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A CLASSIFICATION SYSTEM FOR THE EPILITHIC ALGAL COMMUNITIES OF THE NETHERLANS' COAST

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Up to now little has been written concerning the algal vegetation of the Dutch coast. VAN GOOR (1923) was the first investigator who occupied himself with the description of algal communities in our waters; in the western part of the Waddensea and in the former Zuyderzee he distinguished 8 "associations". Some years later SLOFF (1925–'26) described the zonation of the *Fucaceae* in the littoral belt of Bergen op Zoom and Koffiehoek (Island of Tholen). This subject was studied again by ZANEVELD (1937), who tried to find a correlation between the position of the *Fucaceae* belts at Den Helder and the different tidal levels. Since 1950 the phytocenological study of the Dutch coast was taken in hand by the author with the following intentions: 1 °. to give as complete a description as possible of the epilithic algal communities, 2°. to devise a system for the classification of these communities and 3°. to inquire into the factors which determine differentiation of the vegetation into well-characterized units.

METHODS

For analysing the floristic composition of the different vegetation types the survey-method of BRAUN–BLANQUET was used (KORNAŚ and MEDWECKA–KORNAŚ, 1950). In a certain area with a homogeneous vegetation all species were noted with estimations of their abundance and dominance, expressed by means of a figure according to the scale of BRAUN–BLANQUET. In some cases also the sociability was noted. Examples of such surveys have already been published by KORNAŚ and MEDWECKA–KORNAŚ (1950), WAERN (1952) [1] and DEN HARTOG (1953). In Dutch waters we can suffice with this method, since the algal vegetation usually descends no deeper than about $1\frac{1}{2}$ m. below mean low watermark; in deeper water no suitable substrates are present, and there only some solitary algae may be found (VAN GOOR, 1923). In seas where the algae grow also in deeper water the vegetation can be surveyed by diving (WAERN, KORNAŚ), or by applying a frequency-method to the study of the dredgings (FELDMANN, 1938).

[1] WAERN used the scale of HULT, SERNANDER and DU RIETZ.

UNITS

Vegetation-units can be recognized very easily in the field by the dominant species. The boundaries between them are often very sharp, in consequence of the zonation and the differences in physiognomy. The constancy of the floristic composition of a certain vegetation is determined by means of a synthesis of the surveys made in that vegetation. These vegetation-units, characterized by the dominance and the constancy of one or more species, are called sociations (DU RIETZ, 1931; WESTHOFF, 1951).

Moreover, some of these sociations have characteristic species or a characteristic combination of species. Therefore they may be considered associations in the sense of BRAUN–BLANQUET (WESTHOFF, 1951). Sociations as well as associations are units of the same rank; however, in this paper only the more general term sociation is used.

So far 25 sociations and associations have been observed by the author along the Dutch coast. An account on them will be published later.

In order to obtain a survey of these communities it is necessary to class them into units of a higher order. In phytocenology associations and sociations are classed into alliances (NORDHAGEN, 1936), according to their floristic similarity. In phycocenology, however, it would as yet be premature to establish alliances, as we do not possess complete descriptions of algal communities from sufficiently large regions. Therefore the formations, the higher vegetation-units, used below, are not based on the floristic principle, but on the physiognomy and the stratification of the vegetation. Moreover, for classing these units the position in the succession-sere and in the zonation are important. These formations are the units of higher rank which for the time being have to be used in algal cenology.

PHYSIOGNOMY

The physiognomy and structure of the algal vegetations is considered a very important character for their classification. Many authors exclusively described the communities as physiognomic units, without discussing the floristic composition (KJELLMAN, 1878; BØRGESEN, 1905; KYLIN, 1907; JONSSON, 1912; VAN GOOR, 1923, a.o.); the conspicuous species only were mentioned. Nevertheless, a good idea of these communities may be formed. This is not surprising, since the variety of forms is much greater in the algae than in the phanerogams. There are gigantic *Laminariaceae* and robust *Fucaceae*, but delicate filamentous algae and minute unicellular forms also occur. Moreover, in taxonomically completely different groups there are quite similar growth-forms; for instance *Ectocarpus* in the *Phaeophyceae*; *Cladophora* in the *Chlorophyceae* and *Callithamnion* in the *Rhodophyceae* represent the same basic life form. OLTMANNS (1908), FUNK (1927), NIENBURG (1930) and some others have tried to construct a system on these variations in growth form. They considered these life forms as ecological adaptations. In a somewhat changed form their system is used by the author.

The most important growth forms of the region are:

1. **Laminaria**-type: *Laminaria, Alaria, Saccorhiza.*
2. **Fucus**-type: *Fucus, Ascophyllum, Pelvetia, Himanthalia, Bifurcaria.*
3. **Cystoseira**-type: *Cystoseira, Sargassum, Halidrys.*
4. **Desmarestia**-type: *Desmarestia.*
5. Crustaceous algae (**Hildenbrandtia**-type), forming crusts closely attached to the substrate; *Hildenbrandtia, Lithothamnion* [1], *Melobesia, Ralfsia, Lithoderma.*
6. Filiform algae (**Ulothrix**-type), monosiphonous and polysiphonous, simple filaments, sometimes with rhizoids: *Ulothrix, Urospora, Gayella, Rhizoclonium, Bangia, Percursaria.*
7. Tubular algae (**Enteromorpha**-type), algae with long, simple or ramified hollow fronds: *Enteromorpha, Blidingia, Asperococcus, Dumontia, Scytosiphon.*
8. Membranaceous algae (**Ulva**-type), forming irregular flat membranes: *Ulva, Monostroma* [2], *Porphyra, Petalonia.*
9. Dendritic algae (**Cladophora**-type), forming branched tufts: *Cladophora* [3], *Bryopsis, Ectocarpus, Sphacelaria, Callithamnion, Ceramium, Cystoclonium.*
10. Fruticose algae (**Chondrus**-type), flat branched ribbonlike or leafy fronds: *Chondrus, Gigartina, Dictyota, Delesseria, Rhodophyllis.*
11. Gelatinous algae (**Nemalion**-type), algae with very gelatinous, branched fronds: *Nemalion, Mesogloia, Scinaia.*
12. Coralline algae (**Corallina**-type), tufted chalk-incrusted forms: *Corallina, Jania.*
13. Pulvinate algae (**Vaucheria**-type), forming cushionlike structures: *Vaucheria, Rhodochorton.*
14. Microscopical algae, algae smaller than 2 mm, which occur singly. Many epiphytes, endophytes and parasites belong to this group.

The various species belonging to the same growth form do not occur singly, but appear, as a rule, collectively; therefore the vegetation types can be characterized by means of the dominant growth form, i.e. with that which determines its physiognomy.

KJELLMAN (1878) was the first who used for these physiognomic units the term "formation". He wrote: "Unter einer Algenformation sollte folglich ein Abschnitt der ganzen Algenvegetation verstanden werden, der durch ein eigentümliches Vegetations-Gepräge ausgezeichnet ist. Im Allgemeinen erhalten diese Abschnitte dadurch dieses Gepräge dass ein oder einige Algenarten die Hauptmasse ihrer Bestandteile ausmachen".

It is clear that this rather vague definition may be interpreted in different ways. According to it all physiognomic units can be regarded as formations. We may speak of a *Pelvetia*-formation, because *Pelvetia canaliculata* gives this vegetation a certain aspect, but with the same right we can speak of a *Fucaceae*-formation, while the joint *Fucaceae* too give the vegetation a certain physiognomic aspect.

In 1905 BØRGESEN proposed to use for the smaller units the term "association". "The associations are often united in a natural way in larger communities, where they live together under the same or very similar biological and ecological conditions. I propose the name of formation for these more comprehensive groups". Thus BØRGESEN distinguished a "*Pelvetia*-association" and a "*Fucaceae*-formation".

Unfortunately BØRGESEN did not use his own distinction consistently; consequently it is not always clear whether he means a formation or

[1] Some species of this genus do not belong to this growth form, e.g. *Lithothamnion calcareum* is better referred to the coralline algae.

[2] *Monostroma groenlandicum* is a tubular alga.

[3] *Cladophora basiramosa* is a filiform alga (it resembles *Rhizoclonium*).

an association. KYLIN (1907) criticized this inconsistency; all units which he could distinguish were called by him "formations".

COTTON (1912) had a completely different conception of "formation" and reserved this term "for communities which occur together in a definite type of habitat". He distinguished only a rocky-shore formation, a sandy-mud formation and a saltmarsh formation. So in this sense a formation is not a phytocenological unit, but a pedological one.

JONSSON (1912) avoided the term formation because in his opinion it has been used in a wrong way by the other phycologists. He distinguished therefore associations only, with regard to which he makes the following remark: "Where I think they are closely allied I combine them into communities". He defined these communities after their dominating life forms (Community of filiform algae; Community of crust algae; Community of *Fucaceae*; Community of *Laminariaceae*; Community of Deepwater-*Florideae*).

SETCHELL (1917), FUNK (1927) and FELDMANN (1938) used the term formation only for the comprehensive vegetation-units which are characterized by the dominating life forms, i.e. in the sense of JONSSON's communities. Therefore KJELLMAN's definition should now be formulated more precisely as follows: An algal formation is a part of the algal vegetation whose aspect is determined by the dominance of a certain life form or the joint dominance of some life forms.

STRATIFICATION

When we analyse a certain algal vegetation, we will find that besides the dominant growth form other growth-types occur; they form the undergrowth and the epiphytes. The congregation of different growth-forms in one community gives the latter a definite stratification. Thus we can distinguish in the *Fucaceae*-communities (*Fucus*-formation) 3 layers: 1 ° a layer of crustaceous algae, 2 °. a layer of dendritic and fruticose algae and 3 °. a *Fucus*-layer; moreover, epiphytic species occur on the *Fucaceae* as well as on the dendritic and fruticose algae. Sometimes one of these layers is absent, but potentially the *Fucus*-formation is three-layered. One-layered (*Hildenbrandtia*-formation), two-layered (*Cladophora*-formation) and four-layered formations (*Laminaria*-formation) occur also along the European coast. Every formation has its characteristic potential stratification.

ZONATION

When we look at the slope of a dike with a well-developed algal vegetation, our attention is immediately drawn to the zonation of the algae. The occurrence of the larger brown algae in belts has of old attracted the attention of algologists; nevertheless little is known concerning the causes of the zonation. The ecologists of the British school (BARKMAN, CHAPMAN, COLMAN, SOUTHWARD, T. A. and A. STEPHENSON, ZANEVELD a.o.) impute the phenomenon to the tidal movement and the complex of factors coupled with it; but along the Swedish West-coast the same zonation occurs independent of the tides (KYLIN, LEVRING, SJÖSTEDT, a.o.).

A zonation of *Chlorophyceae* has been described by HAMEL (1940, 1942) from the Basque coast; in Dutch waters such a zonation, mainly consisting of *Ulvales*, has also been found. Moreover a zonation of *Rhodophyceae* has been discovered, which has its most complete development on the piles which strengthen the Oranjedijk near Vlissingen. There we see from the top downwards the following belts:

1. *Catenella repens*
2. *Callithamnion hookeri*
3. *Ceranium deslongchampii*
4. *Polysiphonia urceolata*

NIENBURG (1930) used growth forms to divide the coastal region into a series of belts, each characterized by a distinct formation (in the modern sense). The present investigations have made his system untenable, since communities typified by completely different growth forms were found at the same level (See the table on p. 131).

SUCCESSION

Very important for a classification system is the phenomenon of succession, which can be studied particularly well along the Dutch coast. By the continuous activities of man on dikes and breakwaters (dumping of stone blocks, renewing of piles, bituminizing of the dike-slope) the vegetation is destroyed again and again. And independent of the season the same algae always colonize the vacant spots in the same manner. Within 6 weeks the stones dumped in the littoral belt are covered with *Enteromorpha*, *Porphyra*, *Ulothrix* and *Ulva*. Later, all kinds of dendritic algae settle among them, and soon also the first germlings of the *Fucaceae* appear. After some years the whole spot has been occupied by the *Fucaceae*, each in its own belt. The undergrowth consists of dendritic algae; only a few tubular and membranaceous algae occur at that stage. In other localities establishment of *Fucus* between the *Enteromorpha*-vegetation progresses more slowly or sometimes entirely fails. In that case dendritic and fruticose algae get a chance of succeeding the *Enteromorpha-Porphyra*-sociation and not being untimely superseded by the *Fucaceae* they may form a luxurious growth. On the bituminized northern mole of Harlingen a luxurious community of *Ceranium deslongchampii* has succeeded the *Enteromorpha-Porphyra*-sociation, as on bitumen *Fucaceae* do not grow at all or only poorly.

In localities exposed to the surf and at the same time strongly washed with sand, e.g. on breakwaters along the beach, the *Enteromorpha-Porphyra*-sociation maintains itself permamently.

It is remarkable that the succession has a divergent character, the terminal stages being more numerous than the initial ones. In the tidal zone only two pioneer communities occur. The *Blidingia*-sociation, wich occurs in the upper part of the littoral belt, develops into 2 terminal stages, viz. the *Pelvetia*-sociation and the *Fucus spiralis*-sociation. The low-littoral *Enteromorpha-Porphyra*-sociation, which is completely homogeneous, differentiates even into 4 terminal stages.

Looking at the table one will observe that in the littoral belt all terminal stages except one have relation to the sociations of the large

brown seaweeds. Between the belts of *Fucus serratus* and *Laminaria* along the coasts of the Channel (BEAUCHAMP, 1914; DAVY DE VIRVILLE, 1940), in the Faeröes (BØRGESEN, 1905) and along the Norwegian Westcoast (LEVRING, 1937) a belt of *Himanthalia elongata* occurs. Along the Dutch coast *Himanthalia* cannot grow, and its sociation is replaced by the *Polysiphonia-Chaetomorpha*-sociation, in which mainly dendritic and fruticose algae are represented. The latter sociation is not a real terminal stage but it maintains itself because the circumstances for the establishment of the terminal *Himanthalia* sociation are not realized. Also in the sublittoral a place has been left open, because the communities of *Desmarestia* and of *Cystoseira* are wanting in the Netherlands.

THE CLASSIFICATION SYSTEM

The discussion of the stratification as well as of the succession has shown that the formations are not all equivalent from a structural

THE ALGAL COMMUNITIES OF THE DUTCH COAST

<table>
<tr><td>Supra-littoral</td><td>"Buff zone"</td><td>Prasiola
Bangia-Urospora</td><td colspan="2"></td><td>M.H.W.</td></tr>
<tr><td rowspan="4">Eulittoral</td><td rowspan="4">Hilden-brandtia</td><td>Blidingia</td><td>Catenella</td><td>Pelvetia
Fucus spiralis</td><td rowspan="4">M.L.W.S.</td></tr>
<tr><td rowspan="3">Enteromorpha compressa-Porphyra
+
Enteromorpha intestinalis</td><td>Callithamnion hookeri</td><td rowspan="3">Ascophyllum
+
Fucus vesiculosus</td></tr>
<tr><td>Ceramium deslongchampii
+
Chondrus
+
Gigartina</td></tr>
<tr><td>Polysiphonia-Chaetomorpha</td><td>Fucus serratus</td></tr>
<tr><td>Sublittoral</td><td></td><td>Ulva</td><td>Codium-Hypoglossum</td><td></td><td>Laminaria</td></tr>
</table>

EXPLANATION OF THE TABLE

From left to right the communities are arranged according to their sociological progression. In general outline this classification corresponds to the succession, but there are some important deviations (e.g. the place of the *Hildenbrandtia*-sociation). From the top downwards the communities are classed according to their place in the zonation. Sometimes more than one community of a formation occurs in the zonation at the same level; in that case they have in other respects different ecological preferences; for instance the *Ascophyllum*-sociation occurs in very sheltered localities and avoids more exposed ones, while on the contrary the *Fucus vesiculosus*-sociation prefers more exposed spots.

One community, viz. the *Monostroma- Dumontia*-sociation,which occurs in littoral pools, could not be fitted into the table without deviating from general plan.

Mean high water mark (M.H.W.) is fixed as the upper limit of *Balanus balanoides*.

Mean low water mark at springtide (M.L.W.S.) is leveled with the upper limit of the *Laminaria*-vegetation in the Waddensea and with the *Codium*-vegetation in the province of Zeeland. It is clear that the corresponding tidal levels of an exposed and a sheltered coast do not coincide (DU RIETZ, 1940, 1947).

point of view. The communities which possess a life formpattern consisting of tubular and membranaceous algae, form the little differentiated pioneer vegetation, whereas the terminal stages are formed by the highly organized *Fucaceae-* and *Laminaria*-sociations. The communities of the dendritic and fruticose algae are only transitional stages in the succession. Thus it is possible to arrange the formations according to their position in the succession and their degree of organisation, in short to their sociological progression.

Along the Dutch coasts 7 formations can be distinguished:

1 °. **Hildenbrandtia**-formation, an one-layered formation of crustaceous algae which can develop into more highly organized formations. To this formation belong among others the *Hildenbrandtia prototypus*-sociation and the supralittoral "buff zone" (T. A. and A. STEPHENSON, 1954), a belt of nigrescent *Cyanophyceae* and *Protococcacae*. Also the supralittoral lichen-vegetation in which *Verrucaria maura*, *Caloplaca marina*, *Xanthoria parietina*, etc. occur, may be included in this formation.

2 °. **Prasiola**-formation, a two-layered formation of filiform and small membranaceous algae which are confined to supralittoral nitrate-rich stones.

Along the Dutch coast only the *Prasiola stipitata*-sociation occurs.

3 °. **Bangia**-formation, a two-layered pioneer formation of filiform algae, which is a permanent stage in the supralittoral belt.

The supralittoral *Bangia-Urospora*-sociation may be classed in this formation.

4 °. **Enteromorpha**-formation, a two-layered pioneer formation of tubular, membranaceous and filiform algae. The *Blidingia*-sociation and the *Enteromorpha-Porphyra*-sociation have to be assigned to it.

The three last-mentioned formations correspond in some respects; therefore also other classifications have been proposed. For instance in the Faeröes BØRGESEN (1905) distinguished between 1°. a "*Chlorophyceae*-formation", which includes the *Prasiola*-formation and a part of the *Enteromorpha*-formation, 2°. a "*Porphyra*-association", belonging to the *Enteromorpha*-formation, and 3°. a "*Bangia-Urospora*-association". The system of JONSSON (1912) resembles much more the classification proposed here, for he distinguished between 1°. a "*Prasiola stipitata*-association", 2°. a "Community of filiform algae" and 3°. an "*Enteromorpha*-association". He incorporated, however, the "*Porphyra*-association" into the community of filiform algae, which for the rest corresponds totally with the *Bangia*-formation.

The distinction between the *Bangia*- and the *Enteromorpha*-formation is not always clear because the filiform alga *Ulothrix flacca* often is abundant in the littoral communities of the latter formation. In most cases *Enteromorpha* or *Porphyra* are the dominant genera, but in some localities in the Wadden Sea *Ulothrix flacca* is sometimes predominant. As such a vegetation of *Ulothrix flacca* is only a variant of the *Enteromorpha*-vegetation mentioned above, the author regards it in spite of the filiform structure of the dominant as such.

5 °. **Cladophora**-formation, a two-layered formation in which dendritic and fruticose algae are dominant. It may be considered as a transitional formation arising from communities of the *Enteromorpha*-formation and developing into the formations of the large brown algae.

The *Polysiphonia-Chaetomorpha*-sociation (VAN GOOR, 1923) may be classed in this formation.

6 °. **Fucus**-formation, a three-layered formation of *Fucaceae*. It is the terminal formation in the littoral succession. Members of this formation are, in the Netherlands, the *Pelvetia*-sociation, the *Fucus spiralis*-sociation, the *Ascophyllum*-sociation, the *Fucus vesiculosus*-sociation and the *Fucus serratus*-sociation.

7 °. **Laminaria**-formation, a four-layered formation of *Laminariaceae*. It is the terminal formation in the (upper) sublittoral succession-sere.

Along the Dutch coast this formation is three-layered. In the boreal seas where the *Laminaria*-formation has its most luxurious development, a fourth layer consisting of *Desmarestia* species occurs in the undergrowth (BØRGESEN, 1905; KYLIN, 1907; JONSSON, 1912). In the Channel the *Desmarestia*-layer sometimes is replaced by a *Cystoseira*-layer.

Most of the formations occur not only on the tidal coast, but are found also — partly in the form of other sociations — in the seawater canals of Walcheren and Zuid Beveland, where tides are failing. Only the *Fucus*- and *Laminaria*-formation are restricted to the tidal coast, at least in the Netherlands. The other formations, except that of *Prasiola* [1] are widely distributed in brackish waters too. The *Enteromorpha*-formation disappears at the transition from brackish into fresh water, although in auxotrophiated fresh water *Enteromorpha* species may occur. Finally, only three formations occur in sea as well as in fresh water, viz. the *Hildenbrandtia*-, *Bangia*-, and *Cladophora*-formations.

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[1] *Prasiola*-vegetations have been found on the banks of some Swedish lakes (WAERN, 1952). In the Netherlands an aerial *Prasiola crispa*-community is common on the trunks of trees.

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