated by the annual therophytic pioneer *Suaeda maritima*, often associated with *Spergularia maritima, Puccinellia maritima, Aster tripolium* and *Salicornia europaea*.

It appears on bare ground in depressions of the geolittoral zone with lower salt concentration or in tidal creeks.

The *Suaeda maritima* community most likely replaces the *Salicornia europaea* community on coarser texture.

The community has only been reported in a few studies (e.g. Iversen, 1932, 1936; Jessen, 1968).

Spergularia maritima-Puccinellia distans community

Spergulario-Puccinellietum distantis

Spergularia maritima, Puccinellia distans and occasionally *Spergularia salina* are dominating the rather open and fragmentary pioneer vegetation. *Spergularia maritima* may form large rounded cushions, but more often scattered individuals occur. The vegetation is often accompanied by *Puccinellia maritima* and *Juncus buffonius, Plantago maritima, Agrostis stolonifera, Salicornia europaea* and *Triglochin maritimum* may also appear.

The community develops in places with irregular changing conditions and depressions (e.g. salt pans) with stagnant water in the middle-upper geolittoral zone (Gillner, 1960; Bakker *et al*., 1993). It may occasionally occupy areas where the primary communities have been split up or totally destroyed, e.g. through the action of winter ice and waves on an easily erosive substrate (Gillner, 1965). It forms vegetation mosaic with the *Salicornia europaea* community in salt pans with lower salinity (#5).

The *Spergularia maritima-Puccinellia distans* community is very unstable and

dependent on intensive grazing ("cattle-track" community). When grazing ceases the community will be replaced by the *Puccinellia maritima* or the *Juncus gerardi* community, depending on the moisture (Gillner, 1960).

The community is sparsely documented in this investigation, where vegetation mosaic with the *Salicornia europaea* is found (#5) (Iversen, 1936; NERI, 1996; Raunkiær, 1910; Vestergaard *et al*., 1978). The community is also reported in Påhlsson (1994) and Vestergaard (1987).

Puccinellia maritima community

Puccinellietum maritimae

In the initial phase of this community, *Puccinellia maritima* is a delicate plant, but soon it spreads out to form a thick turf (optimal phase), growing in all directions and catching fresh material at every tide until it forms shallow mounds that merge into each other (Ellenberg, 1988). Where the sediment is very soft, grazing turns the surface into a system of hollows and hummocks, which favours the vegetative growth of *Puccinellia* and *Agrostis stolonifera*. In sandy places *Glaux maritima* is often co-dominant. In badly drained areas (e.g. salt pans) in the upper parts of the *P. maritima* community, where the salt concentration is high, *Plantago maritima* and *Triglochin maritima* are frequent. Often *Aster tripolium, Limonium vulgare*, *Suaeda maritima, Spergularia maritima* and *Halimione portulacoides* may be prominent.

According to Ellenberg (1988) *P. maritima* can establish itself once the tidal flats have become silted up to about 20 cm below the mean high water mark. Mostly it first comes in at a slightly higher level (mean high water mark), where it replaces the *Spartina-* or *Salicornia* communities (#7). The initial phase of the *Puccinellia maritima* community thus appears in the transition from higher hydrolittoral to the lower geolittoral. *Puccinellia maritima* thrives well both in very wet soil and in soil which is rather dry at times, as well as on sandy or clayey ground. It grows best, though, on a wet and clayey bottom (Warming, 1906). *Puccinellia maritima* dominates where the maximum salt concentration is above 25‰, whereas it has difficulty in asserting itself in concentration between 25 and 9‰ (Mikkelsen, 1949a). It may though occur in larger depressions or creeks in areas where the salt concentration of the sea water is even lower. Where the conditions are more brackish, as in the Baltic Sea, this community is replaced by an *Agrostis stolonifera* dominated vegetation in the *Juncus gerardi* community.

Grazing is an important factor in maintaining the almost complete dominance of *Puccinellia maritima* in this community. According to Bakker (1985) a high grazing pressure may though cause a decrease in the cover of *Puccinellia maritima* and replace the community with a *Spergularia maritima-Puccinellia distans* community (Gillner, 1960). If management ceases in a *Puccinellia maritima* community, the vegetation in the lower geolittoral zone is easily replaced by a *Scirpus maritimus* community (#6) (Vestergaard, 1976; Pehrsson, 1988) or *Halimione portulacoides* community (Jensen, 1985; Bakker *et al*., 1993).

According to this study (#4, #7 & #8) and the literature, the *Puccinellia maritima* community is very common and widespread (e.g. Beeftink, 1959; Gravesen, 1969; Gravesen & Vestergaard, 1969; Grøntved, 1963; Iversen, 1932, 1936; Jensen, 1976; Jessen, 1968; Mikkelsen, 1949a, 1949b; Petersen, 1982; Påhlsson, 1994; Raunkiær, 1910; Vestergaard, 1982; Vestergaard, 1987; Warming, 1906).

Halimione portulacoides community

Halimionetum portulacoides

In this community the chamaephyt *Halimione portulacoides* is dominating the vegetation. In the transition zone to the *Puccinellia maritima* community, where the vegetation is more open, *Limonium vulgare* and *Plantago maritima* may occur in large quantities (see # 2). In the upper parts *Artemisia maritima* occurs locally, sometimes in large quantities (Beeftink, 1959). Other species such as *Aster tripolium*, *Triglochin maritimum, Suaeda maritima* and *Spergularia media* appears in varying quantities.

The *Halimione portulacoides* community is situated in the lower geolittoral zone between the *Puccinellia maritima-* and *Festuca rubra* communities, where the salt concentration of the sea water is high. It finds its main habitat on well-aerated silty banks along tidal creeks and in small silted creeks in the lower geolittoral (Beeftink *et al*., 1978; Bakker, 1989).

Thirty-five years after grazing ceased in a salt marsh vegetation dominated by *Puccinellia maritima* and *Salicornia europaea* at Skallingen, Jensen (1985) found that the vegetation had changed into a *Halimione portulacoides* community. At the outer salt marshes on Skallingen the *Halimione portulacoides* community had been replacing the *Puccinellia maritima* community since 1930. At very low grazing pressure or in a transitional phase after the resumption of grazing the *Halimione portulacoides* community may be dominated by *Limonium vulgare* (Jensen, 1985; Bakker, 1989). At higher grazing pressure *Halimione portulacoides* is suppressed as it appears to be sensitive to various sorts of physical damage, i.e. human trampling and treading by cattle and sheep, which is partly due to damage of the shoots and partly to compaction of the sediment (Jensen 1985). Mowing reduces the growth of *Halimione portulacoides* to small scattered individuals (Beeftink *et al*., 1978).

Apart from single occurrences in the inner Danish waters *Halimione portulacoides* is indigenous to the Wadden Sea in Denmark. The community is documented from Skallingen (Beeftink, 1959) (# 2), but also reported in Petersen (1982) and Påhlsson (1994). When Raunkiær studied the vegetation at Skallingen in 1909 *Halimione portulacoides* was not observed (Raunkiær, 1910). It is now abundantly occurring in the younger outer salt marshes on Skallingen (Petersen, 1982). Spreading to other areas is prevented by too high frequency of frost in the winter and by lack of effective tidal influence (Vestergaard, 1989).

Juncus gerardi community

Juncetum gerardii

This community is characterized by *Juncus gerardi, Agrostis stolonifera* and/or *Festuca rubra*. The species *Plantago maritima, Glaux maritima* (in the lower parts of this zone), *Artemisia maritima, Triglochin maritima, Aster tripolium* and *Limonium vulgare* are usually present as scattered shoots or may dominate locally at rather high salinity. Where the salinity is rather low the *Juncus gerardi* community is associated with oligohalabious species such as *Potentilla anserina, Carex extensa, Alopecurus geniculatus* and *Eleocharis uniglumis* (Iversen, 1936; Mikkelsen, 1949a). Small individuals of *Scirpus maritimus* and *Phragmites australis* may occur on grazed salt marshes where the salinity is rather low (Vestergaard, 1976). A fragmentary or thin bottom layer of bryophytes is often present (Tyler, 1969 and Påhlsson, 1994).

Where hay is made the vegetation may be rich in *Festuca rubra* and may include species such as *Odontites littoralis, Rhinanthus serotinus, Holcus lanatus* and *Ophioglossum vulgatum* (Gillner, 1960, 1965 p. 99; Gravesen, 1969 Table VI; Warming, 1906 p. 209).

A *Festuca rubra* ssp. *littoralis*-dominated variant with *Armeria maritima* and *Plantago maritima* has been found at Skallingen (Beeftink, 1959) (#10). *Festuca ru-*

bra ssp. *littoralis* is an ecological race which can endure salt ground water more than *Juncus gerardi* (Petersen, 1982). This variation is favoured by decomposed seadrift and borders the *Puccinellia maritima* community in young salt marshes. It is restricted to the south-western Jutland and appears when grazing ceases.

The species composition of the Juncus gerardi community depends on soil moisture, salinity, the presence of decomposed seaweed and the management regime (Gillner, 1960). In salt marshes with very high salt concentrations, *Juncus gerardi* dominates the middle geolittoral zone. *Juncus gerardi* comprises both very wet and relatively dry soils and dominates in salt marshes with 5 to 30‰ salt in the soil water (Mikkelsen, 1949a). In the sandy salt marshes further landwards, where the rainwater can remain in the hollows for a while, Juncus gerardi may though dominate as a brackish-water plant (Petersen, 1982). *Festuca rubra* dominated salt marshes occurs in the well-drained parts of the middle geolittoral zone and on creekbanks where the sediment is well drained, oxygenated and under low tidal influence. *Agrostis stolonifera* may dominate in the lower geolittoral where the sea water salt concentration is low, e.g. the Baltic Sea.

The *Juncus gerardi* salt marsh borders the *Puccinellia maritima* community or the *Eleocharis uniglumis* community in the lower geolittoral zone and in the upper parts of the geolittoral it borders the *Festuca rubra* maritime grassland. Where the conditions are brackish, as in the Baltic Sea, an Agrostis stolonifera dominated *Juncus gerardi* community may occur in the transition from the higher hydrolittoral zone to the lower geolittoral zone and thus replace the *Puccinellia maritima* community.

The species composition in this community depends largely upon the management regime. Juncus gerardi is favoured by grazing and cutting, probably due to regeneration from rhizome buds (Bakker, 1978; 1989; Vestergaard, 1976; 1994). The competitive power of *Festuca rubra* is reduced considerably by grazing while it is less affected, or even favoured, by cutting (Bakker, 1978; 1989; Jensen, 1985; Mikkelsen 1949a; Vestergaard, 1994). The negative effect from grazing may in part be due to soil compaction by treading by the grazing animals. Agrostis stolonifera is favoured by grazing (Pehrsson, 1988). At very intensive grazing the vegetation is replaced by a Spergularia maritima-Puccinellia distans community (Gillner, 1960). With a decrease in the grazing or hay making intensities the *Juncus gerardi* community will be dominated by *Festuca rubra*. When management ceases, the vegetation may be invaded by *Phragmites australis* and *Scirpus maritimus* and will consequently change into a *Phragmites australis-Scirpus maritimus* community (Pehrsson, 1988; Petersen, 1982). On creekbanks where the sediment is well drained and under low tidal influence, ceased grazing may result in the establishment of an *Artemisia maritima* community (Jensen, 1985).

The *Juncus gerardi* community is the incomparable most important association of the middle and upper geolittoral zone and documented from various salt marshes throughout Denmark (#10-13). The *Festuca rubra* ssp. *littoralis* variation is so far only documented from Skallingen by Beeftink (1959). The *Juncus gerardi* community has been reported in numerous papers (e.g. Beeftink, 1959; Gravesen, 1969; Gravesen & Vestergaard 1969; Grøntved, 1963; Iversen, 1932, 1936; Jensen, 1976; Jessen, 1968; Mikkelsen, 1949a , 1949b; Larsen, 1956; Petersen, 1982; Påhlsson, 1994; Raunkiær, 1910; Runge, 1983; Vestergaard, 1970; Vestergaard *et al*. 1978; Vestergaard, 1982; Vestergaard, 1987; Warming, 1906).

Tetragonolobus maritimus community

The vegetation in this community is dominated by *Tetragonolobus maritimus*

along with species such as *Molinia caerulea*, *Festuca rubra*, *Juncus gerardi*, *Potentilla anserina* and occassionally *Primula farinosa* (Larsen, 1956).

The *Tetragonolobus maritimus* community appears in the upper geolittoral and the epilittoral zones on brackish marshes (Gillner, 1965). The *Tetragonolobus maritimus* community replaces the *Festuca rubra* community at Bornholm.

In Denmark this community is restricted to Bornholm where it is common along the northern coasts (Hansen, 1987; Larsen, 1956; Påhlsson, 1994; Runge, 1983).

***Blysmus rufus* community**

Blysmetum rufi

This community is dominated by *Blysmus rufus* along with *Agrostis stolonifera*, *Festuca rubra*, *Juncus gerardi*, *Phragmites australis* and several other species.

The *Blysmus rufus* community is found from the lower to the upper geolittoral zone and seems to be concentrated to somewhat exposed and rather saline marshes on coarse material (Gillner, 1965). It replaces the *Juncus gerardi* community on coarse ground (Påhlsson, 1994) and it often borders the *Eleocharis uniglumis* community in the lower geolittoral zone (Gillner, 1960).

The *Blysmus rufus* community is restricted to the eastern and southern parts of Denmark (e.g. Påhlsson, 1994; Runge, 1983).

***Artemisia maritima* community**

Artemisietum maritimae

The vegetation in this community is dominated by Artemisia maritima while *Limonium vulgare*, *Festuca rubra*, *Agrostis stolonifera*, *Glaux maritima*, *Juncus gerardi, Plantago maritima, Triglochin maritima, Halimione portulacoides* and *Juncus maritima* may appear in varying quantities.

Artemisia maritima is a dominant on sandy and well-drained soil and in salt marshes with salt concentrations of 18-25‰, but has sporadic occurrences in areas with down to 2‰ salt (Mikkelsen, 1949a). The community is particularly developed at driftlines effected by decomposed seaweed ("Eve"-vegetation), tidal inlets and beach ridges in the lower and middle geolittoral zone (Påhlsson, 1994).

The Artemisia maritima community is negatively effected by grazing (Bakker, 1985). This is partly due to the destruction of the rhizomes of *Artemisia maritima* and *Limonium vulgare* by treading and soil compaction. On the contrary there is no evidence of defoliation (Jensen 1985). By intensive grazing the community converts to a *Juncus gerardi* community dominated by *Juncus gerardi* or a *Puccinellia maritima* community (Bakker & Ruyter, 1981; Påhlsson, 1994).

According to literature the community is quite common in Denmark (Jessen, 1968; Mikkelsen, 1949a; Påhlsson, 1994; Raunkiær, 1910; Vestergaard *et al*. 1978). In this study the community is only documented from Skallingen (e.g. Beeftink, 1959; Iversen, 1936; NERI, 1996) and south-eastern Denmark (Vestergaard, 1982) (# 1).

***Juncus maritima* community**

Oenantho-Juncetum maritimi

The *Juncus maritima* community consist of 1/2 m high stands of *Juncus maritimus* giving this species poor community its grey-green colour (Warming, 1906). *Phragmites australis, Glaux maritima, Plantago maritima, Aster tripolium, Triglochin maritima* and *Carex extensa* may appear along with a number of rare species such as *Apium graveolens, Bupleurum tenuissimum, Samolus valerandi* and *Oenanthe*

lachenalii. Where the stems are less dense, *Vaucheria*-species occur in the bottom (Warming, 1906).

This community develops in sheltered parts of brackish coasts, often directly below the reed swamps (Påhlsson, 1994) or in contact with the *Artemisia* community (Dierssen, 1996). *Juncus maritimus* is tolerant to a broad range of soil salinity and moisture conditions (Ranwell, 1972).

According to Runge (1980) and Sykora (1983) (both cf. Bakker, 1989) *Juncus maritimus* dominated stands are hardly grazed or are not grazed at all, while Dierssen (1996) found that once the community has established itself it is less sensitive to grazing.

The distribution of the Juncus maritima community is limited to the south-eastern Denmark (e.g. Grüner, 1934; Mikkelsen & Olsen, 1956; Iversen, 1936; Vestergaard, 1989; Warming, 1906).

Eleocharis uniglumis community

Eleocharitetum uniglumis

Eleocharis uniglumis and very often *Agrostis stolonifera* dominates the vegetation of this very species-poor community (Tyler, 1969). *Carex paleacea* and *Triglochin maritimum* often codominate the community and the ground is typically covered with *Drepanocladus tetraphylla*. Reed-species, e.g. *Phragmites australis, Scirpus tabernaemontani* and *S. maritimus* may occur with scattered shoots and several species from the *Juncus gerardi* community may appear (Gillner, 1960).

The *Eleocharis uniglumis* community occurs in the lower parts of the geolittoral zone at brackish shores (Tyler, 1969) and is often an indication of fresh-water influence. The ground is usually very soft, clayish and soaked by sea-water during most of the year (Tyler, 1969 & 1971). It replaces the *Puccinellia maritima* community in the lower geolittoral zone in brackish waters, primarily in the Baltic Sea.

The community depends partly on grazing (Gillner, 1960) and when management ceases the vegetation will be replaced by a *Scirpus maritimus* community, with Eleocharis uniglumis corporated as part of the lower stratum (Gravesen, 1969).

The community is reported in several papers (e.g. Gravesen, 1969; Gravesen & Vestergaard, 1969; Grøntved, 1963; Jessen, 1968; Påhlsson, 1994).

Festuca rubra community

The main species in this very variable community is *Festuca rubra*, but a more characteristic plant is *Trifolium fragiferi* - giving this community its Danish name of "jordbærkløvereng". The vegetation is characterised by the occurrence of nitrophilious species such as *Leontodon autumnalis, Potentilla anserina, Trifolium repens* and *Poa pratensis* (Gillner, 1960; Iversen, 1936; Jessen, 1968; Mikkelsen, 1949a).

The *Festuca rubra* community is found in the middle-upper geolittoral zone along shores of varying salinity. The community makes a gradual transition from the *Juncus gerardi* community towards an epilittoral common with fewer halophilic species. The *Elymus repens* community often appears within the *Festuca rubra* community and in salt marshes with narrow drift-lines, a separation of the two communities may be difficult (see #16).

The *Festuca rubra* community is widespread in Denmark and documented from various salt marshes (#14 & #16).

Elymus repens community

Elymetum repentis maritimum

This community is dominated by perennials of which *Elymus repens* is the main species. Common species are in general *Festuca rubra, Poa pratensis, Rumex crispus, Potentilla anserina, P. reptans, Atriplex littoralis, A. latifolia, Glaux maritima, Cirsium vulgare, Iris spuria, Festuca arundinacea, Vicia cracca* and *Galium verum*. Occasionally *Phragmites australis* and partially *Sonchus palustre* create stands tall enough to hide a man (Jessen, 1968) (#23). A *Lepidium latifolium* variation dominated by *Elymus repens, Lepidium latifolium, Rumex crispus, Galium verum* and *Iris spuria* (at Saltholm) may cover large areas (Påhlsson, 1994; Vestergaard *et al*., 1978) (see #21).

The *Elymus repens* community usually occurs in the middle or upper geolittoral zones, but may also appear on beach ridges in the lower part of the geolittoral zone. It appears on sandy soil affected by the humus of seadrift, is generally indifferent as regards the salt factor, but may appear where the salt concentration of the soil water is as high as 30‰ (Mikkelsen, 1949a). The community is favoured by the occurrence of decomposed seaweed, creating an "eve" vegetation and the content of seadrift seems to be more important than the salinity.

The Elymus repens community often appears within stands of the *Festuca rubra* community in the upper geolittoral zone and in salt marshes with narrow drift-lines, a separation of the two communities may be difficult (see #16).

This community occurs in ungrazed areas or in grazed salt marshes where fertilisers are applied (Bakker, 1989).

The *Elymus repens* community is quite common (e.g. Gravesen & Vestergaard, 1969; Jessen, 1968; Vestergaard *et al*., 1978; Vestergaard, 1987) and documented from several salt marshes (#16, #21 & #23). The *Elymus repens-Lepidium latifolium* variation is restricted to the south-eastern parts of the country, e.g. Saltholm (Vestergaard & Vintner, 1985).

Agrostis stolonifera-Triglochin palustre community

This community is dominated by *Agrostis stolonifera* and *Triglochin palustre* along with *Eleocharis uniglumis, Juncus gerardi, Plantago maritima, Potentilla anserina* and *Triglochin maritima*.

The *Agrostis stolonifera-Triglochin palustre* community develops on poorly drained ground on clay or gyttja in every part of the geolittoral zone (Tyler, 1969). It occurs in less salt areas than an *Agrostis stolonifera* dominated *Juncus gerardi* community, e.g. near outlets of fresh water.

It develops under very high grazing intensities. When grazing pressure is reduced in the middle or upper geolittoral zones a slow development towards a *Juncus gerardi* community has been observed (Tyler, 1969; Vestergaard & Vintner, 1985). If grazing ceases, the lower stands of the *Agrostis stolonifera-Triglochin palustre* community may change into typical stands of an *Eleocharis uniglumis* community.

The main distribution area is probably the eastern Denmark, but the community is sparsely reported in the literature (e.g. Iversen, 1932, 1936; Påhlsson, 1994).

Potentilla anserina-Festuca arundinacea community

Potentillo-Festucetum arundinaceae

The *Potentilla anserina-Festuca arundinacea* community is a coarse vegetation dominated by large tussocks of *Festuca arundinacea*, forming a high canopy. *Potentilla anserina, Festuca rubra* and *Agrostis stolonifera* are often abundant (see #20), while *Hordeum secalinum, Elymus repens, Poa pratensis, Holcus lanatus, Trifolium repens* and *Juncus gerardi* are present in varying quantities. It may though have a

higher frequency of salt marsh species.

The community is characteristic of sandy and stony soils affected by the humus of seadrift, kept moist under influence of fresh water seepage or frequent inundation of brackish water (Mikkelsen, 1949a; Påhlsson, 1994; Rodwell, 1992). It occurs in the transition zone between the geo- and epilittoral zones, marking the mean high water line or on banks of tidal creeks.

This community is generally ungrazed.

The *Potentilla anserina-Festuca arundinacea* community appears in the south-eastern parts of Denmark (e.g. Jessen, 1968; Larsen, 1956; Påhlsson, 1994; Vestergaard, 1982; Vestergaard, 1987), but is sparsely documented in this study (#20).

Agrostis stolonifera-Alopecurus geniculatus community

The *Agrostis stolonifera-Alopecurus geniculatus* community is dominated by *Agrostis stolonifera* and *Alopecurus geniculatus* usually creating very small open or closed swards. It is often associated with *Juncus buffonius, Potentilla anserina, Ranunculus sceleratus* and *Glaux maritima*.

This community is found in heavily grazed parts of the upper geolittoral zone where the trampling almost fallows the ground ("trittgesellschaft") (Tyler, 1969). It typically occurs on silty soils kept moist or waterlogged under influence of fresh water seepage (Rodwell, 1992).

It is probably widely distributed in Denmark, but sparsely reported (e.g. Grøntved, 1929; Iversen, 1936; Mikkelsen, 1949a; Vestergaard *et al*., 1978).

Reed swamps

Phragmiteteo-Magnocaricetea

The three most important species in reed swamps on Danish salt marshes are *Phragmites australis, Scirpus maritimus* and *S. tabernaemontani*. In Denmark it has been widely adopted to distinguish between outer ("telmatisk") reed swamps in the hydrolittoral zone (= *Phragmites australis-Scirpus maritimus* community) and inner ("terrestrisk") reed swamps in the geolittoral zone (=*Scirpus maritimus* community).

Phragmites australis-Scirpus maritimus community

Phragmito-Scirpetum maritimi

This community consist of a mixture of *Phragmites australis, Scirpus maritimus* and *S. tabernaemontani* with *Festuca rubra, Agrostis stolonifera* (#9), *Juncus gerardi* and *Elymus repens* in the bottom layer. Most often there are scattered plants of a wide range of species: e.g. *Triglochin maritima, Plantago maritima, Oenanthe lachenalii, Cochlearia officinalis, Apium graveolens* and *Atriplex hastata*. Near seepages of fresh water, the vegetation may contain meadow species such as *Trifolium repens, Holcus lanatus* and *Poa pratensis* (#15).

This community is restricted to the geolittoral zone. *Juncus gerardi* dominates the bottom layer in the lower geolittoral zone with very high salt concentrations of the sea water, *Agrostis stolonifera* dominates in brackish waters (#9), e.g. the Baltic Sea (Påhlsson, 1994; Vestergaard, 1994) and *Festuca rubra* mostly appears in the middle and upper geolittoral zones (Påhlsson, 1994) (#15).

The *Phragmites australis-Scirpus maritimus* community appears in salt marshes with a very low grazing pressure or where grazing has ceased. In a three year mowing experiment at Øslemagle Revle (barrier island) at the Baltic Sea, Vestergaard (1985) observed considerable changes in the composition of the dominant species

in a *Phragmites australis-Scirpus maritimus* community. Both *Scirpus maritimus* and *Agrostis stolonifera* increased, while *Phragmites australis* decreased significantly when mowing was renewed. According to Vestergaard (1994) a *Phragmites australis-Scirpus maritimus* community dominated by *Scirpus maritimus* is more resistant than when *Phragmites australis* dominates the vegetation. He found that a *Phragmites*-dominated stand changed into an *Agrostis stolonifera* dominated *Juncus gerardi* community within a few years when mowing was introduced.

The *Phragmites australis-Scirpus maritimus* community is widespread, well documented in this study (#9 & #15), and numerously reported in the literature (e.g. Böcher, 1946; Gravesen, 1969; Gravesen & Vestergaard, 1969; Grüner, 1934; Grøntved, 1963; Iversen, 1936; Jensen, 1976; Jessen, 1968; Larsen, 1956; Petersen, 1982; Påhlsson, 1994; Vestergaard, 1976; Vestergaard, 1985; Vestergaard, 1987; Warming, 1906).

It is increasing in Denmark as a consequence of ceasing management.

Scirpus maritimus community

Scirpetum maritimi, Scirpetum tabernaemontani and Phragmitetum australis

The *Scirpus maritimus* community is dominated by *Scirpus maritimus, Phragmites australis* or *Scirpus tabernaemontani* forming a tall dense cover (Gillner, 1960, p. 42). The bottom layer of the reeds is distinguished by a vegetatively propagating Vaucheria, often forming a compact blackish green blanket, where the reeds are less densely closed (Tyler, 1969). The physiognomy and, to a certain extent, the floristic composition of the reeds are influenced by the exposure of the site and the texture of the substrate.

The community is characteristic of the hydrolittoral zone. In sheltered sites *Phragmites australis* predominates, while the two *Scirpus species* appear to have more competitive power on sandy and easily erosive ground (Tyler, 1969). *Scirpus tabernaemontani* is very sensitive to wind- and water exposure (Gillner, 1960), while *Scirpus maritimus* tolerates a higher degree of exposure and a somewhat higher salinity than both *Phragmites australis* and *Scirpus tabernaemontani* (Gillner, 1965). At very low salinity *Phragmites australis* is the most prominent species and halophytic species are less prominent. This situation is represented by its own community (*Phragmites australis* community - not included in this study). The *Scirpus maritimus* community replaces the *Salicornia maritima* community where the conditions are more brackish.

The *Scirpus maritimus* community on clay seems quite stable, while reeds on sand or silt is more susceptible to repeated reed cutting and heavy grazing. It will easily replace a *Puccinellia maritima* community if management ceases (#6) (Vestergaard, 1976; Pehrsson, 1988).

The *Scirpus maritimus* community occurs throughout Denmark (e.g. Böcher, 1946; Gravesen & Vestergaard, 1969; Grøntved, 1963; Iversen, 1936; Jessen, 1968; Larsen, 1956; Petersen, 1982; Påhlsson, 1994; Runge, 1983; Vestergaard, 1987; Warming, 1906) and is well documented in this study (#6, #18 & #19).

Elymus pungens community

Atriplici-Elymetum pungens

Elymus pungens creates a dense canopy and prevents the establishment of other species in this species-poor community (Bakker, 1989).

It appears along banks of tidal creeks on soils with a very high silt content,

somewhat higher on the salt marshes and locally in the lower geolittoral (Andresen *et al*., 1990; Beeftink, 1959; Bakker, 1989). The vegetation depends on a marked nutrient supply and tolerates high salt concentrations (Beeftink *et al*., 1978; Dierssen, 1996).

The *Elymus pungens* community often appears with the *Artemisia maritima* and *Halimione portulacoides* communities and may replace the *Artemisia maritima* community where the banks are silted up with much fine material (Beeftink, 1959; Dierssen, 1996).

It is restricted to ungrazed salt marshes (Bakker, 1985, 1989; Dierssen, 1996) and appears in *Juncus gerardi* and *Artemisia maritima* salt marshes where grazing has ceased (Bakker, 1985, 1989). Andresen *et al*., (1990) found that an *Elymus pungens* community had developed in the upper geolittoral zone 8 years after management had ceased in a salt marsh in Leybucht (The Netherlands).

This community is so far restricted to south-western Jutland. According to Hansen, (1945, 1948, cf. Beeftink, 1959) the most northern record of this community in the 1940´s was from the isle of Fanø. The present distribution is mostly unknown, but the community is propably extending in Denmark as a consequence of eutrophication and ceasing management (Bakker *et al*., 1993).

Sagina maritima-Cochleare danica community

Sagino-Cochlearietum danicae

The *Sagina maritima-Cochleare danica* community covers only very small patches and is characterised by a few weakly competitive species, of which *Sagina maritima* and *Cochlearia danica* must be considered constant, but *Bupleurum tenuissimum, Plantago coronoporus* and *Erophila verna* may also occur. Often the vegetation covers only 30-50% of the ground (Gillner, 1960).

The *Sagina maritima-Cochleare danica* community is typical for the transitional zone between dune and salt marsh and low elevations within salt marshes e.g. anthills by *Lasius flavus*. The community demands open, dry and warm soil and is also found in the epilittoral zone (Gillner, 1965).

The vegetation seems to depend on grazing.

This rare community covers only very small patches and has not been documented in this study. It is reported in the literature by Grüner (1934), Iversen (1936: tab. 56) and Vestergaard *et al*., (1978).

This examination of the distribution of Danish Salt marsh communities is suffering from lacking data, which probably to a large extent would modify the precocious conclusions of ecology and distribution. Yet, these data are the only data available at the present time.

To obtain a more complete and accurate picture of the distribution, ecology and status of Danish plant communities in general, and of salt marsh communities in particular, it is recommended to initiate a systematic survey of Danish natural areas and their contents of plant species and communities.

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