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THE ALGAL COMMUNITIES OF THE NORTHEASTERN PART OF THE SALTMARSH "DE MOK" ON TEXEL (THE NETHERLANDS)

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SUMMARY

For more than a year, the algal vegetation of a particular part of the saltmarsh "De Mok" was studied, by means of permanent quadrats. Three communities of surface algae were distinguished: the *Vaucheria subsimplex/Enteromorpha prolifera/Microcoleus* community, the *Vaucheria coronata/ Enteromorpha prolifera/Microcoleus* community and the *Vaucheria coronata/ Rhizoclonium/Microcoleus* community. Each of these occupied a consecutive zone, from low to high, in the marsh and had a number of characteristic species, for some of which a significant correlation to higher or lower situated permanent quadrats could be shown.

A *Blidingia minima* community, epiphytic on *Salicornia* stems, with the red alga *Bangia atropurpurea* as a characteristic species, was intermingled with the *Enteromorpha prolifera* unit of the first community during a part of the year.

1. INTRODUCTION

During the last five years, the number of studies on the algal vegetation of Dutch saltmarshes has increased considerably. Especially in the Southwest Netherlands, this vegetation has been studied thoroughly. From this area, descriptions of algal communities (NIENHUIS 1970), of the periodicity in various algal vegetations (NIENHUIS & SIMONS 1971, POLDERMAN 1974a, SIMONS 1975b) and of the general zonation pattern of saltmarsh algae (NIENHUIS 1973) have been given. Recently, a monograph of *Rhizoclonium riparium* (NIENHUIS 1975) appeared. SIMONS (1975 s.l.) studied *Vaucheria* species both in this area and in the Dutch Wadden area. Comparatively little information has been published from the latter area, although special groups of saltmarsh algae have been dealt with, viz. *Vaucheria* (SIMONS 1974a, 1975a), *Bostrychia scorpioides* (Huds.) Mont. and *Catenella repens* (Lightf.) Batt. (DEN HARTOG 1955, 1958), *Chrysomeris ramosa* (POLDERMAN & PRUD'HOMME VAN REINE 1973) and *Bangia atropurpurea* (POLDERMAN 1972). General remarks on combinations and communities of saltmarsh algae in the Wadden area were made by DEN HARTOG (1973). The zonation of algae in a brackish polder was described by POLDERMAN (1975).

Within the scope of a study of the algal vegetation of saline areas in the Wadden area (POLDERMAN in prep.) special interest was taken in the algal vegetation of "De Mok", because a clear and relatively undisturbed zonation pattern extends over larger areas in this marsh. It also offered the opportunity to include *Bangia atropurpurea* in the proposed study. Up to now this species has only been reported from two saltmarsh areas in the Wadden Sea: Griend, on a creek-wall (VAN DER WERFF 1950), and "De Mok".

The present paper deals with the distinction of algal communities; the syntaxonomic implications of this will be dealt with in a later paper (POLDERMAN in prep.).

2. TOPOGRAPHY

The saltmarsh "De Mok" borders a shallow bay, "De Mokbaai" in the south of Texel. "De Mokbaai" is connected with the Wadden Sea. In the south, west and northwest, bay and marsh are bordered by dunes. The northeastern part of the marsh is bordered by a sea-wall (a relatively narrow artificial dune ridge behind which a saline seepage area "De Petten" is situated). The marsh is divided by a shallow trench, which used to be an extension of the drainage canal of southwest Texel, "De Moksloot". The water outlet from "De Moksloot" was controlled by a sluice, which is now permanently blocked. The southern part of "De Mok" is subject to strong seepage of fresh water, especially when in the wet seasons the water level of the dune land builds up. In the northeastern part seepage conditions seem to be in the opposite direction, judging from the brackish area inland.

The northeastern part of the marsh is almost devoid of "saltmarsh reeds" (*Spartina townsendii* H. et J. Groves, *Scirpus maritimus* L., *Juncus maritimus* Lamk. and *Phragmites australis* (Cav.) Trin. ex Steud.), which are dominant in the remaining part of the marsh. Between the bank of the trench and the sea-wall, a slight depression slopes down in an easterly direction. Its phanerogamic vegetation, dominated by grasses, is kept low by intensively grazing and trampling sheep, which are concentrated in the northeastern part of the marsh.

The differences in hydrology and vegetation between the northeastern part and the remaining saltmarsh justify a separate study of the algal vegetation of both.

3. METHODS

3.1. Selection of permanent quadrats

The area studied extended from the lowest part of the depression to the base of the sea-wall. In it, a *Salicornietum* (non *strictae*) was present in a zone over about 5 m. Towards the sea-wall, it was followed up by various stages of the *Puccinellietum maritimae* over 35 m and by a *Juncetum gerardii* over 5 m. A series of seven permanent quadrats (PQ) was projected in a transect line perpendicular to the zonation, each PQ being representative of a vegetation type:

PQ 1. A *Salicornietum* of *Salicornia europaea* L. (div. sspp., non *stricta*), *Suaeda maritima* L. and *Spergularia media* (L.) Griseb.

PQ 2. A young *Puccinellietum maritimae* of *Puccinallia maritima* (Huds.) Parl. with *Salicornia europaea*, *Suaeda maritima* and *Spergularia media*, 1.7 cm above the level of PQ 1.

PQ 3. A *Puccinellietum maritimae* of *Puccinellia maritima* varying in cover percentages between 20% in winter and 80% in summer, with scattered the three companion species mentioned for PQ 2, 3.6 cm above PQ 1.
PQ 4. A *Puccinellietum maritimae* with scattered *Glaux maritima* L. and *Plantago maritima* L. added to the companion species, 4.9 cm above PQ 1.
PQ 5. A *Puccinellietum maritimae* of *Puccinellia maritima* with six companion species, of which the last, *Juncus gerardii* Loisl. covered up to 10% during the year, 14.7 cm above PQ 1.
PQ 6. A *Puccinellietum maritimae* similar to the previous, but with *Juncus gerardii* covering 5-30%, 19.9 cm above PQ 1.
PQ 7. A *Juncetum gerardii* of *Juncus gerardii* and *Plantago maritima* with *Parapholis strigosa* (Dum.) Hubb. among the companion species, 37-41 cm above PQ 1. Drift-accumulation material was deposited infrequently.

Between PQ 6 and 7 the inclination angle of the marsh increases rapidly towards the sea-wall. For that reason the *Juncetum gerardii* forms only a narrow strip. The names of the plant communities used are those given by WESTHOFF & DEN HELD (1969).

The quadrats, measuring 50 × 50 cm, were studied from 1-4-'74 to 9-2-'75 with intervals of 2-6 weeks.

3.2 Surveying of the permanent quadrats

The same sampling and analysis method as described by POLDERMAN (1975) was used. The size of the samples seldom exceeded 1 cm^2, but was usually smaller. Preceding investigations had shown that the minimum area of the vegetation components was far less than 1 cm^2. Often a *Vaucheria* sample had to be cultivated in order to induce fruitings necessary for identification. In the initial period of the investigation, the facilities for this were not yet available, while later it was not always possible to obtain fruitings from single filaments (*table 2*).

3.3 Taxonomic notes

For the Xanthophyceae, the nomenclature by CHRISTENSEN & THOMSEN (1974) was used. The taxonomy of *Bangia atropurpurea* was interpreted in accordance with GEESINK (1973). For the coccoid and filamentous *Cyanophyceae* the same taxonomic concepts were applied as in previous papers (POLDERMAN 1974a, 1975). More detailed information on the taxonomic concepts used for saltmarsh *Cyanophyceae* will be published later (POLDERMAN in prep.). For the *Chrysophyceae*, the nomenclature of PARKE & DIXON (1968), partly revised by GAYRAL & LEPAILLEUR (1971), was used provisionally. *Enteromorpha torta* was not distinguished (POLDERMAN 1975), but an "*intestinalis*" form of *E. prolifera* (NIENHUIS 1969, 1975) was treated as a separate taxon, for ecological reasons only.

4. THE ALGAL VEGETATION

Three algal components occurred, recognizable in the field: *Vaucheria*, filamentous *Chlorophyceae* and *Cyanophyceae* (mainly *Oscillatoriaceae*). Usually, the algal vegetation was a mosaic of two or three components. The components were recognizable by their dominants, but they contained also other species, dominant elsewhere, in minor quantities. Occasionally, the components were not clearly separated into three groups as when, for instance, *Vaucheria/Enteromorpha* components occurred. A species could also be dominant in two components which appear different to the eye. Also, species are capable of forming differently structured components. For this reason, in the final description of the vegetation, not the components in the field, but the dominant and companion species are important. *Figure 1*, dealing with the periodicity of the most important groups of saltmarsh algae, is thus not the direct projection of the situation in the field, as was observed with the eye, but a reconstruction after analysis of the field components.

In the area three zones were distinguished based on the similarity in the phanerogamic flora. The first included PQ 1-3, the second PQ 4-6 and the third PQ 7.

4.1 PQ 1-3

In these quadrats, the filamentous green algae and the *Oscillatoriaceae* had most of the cover *(table 2)*. The first reached maximum cover values in the period January-May and October-January. The most important mat-forming Chlorophycea was *Enteromorpha prolifera (table 2)*, in the beginning of autumn partly occurring as *forma "intestinalis"*. Often *E. prolifera* was accompanied by a co-dominant Chlorophycea: in winter *Ulothrix flacca*, during spring, summer and autumn *Blidingia minima*, in autumn, also, *Percursaria percursa* and *E. flexuosa*.

Among the *Oscillatoriaceae*, *Microcoleus chthonoplastes* and *Oscillatoria nigroviridis* often exceeded cover values of 5%. At the end of spring *O. nigroviridis* was reduced to low numbers *(table 2)*. In PQ 3 *Symploca atlantica* took its place immediately. In PQ 1 and 2 it lasted until July before *S. atlantica* and *Microcoleus lyngbyaceus* emerged as dominants. *Schizothrix calcicola* was dominant for a very short period in summer. It lost its dominant role at the same time as *M. lyngbyaceus*. *Symploca atlantica* shared the rises and the falls in the cover of the *Cyanophyceae* with *M. chthonoplastes* for the rest of the period of study.

In PQ 2, *Vaucheria* reached its maximum values of 10% and 5% cover in March and November respectively. During summer, *Vaucheria* was hardly present in the form of filaments. In the three PQs, fruitings were obtained of *Vaucheria subsimplex*, *V. intermedia*, *V. velutina* and *V. compacta*.

In this quadrat *Ulothrix pseudoflacca*, *U. subflaccida*, *Rhizoclonium riparium*, *Bangia atropurpurea*, *Spirulina subsalsa* and *Oscillatoria brevis* were constant species, without a conspicuous seasonal variation. Considered over PQ 1-3,

Table 1. List of species collected in 7 permanent sample plots in "De Mok" in the period of investigation and their relative frequencies (%) during the seasons (4-1-'74 to 15-1-'75).

Season:	winter	spring	summer	autumn
Xanthophyceae:				
Vaucheria subsimplex Cr. fr.	18	–	–	14
Vaucheria velutina C. Ag.	4	4	10	4
Vaucheria arcassonensis P. Dang.	4	11	–	–
Vaucheria intermedia Nordst.	25	7	14	57
Vaucheria compacta Nordst.	7	–	–	4
Vaucheria coronata Nordst.	39	39	29	24
Planktonema lauterbornii Schmidle	26	39	5	7
Tribonema spec.	4	–	–	–
Rhodophyceae:				
Bangia atropurpurea (Roth) C.Ag.	14	29	33	18
Phaeophyceae:				
Pilayella littoralis (L.) Kjellm.	4	–	–	–
Ectocarpus siliculosus (Dillw.) Lyngb.	*	–	–	–
Ectocarpaceae spec.	25	4	5	–
Chlorophyceae:				
Prasiola stipitata Suhr in Jessen	–	–	–	4
Ulothrix verrucosa Lokhorst	*	–	–	–
Ulothrix flacca (Dillw.) Thur.	68	18	–	25
Ulothrix pseudoflacca Wille	75	93	29	69
Ulothrix subflaccida Wille	79	82	48	79
Ulva lactuca L.	–	–	–	4
Ulvaria oxysperma (Kütz.) Blid.	7	11	14	7
Blidingia minima (Näg. ex Kütz.) Kyl.	82	93	81	85
Capsosiphon fulvescens (C.Ag.) Setch. & Gard.	–	4	–	4
Percursaria percursa (C.Ag.) Rosenv.	64	71	76	100
Enteromorpha flexuosa (Wulf. ex Roth) J.Ag.	29	7	24	46
Enteromorpha prolifera (O.F.M.) J.Ag.	79	100	76	100
Enetromorpha prolifera f. "*intestinalis*"	18	14	29	25
Cladophora laetevirens (Dillw.) Kütz.	–	–	–	4
Cladophora spec.	–	4	–	4
Rhizoclonium riparium (Roth) Harv.	79	93	76	96
Pseudotetraspora marina Wille	4	7	–	–
Chrysophyceae:				
Chrysomeris ramosa Carter	–	4	–	–
Apistonema pyrenigerum Pascher	18	32	71	29
Ruttnera maritima (Anand) Parke	–	4	19	–
Ruttnera chadefaudii Bourr. et Magne	–	10	19	4
Cyanophyceae:				
Anacystis dimidiata Dr. et D.	14	11	24	18
Anacystis montana (Lightf.) Dr. et D.	4	21	52	21
Agmenellum thermale (Kütz.) Dr. et D.	4	–	–	4
Gomphosphaeria lacustris Chodat	11	–	–	–

Season:	winter	spring	summer	autumn
Entophysalis deusta (Menegh.) Dr. et D.	–	17	33	7
Anabaena variabilis Born. et Flah.	–	4	10	4
Nodularia harveyana Born. et Flah.	14	32	52	25
Nostoc spec.	–	7	–	–
Calothrix aeruginaea Born. et Flah.	4	4	5	–
Calothrix confervicola Born. et Flah.	–	–	5	14
Plectonema battersii Gom.	7	–	–	–
Spirulina subsalsa Gom.	64	25	24	29
Microcoleus chthonoplastes Gom.	97	96	100	100
Microcoleus lyngbyaceus Gom.	100	96	95	100
Microcoleus tenerrimus Gom.	–	–	–	11
Microcoleus vaginatus Gom.	4	–	–	7
Oscillatoria brevis Gom.	79	64	52	43
Oscillatoria nigroviridis Gom.	97	100	86	75
Symploca atlantica Gom.	75	86	100	93
Schizothrix calcicola Gom.	68	64	71	75
Total number of surveys	28	28	21	28

* = found on 27–1 or 9–2, in 1975.

Nodularia harveyana and *Ulvaria oxysperma* also belonged in this group. In PQ 2, these two had their optimum with four other species: *Anacystis montana, Apistonema pyrenigerum, Ruttnera chadefaudii* and *Entophysalis deusta,* namely in summer and autumn. *Apistonema* even reached a 5% cover in PQ 2 in summer *(table 2)*. The four last-mentioned species showed the same seasonal rhythm in all zones *(table 1)*.

Other species, especially those found in winter and autumn only, had obviously floated in. *Ectocarpaceae, Cladophora* spec. (PQ 1, 3) and *Agmenellum thermale* (PQ 3) probably originated from the mud-flats in the "Mokbaai". *Tribonema* spec., *Planktonema lauterbornii* and *Gomphosphaeria lacustris* probably originated from freshwater bodies elsewhere. They were generally accompanied by freshwater *Chlorococcales, Scenedesmus quadricauda* (Turp.) Bréb. and *Pediastrum boryanum* (Turp.) Menegh., of which intruding into brackish and marine habitats is well-known. These *Chlorococcales* were not consequently noted down and therefore not included in the list of species *(table 1)*.

A rather unexpected species frequently floating in was *Blidingia minima.* This species occurred in loose-lying tufts, or entangled in *Salicornia,* when recognizable as having floated in. *B. minima* was the most important species of the epiphyte community on *Salicornia,* in which community *Enteromorpha* spp., *Rhizoclonium riparium* and three *Ulothrix* species co-dominated in the cold seasons. Many records of *Bangia atropurpurea* were from this epiphyte vegetation. During spring, *Salicornia* stems fell over and the epiphytes became intermingled with the surface algae. In that period *B. atropurpurea* was found in mats of green algae with *E. prolifera* or *B. minima* as dominants, but also in *Oscillato-*

Tabel 2. Changes in the algal vegetation of PQ 2, as an example of the PQ's 1–3.

Sampling Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Total cover	90	30	70	80	90	65	50	100	100	100	100	100	100	100	35	60
Vaucheria intermedia	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Vaucheria subsimplex	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	1
Vaucheria spec.	1	1	1	10	1	1	1	(1)	–	–	1	1	5	–	–	1
Planktonema lauterbornii	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–
Tribonema spec.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(1)
Bangia atropurpurea	1	(1)	1	–	1	–	–	(1)	(2)	–	–	–	–	–	–	(1)
Ectocarpus siliculosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Ectocarpaceae spec.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(1)	–
Ulotrix flacca	10	15	1	(1)	–	–	–	–	–	–	–	–	–	1	(1)	(1)
Ulothrix pseudoflacca	1	1	1	1	1	1	2	1	(1)	–	1	–	1	1	1	1
Ulothrix subflaccida	1	1	1	1	–	1	–	(1)	(1)	1	1	1	1	–	–	(1)
Ulvaria oxysperma	–	–	–	–	–	–	–	1	–	1	1	–	–	–	–	–
Blidingia minima	2	1	2	3	5	1	3	10	2	1	2	5	15	10	1	1
Capsosiphon fulvescens	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Percursaria percursa	1	1	3	1	–	1	2	1	2	3	15	2	5	2	1	1
Enteromorpha flexuosa	–	–	–	–	–	–	1	–	–	–	1	–	2	5	(1)	–
Enteromorpha prolifera	30	15	50	50	55	15	2	2	10	2	35	60	70	85	2	1
id. f." *intestinalis*"	–	–	–	–	–	–	–	–	1	2	10	1	3	1	–	–
Rhizoclonium riparium	1	1	1	1	1	–	2	–	1	1	1	–	2	2	1	1
Apistonema pyrenigerum	–	–	–	–	–	–	1	–	2	5	1	–	–	–	–	–
Ruttnera chadefaudii	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–
Anacystis dimidiata	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Anacystis montana	–	–	1	–	–	–	–	1	3	2	2	1	1	–	–	–
Gomphosphaeria lacustris	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Entophysalis deusta	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–
Anabaena variabilis	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Nodularia harveyana	–	–	–	–	–	1	–	–	1	1	1	1	–	–	–	–
Calothrix aeruginaea	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Calothrix confervicola	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–
Spirulina subsalsa	1	1	2	–	–	–	1	1	–	1	1	–	–	–	–	–
Microcoleus chthonoplastes	40	3	5	10	25	50	50	90	70	20	15	30	5	1	35	45
Microcoleus lyngbyaceus	1	1	1	3	1	2	1	2	10	15	2	2	1	1	1	2
Microcoleus tenerrimus	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Oscillatoria brevis	–	1	1	(1)	–	1	1	1	–	–	1	–	1	–	–	(1)
Oscillatoria nigroviridis	10	3	15	10	5	2	3	1	3	2	2	2	1	–	1	1
Symploca atlantica	–	1	3	2	1	2	2	1	10	20	25	5	1	1	2	15
Schizothrix calcicola	–	1	1	–	–	1	2	1	2	40	1	–	1	1	–	1

(1) occurring as epiphyte only

Sampling Dates:

1: 2-2-'74	7: 11-6-'74	13: 19-11-'74
2: 15-2-'74*	8: 9-7-'74	14: 14-12-'74
3: 5-3-'74	9: 26-7-'74	15: 15-1-'75
4: 21-3-'74	10: 28-8-'74	16: 27-1-'75
5: 17-4-'74	11: 3-10-'74	
6: 15-5-'74	12: 20-10-'74	

* On this date only PQ 2 was sampled.

riaceae mats. The *Bangia* population was rather poor in individual specimens, and although thalli, forming spores, were observed in the period February-May, the occurrence of *Bangia* in floating *Blidingia minima* tufts indicated that the population was sometimes supplied with new material from elsewhere.

4.2 PQ 4-6

The level of PQ 4 is closer to PQ 1-3 than to PQ 5-6, but because of its phanerogamic flora and vegetation composition it was decided to combine PQ 4 with PQ 5-6.

The low total cover values of the algae in this zone, of which PQ 5 was chosen as an example, are lower than in PQ 2 in the month June, but higher in the winter months *(fig. 1)*. These differences can be ascribed to a lower overflowing frequency of PQ 5, which is 13 cm higher situated than PQ 2. In June, this has, as a consequence, that hypersalinity is reduced less frequently in PQ 5, which condition is unfavourable for algal growth. In winter a lower overflowing frequency means less deposition of silt, which is also a factor unfavourable for algal growth.

From January to May and from November onwards, *Vaucheria* was the most covering vegetation component. It had a minimum cover of 5% in July *(fig. 1)*. All *Vaucheria* species listed in *table 1* were found fruiting in this zone, but generally *V. coronata*, *V. arcassonensis* and/or *V. intermedia* were dominant, the

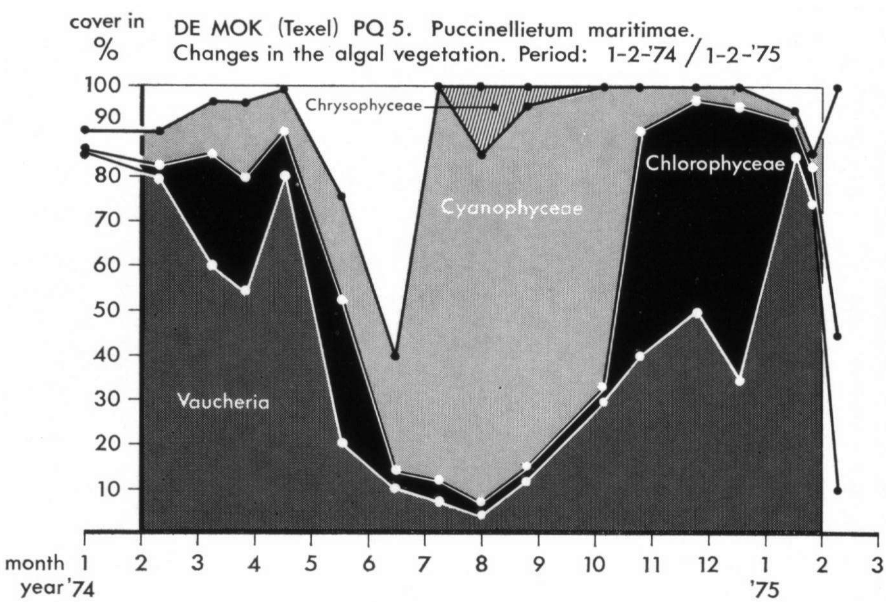

Fig. 1.

first two mainly in spring and *V. intermedia* mainly in autumn *(table 1)*. In summer and winter *V. coronata* and *V. intermedia* were infrequently found together (e.g. *table 3*, PQ 5).

The *Chlorophyceae* reached their maximum cover values in the same periods as in the previous zone: just after the decline and just before the recovery of *Vaucheria (fig. 1)*. *Enteromorpha prolifera* was always dominant among the green algae, with *Percursaria percursa* as a co-dominant, in the period July-November. *Enteromorpha flexuosa* co-dominated once.

In the winter of 1974, *Microcoleus chthonoplastes* and *Oscillatoria nigroviridis* were the dominant *Cyanophyceae*, covering up to 20% each (e.g. *table 3*, PQ 4 and 5). In the following months the same process as in the *Oscillatoriaceae* vegetation of the previous zone took place. In the *Vaucheria*-rich PQ 6, the cover of the *Oscillatoriaceae* (by *Microcoleus chthonoplastes*, *M. lyngbyaceus* and *Symploca atlantica*) exceeded 20% in August only. During summer, the *Chryso-*

Tabel 3. The cover of the algae in PQ 1-7 on 5-3-'74.

PQ	1	2	3	4	5	6	7
Total cover algae	45	70	95	100	95	85	100
Vaucheria coronata	–	–	–	10	60	85	40
V. intermedia	–	–	–	–	sp	–	–
V. arcassonensis	–	–	–	–	–	–	1
Vaucheria spec.	1	1	2	–	–	–	–
Planktonema lauterbornii	1	1	–	1	1	–	–
Bangia atropurpurea	1	1	–	–	–	–	–
Ectocarpaceae spec.	–	–	–	–	–	1	–
Ulothrix flacca	3	1	15	2	2	1	–
Ulothrix pseudoflacca	1	1	1	2	2	1	5
Ulothrix subflaccida	1	1	1	1	1	1	1
Ulvaria oxysperma	1	–	–	–	–	–	–
Blidingia minima	2	2	1	1	1	–	1
Enteromorpha prolifera	25	50	45	75	25	3	2
id. f. "*intestinalis*"	–	–	–	1	–	–	–
Percursaria percursa	1	3	1	1	2	–	2
Rhizoclonium riparium	1	1	(1)	1	1	–	55
Anacystis dimidiata	–	1	–	–	–	–	–
A. montana	–	1	–	–	–	–	–
Agmenellum thermale	–	–	–	–	–	1	–
Gomphosphaeria lacustris	–	1	–	–	–	–	–
Nodularia harveyana	–	–	1	–	–	–	–
Spirulina subsalsa	1	2	2	1	1	2	–
Microcoleus chthonoplastes	10	5	2	10	2	2	2
M. lyngbyaceus	1	1	1	2	1	1	3
Oscillatoria brevis	1	1	1	1	1	1	2
O. nigroviridis	10	15	35	5	10	2	3
Schizothrix calcicola	1	1	1	2	–	1	1
Symploca atlantica	1	3	1	2	–	–	1

sp = oospores
(1) = occurring as epiphyte only.

phyceae Apistonema pyrenigerum, *Ruttnera maritima* and *R. chadefaudii* covered some 20% in the PQ's 5 *(fig. 1)* and 6. These *Chrysophyceae* did not form special vegetation components in this area. They occurred in *Chlorophyceae* and *Cyanophyceae* mats.

The differences between the non-dominant species of this and the previous zone were only in minor details. *Ulothrix flacca* and *Blidingia minima* could be added, whereas *Gomphosphaeria lacustris* and *Tribonema* spec. had not been found. Two species generally occurring in mesohaline and oligohaline habitats were found: *Chrysomeris ramosa*, *Pseudotetraspora marina*. The last-mentioned species was described by WILLE (1906), from a wooden post in the supralittoral belt. DEN HARTOG (pers. comm.) found it in Southwest England (Jennycliff, near Plymouth (Devon)) in supralittoral water trickles on the rocky shore. The species has shown to be a common saltmarsh alga in the whole North Sea area (POLDERMAN in prep.). It was found once in PQ 6 and twice in PQ 7. *Bangia atropurpurea* was only an occasional species in PQ 4-6.

4.3 PQ 7

In the zone of the *Juncetum gerardii*, *Rhizoclonium riparium* was the predominant species, generally covering over 75%. During the year of study, when the total algal vegetation covered 90–100%, the lowest cover value of *R. riparium* was 35% in August, when at the same time *Microcoleus lyngbyaceus* reached its maximum cover value of 60%. *M. lyngbyaceus* showed similar tendencies in its cover during the course of the year as in the previous zones. The cover values of *M. chthonoplastes* and *Oscillatoria nigroviridis* remained low during the whole period of study. *Symploca atlantica* was the only other Oscillatoriacea with cover percentages over 5%. This occurred in the period July-December.

Co-dominant green algae were *Enteromorpha prolifera* (infrequently over the year) and *Ulothrix pseudoflacca* (in winter, *table 3*). *Ruttnera maritima* and *R. chadefaudii* covered over 5% in the period June-August.

Vaucheria initially showed the same tendency in its cover values as in the previous zone *(fig. 1)*: high values in winter *(table 3)*, a decline in spring, rather low values in summer and a recovery in autumn. However, this last-mentioned recovery did not continue in PQ 7. During the rest of the period of study the *Vaucheria* cover stayed below 10%. Only *V. coronata*, *V. arcassonensis* and *V. intermedia* were found. The *Vaucheriae* showed the same periodicity as in the previous zone.

Ulothrix subflaccida, *Blidingia minima*, *Percursaria percursa*, *Nodularia harveyana*, *Oscillatoria brevis* and *Schizothrix calcicola* belonged to the constant, but non-dominant species. *Ulothrix flacca*, *Bangia atropurpurea*, *Ectocarpaceae* spp. and *Planktonema lauterbornii* were found occasionally. Two species of *Oscillatoriaceae* were found rather particular to this zone: *Microcoleus vaginatus* and *M. tenerrimus*. LINDSTEDT (1943) noted that the first species mainly occurred in freshwater habitats of his area of study, the Swedish west coast. Another species extending from freshwater habitats into saltmarshes is *Ulothrix verru-*

cosa. It was found in PQ 7 only. The species has been collected in comparable habitats in several other saltmarshes in the Wadden area (POLDERMAN in prep.).

5. DISCUSSION

The changes in the algal vegetations during the seasons *(fig. 1, table 2)* can be explained by the structure and the mode of growth of the groups of species composing these vegetations. This could be shown in an inland seepage area near Vlissingen, in a vegetation system of *Vaucheria* and *Rhizoclonium riparium* (POLDERMAN 1974a). In that system *Vaucheria* disappeared first in a period of drought, followed later by *Rhizoclonium*. The same was observed for *Vaucheria* and the filamentous green algae in "De Mok" *(fig. 1, table 2)*. The survival of the two remaining groups of algae in "De Mok", the *Cyanophyceae* of the genera *Symploca*, *Microcoleus* and *Schizothrix*, and the *Chrysophyceae* of the genera *Apistonema* and *Ruttnera* can also partly be explained by their structure. The species of these genera possess a mucous sheath, which is well-protective during a prolonged period of drought.

The PQ method, by means of which the area was studied is not very suitable, if it is necessary to establish correlations between species over a longer period, as the samples are continually taken from the same limited area.

Because the quadrats had been chosen as being representative of the area studied, with respect to the zonation pattern, it was possible to obtain data on the correlation between the abundance of a species and the level of the marsh. The correlations were calculated by means of the Spearman rank correlation test. A species was only submitted to the test, if it was sufficiently present and

Table 4. List of species submitted to the statistical tests.

	A	B	C	D	E	F
Vaucheria coronata	8	5	0	pos	< 0.001	1,2
Vaucheria intermedia	8	2	0	pos	< 0.001	1,4
Blidingia minima	11	0	3	neg	< 0.001	2,3,4
Enteromorpha prolifera	15	0	2	neg	0.003	1,2,3,4
Rhizoclonium riparium	15	2	0	pos	< 0.001	1,2,3,4
Microcoleus lyngbyaceus	11	2	0	pos	< 0.001	2,3,4
Symploca atlantica	11	0	0	neg	0.28	2,3,4
Microcoleus chthonoplastes	15	0	1	neg	< 0.001	1,2,3,4
Oscillatoria nigroviridis	8	0	3	neg	< 0.001	1,2

A: number of sampling dates for which the Spearman rank correlation (R_s) between the cover and the level of the quadrats was calculated.
B: number of significant positive R_s. probability level (P) < 0.05.
C: number of significant negative R_s. ($P < 0.05$).
D: average Spearman correlation.
E: Probability level of average Spearman correlation.
F: seasons over which testing was done – 1. winter; 2. spring; 3. summer; 4. autumn.

also showed a clear variation in its cover values. For this it had to fulfill two demands: 1. It had to occur in 25% of the surveys in at least two seasons *(table 1)*. 2. It had to occur three or more times with cover values over 5% in these seasons. The nine species selected this way were only tested over the seasons, in which both demands were fulfilled *(table 4)*. For each sampling date in the suitable season the Spearman rank correlation was calculated. For example, on 5-3-'74 *(table 3)*, the Spearman correlation between the cover of *Vaucheria coronata* and the level of the quadrats was as follows:

rank number quadrats	1	2	3	4	5	6	7	(correspond with level. see 3.1)
cover *V. coronata*	0	0	0	10	60	80	40	
rank *V. coronata*	2	2	2	4	6	7	5	(total pairs n, = 7)
difference in ranks	−1	0	+1	0	−1	−1	+2	(sum total = 0)
squared difference	1	0	1	0	1	1	4	(sum total $\Sigma d^2 = 8$)
ties (t)		3		1	1	1	1	(equal observations, in second ranking)
t^3		27		1	1	1	1	(sum total $\Sigma t^3 = 31$)

$$\text{Spearman correlation } R_s = \frac{n^3 - \frac{1}{2}\Sigma t^3 - 6\Sigma d^2}{\sqrt{(n^3-n)(n^3-t^3)}} = \frac{343-15.5-48}{\sqrt{336 \cdot 312}} = 0.854$$

This correlation coefficient is significant, with a probability level (P) smaller than 1%. On five out of eight sampling dates *V. coronata* had a positive correlation with the level of the quadrats, which was at least significant on the 5% level *(table 4)*.

The hypothesis that on each of these dates the abundance of *V. coronata* was independent of the level in the marsh was tested by means of the sum of the eight rank correlation coefficients, which was 6.139 for *V. coronata*. Under the hypothesis this sum is approximately normally distributed with the mean 0 and the variance equal to 8/(7-1), as each of the coefficients has a variance of 1/(7-1), with 7 being the total of the pairs of the Spearman test. The significance of the sum of the rank correlation coefficients can be established by dividing it by the standard deviation (the square root of the variance), for the example $\sqrt{8/(7-1)} = 1.154$, and referring to the table of the normal distribution (e.g. DE JONGE 1958/60). A value over 1.96 is significant on the 5% level. The value of 5.31, found for *V. coronata* is significant on a level below 0.1% ($P < 0.001$).

According to the last test, it can be stated that the positive correlation existing on an average between the cover value and the level of *V. coronata* in the marsh, during winter and spring, is very significant.

The same was found for *Vaucheria intermedia* in winter and autumn, and for *Microcoleus lyngbyaceus* and *Rhizoclonium riparium* over longer periods. Negative correlations with the increasing level of the quadrats (or positive correlations with the decreasing level of the quadrats) could be established for *Blidingia minima* (winter excluded), *Enteromorpha prolifera* and *Microcoleus chthono-*

plastes (whole year) and *Oscillatoria nigroviridis* (winter and spring).

A number of data, derived directly from the tables were also available. *Table 3* indicates that *Bangia atropurpurea* occurs especially in the lower quadrats. *Table 2* shows a considerable number of records of this species in PQ 2. Combining these two tables and those not published, *Bangia atropurpurea* can be seen to be characteristic of PQ 1-3, and especially of epiphyte *Blidingia minima* vegetations. In *table 3, Ulothrix flacca* has a relatively high cover value in PQ 3. In *table 2*, this species appears to have similar cover values in PQ 2 in winter. These data indicate that *Ulothrix flacca* is characteristic of the zone represented by PQ 1-3. There are no data that contradict this supposition.

In PQ 1-3, the filamentous *Chlorophyceae* had *Enteromorpha prolifera* as their most abundant representative. The species had a significant negative correlation to the level of the marsh on two occasions (*table 4*), and on an average the correlation between the cover of *Enteromorpha prolifera* and the level of the marsh was also significantly negative. Co-dominant species were *Ulothrix flacca, Blidingia minima, Enteromorpha flexuosa* and *Percursaria percursa.* In literature, algal communities dominated by *Chorophyceae*, whether situated low or high in the saltmarshes, have been classified into a "General *Chlorophyceae* Community" (CARTER 1933, NIENHUIS 1970). The Chlorophycean vegetation unit of this zone is distinguished from that of the higher zones by the abundance of *Blidingia minima (table 4)* and of *Ulothrix flacca,* as explained abave. For *Blidingia minima* separate communities have been distinguished, occurring on firm substrates, rocks (the *Blidingietum minimae,* DEN HARTOG 1959) or stems of higher plants (the *Blidingia minima* sociation, NIENHUIS 1970). The last mentioned author pointed at the relation between these communities. DEN HARTOG (1973) confirmed this. In "De Mok" a vegetation dominated by *Blidingia minima, Enteromorpha prolifera* and sometimes *Rhizoclonium riparium* (POLDERMAN 1972) formed an independent vegetation unit on *Salicornia* stems, with *Bangia atropurpurea* as a characteristic species. From the first record of this species in "De Mok" (POLDERMAN 1972) it was assumed that this vegetation with *Bangia* was an indication of the ecological relationship between the *Bangieto-Urosporetum* (DEN HARTOG 1959) and the vernal *Ulothrix* sociation (NIENHUIS 1970) because *Ulothrix pseudoflacca, U. subflaccdia,* and *Blidingia minima,* species of the two communities, were also present. In 1972 *Bangia* was not found again. The species was therefore assumed to have a rather ephemerous character in saltmarshes. The present studies have shown that *Bangia* is present during the whole year *(table 1, 2)*, and also that the species is generally present in mats dominated by *Blidingia minima* in epiphytic conditions and in soil surface vegetations. These new and more numerous data prove that *Bangia atropurpurea* is a characteristic companion of the *Blidingia minima* community, epiphytic on *Salicornia* in "De Mok".

For *Ulothrix flacca,* a vernal *Ulothrix* sociation has been described. The results from "De Mok" suggested a hibernal, rather than a vernal, *Ulothrix* sociation, because the species reached its highest cover in February. In PQ 1-3, *Blidingia minima* (not the epiphytic populations) and *Ulothrix flacca* did not form mats with a special character, but they were incorporated in the *Chlorophyceae* mat. Therefore they were dealt with as belonging to the same unit as *Enteromorpha prolifera.*

In PQ 1-3, the *Vaucheria* unit has also its characteristic representatives. It is formed by a combination of *Vaucheria subsimplex* (the most frequent), *V. velutina* and *V. compacta,* rarely accompanied by *V. intermedia.* NIENHUIS (1970) reported a *Vaucheria thuretii (velutina) – V. sphaerospora (subsimplex)* sociation as an independent vegetation unit from the Springersgors (Southwest Netherlands). This unit had also *V. intermedia* as a companion species. SIMONS (1974b) reported the combination without *V. intermedia* in general for saltmarshes bordering euhaline or polyhaline water.

The *Cyanophyceae* unit of PQ 1-3 consisted of four frequent dominants, *Microcoleus chthonoplastes, M. lyngbyaceus, Symploca atlantica* and *Oscillatoria nigroviridis,* and one occasional, *Schizothrix calcicola.* According to its cover values *M. chthonoplastes* is correlated to the lower levels of the marsh, but *M. lyngbyaceus* is correlated to the higher levels *(table 4).* Although the number of significant Spearman correlations was low for both species *(table 4* A-C), the conclusion is justified that the two species have different ecological optima in the marsh. The two species have broad ecological ranges *(table 3).* They occurred frequently together with cover values over 5% *(table 2).* The combination *M. chthonoplastes – M. lyngbyaceus* is one of the most reported *Cyanophyceae* combinations (NIENHUIS 1970). The same author also mentions literature on pure vegetations of one of the two. Judging from *table 2,* it can be concluded that PQ 1-3 is within the overlapping area of the ecological ranges of the two species.

Oscillatoria nigroviridis showed more significant correlations to the lower situated quadrats than the two *Microcoleus* species dealt with above. These correlations (*table 4* A-C) were found during the first half year of 1974. In that period *O. nigroviridis* decreased in quantity *(table 2)* but not in frequency *(table 1).* No recovery of *O. nigroviridis* took place. In contrast to many other declines of species in the marsh *(Vaucheria, Enteromorpha)* that of *O. nigroviridis* was not part of a cyclic process. CARTER (1932) mentions the combination of *O. nigroviridis* with *Microcoleus chthonoplastes* and *M. lyngbyaceus.* Neither CARTER (1932) nor NIENHUIS (1970) mention the combination of these two *Microcoleus* species and *Symploca atlantica.*

The algal vegetation provided some evidence that PQ 4 could be better grouped with PQ 5-6 than with PQ 1-3. Three species with a significant positive correlation to the higher levels of the marsh were frequently dominant, in PQ 4, *Vaucheria coronata, V. intermedia* and *Microcoleus lyngbyaceus.* Two species more characteristic of the lower levels of the marsh, *O. nigroviridis* and *Blidingia minima,* never reached cover values of 10% or more. Another species found characteristic of PQ 1-3, *Ulothrix flacca,* was never more than occasional in PQ 4. Only two species with a correlation to the lower quadrats reached very high cover values in PQ 4, *Enteromorpha prolifera* and *Microcoleus chthonoplastes.* As *Vaucheria coronata, Oscillatoria nigroviridis* and *Blidingia minima* can be considered as the strongest indicators (*table 4* A-C), the data mentioned above can be used as supporting evidence that the algal vegetation of PQ 4 is closer allied to that of PQ 5-6 than to that of PQ 1-3.

The *Cyanophyceae* unit of PQ 4-6 did not show special differences to that of PQ 1-3. PQ 4-6 was also within the area of the ecological overlap of *Microcoleus chthonoplastes* and *M. lyngbyaceus.*

The *Chlorophyceae* unit of PQ 4-6 differed mainly quantitatively. *Enteromorpha prolifera* and *Percursaria percursa* were the only frequently dominant species. Although *E. prolifera* was found with a certain correlation to the lower quadrats, it was still the most characteristic Chlorophycea of PQ 4-6, because of its constant dominance.

The greatest differences between PQ 1-3 and PQ 4-6 were found in the *Vaucheria* unit of the latter. Its species, *Vaucheria intermedia* and *V. coronata*, had a significant correlation to the higher marsh, judging from their cover (*table 4*). With *V. arcassonensis* absent in PQ 1-3, they formed a characteristic combination, reported before by many authors (see SIMONS 1975 s.l.).

In PQ 7, the same *Vaucheria* unit was found. A slight distinction from that in the zone of PQ 4-6 was the complete absence of *Vaucheria subsimplex*, *V. velutina* and *V. compacta.*

The greatest difference from the mosaic vegetations of the other zones was in the *Chlorophyceae* unit. In PQ 7, this unit was dominated by *Rhizoclonium riparium*, with *Enteromorpha prolifera* playing a minor role. During the whole year, the cover of *Rhizoclonium riparium* was, on an average, significantly positively correlated to the level of the marsh; but on two occasions only (11-6 and 26-7-'74) the Spearman correlation coefficient was significant on the 5% level. In winter, the co-dominance of *Ulothrix pseudoflacca* was a characteristic element (*table 3*). The vegetations of *U. pseudoflacca* and of *U. subflaccida* appear to be separate from the *Ulothrix flacca* vegetations. The seasonal occurrence of the first two was also different to that of *Ulothrix flacca.* The frequencies in *table 1* show that *U. subflaccida* and *U. pseudoflacca* are not such strictly vernal forms, as CARTER (1932) stated. In contradistinction to *U. flacca* they also form a winter-spring element of algal vegetations on the landward side of the dikes (POLDERMAN 1974a, 1975; SIMONS 1975b). A vegetation of phanerogams, similar to PQ 7, is described by NIENHUIS (1975) as having *Rhizoclonium riparium* as the dominant alga. In such vegetations NIENHUIS (l.c.) noticed *Microcoleus lyngbyaceus (Lyngbya aestuarii)*, *M. chthonoplastes* and *Schizothrix calcicola* as co-dominant blue-green algae. In PQ 7, *M. lyngbyaceus* and *Symploca atlantica* only were occasional (co-)dominants. In this respect, the *Cyanophyceae* unit of PQ 7 differed from that in the other zones. The presence of *Microcoleus vaginatus* in PQ 7 was another difference, but as yet the differences cannot be considered important enough to basically distinguish the *Cyanophyceae* unit of PQ 7 from the other two.

In the PQ's 2, 5, 6 and 7, *Chrysophyceae* covered 5-20% during summer. They form independent vegetation units elsewhere in the Wadden Sea (POLDERMAN in prep.), or take part in widespread algal communities, such as the *Rivu-*

laria-Phaeococcus community (CARTER 1933). In such conditions, the *Chrysophyceae* have a more or less constant position. In "De Mok", their appearance was rather temporary *(table 1)*, comparable to the way of occurrence of *Ulothrix flacca*. The *Chrysophyceae* were more abundant in the middle part of the marsh than in the zones of PQ 1-3 and of PQ 7. However, the data were not sufficient to support this impression with statistical evidence.

In a preliminary survey of algal combinations in the Wadden Sea, DEN HARTOG (1973) mentioned the probability that the "Communities dominated by *Cyanophyceae*" and the "General *Chlorophyceae* Community" belong to one master-complex. NIENHUIS (1970) already mentioned transitional vegetation types between the two. In the conception of most authors, certain *Vaucheria* spp. are not considered independent of the General *Chlorophyceae* Community (see NIENHUIS 1970). The vegetations of the various zones in "De Mok" can be considered as master-complexes (DEN HARTOG 1973), each composed of three units, which under different conditions occur as independent communities. The three master-complexes distinguished in PQ 1-3, PQ 4-6 and PQ 7 of "De Mok" each have so many particular characteristics that they can be considered to be separate communities. Such master-complexes do not only exist in vegetations related to the "General *Chlorophyceae* Community". From "De Kom" on Terschelling, a master-complex community was reported consisting of a *Sphacelaria britannica* Sauv. unit, a *Catenella repens* unit and a *Vaucheria coronata* unit (POLDERMAN 1974b). When optimally differentiated that community contains also a *Chlorophyceae* and a *Cyanophyceae* unit.

As the units in these master-complex communities have many if not all species in common, so that often, within the vegetation, the variation is only caused by a different local dominant, it is, in my opinion, better to consider such mosaic vegetations as independent communities and not as merely accidental conglomerates of separate vegetation units.

6. CONCLUSIONS

1. The mosaic vegetation of algae in PQ 1-3 can be described as a community characterized by *Vaucheria subsimplex*, *V. velutina*, *V. compacta*, by *Enteromorpha prolifera*, *Ulothrix flacca*, *Blidingia minima* and by *Microcoleus chthonoplastes*, *M. lyngbyaceus*, *Symploca atlantica* and *Oscillatoria nigroviridis*. The community can be indicated as *Vaucheria subsimplex/Enteromorpha prolifera/Microcoleus* community.

2. The algal vegetation of PQ 4-6 is characterized by *Vaucheria coronata*, *V. intermedia*, *V. arcassonensis*, by *Enteromorpha prolifera*, *Percursaria percursa* and by *Microcoleus chthonoplastes*, *M. lyngbyaceus*, *Symploca atlantica*. As *Percursaria percursa* plays a subordinate role, the community can best be indicated as the *Vaucheria coronata/Enteromorpha prolifera/Microcoleus* community.

3. In PQ 7, the algal vegetation is characterized by *Vaucheria coronata*, *V. intermedia*, *V. arcassonensis*, by *Rhizoclonium riparium*, and by *Microcoleus lyngbyaceus*, *Symploca atlantica*. Despite the slight differences in the composi-

tion of the *Cyanophyceae* unit, the community can be characterized as the *Vaucheria coronata/Rhizoclonium/Microcoleus* community.

4. The epiphyte vegetation on *Salicornia* stems belonged to the *Blidingia minima* community.

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