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SPIROGYRA SPECIES AND ACCOMPANYING ALGAE FROM DUNE WATERS IN THE NETHERLANDS

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SUMMARY

A survey is given of the occurrence of filamentous algae from dune pools situated in the calcium carbonate-rich dune area at Oostvoorne and Egmond-Castricum as well as the calcium carbonate-poor Wadden area at Terschelling.

Spirogyra and *Oedogonium* were important and often dominant components at these sites and were represented by at least 35 and 20 species respectively. Accompanying species belonged to *Zygnema, Mougeotia, Bulbochaete, Microspora* and *Tribonema*. In several pools *Chara* was dominant. Mass occurrence of filamentous algae was frequently observed. The seasonal dynamics of the components in floating mats were described.

Periodicity phenomena of components and individual *Spirogyra* and *Oedogonium* species were studied. A peak in spore production of *Spirogyra* was situated in the second half of May and the first half of June.

Based on physico-chemical data, the water of most of the investigated pools can be characterized as mesotrophic freshwater with a moderate or high amount of calcium and bicarbonate. Water quality differences between Terschelling (low alkalinity) and Egmond-Castricum/Oostvoorne (high alkalinity) were reflected in their species composition. Most of the species from the dune pools are also known from other more nutrient-rich habitats in The Netherlands, but there are differences in quantities and combinations of species.

1. INTRODUCTION

Zygnematalean algae represent an important component of algal growth in many shallow water bodies such as peat lakes, ditches and ponds in The Netherlands. Species of *Spirogyra* and to a lesser extent *Oedogonium* often reach dominance in dune pools, forming blanketing mats.

Formerly natural dune pools were widespread over the whole coastal area (BAKKER et al. 1979), but recently the groundwater level has become reduced by water withdrawal for public purposes. Nowadays natural dune waters are restricted to only a few areas.

Only a few published studies exist on the hydrobiology of natural dune waters (LEENTVAAR 1963, 1967, 1981). In these studies most attention was paid to phyto- and zooplankton.

From 1980 onwards regular observations were made on the occurrence of filamentous algae at some localities: pools in the dunes near Oostvoorne in the province of Zuid-Holland, small artificial ponds in the area between Egmond and Castricum in the province of Noord-Holland and large pools (lakes) on

Terschelling island in the Northern Wadden area (*fig. 1*). Terschelling is situated in the calcium carbonate-poor (less than 1% $CaCO_3$ dry soil) 'Waddendistrict', and the other localities in the calcium carbonate-rich (1–9% $CaCO_3$) 'Dune-district'.

The freshwater bodies in dunes are largely undisturbed by human activities, which is reflected in the abundance of characean algae at many localities.

Besides filling a gap in our knowledge, one of the objectives of this study was to compare these data with those from the generally much more influenced and eutrophicated freshwater habitats outside the dune region.

2. MATERIAL AND METHODS

At intervals of about three weeks during spring and summer frequent observations at selected localities were carried out at Oostvoorne during 1980 and 1982, at Egmond-Castricum in 1981 and 1982 and at Terschelling in 1982.

Samples were kept alive a few days for identification and were later fixed in a mixture of formaldehyde 40%, acetic acid and ethyl alcohol 50%. On some occasions isolates were made from vegetative *Spirogyra* filaments in order to obtain reproductive structures with the aid of an induction method designed at our laboratory (SIMONS et al. 1984).

At some localities observations on small epiphytic algae were made using glass slides as artificial substrates, which were kept floating in a perspex holder connected to a cork.

Relative abundances of species or genera were estimated and expressed according to a scale with 6 intervals: + = 1–10%, 1 = 10–20%, 2 = 20–40%, 3 = 40–60%, 4 = 60–80%, 5 = 80–100%.

Fig. 1. Map of The Netherlands with the 3 study areas: 1: Oostvoorne, 2: Egmond-Castricum, 3: Terschelling.

Table 1. Presence of aquatic macrophytes from pools in the study area at Oostvoorne.

Pool number	1	2	3	4	5	6	7
Alisma plantago-aquatica			+	+	+	+	+
Echinodorus ranunculoides			+	+			
Eleocharis palustris	+		+	+	+	+	
Equisetum fluviatile				+			
Equisetum palustris			+			+	
Hippuris vulgaris	+			+		+	+
Hydrocotyle vulgaris	+		+	+		+	+
Lemna minor	+			+	+		
Lycopus europaeus				+			
Mentha aquatica	+		+	+	+	+	+
Myosotis palustris			+	+			
Phragmites australis	+	+		+	+	+	
Potamogeton coloratus			+	+			
Potamogeton gramineus	+		+	+			+
Ranunculus aquatilis var. *aquatilis*	+			+			+
Ranunculus aquatilis var. *diffusus*	+		+	+		+	
Ranunculus flammula	+		+	+		+	
Scirpus lacustris				+			
Scirpus maritimus	+			+	+		
Typha angustifolia				+			
Typha latifolia	+			+			
Leptodictyum riparium	+	+	+	+			
Chara aspera				+			+
Chara hispida	+	+	+	+	+	+	
Chara vulgaris	+			+		+	

The *Spirogyra* species were identified using the flora's of KADLUBOWSKA (1984), KOLKWITZ & KRIEGER (1940), RANDHAWA (1959) and TRANSEAU (1951). *Oedogonium* species were identified following GEMEINHARDT (1939) and GONZALVES (1981). *Chara* species were named according to MAIER (1972), and other accompanying algae following PRESCOTT (1970) and PRINTZ (1964). The nomenclature of the phanerogamic plants is in accordance with HEUKELS & VAN DER MEIJDEN (1983).

Chemical and physical data were obtained from the research institute 'Weevers Duin' at Oostvoorne, from the water board agency 'Provinciaal Waterleidingbedrijf van Noord-Holland' (Castricum) for Egmond-Castricum, and from the Laboratory for Aquatic Ecology, University of Nijmegen for Terschelling.

3. DESCRIPTION OF STUDY AREAS

3.1. Oostvoorne (OV)

For a general survey of the dune vegetation of Oostvoorne, see VAN DER MAAREL & WESTHOFF (1964).

Table 2. Physical and chemical characteristics of 7 pools at Oostvoorne, based on data from the periods April to September 1980 and May to July 1982. For pH the total range of values is given and for the other parameters mean values which are based on 2–5 determinations at different times. Electrical conductivity (EC) is expressed as $\mu S\ cm^{-1}$ (20°C). Alkalinity (HCO^{3-}) is expressed in $meg \cdot l^{-1}$. The concentrations of dissolved chemical components are given in $mg\ l^{-1}$.

Parameter	Pool number						
	1	2	3	4	5	6	7
pH (range)	6.9–10.0	7.4–8.4	7.9–9.0	7.4–8.5	7.3–8.8	6.9–9.2	7.8–9.6
EC	589	532	503	686	633	417	698
Cl^-	73	45	60	98	67	53	100
Ca^{2+}	89	105	74	119	99	54	85
Mg^{2+}	8.8	6.6	6.7	9.4	8.9	8.1	9.4
PO_4^{3-}-P	0.009	0.04	0.08	0.02	0.01	0.02	0.009
P_{tot}	0.034	0.128	0.017	0.06	–	–	0.065
NH_4^+-N	0.11	0.119	0.07	0.08	0.12	0.19	0.02
NO_3^--N	0.11	0.07	0.12	0.08	0.11	0.22	0.02
K^+	1.5	0	0–5	0–5	–	–	4.5
SO_4^{2-}	68.7	51.3	90.2	66.0	–	–	178
Alkalinity	5.0	4.5	2.6	4.2	–	3.1	2.3

The sampling localities were situated in primary valleys in the central part of a dune area of which the northwestern side is bordered by a dune ridge, the outermost coastal border until 1910. In this valley system, 6 small ponds were selected as well as one pool (7), situated north of the 1910 ridge in a younger primary valley, called Bitterlingvallei.

The two largest pools measure 44 × 15 m^2 (1) and 25 × 13 m^2 (4). The smaller pools measure from 4–50 m^2. In the central part of most pools there is a relatively deep pit with a depth of about 1 m, around which the water depth varies from 0–50 cm. Most pools dry up during late spring and early summer. Depending on the weather conditions, the central pits may contain water during the whole year. The surrounding vegetation of the pools is kept low by annual mowing. The herb vegetation around the pools is mostly bordered by shrubs of *Salix repens* and trees (*Alnus glutinosa, Betula pendula, Populus canescens*).

The aquatic vegetation of the pools is presented in *table 1*. In many pools the density of *Chara hispida* is very high; *Potamogeton gramineus* is of rather common occurrence. Remarkable is the presence of *Potamogeton coloratus* in pools 3 and 4, which is a very rare species in The Netherlands (Eelman & van der Ploeg 1979). The moss *Leptodictyum riparium* occurs in 4 pools.

The physico-chemical data presented in *table 2* show that the pools are very much alike concerning the physico-chemical features. Nutrients were measured at low levels. According to the total amounts of soluble phosphate, the pools could be called meso-eutrophic (Vollenweider 1968). The calcium level is rather high. Chloride content is always lower than 100 mg l^{-1} indicating no large influence of salt spray.

3.2. Egmond-Castricum (EC)

The sampling localities were situated in the dune area between Egmond-Binnen and Castricum, of which the vegetation has been described earlier (Doing 1966). The investigated pools ly behind the outer coastral dune ridge in a system of primary valleys called Reggers Sandersvlak and De Kil going from north to south. Of the pools present, measuring 5–6 m in diameter and 0.5–1.0 m deep, 18 were selected for detailed investigation.

These round pools were formed by disarming explosives from world war II. Most pools contain water in all seasons, lowered during summer by evaporation. Hardly any phanerogamic aquatic plants are present, but in several pools considerable quantities of *Chara hispida*, at some localities together with *C. contraria*, were recorded. In some pools *Phragmites australis* and sometimes *Typha latifolia* and *Scirpus lacustris* also occur. The pools are bordered by luxuriously developed *Salix repens* and/or *Hippophaë rhamnoides* shrubs. The aquatic moss *Leptodictyum riparium* often grows at the boundary between water and land.

Approximately 7 km south of this site, a location called Sikkelduin is situated encircling a recently blown out secundary valley in which a rather large pool occurs measuring 154 m^2 with a maximum water depth of 1 m. In this pool a vegetation of *Eleocharis palustris* with patches of *Typha latifolia* has developed. Another water body called IJsbaan situated in the inner dune area near Castricum was also studied. Maximum water depth there is about 1 m. The greater part of this pool dries up during the summer. As aquatic species *Apium inundatum* and *Echinodorus ranunculoides* occur at some places.

The physico-chemical data are summarized in *table 3*. The small pools 1.1, 1.2, 3.4, 3.6, 3.7, 3.9, 3.10, and Sikkelduin are very much alike with respect to most parameters. The water properties (low nutrients, high calcium and alkalin-

Table 3. Physical and chemical characteristics of 9 pools at Egmond-Castricum, based on data from a period between April 1981 and November 1982. Values are expressed as in *table 2*, and based on 1 (pool 3.7 and 3.9) or 8–10 determinations at different times. Si: Sikkelduin, IJsb.: IJsbaan.

Parameter	Pool number								
	1.1	1.2	3.4	3.6	3.7	3.9	3.10	Si	IJsb.
pH	7.1–8.8	7.6–8.3	7.1–7.8	7.1	7.4	6.9–8.1	7.3–7.4	6.9–8.4	7.3–8.8
EC	640	710	680	590	590	720	625	665	390
Cl^-	102	115	93	57	65	104	90	89	60
Ca^{2+}	73	79	95	96	88	98	80	96	56
Mg^{2+}	9.6	10.3	9.0	7.5	8.4	10.0	7.5	7.6	5.7
PO_4^{3-}-P	0.01	0.02	0.02	0.01	0.01	0.02	0.01	0.01	0.01
P_{tot}	0.07	0.12	0.25	0.34	0.07	0.06	0.03	0.17	0.15
NH_4^+-N	0.04	0.76	0.03	0.06	0.01	0.01	0.02	0.02	0.03
NO_3^--N	0.06	0.03	0.05	0.01	0.02	0.04	0.03	0.01	0.06
Kjeld.N	1.3	6.8	2.4	5.3	0.6	1.0	0.7	1.9	3.4
K^+	1.8	5.5	2.6	3.5	2.3	2.3	–	1.8	5.5
SO_4^{2-}	33	41	45	46	28	28	–	44	24
Alkalinity	3.35	3.70	4.13	4.51	4.36	4.60	3.70	4.26	1.40

ity, chloride content about 100 mg l^{-1}, conductivity 570–720, pH 7.1–8.8) show much resemblance with the OV pools. The locality 'IJsbaan' is distinct in several aspects. The conductivity, chloride, calcium, and alkalinity reach considerably lower values. This relatively soft water character is indicated by the Littorellion species *Apium inundatum* and *Echinodorus ranunculoides*. The high total N-content may be related to the thick sapropelium layer.

3.3. Terschelling (Tersch.)

In the lime-poor dune area of the Frisian island Terschelling, several large pools (lakes) are present. In only some of these, called Griltjeplak, Badhuisplak and Liesingerplas *Spirogyra* species occurred in considerable quantities.

The most western locality, Griltjeplak, is situated in a primary dune valley and measures about 250 × 150 m^2, with a maximum water depth of 75 cm. In summer the pool usually dries up. Aquatic plant species of the Littorellion alliance occur there: *Littorella uniflora, Potamogeton polygonifolius, Echinodorus ranunculoides,* and *Juncus bulbosus*. For a habitat characterisation of this vegetation type see SCHOOF-VAN PELT (1973). Other species at this site are: *Phragmites australis, Cladium mariscus, Menyanthes trifoliata* and *Fontinalis antipyretica*. The pool is bordered by dunes with dense shrubs of *Myrica gale, Salix repens* and *Hippophaë rhamnoides*. South of this locality, in a muddy basin with *Alnus glutinosa* provisionally designated as 'Paulusplak', large *Spirogyra* mats were occasionally recorded.

The Badhuisplak is a pool measuring about 150 × 60 m^2, with a maximum water depth of 120 cm. Water plants present were *Myriophyllum spicatum, M. alterniflorum, Potamogeton gramineus, P. natans* and many *Fontinalis antipyretica*. Dense stands of *Cladium mariscus* and *Phragmites australis* occur in the borders and at some places *Equisetum fluviatile* together with *Potentilla palustris* dominate. This pool does not dry up in summer and the water is influenced by a colony of gulls. On some occasions samples were taken from a valley north-

Table 4. Physical and chemical characteristics of 3 pools at Terschelling, based on data from spring and summer 1982 and 1984. Values are expressed as in *table 2*.

		Locality		
Parameter	n	Griltjeplak	Badhuisplak	Liesingerplas
pH	12	6.8–7.8	5.5–7.5	6.3–8.2
EC	2	240–290	185–270	–
Cl^-	7	55–100	63–143	77–127
Ca^{2+}	2	16–19	6.4–7.2	11.6–16.8
Mg^{2+}	2	8.3–9.9	4.2–6.9	9.9–19.2
Alkalinity	5	1.12–1.43	0.21–1.59	0.4–0.9
PO_4^{3-}-P	2	0.02–0.09	0.01–0.13	0.02–0.21
NH_4^+-N	2	0.07–0.16	0.07–0.11	0.07–0.21
NO_3^--N	2	0.03–0.28	0.03–0.17	0.02–0.68
K^+	2	2.9–5.5	1.2–4.8	3.1–10.5

west of Badhuisplak, provisionally called 'Orchisplak', which contained some water at the deepest point and plants like *Potentilla palustris*, *Eriophorum angustifolium*, *Carex disticha* and *C. nigra*.

The Liesingerplas, near the village Lies, is a low-lying flat grassy area with drains. Water depth does not reach more than 20 cm. *Apium inundatum* grows there luxuriously, accompanied by *Littorella uniflora*, *Callitriche hamulata*, *Equisetum fluviatile* and *Leptodictyum riparium*.

The estimated physico-chemical data from these 3 localities are presented in *table 4*. Summarizing these data, it can be stated that the water differs from the OV and EC pools in many respects. The most important differences are the considerably lower values of conductivity, chloride, calcium, and alkalinity.

4. RESULTS

4.1. The components of floating algal masses

Mass occurrence of filamentous algae was recorded from the beginning of May till August or September. Especially at OV and EC algal mats were present at many sites during a long period, reaching a coverage of 70–80% of the total water surface. At OV algal mats occurred in all pools, but at EC this was the case at only 10 sites. At EC no mass development of filamentous algae was recorded in ponds where *Chara* was dominant.

The composition of the mats appeared to vary considerably during the season. Species of the following genera made up the different components: *Spirogyra*, *Mougeotia*, *Zygnema*, *Oedogonium*, *Microspora*, and *Tribonema*. At OV species of *Vaucheria* and *Cladophora* were sometimes represented as well. The record of the very rare species *Vaucheria birostris* on the muddy soil of pool 1 at OV was very remarkable. The date of this record was July 21, which is nearly the same date (July 20) as when this species was first found in a cart-track in a moist dune valley on the Wadden island Schiermonnikoog (SIMONS 1974). Other *Vaucheria* species observed in pools at OV were *V. geminata* and *V. bursata*. At Tersch. *Mougeotia* was of greater importance than at EC and OV, and only at Tersch. *Klebsormidium* attained mass occurrence at one site (Badhuisplak). Filamentous bluegreens and species of *Bulbochaete* and *Cylindrocapsa* were present as minor components at several sites.

At OV and EC regular observations were made on the species composition and these are graphically presented for some localities (*figs 2* and *3*). From the figures it appears that each locality shows a distinct pattern of species composition and dynamics. *Spirogyra* and *Oedogonium* reached dominance at nearly all localities and often showed reproductive structures. *Tribonema* and *Microspora* may grow in considerable quantities early in the season (sites OV 1, 3, 4; EC 3.10, 3.11) and outcompete other species (EC 3.10, 3.11). At 2 localities (EC 0.1, EC 3.4) *Mougeotia* reached a large biomass early in season. *Mougeotia* and *Zygnema* only seldom attained large quantities and were nearly always present in the vegetative state.

Observations at OV were terminated in the end of July when most ponds were drying up. At EC mass occurrence disappeared in August or September.

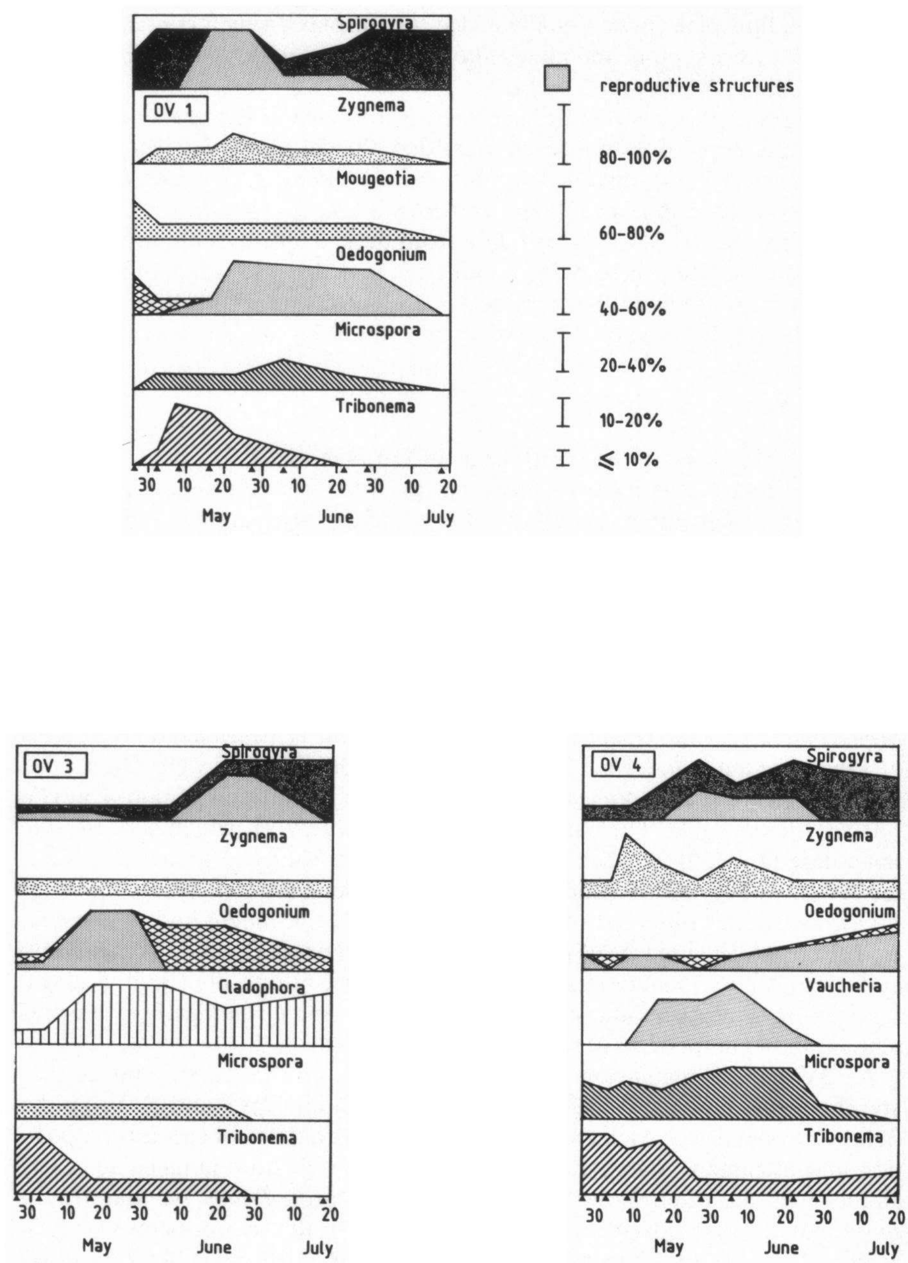

Fig. 2. Seasonal dynamics of the main components in floating mats from 3 pools at Oostvoorne (OV1, OV3, OV4).

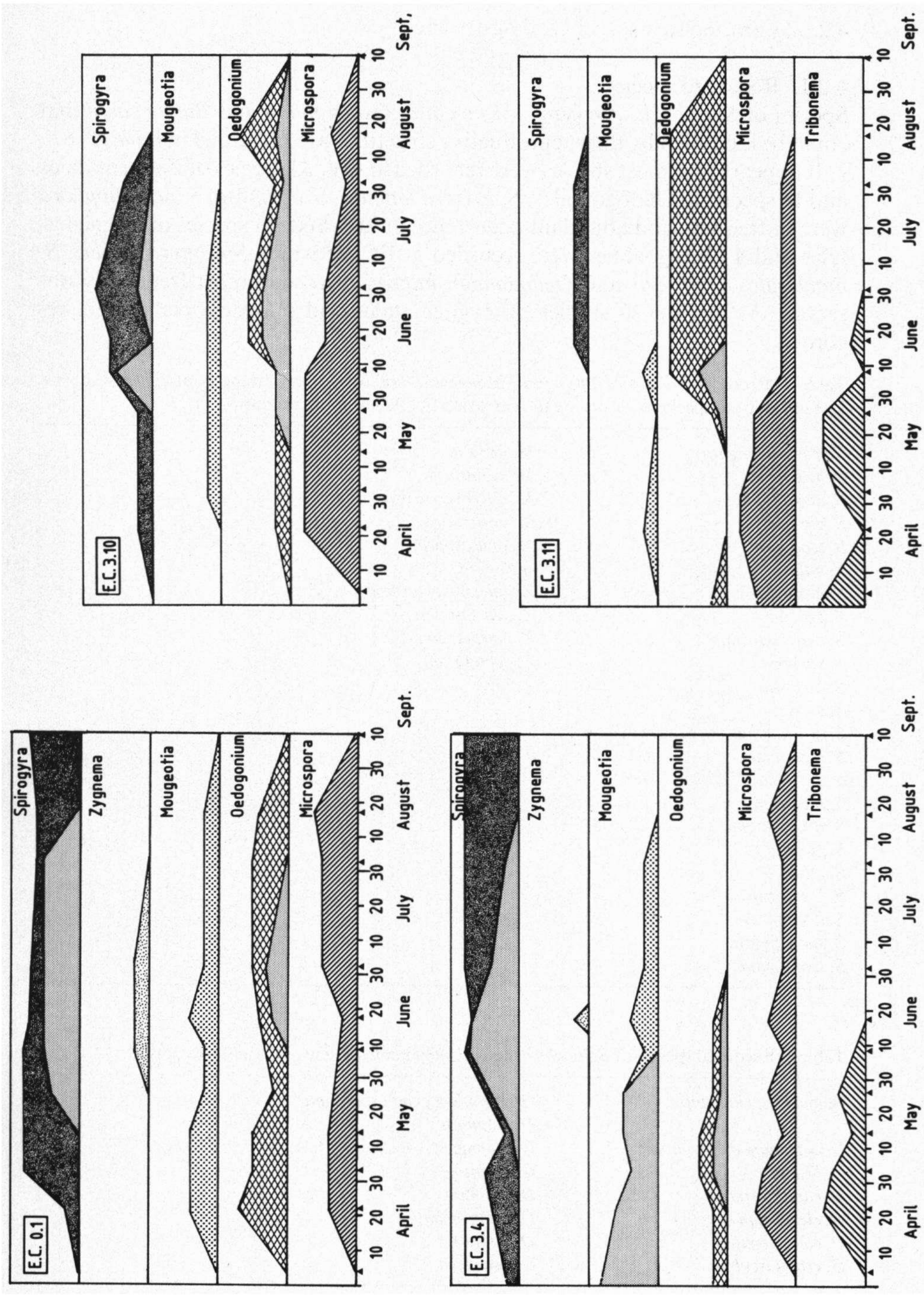

Fig. 3. Seasonal dynamics of the main components in floating mats from 4 pools at Egmond-Castricum (EC 0.1, EC 3.4, EC 3.10, EC 3.11).

4.2. Zygnematales and Oedogoniales

4.2.1. Recorded species

Species of *Spirogyra, Zygnema, Mougeotia, Oedogonium* and *Bulbochaete* that could be identified by their reproductive structures are presented in *tables 5–8*.

It appears that most species were recorded at OV: 33 species of Zygnematales and 15 species of Oedogoniales. *Spirogyra longata, S. bellis* and *S. acanthophora* were of frequent and abundant occurrence at OV. Sixteen species of Zygnematales and 4 Oedogoniales were recorded at EC, of which *Spirogyra weberi, S. majuscula, S. gracilis* and *Oedogonium intermedium* were most frequently observed. At Tersch. 20 species of Zygnematales and 6 Oedogoniales were recorded.

Table 5. Recorded species of *Spirogyra, Mougeotia,* and *Zygnema* in dune pools at Oostvoorne. The sequence of species is according to decreasing frequency of observations.

Spirogyra longata	*Mougeotia laevis*
S. bellis	*M. scalaris*
S. acanthophora	*M. microverrucosa*
S. parvula	*M. gotlandica*
S. teodoresci	*M. microspora*
S. inflata	
S. neglecta	*Zygnema pawhuskae*
S. gracilis	*Z. peliosporum*
S. catenaeformis	*Z. pawneanum*
S. varians	*Z. pectinatum*
S. farlowii	
S. weberi	
S. grevilleana	
S. majuscula	
S. silesiaca	
S. setiformis	
S. frankliniana	
S. punctata	
S. nitida	
S. condensata	
S. daedaloides	
S. subpapulata	
S. tenuissima	

Table 6. Recorded species of *Bulbochaete* and *Oedogonium* in dune pools at Oostvoorne.

Bulbochaete mirabilis	*Oedogonium echinospermum*
	O. magnum
Oedogonium abbreviatum	*O. oblongum*
O. brauni	*O. orientale*
O. capilliforme	*O. patulum*
O. cleveanum	*O. pringsheimii*
O. concatenatum	*O. rivulare*
O. crassiusculum	*O. vaucherii*

Table 7. Recorded species of *Spirogyra, Mougeotia,* and *Oedogonium* from dune pools in the area between Egmond-Binnen and Castricum. The sequence of species is according to decreasing frequency of observations.

Small artificial pools	IJsbaan
Spirogyra weberi	*S. fluviatilis*
S. majuscula	*S. rivularis*
S. gracilis	*S. majuscula*
S. colligata	*S. nitida*
S. parvula	*S. juergensii*
S. inflata	*S. gracilis*
S. bellis	
S. juergensii	
S. setiformis	
S. teodoresci	
S. varians	
Mougeotia scalaris	
M. virescens	
Oedogonium intermedium	
O. rivulare	
O. braunii	
O. vaucherii	

Comparing the species composition at the three sites, it appears that the areas EC and OV show much resemblance in species composition and that Tersch. is rather distinct in this respect. Eight of the total 15 *Spirogyra* species found at Tersch. were not recorded at EC and OV, while at EC only 5 *Spirogyra* species of the total of 14 species were not recorded at OV. For *Oedogonium* the same applies. Hence, the species composition of Zygnematales and Oedogoniales at the lime-spoor Tersch. is clearly different from the limerich southern dune areas.

4.2.2. Taxonomic remarks about *Spirogyra* species

The morphology of most species was in accordance with the existing species descriptions (Kadlubowska 1984). However the variability in several species appeared to be larger than indicated in the flora's, especially concerning dimensions of spores, morphology of gametangium cells, and diameter of filaments. On some occasions it was difficult to decide between two species due to overlap in dimensions. Several species complexes are discernable in *Spirogyra* where often only quantitatively based species differences exist. Species belonging to such complexes are for instance, *Spirogyra silesiaca* (overlap with *S. colligata*), *S. weberi* (overlap with *S. semiornata*), *S. parvula* (hardly discernable from *S. chenii*), *S. catenaeformis* (in a complex with *S. varians, S. affinis,* and *S. teodoresci*) and *S. nitida* (in a large complex with among others *S. setiformis*). In such cases species names were chosen which fitted best with the existing descriptions.

In one species, namely *Spirogyra frankliniana,* ripened spores were found to

Table 8. Recorded species of *Spirogyra, Zygnema, Mougeotia, Mougeotiopsis, Oedogonium,* and *Bulbochaete* in dune pools at Terschelling. The sequence of *Spirogyra* species is according to decreasing frequency of observations. D: Reaching dominance in floating mats.

Names of pools	Badhuisplak	Orchisplak	Griltjeplak	Paulusplak	Liesingerplak
Spirogyra fennica	+				
S. flavescens	+				
S. fragilis	+				
S. hassallii				+	
S. inflata	+				
S. majuscula		+D			
S. maxima	+D				
S. mirabilis	+				
S. neglecta		+			
S. papulata	+				
S. parvula	+				
S. setiformis			+D		
S. singularis	+				
S. tenuissima	+				
S. varians				+D	
S. variformis					+D
S. nitida					+D
Zygnema calosporum	+				
Z. pawhuskae		+			
Mougeotia virescens	+				
M. parvula	+				
Mougeotiopsis calospora	+				
Oedogonium borisianum	+				
O. fragile					+
O. pungens	+				
O. rufescens	+				
Bulbochaete angulosa	+				
B. furberae	+				

be roughly structured and not smooth as indicated in the flora's. This observation will be published elsewhere.

4.2.3. Periodicity of *Spirogyra* and *Oedogonium* species

Reproductive structures of *Spirogyra* and *Oedogonium* species were recorded from the end of April till the second half of August. All available observations for *Spirogyra* species from OV were summed and presented in *fig. 4*. The peak occurred in the third part of May, and a second smaller peak in the first part of June. For *Oedogonium*, data are not sufficient to allow quantification, but appear similar to *Spirogyra*.

The earliest record of reproduction in *Spirogyra* concerned the species *S. inflata* at all three study areas, and the latest regard *S. bellis* at OV, *S. majuscula, S. setiformis* and *S. weberi* at EC, and *S. nitida* and *S. parvula* at Tersch. Apart from *S. parvula* and *S. weberi* the late records concern species with relatively wide filaments (> 50 μm). This is a general phenomenon described earlier by TRANSEAU (1916).

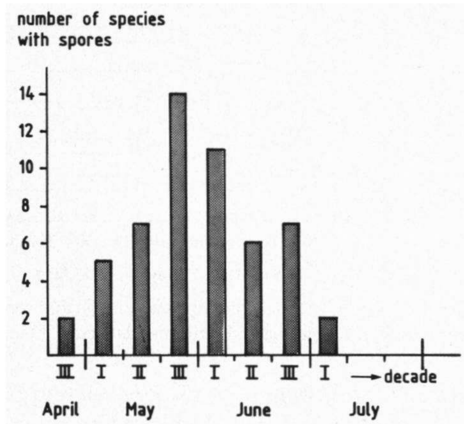

Fig. 4. Seasonal frequency of spore production from all recorded *Spirogyra* species at Oostvoorne.

Concerning individual species, it appears that periodicity of vegetative and reproductive occurrence differed at various locations. This is illustrated for *Oedogonium intermedium* at 10 localities at EC in *fig. 5*. The end of the reproductive period for *Oedogonium intermedium* occurred at the beginning of July at most localities, whereas the start of reproduction was more variable. Also the length of vegetative and reproductive periods within a species may vary per location. When the data from comparable locations for a species are taken together, as

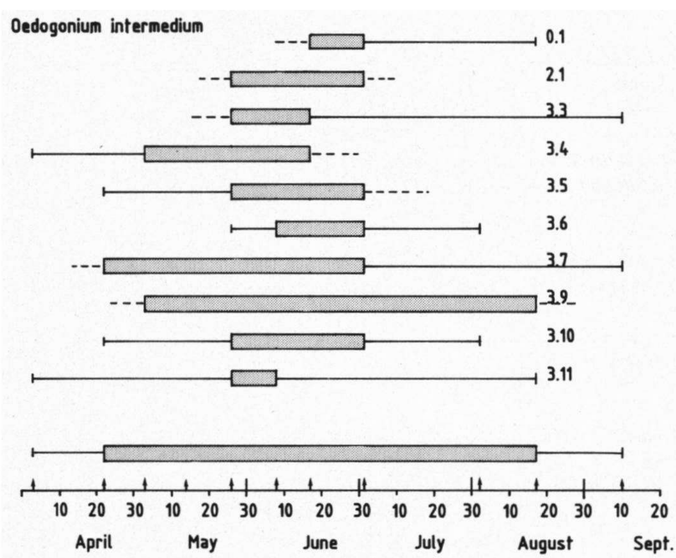

Fig. 5. Periodicity of vegetative stages (lines) and reproductive stages (blocks) of *Oedogonium intermedium* at 10 sampling localities at Egmond-Castricum. Dates of observations are indicated by arrows. The lowest line/block summarizes the data from all localities.

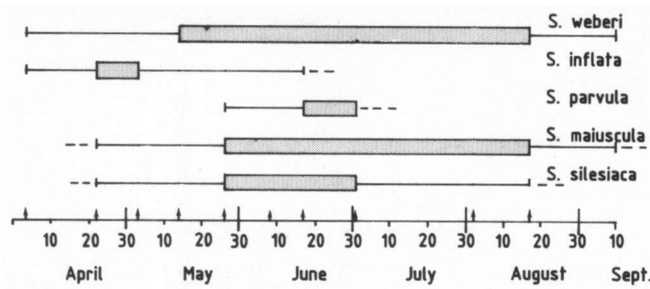

Fig. 6. Periodicity of vegetative stages (lines) and reproductive stages (blocks) of 5 *Spirogyra* species from different localities at Egmond-Castricum. Dates of observations are indicated by arrows.

is done for *Spirogyra* at EC (*fig. 6*), it appears that each species shows a specific pattern of periodicity. Species as *Spirogyra weberi* and *S. majuscula,* which were most frequently recorded at EC have relatively long reproductive periods. This was also the case for *Spirogyra acanthophora* and *S. bellis* at OV.

4.2.4. Small epiphytic algae

From the observations on glass slides, it appeared that in the group of small

Table 9. Epiphytic algal species which were regularly recorded on glass slides as artificial substrate.

Study area	OV	EC	Tersch.
Chlorophyceae:			
Chaetopeltis orbicularis	+	+	+
Gongrosira sp.	+	+	+
Chaetosphaeridium globosum	+	+	+
Coleochaete scutata	+	+	+
C. pulvinata	−	−	+
C. irregularis	−	−	+
Dicranochaete reniformis	−	+	+
[a]*Stigeoclonium farctum*	+	+	+
[a]*S. tenue*	+	+	+
[a]*S. helveticum*	+	+	+
Microthamnion kützingianum	−	+	+
Palmodictyon varium	+	−	+
Chrysophyceae:			
Chrysochaete brittanica	+	+	+
Dinobryon divergens	−	−	+
D. cylindricum	−	−	+
D. sociale	−	−	+
Epipyxis utriculus	+	+	+
Xanthophyceae:			
Ophiocytium arbuscula	+	+	+
O. cochleare	+	+	+
O. capitatum	+	+	+
O. parvulum	+	−	+
O. ilkae	−	−	+

[a] in accordance with the taxonomic conception of SIMONS et al. (1986)

epiphytic algae some species were of regular occurrence. These species are presented in *table 9*. From this survey it appears that several species were only recorded at Tersch. It must be kept in mind that most observations of this kind were done at EC and Tersch.

5. DISCUSSION

5.1. Water quality

From the physico-chemical data, most of the investigated waters can be characterized as undisturbed nutrient-poor freshwater with a moderate (at Tersch.) or high amount of calcium and bicarbonate (at EC and OV).

The pools are fed by rain water and subsurface seepage of groundwater. The groundwater influence is reflected by relatively high chloride contents with values above 50 mg l^{-1} (LEENTVAAR 1981). As the observed chloride values were mostly below 100 mg l^{-1}, no large influence of salt spray was detected.

The measured values of nitrate and phosphate were low compared with the mean values for natural groundwater in dunes as given by BAKKER et al. (1979). This means that the waters at EC were not influenced by the neighbouring artificial infiltration of Rhine water commonly the case nowadays for the supply of extractable water for public purposes.

5.2. Mass occurrence

At many sites filamentous algae reached mass occurrence in spring and summer. Mass occurrence under low nutrient conditions is strange at first sight. One of the explanations may be that a considerable input of nutrients is in balance with the uptake by organisms, in which case no or only a small 'surplus' of nutrients in the free water can be measured. The nutrient turnover can be considerable by the high rate of mineralisation at the circumneutral pH (BAKKER et al. 1979). Input, especially of nitrate will be enhanced by neighbouring shrubs of *Hippophaë rhamnoides* of which symbiontic N-fixation may reach values up to 275 kg N/ha (OREMUS 1982). Also the input by rainwater in the small volumes of pools must not be neglected. Measurements from rainwater samples at a station near Rotterdam (not far east from OV) yielded a yearly mean value of 6.31 mg N l^{-1} and from a station in the northwestern part of the country (De Kooy) a yearly mean value of 2.51 mg N l^{-1} was measured (KNMI/RIV 1982). The nutrients will be quickly available as nutrient adsorption to organic substances in the sandy soil will be relatively low. Carbon will not be limiting by the moderate or high alkalinity levels, assuming that most filamentous algae from alkaline habitats use bicarbonate as C-source (ROUND 1973).

A comparable situation may exist for planktonic algae, as LEENTVAAR (1981) showed that in dune lakes most planktonic algae are characteristic for eutrophic situations.

In pools at EC with dominance of *Chara*, floating algal masses were never observed, possibly due to the excretion of sulphur-containing allelopathic substances recently demonstrated in *Chara* (WIUM-ANDERSEN et al. 1982).

The disappearance of the algal mats in late summer may be related to nutrient depletion, infection by fungi, pH instability, or self shading.

The genera forming the floating masses were the same in all areas, except at OV where *Cladophora* and *Vaucheria* were important components in some pools. The occurrence of *Cladophora* and *Vaucheria* only at OV may be related to the relatively high nutrient status there (compare *table 2* with *tables 3* and *4*). That genera like *Cladophora* are bound to more eutrophic situations, is supported by the frequent and abundant occurrence of *Cladophora,* together with *Hydrodictyon, Enteromorpha* and filamentous bluegreens in dune waters fed by infiltration of river water.

Spirogyra and *Oedogonium* often reached dominance, on several occasions preceded by dominance of *Tribonema* and/or *Microspora* early in the season. According to WHITFORD & SCHUMACHER (1963) and DE VRIES & HILLEBRAND (1986) temperature is the regulating factor for this phenomenon. At temperatures above 15 °C the growth of *Tribonema* and *Microspora* would be reduced and that of *Spirogyra* and *Oedogonium* enhanced, which is supported by the observations.

5.3. Species composition

Spirogyra and *Oedogonium* species make up the most important components in dune pools, and were represented by 35 and 20 species respectively. Of the 35 *Spirogyra* species, only 4 have not yet been recorded outside the dune area. Up to now, about 70 species of *Spirogyra* were recorded in The Netherlands by the present author (to be published).

Some general statements can be made about the relation between species composition and physico-chemical factors. The observed difference in species combination between OV and EC on the one hand, and Tersch. on the other, may be related to the lower calcium content and alkalinity at Tersch. The species composition of especially the *Spirogyra* species from OV and EC showed much mutual resemblance, reflecting the large similarity in habitat factors. At EC the locality 'IJsbaan' which is distinct from the small pools, with lower calcium and alkalinity, a distinct combination of *Spirogyra* species was recorded with among others *S. majuscula* and *S. nitida. S. majuscula* and *S. nitida* were also abundant at a few sites on Tersch. *S. nitida* was often recorded from several inland Littorellion situations, which are comparable with the habitats at Tersch.

When comparing dune waters with inland waters, some tendencies can be indicated. Firstly, most species are not restricted to the dune area, but some species are more abundant there than in inland freshwater habitats in The Netherlands, e.g. *Spirogyra acanthophora, S. bellis, S. colligata, S. frankliniana, S. inflata, S. longata, S. majuscula, S. parvula* and *S. silesiaca.* Some species such as *S. juergensii, S. farlowii,* and *S. singularis* rarely occur in the dune waters but are common in eutrophic polder ditches. Presumably, the main reason for these differences is the lower nutrient status of the dune waters compared to most inland eutrophic habitats.

Only a few data are available for the comparison of the dune situation with other nutrient-poor situations in The Netherlands. An interesting opportunity for such a comparison is a recent study on the distribution of zygnematalean filamentous algae in the low-mountainous Western German Spessart region near Frankfurt (GÜNTHER 1985). The investigated small temporary pools in the Spessart are nutrient-poor with low chloride and calcium contents, low alkalinity, and pH values from 5.3–6.8. *Spirogyra* species frequently occurring there are *S. parvula, S. inflata, S. varians, S. teodoresci, S. mirabilis* and *S. nitida.* Except for *S. mirabilis* these species were also recorded in all investigated dune areas. At OV and EC *S. parvula* and *S. inflata* were rather common and *S. nitida* occurred at Tersch. Apparently such species show preference for nutrient-poor situations. Moreover, *Spirogyra mirabilis* and *S. nitida* are able to grow well under conditions of low calcium, chloride, alkalinity and pH, as in the Spessart region and Tersch. However, a species like *Spirogyra nitida* must have a very wide ecological amplitude, as it occurs also in very eutrophic and hardwater ditches in The Netherlands.

Most of the *Spirogyra* species are inhabitants of hardwater environments (HOSHAW 1968). This is supported by the fact that in the softwater Spessart region only 14 *Spirogyra* species were found against 26 species in the hardwater dune habitats of OV and EC.

5.4. Periodicity

Regarding the seasonal periodicity, some generalisations can be made concerning the spore producing *Spirogyra* and *Oedogonium* species. The observed peak in spore production in the second half of May and the first half of June in *Spirogyra* is a general phenomenon for The Netherlands as a whole, presumably primarily regulated by climatic factors. One of the chemical factors which is important in inducing reproduction is N-depletion (SIMONS et al. 1984). No decrease of N in the course of time could be determined in the water of the pools. Yet the possibility exists that for the growing algal mass this nutrient will become depleted at a certain stage. This assumption is supported by some observations at OV where renewed vegetative growth turned a yellowish algal mat with reproductive stages brightgreen after rainfall with nutrient-input. Other modulating factors may play a role so that each species shows a distinct pattern of growth and reproduction.

In *Zygnema* and *Mougeotia* sexual reproduction was rare. For *Zygnema* it is known (PESSONEY 1968) that this genus easily forms asexual spores (akinetes and aplanospores).

5.5. The biological significance of spores

The zygospores of *Oedogonium* and *Spirogyra* are decay-resistant resting spores of which the thick walls were shown to contain sporopollenin, at least in *Spirogyra* (DE VRIES et al. 1983). This is an important life-strategy for organisms living in small and in this case often ephemeral water bodies. Spores are more frequently observed in small water bodies such as pools and ditches in The Netherlands than in larger water bodies. PESSONEY (1968) made the same observation working in small water habitats in the vicinity of Austin, Texas. MROZINSKA-

WEBB (1976) states that in Southern Poland the highest rate of sexual reproduction in *Oedogonium* occurred in periodically filled ponds, with a peak in June.

Most *Spirogyra* species appear to be homothallic, at least in culture (HOSHAW 1968; SIMONS et al. 1984). However, different clones of species with scalariform conjugation are expected to exchange genetic material in natural situations, which could be reflected in morphological variability in the offspring. Within an area like OV, morphological characters such as filament diameter only varied in a narrow range for most species, suggesting that in such a small area material belonging to only one clone occurred. Even over different areas little morphological variation could be detected in most species, e.g., in *Spirogyra inflata* filament diameter varied between 15 and 21 μm at the three study areas. Hence, it seems that spores are more important for surviving critical periods than for maintaining genetical variability, at least in the area studied.

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