THE EPILITHIC ALGAL COMMUNITIES OCCURRING ALONG THE COAST OF THE NETHERLANDS

C. DEN HARTOG *)
(Hugo de Vries Laboratory, Amsterdam)

(received April 21st, 1959)

CONTENTS

---

*) Present address: Hydrobiological Institute div. Delta-research, Yerseke, Holland.

CHAPTER I

INTRODUCTION

1. EARLIER WORK ON THE ALGAE OF THE NETHERLANDS

In her "Review" of the literature dealing with the Algae of the Netherlands Koster (1939) reports that the oldest data on the marine Algae occurring in this country are to be found in the work of De Gorter (1781), but as the author kindly informed me, she has since then found out that Commelin had already in 1683 mentioned some marine Algae in his "Catalogus Plantarum indigenarum Hollandiae". His very summary descriptions, however, do not always allow the recognition of his species. So it is certainly not clear what he means with his "*Alga membranacea ceranoides*" (p. 3). His "*Alga nigro capillaceo folio*" (p. 3), however, is doubtless *Chorda filum*. His "*Fucus maritimus vel Quercus maritima vesiculas habens* (Zee-eyken)" and his "*Fucus maritimus nodosus* (Knobbelachtigh Wierd)", which he mentioned on p. 37, are respectively *Fucus vesiculosus* and *Ascophyllum nodosum*, but his "*Fucus maritimus alter tuberculis paucissimis* (Klein Knobbelachtigh Wierd)" is less easily identifiable; it may have been *Fucus spiralis* or else a *F. vesiculosus* with a small number of bladders, but it is also conceivable that it was a depauperated regeneration form of *Ascophyllum nodosum*. His "*Alga angustifolia vitrariorum*" (p. 3) and his "*Fucus angustifolius ligulas referens* (p. 36), for each of which the Dutch name "Wiert" is recorded, refer to the grass-wrack *Zostera*. At a later date Baster gave in an essay called "Van de zee-rui of strandwier" included in his "Natuurkundige Uitspanningen, behelzende eenige Waarneemingen over sommige Zee-planten en Zee-insecten, benevens derzelver Zaadhuisjes en Eyernesten" (Vol. 2, p. 129—141, 1765) clear descriptions illustrated by good figures of *Fucus spiralis* (under the name *F. ceranoides*), *F. vesiculosus*, *F. serratus* and *Ascophyllum nodosum* (under the name *Fucus nodosus*).

R. B. VAN DEN BOSCH was the first to make the Algae of the Netherlands the object of a detailed study. His most important communication on this subject appeared in 1853 in the "Prodromus Florae Batavae 2"; his other papers were confined to Algae occurring in the waters of the province of Zeeland, and had already been published at an earlier date in the "Nederlandsch Kruidkundig Archief". Several of the species recorded by him were not found again until quite recently.

SURINGAR's "Observationes Phycologicae in Floram Batavam" appeared in 1857; this work too, the author's doctor's thesis, is an important contribution to our knowledge. In 1870 he published in the "Flora van Nederland" (in "Algemene Statistiek van Nederland") a list which contained the names of all Algae that so far had been recorded from the Netherlands. After that only some short notes on our algal flora appeared from his hand.

BUSÉ, VRIJDAG ZIJNEN and SPREE collected at about the same time a fairly large number of specimens that are preserved in the herbarium of the "Koninklijke Nederlandse Botanische Vereniging", but with the exception of the last-named collector they published nothing on their findings. The well-known phycologist Mrs. A. WEBER-VAN BOSSE, too, published but little on the Algae of the Netherlands. Two very short papers (1886 and 1891) form her entire contribution to our knowledge of the latter.

Between 1898 and 1909 several short notes appeared in the reports on the investigations carried out at the Zoological Station, Den Helder, which were published in the "Tijdschrift van de Nederlandse Dierkundige Vereniging". These notes are not mentioned in KOSTER's "Review" (1939).

However, it was not before the third decennium of this century that once more important phycological studies on the Algae of the Netherlands appeared. In 1922 VAN GOOR published a paper on the algal flora of the Zuyderzee; and this was followed in 1923 by his book "Die holländischen Meeresalgen, insbesondere der Umgebung von Helder, des Wattenmeeres und der Zuidersee". The last-named publication, which consists of an enumeration of the species, a part dealing with the algal communities, and one devoted to the geographic distribution of the Algae, is valued by phycologists in the Netherlands as well as abroad as the standard work on the marine phycology of the Netherlands. However, as VAN GOOR's investigations were confined to a part of the area, his book cannot be regarded as fully representative of the whole of the Netherlands. It should also be noted that he collected his material, as appears from his book, mainly from the deck of a ship, i.e. by the aid of a net and a dredge, and that he visited but rarely the slopes of the embankments and the salt marshes.

VAN GOOR's work, unfortunately, failed to exercise in the Netherlands a stimulating influence on the study of the Algae. At least up to the end of the second world war the number of publications remained very small. In this period we only find a popular essay by SLOFF (1925—1926) on the Algae growing on the slopes of dikes, a study by ZANEVELD (1937) on the influence of desiccation on the zonation of the Fucaceae, and two short communications by KOSTER (1936 and 1937) on the algal flora of the West Frisian Islands.

After the second world war the study of marine phycology showed a revival in the Netherlands. Under the guidance of Dr J. TH. KOSTER in the "Rijksherbarium" at Leiden publications were prepared dealing with *Cladophora* (SLOOTWEG, 1948), *Polysiphonia* (VELDKAMP, 1950), Algae attached to floating objects (LUCAS, 1950), *Ceramium diaphanum* (LUCAS, 1953), Algae from the northern pier at Hook of Holland (VAN DEN HOEK, 1958), and the algal microvegetation in and on barnacle shells (VAN DEN HOEK, 1958), whereas she herself published papers on rare and noteworthy Algae in the Netherlands (1952), on the algal vegetation of Zeeland (1954), and on *Rhizoclonium* (1955).

2. THE PRESENT INVESTIGATION

Since KJELLMAN published his first sociological descriptions of the algal vegetation along the sea coasts, viz. of that of the Murmansk Coast (1877) and of that of the Skagerrak (1878), numerous phycologists in northern and western Europe have made it their task to describe, as accurately as possible, definite stretches of the coasts. HANSTEEN (1892), GRAN (1893), and BOYE (1895) described the algal growth on the southern and western coasts of Norway; COTTON (1912) gave a survey of the algal vegetation of Clare Island; BØRGESEN (1905) sketched the algal growth of the Faeroes; the algal communities of Iceland were described in detail by JONSSON (1912), whereas KYLIN (1907, 1918) studied the west coast of Sweden. Especially the monumental work of BØRGESEN was a valuable contribution to our knowledge, for in the latter we find marvellous descriptions of the physiognomic aspect, and by means of the latter these communities are so strikingly depicted that, notwithstanding the fact that but few specific and generic names are mentioned, it is impossible to misunderstand them.

With regard to the taxonomic units of which the communities described by these authors are composed, we are, however, but imperfectly informed, as the latter confined their attention mainly to the physiognomic aspect, and failed to give qualitative and quantitative data on the floristic composition. From their works we learn only the geographic distribution of the community in which a definite species predominates, and the ecological conditions to which the community is bound, but it is impossible to compare the floristic composition of communities found in different parts of the area, as the species occurring in the various communities were not listed.

Of the algal communities occurring in the vicinity of Banyuls a qualitative description, i.e. one comprising species lists that, as far as possible, are complete, was given by FELDMANN (1938). In this way a comparison with other regions became possible, and since then it was found out that most of the vegetation units that were recognized by him, occur throughout the whole western part of the Mediterranean Sea.

FELDMANN, however, had a predecessor in BERNER (1931), who had studied, not only qualitatively but also quantitatively, the composition of the algal communities in the vicinity of Marseilles, but who had used such an intricate recording method that he had not been able to attract followers. Not until the period following the world war more quantitative data were published. Then KORNAŚ and MEDWECKA-KORNAŚ (1950) gave a detailed survey of the algal vegetation in the Gulf of Gdańsk (Danzig), and SUNDENE (1953) described the vegetation units occurring in the Oslo Fjord. These investigators used the recording method which had proved its usefulness in the study of the terrestrial vegetation. This method was applied also by WAERN (1952), who studied the algal communities occurring along the coast of the Baltic Sea. In their study of the algal vegetation of the Mediterranean Sea MOLINIER and PICARD, too, used it.

With regard to the algal communities of the Netherlands hardly any data were available. VAN GOOR (1923) had confined himself to a short description of the physiognomic aspect, and his descriptions, moreover, are confined to a small part of the coast. Another drawback of his work is that he takes the association in a very wide delimitation, which makes a correct interpretation of his results very difficult.

In order to fill these gaps in our knowledge, in 1950 the present investigation was started. Its aims were:

1°. a qualitative and quantitative description, as complete as possible, of the epilithic algal communities occurring in the southern part of the North Sea, especially along the coast of the Netherlands;
2°. the development of a classification of the epilithic algal communities;
3°. the study of the causes that are responsible for the differentiation which splits the vegetation in well-defined units.

In the following years our first and second object were achieved (cf. Chapters IV and V). In 1955 already a provisional classification could be proposed, and since then supplementary studies along the English Channel and along the Mediterranean Sea have permitted us to enlarge and to improve this classification.

The third aim so far eluded our grasp. It is true that a large number of ecological data were collected (Chapter III), but the latter did not enable us to find a satisfactory explanation for the discontinuities observed in the vegetational cover. As a large number of factors are involved, and as their interaction is apparently very intricate, it was so far impossible to disentangle this Gordian knot.

A phycocoenological investigation demands a thorough knowledge of all the various stages of development through which the Algae have to pass. In order to obtain this knowledge I studied the Algae not only in their natural habitat, but also indoors by comparing material lent from various herbaria. These herbaria were 1° the "Rijksherbarium", Leiden, in which are incorporated the herbarium of the Koninklijke Nederlandse Botanische Vereniging, the "Filiaal"-collection of the "Comité ter Bestudering van de Nederlandse Mariene Flora en Fauna" and the herbarium of the author, 2° the herbarium of the Hugo de Vries Laboratory of the Municipal University, Amsterdam, 3° the collection of the Zoological Station, Den Helder, mainly brought together by Van Goor, and 4° the collection of Mr A. F. Mulder, Heilo. The many distributional and taxonomic data that were obtained in this way, will be published in the near future.

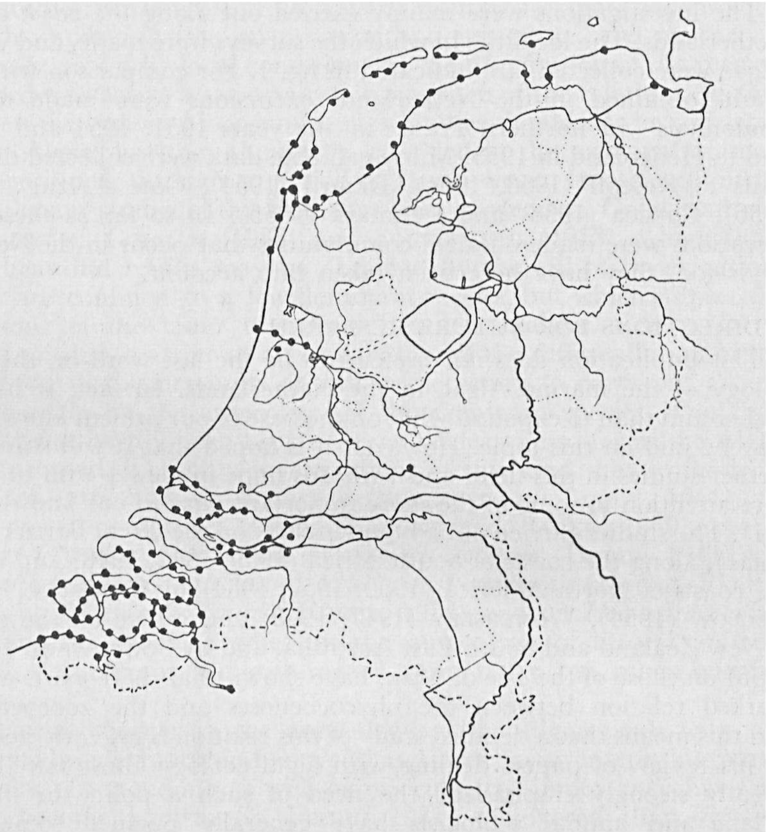


Fig. 1. Map of the Netherlands showing the localities surveyed by the author.

In this work for the nomenclature of the Algae use is made of Parke's "checklist" (1953) and of the addenda and corrigenda to the latter (1956, 1957). In the few instances in which other names are used, the reason for not adopting the recommended name will be given in a foot-note.

The investigations were confined to the Rhodophyceae, Phaeophyceae, Chlorophyceae, Xanthophyceae and Cyanophyceae; the Diatomeae were left out of consideration.

The algal vegetation on the sand and clay soils of the fore-shore and of the "wadden" (the banks in the lagune behind the West Frisian Islands) were not included. This algal vegetation appears partly in the form of an undergrowth of the phanerogamic vegetation, viz. in the *Puccinellio-Salicornion* (lower salt marsh), in the *Armerion maritimae* (higher salt marsh) and in the *Scirpetum maritimi* (brackish salt marsh), and partly in the form of independent communities. Particulars on this subject were published by WESTHOFF (1947) WESTHOFF and BEEFTINK (1950), KOSTER (1952, 1954, 1955) and DEN HARTOG (1955, 1956, 1958).

The investigations were mainly carried out along the coast of the Netherlands. The localities in which the surveys were made, and where Algae were collected, are indicated in fig. 1. For comparison with the results obtained in the Netherlands excursions were made to "le Boulonnais" in northern France in the years 1951, 1954 and 1955, and to Heligoland in 1955. Many valuable data were collected during visits to Roscoff (1953, 1954), Dinard (1954), Côte d'Azur (1954, 1956), Corsica (1956) and Denmark (1955). In so far as these observations were made on algal communities that occur in the Netherlands too, they have here been taken into account.

3. DIRECTIONS FOR FUTURE RESEARCH

This publication does not pretend to be the last word on the coenology of the marine Algae in the Netherlands. In fact, it has no higher aim than to expound what on the base of our present knowledge may be said on this topic. However, it is hoped that it will stimulate further studies in this field, and with this hope in view I wish to draw here attention to some of the more important gaps in our knowledge.

1°. The studies carried out by STEPHENSON on the Great Barrier Reef (1931), along the coasts of South Africa (1939, 1942, 1948) and along the coasts of North America (1950, 1952, 1954), by CHAPMAN (1950), DELLOW (1954), WOMERSLEY (1947, 1948) and others on the coasts of New Zealand and South-East Australia, and by SOUTHWARD (1953, 1956) on those of the Isle of Man, have shown that there exists a very marked relation between the phycocoenoses and the zoocoenoses, and this means that a detailed study of this relation is urgently needed. In his review of papers dealing with algal ecology CHAPMAN (1946) already strongly emphasized the need of such a policy in stating "Plant and animal ecologists have generally pursued somewhat different paths, but it is impossible for the marine algal ecologist not to take cognizance of the work of his zoological co-workers. It is, of course, possible to carry out marine algal studies without regard to the associated animals, but such work can be regarded only as incomplete. The necessity to consider both plants and animals has rendered the subject fraught with more difficulties than it would otherwise possess, but it is impossible to avoid them."

As the intertidal fauna is in the Netherlands but poorly represented, this relation is here not very striking. As a case in point we may mention the competition for space between mussel and barnacle populations on the one hand and the *Blidingietum minimae*, the *Enteromorpheto-Porphyretum* and the *Fucetum vesiculosi* on the other, as it is witnessed in exposed situations; in this instance the result is probably not determined by priority of arrival alone, but also by peculiarities of the cyclic succession (SOUTHWARD, 1956).

2°. Besides this survey, in which the description of the various algal communities stands in the centre of our interest, we are also in need of detailed studies of the mutual relations between the algal communities. Such studies will have to be carried out in definite localities of the coast, which to this end will have to be selected with great care. Such studies carried out in an area of restricted extent, will provide us with important data on zonation and succession, and on the influence exercised by local conditions on the distribution of the species.

In order to arrive at an accurate conception of the relations existing between the various biocoenoses, such studies should not be restricted to the Algae, but they should be extended to the principal animals and continued through a period of several years. In other countries already many studies of this kind have been carried out. Good examples are those of COLMAN (1933) and SOUTHWARD (1953), which show what beautiful results may be obtained by the aid of investigations which are confined to a few dominant species, but which subject the behaviour of the latter to a very detailed analysis.

3°. In order to arrive at an explanation of the differentiation of the vegetation in distinct units, it will be necessary to carry out an extensive study on the autecology of the dominant species. This field of study has hardly been broken as yet, at least in so far as the Algae are concerned. The only investigations of this kind that so far have appeared, are those on Fucaceae (BURROWS and LODGE, 1951), on *Fucus vesiculosus* and *F. serratus* (KNIGHT and PARKE, 1950), on *F. distichus* (POWELL, 1957), on *Ascophyllum nodosum* (DAVID, 1943), on *Bifurcaria brassicaeformis* (ISAAC, 1951), on *Laminaria saccharina* (PARKE, 1948), on *Macrocystis pyrifera* (CRIBB, 1954) and on *Hormosira banksii* (WOMERSLEY, 1957). Studies on the autecology of littoral animals are more numerous, but with regard to the latter, too, much remains to be done.

A special chapter in the autecology of the Algae deals with the study of the pleomorphic life cycle, and here many interesting particularities of taxonomic as well as of ecological importance have already become known. So JORDE (1931) discovered that *Urospora mirabilis* is the sexual generation of *Codiolum gregarium*. KORNMANN (1938) detected the existence of a similar relation between *Halicystis ovalis* and *Derbesia marina*. The Bonnemaisoniaceae, too, appeared to possess a heteromorphic life cycle (J. and G. FELDMANN, 1942, 1952). DREW (1949) discovered that *Conchocelis rosea* is but a phase in the life cycle of *Porphyra* and of *Bangia*.

The studies carried out by KORNMANN on *Acinetospora crinita* (1953), on *Giffordia fuscata* (1954) and on *Ectocarpus confervoides* (1956), by BLIDING on *Enteromorpha* (1933, 1938, 1939, 1944, 1948, 1955), and by FÖYN on *Ulva lactuca* (1955) prove sufficiently that this subject is as yet by no means exhausted.

ACKNOWLEDGEMENTS

In the first place I wish to express my gratitude to my tutor, Prof. Dr J. HEIMANS (Amsterdam) for his never failing encouragement. Many thanks are also due to Dr J. TH. KOSTER (Leiden), who identified the Cyanophyceae and also many other Algae in my collections, who controlled part of my own identifications, and who showed a lively interest in the progress of my work. To Prof. Dr H. ENGEL (Amsterdam) I am indebted for my initiation in marine biogeography and for a large part of my zoological knowledge. In the identification of some supralittoral lichens I received the assistance of Dr R. A. MAAS GEESTERANUS (Leiden), whereas Dr C. BLIDING (Borås) identified some of my *Enteromorpha* species, and Dr T. CHRISTENSEN (Copenhagen) my *Vaucheriae*. Much assistance I received from Messrs. A. F. MULDER (Heilo), C. SWENNEN (the Hague) and A. S. TULP (Leeuwarden), who accompanied me on many excursions, and whose zoological knowledge was a great help to me. Messrs. C. VAN DEN HOEK (Leiden) and J. A. W. LUCAS (Rotterdam) provided me with valuable phycological information. Dr H. TEN KATE (De Bilt) and Dr H. POSTMA (Den Helder) kindly assisted me with meteorological and hydrographic data. To Prof. Dr H. BOULANGÉ (Lille) and Dr R. LAMI (Paris) I offer my best thanks for the hospitality I received from them during my visits to the biological stations at Ambleteuse and Dinard. Prof. Dr C. E. B. BREMEKAMP (Bilthoven) translated the original text into English.

I also wish to express my indebtedness to the "Amsterdamse Universiteitsvereniging" for a grant which enabled me to take part in a phycological excursion to Roscoff, which was organized by the 8th International Botanical Congress and supervised by Prof. Dr J. FELDMANN.

To the Nederlandse Organisatie voor Zuiver Wetenschappelijk Onderzoek many thanks are due for its subventions for the translation of the original text and the publication of the paper.

Finally I wish to thank all persons who assisted me in my work either by the sending of reprints or in some other way.

SUMMARY

In Scandinavia the study of phycocoenology has already been attended to for a long time, but in the Netherlands it has received so far but little attention. Until a short time ago the Algae were studied in this country mainly from the points of view of taxonomy and floristics, e.g. by VAN GOOR (1923). Since the time of VAN GOOR, however, here, too, a few contributions to our knowledge of phycocoenology have appeared.

Originally phycocoenologists confined themselves to a general description of the algal vegetations. However, as they failed to give lists of species and quantitative data, a comparison of the algal vegetations found in different areas, remained difficult, if not impossible. Up to this day the number of publications in which complete descriptions of the algal vegetations are given, remain scarce, and quantitative data are even more scarce. In this work all epilithic algal communities which the author could study on the coasts of the Netherlands, are described, and these descriptions are not only qualitative, but as far as possible also quantitative. The results cannot yet be regarded as final, as the causes by which the development of the communities is determined, are as yet insufficiently known, and as several subjects are still to be studied, e.g. the relation between the algal vegetation and the fauna, and the autecology of the predominating organisms. Detailed studies in carefully selected areas of restricted extent are also required.

CHAPTER II

THE COAST OF THE NETHERLANDS FROM A PHYCO-GEOGRAPHIC POINT OF VIEW

1. PHYCO-GEOGRAPHIC DISTRICTS

Already at first view the coast of the Netherlands appears to be divisible in three districts, each of them with its own, physiographic as well as bio-geographic character. These districts are:

1°. the "Waddenzee" district;
2°. the beach district; and
3°. the deltaic district.

Below I will sketch these districts in broad outline in order to give an impression of the diversity that is found in the region as a whole.

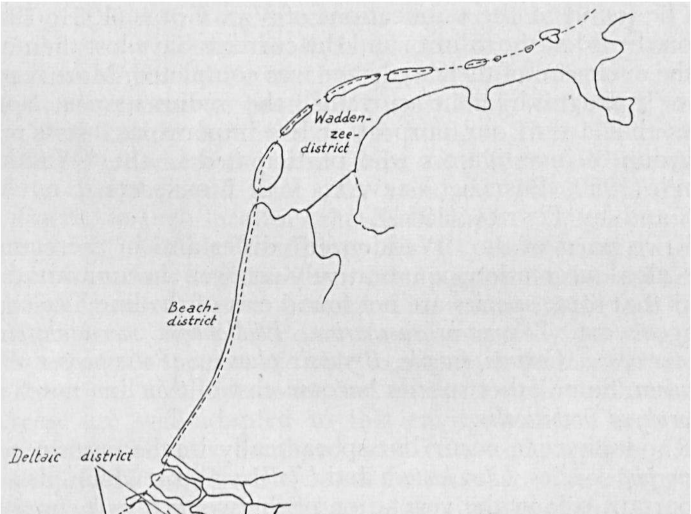


Fig. 2. Algal geographical districts of the coast of the Netherlands.

1.I. THE "WADDENZEE" DISTRICT

The district of the "Waddenzee" extends from Den Helder to the coast of Schleswig-Holstein. It is a shallow and quiet basin in which hardly any surf occurs, and of which à large part falls dry at ebb-tide. The soil consists of sand, silt or clay. The coasts of Friesland and Groningen are very rich in mud, but the coast of the West Frisian Islands consists mainly of sand.

The western and the eastern part of the "Waddenzee" differ considerably. The western part has a good circulation through the Vlie Stroom and the Texel Stroom; it is, moreover, much larger, so that the influx of fresh water, mainly originating from the IJsselmeer, exercises but a relatively small influence. Only in the vicinity of the discharging-sluices and the draining mills the water appears to be brackish, and this brackishness decreases in a concentric way (POSTMA, 1954).

The eastern part is weakly polyhaline to mesohaline, owing to the much larger influx of fresh water from the draining canals (in the German portion also by the water of the Ems, the Jade, the Weser and the Elbe) and to the smaller size of the basin (VAN VEEN, 1950). The sedimentation is here, moreover, much stronger than in the western part, a phenomenon which is often observed where sea water comes in contact with fresh water.

Older data with regard to the western part of the "Waddenzee" are to be found in the publications of VAN GOOR (1921, 1923), but those on the tides, the salinity and the currents have lost their actuality since the enclosure of the Zuyderzee was completed. More recent data on the hydrography, the currents, the sedimentation and some features that are to our purpose of less importance, were published by a group of investigators who participated in the "Wadden symposium" (1950, POSTMA, VERWEY, VAN VEEN, etc.), by VERWEY (1952) and by POSTMA (1954).

The two parts of the "Waddenzee" differ also in the composition of the algal vegetation, qualitatively as well as quantitatively. It appears that some species are not found east of the line Terschelling—Harlingen, e.g. *Laminaria saccharina*, *Phyllophora membranifolia*, *Gracilaria verrucosa*, *Codium fragile*, *Bryopsis plumosa*, *Polysiphonia nigra* and *P. denudata*. Some other species become east of this line much scarcer, e.g. *Porphyra umbilicalis*.

As Rhodophyceae occur but sporadically in the eastern part, the *Enteromorpha* species, *Ulva lactuca* and *Ulothrix flacca*, which play already an important role in the vegetation of the western part, now become dominant. Apart from this change in the general aspect of the vegetation, we note that the *Fucetum vesiculosi*, which predominates in the western part, is replaced in the far more sheltered eastern part nearly everywhere by the *Ascophylletum nodosi*.

Another characteristic feature of the western part of the "Waddenzee" are the "floating algal communities". The latter begin their development on the dead shells of *Cardium edule*, *Mya arenaria* and *Mytilus edulis* which are found on the tidal flats. When the flats are submerged, these shells may become detached from the substrate because of the upward pressure to which the tufts of Algae (*Polysiphonia nigrescens*, *Ceramium rubrum*, *Gracilaria verrucosa*, *Ectocarpus siliculosus*, *Ulva lactuca*, *Enteromorpha* species, *Cladophora crystallina*, etc.) are subjected, and in this way the larger tufts finally become a sport to the tide currents (DEN HARTOG, 1958).

1.II. THE BEACH DISTRICT

The beach district comprises the coast of the North Sea, i.e. the sandy beach at the foot of the sea dunes. As it is strongly exposed to the action of the surf, it is normally an unsuitable substrate for the development of an algal vegetation. On the breakwaters and harbour moles, however, a rather poor algal growth has established itself; these Algae apparently are able to withstand the action of the surf and the sprinkling with sand. Other algal communities are found in more or less sheltered corners only.

The sprinkling with sand is especially common on the breakwaters that project from the beach into the sea. At the "Hondsbosse Zeewering" (the large dike extending south of Petten for nearly three miles along the sea) and at the western part of the "Helderse Zeedijk" (the dike to the west of Den Helder) the effect of its action is easily recognizable. The *Fucus* species no longer occur in groups, and may even be lacking entirely; occasionally small plants are present, but well-developed and mature specimens are extremely rare. The associations that are found in such places, are the *Enteromorpheto-Porphyretum* accompanied by much *Ulva*, and the *Blidingietum minimae*. *Enteromorpha linza* seems to profit by a sprinkling with sand; at least, it is very abundant in localities of this kind, at Den Helder as well as at Petten, even where the sand forms a sediment. Where the surf is so strong that the sand is at once removed, *Fucus* appears to be entirely absent; in such localities the *Enteromorpha-Porphyra*-association still finds fairly suitable conditions for its maintenance, whereas barnacles and mussels begin to form large agglomerations. The effect of the grinding sand is very strong. The young thalli are buried, destroyed or swept away, and only the most rapidly growing Algae, such as *Enteromorpha* species, are able to maintain themselves. By their peculiar structure, a hollow thallus and an elastic cell-membrane, these *Enteromorphae* are well-adapted to this environment. The tissues of *Fucus* are often distinctly damaged, and *Ulva* and *Porphyra*, too, may show the marks of the grinding sand. In contrast with *Ulva*, *Porphyra umbilicalis* reaches a very large size in this environment.

Where sand is absent, e.g. on the large moles of the IJmuiden harbour, there is a somewhat richer development. Apart from the algal communities that have already been mentioned, we meet here, especially during the six colder months a beautifully developed *Bangia-Urospora* growth, and also strongly ramified Algae like *Ceramium deslongchampii*, *Polysiphonia urceolata* and *Callithamnion scopulorum*. The *Acrosiphonia* variant of the *Polysiphonieto-Chaetomorphetum* is entirely bound to the harbour moles with their strong surf.

1.III. THE DELTAIC DISTRICT

The deltaic district, the alluvial tract at the mouth of the rivers Rhine, Meuse and Scheldt, is, like the district of the "Waddenzee", not fully uniform. According to the degree of salinity it may roughly be divided in five zones, which, however, pass gradually one into the other. These zones are:

1. the fresh-water zone	$< 0.3\ ^0/_{00}$ Cl′ *)
2. the oligohaline zone	$0.3 — 1.6\ ^0/_{00}$ Cl′
3. the mesohaline zone	$1.6 — 9.0\ ^0/_{00}$ Cl′
4. the polyhaline zone	$9.0 — \pm\ 16.5\ ^0/_{00}$ Cl′
5. the euhaline zone	$> \pm\ 16.5\ ^0/_{00}$ Cl′

I did not use the classification proposed by REDEKE (1922, 1932), which in the past has generally been applied in the Netherlands, but that of VÄLIKANGAS (1933) and REMANE (1940), because the latter has been based on changes in the composition of the fauna, and is therefore a far more natural one. For the distribution of the Algae, too, it proved to be a most useful system. REDEKE draws the line between fresh water and oligohaline water at $0.1\ ^0/_{00}$ Cl′, but this line is entirely arbitrary. Marked changes in the algal vegetation are noted at $0.3\ ^0/_{00}$ Cl′, as above this line fresh-water species like *Ulothrix tenerrima*, *Microspora floccosa* and *Hormidium flaccidum* show a strong decrease, and as below it *Enteromorpha intestinalis* is only exceptionally met with. The boundary line between euhaline water and polyhaline water lies for the Algae distinctly below $17.0\ ^0/_{00}$ Cl′, the value adopted by REDEKE; it is found at circ. $16.5\ ^0/_{00}$ Cl′. However, we should not overestimate the importance of these boundary lines, as there are more or less gradual transitions between the successive zones. The boundary lines, moreover, are not all the time found at the same place, but shift with the tides. The $10\ ^0/_{00}$ Cl′ isohaline, for instance, lies at high tide considerably farther to the east than at low tide. The Algae therefore are exposed to considerable fluctuations in the degree of salinity.

The five zones are not all of the same importance. The euhaline, the mesohaline and the fresh-water zone are the only ones that possess their own species, i.e. species that occur but rarely or not at all in another zone. The polyhaline zone has no species of its own; the Algae that occur in this zone are marine ones of the euryhaline type and further species that, though confined to brackish water, show a rather wide salt tolerance. The oligohaline zone has no algal flora of its own either, and the Algae that are met with in this zone are partly fresh-water species with a marked salt tolerance and partly species that occur also in the zones with a higher degree of salinity.

In the deltaic district the euhaline zone is almost entirely restricted to the East Scheldt, as this arm of the sea does not function as an estuary, and is therefore but slightly affected by the influx of fresh water (see, however, KORRINGA, 1940, and p. 47 of this work). Because of its secluded place its waters are quiet, and they offer therefore a suitable environment for the development of various species

---

*) The classification of the various kinds of water according to their degree of salinity that was proposed at the "Symposium on the Classification of Brackish Waters" held at Venice in April 1958 and recommended for universal adoption, deviates slightly from the one used in this work, the main difference being that the boundary line between oligohaline and mesohaline was drawn at $3.0\ ^0/_{00}$ Cl′. Instead of the term "brackish water", which has been used in various senses, the term "mixohaline" was recommended.

that are unable to maintain themselves in the strong surf of the beach district.

Climatologically, too, the conditions are favourable, especially because the summer temperature of the water is rather high. A considerable number of southern species that are already rare on the Normandy coast, are here represented in large numbers. Some of them reach here the northern limit of their area of distribution, e.g. *Giffordia mitchellae*, *Taonia atomaria*, *Hypoglossum woodwardii*, *Chondria tenuissima*. Some other warm-boreal species, like *Codium fragile*, *Dictyota dichotoma*, *Bryopsis plumosa* and *Griffithsia devoniensis*, are here very common.

Apart from the East Scheldt there is still another area in which the above-named species are well represented, viz. the waters round Flushing. For this reason I have united these parts in a **Scaldian subdistrict.**

The polyhaline zone shows a much smaller diversity in species; it reminds one more or less of the "Waddenzee" district, whose waters, too, are polyhaline. *Bostrychia scorpioides* and *Catenella repens*, which are common in the deltaic district, are, however, in the "Waddenzee" confined to Terschelling, and *Fucus lutarius* does not occur there at all.

The algal vegetation of the mesohaline and the oligohaline zones has not yet been studied. In the neighbourhood of Willemstad the fauna of these zones appeared to be rich in characteristic species; as examples of the latter we may quote *Gammarus zaddachi* and *Cyathura carinata*. As the position of the boundary line between these two zones is not yet sufficiently known in the deltaic district, they may for the time being be united in a meso-oligohaline zone.

For literature on the deltaic district we may refer to the works of KORRINGA (1940, 1951). Data with regard to the algal flora were published by VAN DEN BOSCH (1846, 1853), KOSTER (1952, 1954) and DEN HARTOG (1953, 1954).

1.IV. FLORISTIC CHARACTERIZATION

The subdivision in districts which was outlined in the preceding sections, was based on physico-geographic considerations. Originally I was inclined to suppose that the marked differences between these districts would also be reflected in the floristic composition of their vegetation, but this supposition was but partly confirmed.

It appeared, for instance, that the polyhaline zones of the deltaic district and of the "Waddenzee" district, although differing in their physico-geographic character, show a striking similarity in the composition of their algal flora. Salinity and the sheltered position are here apparently the decisive factors. Corroborative evidence for this view is found in the fact that the algal flora found in sheltered spots of the beach district, e.g. between the harbour moles at IJmuiden, does not differ from that in the polyhaline western part of the "Waddenzee".

Another expression of a parallel development may be recognized in the decrease in the number of species which in the "Waddenzee" as well as in the deltaic district accompanies the decrease in salinity. There are nevertheless some differences. Species like *Catenella repens* and *Bostrychia scorpioides*, which in the deltaic district are common, are in the "Waddenzee" very rare, whereas *Fucus lutarius* and *Pelvetia canaliculata* *) are in the latter entirely absent. On the other hand, *Desmotrichum undulatum*, a cold-boreal species and the subarctic *Chordaria flagelliformis* both occur in the "Waddenzee", although they belong there to the rarities, but they have never been found in the deltaic district. The presence of these species in the "Waddenzee", however, does not justify the conclusion that the algal flora of this district shows a more distinctly boreal character, as in the deltaic district, too, some species with a distinctly boreal area of distribution occur, e.g. *Desmarestia viridis.*

The more southern character of the deltaic district, however, comes more clearly to the fore when we concentrate our attention on the euhaline zone. Here we find a number of species which reach the northern limit of their area of distribution in the East Scheldt, and some other ones that in the Netherlands are confined to the latter and to the neighbourhood of Flushing, e.g. *Dictyota dichotoma, Griffithsia devoniensis, Sphacelaria plumigera, Chondria dasyphylla.*

In the "Waddenzee" the number of species with a predominantly southern distribution is much smaller, and they are confined here to the vicinity of the gates. They are found e.g. along the Texel Stroom and the Marsdiep, viz. on the southern dike of Texel and in the vicinity of Den Helder, and along the Vlie Stroom in West Terschelling. Moreover, such species are in the "Waddenzee" rather rare, and they form there but a very subordinate part of the vegetation.

By summarizing the exposition given above, we arrive at the following characterization of the three phyco-geographic districts:

1. The "Waddenzee" district; polyhaline and sheltered.
   Species with a predominantly southern distribution are but few in number, and they are mainly confined to the vicinity of the Vlie Stroom and the Texel Stroom. However, species with a predominantly northern distribution are also very rare. On account of a difference in salinity this district is to be divided in a western and an eastern sub-district.
2. The beach district; euhaline and exposed.
   Species with a predominantly southern as well as those with a predominantly northern distribution are absent.
3. The deltaic district, on account of the degree of salinity to be divided into a polyhaline estuarine sub-district with a number of species with a predominantly southern distribution, and a euhaline Scaldian sub-district, which may be regarded as an enclave of a southern algal flora.

---

*) This species occurred formerly at Den Helder, but it disappeared there on account of works that were carried out on the "Leidam" (a pier extending into the "Waddenzee").

2. NATURAL ROCKS ALONG THE SOUTHERN PART OF THE NORTH SEA

In the southern part of the North Sea the coast is formed almost entirely of sandy beaches and mud flats. Moles, piers and harbour works are here the only substrates consisting of stone, but these structures are no more than a few centuries old. The algal communities on these artificial substrates are therefore of comparatively recent date, and it often appears that they have not yet reached their final composition, as species with a slow dispersion have not been able to reach these sites.

In order to recognize the true character of the algal communities occurring along the coast of the Netherlands, it is therefore necessary to compare them with corresponding communities growing on natural rocks, and to this end we will have to turn our attention to those rocky coasts that are nearest to the Netherlands. These coasts are that of "le Boulonnais" at the entrance of the English Channel and that of Heligoland. A very summary description of these two regions will here be inserted, but in the near future a more detailed publication will be devoted to them.

2.1. The coast of "le Boulonnais"

"Le Boulonnais" is the hilly country round Boulogne sur Mer. The coast consists here of a number of promontories, i.e. rocks jutting out into the sea, which are separated from each other by sandy beaches.

The promontories consist of large lumps of a chalky sandstone called "Grès de la Crèche". It are partly rests of stony ridges that were denuded by the action of the surf, and partly boulders that were precipitated from the cliffs. On the beach locally a greenish blue clay (Portlandien) becomes exposed, which hardens rapidly by contact with the air, and forms in this way an excellent substrate for the growth of Algae.

From Cape Gris Nez to Le Portel this coast offers a good opportunity for the development of Algae. South of the last-named place there are no more cliffs. During excursions made in the years 1951, 1954 and 1955 I obtained a good idea of the algal vegetation; of most of the vegetation units records were obtained.

The pioneer vegetations are completely identical with those that are found in the Netherlands. It are the *Bangieto-Urosporetum* found in the supralittoral region on the northern mole at Boulogne, the *Blidingietum minimae* and the *Enteromorpheto-Porphyretum* on the most strongly exposed spots in the eulittoral region, and also on the boulders that are scattered over the beach; at the mouth of small water-courses, i.e. where fresh water is mixed with sea water, *Enteromorpha* vegetations are met with consisting of *E. intestinalis*, *E. prolifera* and perhaps some other species of this genus; they belong doubtless to the *Enteromorphetum prolifero-intestinalis*.

In the eulittoral region the final stages, i.e. the associations belonging to the *Fucus* formation, show no important differences with the Fucaceae vegetations found in the Netherlands either, although it must be admitted that the *Fucetum serrati* of the coast of "le Boulonnais" comprises a larger number of species.

Important differences, however, are noted in the associations belonging to the *Cladophora* formation. In the sandy pools of the eulittoral region we find e.g. an association which is characterized by the presence in large numbers of *Gracilaria verrucosa* and *Polyides rotundus* *), the *Gracilarieto-Polyidetum*. This association is found

---

*) DREW (1958) has shown that *Polyides rotundus* (Huds.) Grev. is the correct name of this species, not *P. caprinus* (Gunn.) Papenf.

neither in the Netherlands nor in Heligoland.

In the Netherlands the *Callithamnion scopulorum* community has but a single dominant. On the coast of "le Boulonnais" this community is but rarely met with; as a rule *Callithamnion scopulorum* occurs here in company with *Laurencia pinnatifida, Plumaria elegans, Cladostephus spongiosus, Lomentaria articulata* and *Rhodochorton floridulum*, a community which I should like to call the *Lomentaria-Plumaria* association (*Lomentarieto-Plumarietum*). The two species after which the association is named, are characteristic components of the vegetation that is found in dark fissures in the lower part of the littoral region. Another species which in the Netherlands forms a sociation of its own, viz. *Ceramium deslongchampii*, occurs on the coast of "le Boulonnais" only as a component of this *Lomentaria-Plumaria* association.

In the Netherlands the zone between the *Fucus serratus* community and the *Laminaria* community is dominated by the *Polysiphonieto-Chaetomorphetum*, a community which differs in composition from place to place. On the coast of "le Boulonnais", too, we found algal vegetations which may be referred to this community, although there are important differences, e.g. by the presence of *Rhodymenia palmata, Membranoptera alata, Corallina officinalis, Laurencia pinnatifida, Griffithsia flosculosa*, etc. At the same level, however, we find here another community, viz. the *Rhodymenietum palmatae*, an association that does not occur in the Netherlands; it grows especially on the soft and chalky jurassic claystone (Portlandien). *Chondrus* and *Gigartina* are on the coast of "le Boulonnais" never met with in the form of separate communities.

In the sublittoral region we found but a single community, viz. the *Laminarietum digitato-saccharinae*, and this proved to be richer in species than it is in the Netherlands.

A survey of the communities occurring on the coast of "le Boulonnais" is given in Table I, they are arranged in sociological progression.

TABLE I

Algal communities on the coast of "le Boulonnais"

supra-littoral	?	Bangia-Urospora			M.H.W.
eu-littoral	Hildenbrandtia	Blidingia	Catenella	Pelvetia	
				Fucus spiralis	
		Entero-morpha compressa-Porphyra + Entero-morpha intestinalis	Callithamnion scopulorum		
			Lomentaria-Plumaria + Laurencia + Rhodochorton floridulum	Ascophyllum + Fucus vesiculosus	
				Fucus serratus	
			Polypsihonia-Chaetomorpha + Rhodymenia		M.L.W.S.
sub-littoral			?		Laminaria

Not mentioned in this table are two communities that occur mainly in small pools, viz. the *Monostrometo-Dumontietum* and the *Gracilaria-Polyides* community.

Comparison of the algal vegetation on the coast of "le Boulonnais" with that of the coast of the Netherlands leads therefore to the conclusion that there is a striking resemblance between the two, but that there are also important points of difference.

2.II. HELIGOLAND

Heligoland, the rocky island in the Frisian Gulf, has repeatedly been described by German biologists (HAGMEIER, 1925; HOFFMANN, 1933; NIENBURG, 1925; SCHMIDT, 1928).

It consists of the easily corroding Bunter Sandstone, of which the strata slope down towards the north-east. Originally the island was much larger, but the cliffs along the coast have been exposed for a long time to the eroding action of the surf, and are continually collapsing. In this way extensive abrasion terraces were formed; ledges running from the North-west to the South-east still give a clear indication of the stratification. Towards the end of the 19th century a beginning was made with the construction of a basalt wall round the island, which had to serve as a protection against the eroding action of the sea. This wall was finished during the second world war. At the northern side of the "Düneninsel" the abrasion terraces have another lithological composition, for here they consist of the triassic "Muschelkalk" and of white chalk; sandy beaches, too, are found here, and the eastern end consists of a pebble bank.

The algal flora is, just as on the coast of "le Boulonnais", richer than it is on the coast of the Netherlands, but in composition it differs considerably from that of "le Boulonnais". Several of the species with a predominantly southern distribution that are still present in the Netherlands, are here totally absent. If the eulittoral algal vegetation of Heligoland is compared with that of the Netherlands, it appears that it differs from the latter in details only; the sublittoral region shows to a depth of 10 m a well-developed algal growth.

A noteworthy difference between the algal vegetation of the Netherlands and of Heligoland is the absence in the latter of the *Catenella* and the *Pelvetia* communities. Another point of difference is that the *Fucetum serrati* and the *Laminarietum* are almost always contiguous; only occasionally a *Polysiphonieto-Chaetomorphetum* is present; the latter is notable here for the frequent occurrence of *Rhodomela confervoides*.

As the Fucaceae communities here are almost always uninterrupted, the transitional communities of the *Cladophora* formation are but sporadically represented. On but one place we found in 1955 a growth of *Ceramium deslongchampii*, whereas in shaded spots on the "Lange Anna" *Plumaria elegans* appeared to occur frequently. The pioneer communities of the eulittoral region are in Heligoland, too, completely identical with those that are found in the Netherlands.

In Heligoland the sublittoral region shows a zonation. Whether such a zonation is present on the coast of "le Boulonnais", too, I am unable to say, as I could not study this region sufficiently on account of the surf; in the Netherlands such a zonation is absent. In the uppermost part of the sublittoral region we find the *Laminarietum digitato-saccharinae,* which in localities where strong currents are present, is replaced by a growth of *Halidrys siliquosa* or by one of *Desmarestia aculeata*. Lower down the *Laminarietum hyperboreae* predominates; in this association *Laminaria hyperborea* is the dominant species, but the latter is accompanied by several Rhodophyceae, e.g. *Delesseria sanguinea, Plocamium coccineum, Membranoptera alata, Phycodrys sinuosa* and *Furcellaria fastigiata.* At the very base of the algal zone these magnificent Rhodophyceae sometimes are the only Algae left. In gullies the *Laminarietum hyberboreae* is sometimes replaced by a growth of *Desmarestia aculeata.*

A survey of the vegetation units observed in Heligoland, arranged according to the sociological progression, is given in Table II.

TABLE II

Algal communities on the coast of Heligoland

supra-littoral	Calothrix scopulorum	Prasiola			M.H.W.
		Bangia-Urospora			
eu-littoral	Hildenbrandtia	Blidingia			
				Fucus spiralis	
		Enteromorpha compressa-Porphyra + Enteromorpha intestinalis	Plumaria	Ascophyllum + Fucus vesiculosus	
				Fucus serratus	
			Polysiphonia- Chaetomorpha		M.L.W.S.
sub-littoral	Lithothamnion	Ulva	Ceramium rubrum + Codium	Halidrys	Laminaria digitata-saccharina
			Plocamium-Delesseria	Desmarestia	Laminaria hyperborea

As my visit to Heligoland took place in August, it was too late in the year to find out whether here, too, the *Monostrometo-Dumontietum*, which is a characteristic spring association of small pools in the eulittoral region, was present.

On the whole the algal flora of the Netherlands is intermediate between that of the coast of "le Boulonnais" and that of Heligoland. There are, however, a fairly considerable number of species which occur in Heligoland as well as in "le Boulonnais", but which in the Netherlands are completely absent. To this group belong *Polyides rotundus*, *Rhodomela confervoides*, *Rhodochorton floridulum*, *Membranoptera alata*, *Plocamium coccineum*, *Corallina officinalis*, various *Lithothamnion* species and *Plumaria elegans*. It is to be expected that one day all these species will settle on our coast, too. The greater part of them has already been found on floating objects, and this proves that they are able to reach the coast of the Netherlands in a natural way.

3. SOME REMARKS ON THE GEOGRAPHIC DISTRIBUTION OF THE ALGAE

3.1. Classification of Børgesen and Jonsson

In 1905 Børgesen and Jonsson published a paper on the distribution of the marine Algae in the Arctic Ocean and in the northern part of the Atlantic Ocean. They described in this paper the northern-atlantic and arctic parts of the area of distribution of all Algae occurring north of a line connecting Lindesnaes on the coast of Norway via the border between England and Scotland with the coast of New England in North America, and they arranged these Algae in groups according to their area of distribution. As this classification is also of importance for the Algae occurring on the coast of the Netherlands, we will insert here a survey of their groups.

A. The **arctic** group. This group is not represented in the Netherlands.

B. The **subarctic** group
This group is subdivided into:
   1. species that are common in the Arctic Ocean and fairly common in the northern part of the Atlantic Ocean, i.e. as far south as the most southern island of the Faeroes and the southern end of northern Norway.
   2. species whose area extends from the Arctic Ocean to the English Channel. This group is represented in our flora by several species, e.g. *Monostroma grevillei*, *Chordaria flagelliformis*, *Laminaria digitata.*

C. The **boreal-arctic** group. This group comprises the species whose area extends from the Arctic Ocean through the Atlantic Ocean at least as far southward as the coast of North Africa. The cosmopolitic species are sometimes also included in this group, which in the Netherlands is represented by such species as *Petalonia fascia*, *Scytosiphon lomentaria*, *Ulva lactuca* and *Fucus vesiculosus.*

D. The **cold-boreal** group. This group comprises species occurring in the northern part of the Atlantic Ocean; they reach the southern limit of their area of distribution on the west coast of France, and are but rarely met with in the Arctic Ocean. It is represented on the coast of the Netherlands by several common species, e.g. *Gigartina stellata*, *Phyllophora membranifolia*, *Polysiphonia urceolata*, *Giffordia granulosa* and *Fucus serratus.*

E. The **warm-boreal** group. The species of this group have an area of distribution extending from the Mediterranean Sea and North Africa to a line far to the north. According to the position of the northern limit of the area of distribution BØRGESEN and JONSSON distinguished 3 subgroups, viz.
   1°. species occurring as far to the north as southern Iceland, the Faeroes and northern Norway; to this subgroup belong *Chondrus crispus*, *Porphyra leucosticta*, *Callithamnion corymbosum*, *Leathesia difformis*;
   2°. species whose area extends to northern Scotland and western Norway; in our waters this subgroup is represented by *Antithamnion cruciatum*, *Dictyota dichotoma*, *Giffordia sandriana*, *Catenella repens*, etc.; these species may reach the North Sea from the north as well as from the south;

3°. species whose area of distribution extends northward at the most as far as Southern Scotland; several of them go no further than the English Channel; in our flora this subgroup is represented e.g. by *Hypoglossum woodwardii* and *Taonia atomaria*; the only way by which they reach the North Sea is by means of the English Channel.

Van Goor (1923) was of opinion that a sixth group ought to be added to this list, viz. that of the **intermediate-boreal** species. The area of the latter would extend from the west coast of France to the west coast of Sweden and the Baltic Sea. The majority of these species had been included by Børgesen and Jonsson either in the E_2 group or in the D group.

New findings proved that the area of some of the species was larger than the authors had assumed, and this sometimes necessitated the transference of such species to another group, but this were no changes of fundamental importance.

Børgesen and Jonsson themselves attached no great value to the division of the warm-boreal group into 3 subgroups, as it fell more or less outside the scope of their study, which aimed at a comparison of the algal flora of Iceland and the Faeroes with that of the surrounding regions.

Van Goor (1923) already pointed out that the subdivision of the warm-boreal group is without doubt of importance for a better understanding of the algal flora of the Netherlands. He even distinguished a fourth subgroup (E_4), which comprised the Algae that reach the northern limit of their area of distribution on the Spanish coast, but which may perhaps be washed ashore from time to time on the coast of the Netherlands. Herein, however, we will not follow him.

The species belonging to the E_1 and to the E_2 group may have invaded the North Sea either from the north or from the south, but those of the E_3 group can have reached it only by way of the Strait of Dover. The species of the last-named group are adapted to water of a higher temperature, and the greater part of them do not reach the North Sea; some of them, however, are found in the southern part of the latter, and a few even reach Heligoland.

On the coast of the Netherlands the E_3 group is not without importance. The East Scheldt derives its phycological significance even to a large part from the representatives of this group. It is because of the presence of these species that the algal flora of the Netherlands reveals itself as intermediate between that of the coast of "le Boulonnais" and that of Heligoland. In the latter they are practically absent, in the first they are more numerous.

3.II. Biogeographic boundaries

The way in which the species with a predominantly southern area are distributed and may show a local expansion in the southern part of the North Sea, offers an interesting problem. Even along the relatively short coast of the Netherlands their distribution offers remarkable aspects. It appears, for instance, that a number of these species reach the boundary of their area on this coast, and, even more remarkable, that these boundary lines form two groups, viz. one situated in the East Scheldt and one near Terschelling. The explanation of this curious distribution pattern is to be found in differences in the ecological conditions that are present in these regions (cf. chapter III).

The species that reach the boundary of their area of distribution in the East Scheldt, are:

Giffordia mitchellae	E_3
Taonia atomaria	E_3
Fucus lutarius	E_3
Erythrotrichia investiens	E_3
Hypoglossum woodwardii	E_3
Griffithsia barbata	E_3
Griffithsia devoniensis	E_3*)
Chondria tenuissima	E_3

The species that reach their boundary at Terschelling, are:

Acrochaetium codii	E_3
Catenella repens	E_2
Bostrychia scorpioides	E_3
Polysiphonia denudata	E_3

It appears therefore that the group E_3 may be divided once more, viz. in E_3a, which would comprise those species which reach the East

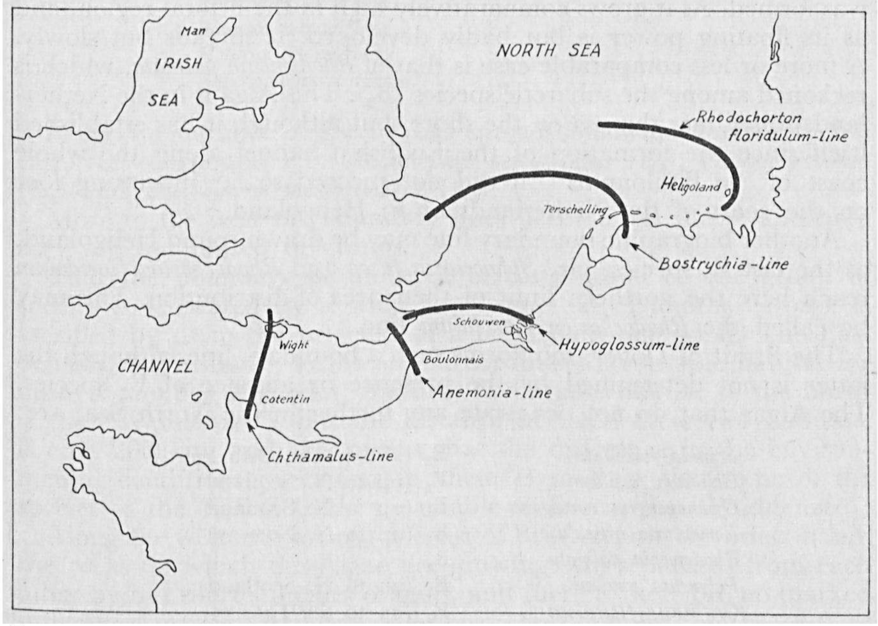


Fig. 3. Biogeographic borderlines in the southern North Sea and in the Channel.

*) This species may belong to E_2, as CHRISTENSEN (1947) collected a floating specimen in Denmark.

Scheldt but which are not found to the north of the latter, and E_3b, for those species which reach Terschelling.

However, it seems more advisable to indicate the position of the boundary of the area in which such a group of species is met with, by means of a special name, as it appears that there are also groups of species belonging to E_3 that reach the boundary of their area of distribution in some other part of the North Sea coast or in the English Channel. For the coast of the Netherlands we might distinguish a *Hypoglossum* line and a *Bostrychia* line.

Among the marine fauna, too, there is a group of species which reach the limit of their area of distribution in the waters of Zeeland, e.g. the Polychaete *Autolytus aurantiaca* (KORRINGA, 1951) and the Nudibranchiates *Goniodoris castanea* and *Thecacera pennigera* (both belonging to E_3). The boundary line of the area of distribution of *Patella vulgata* (E_2), the limpet, fluctuates.

Although the Phaeophycea *Pelvetia canaliculata* belongs to the cold-boreal group (D), it is on the coast of the Netherlands confined to the southern part. It formerly occurred in the "Waddenzee" near Den Helder, but, as mentioned before, it disappeared from this neighbourhood when works were carried out on the "Leidam", and now its northern boundary on the coast of the Netherlands is found in Zeeland. The absence of this species on the coast of Heligoland may be regarded as an indication that this species has reached the southern part of the North Sea in the period after the Strait of Dover was formed. As it grows comparatively high in the littoral region, and as its floating power is but badly developed, it spreads but slowly. A more or less comparable case is that of *Rhodymenia palmata*, which is reckoned among the subarctic species (B_2). This Alga is in the Netherlands sometimes thrown on the shore, but although it has established itself since the formation of the English Channel along the whole coast of "le Boulonnais", it did not succeed so far in getting foot on the coast of the Netherlands or in Heligoland.

Another biographic boundary line may be drawn round Heligoland, as the last E_3 species, viz. *Sphacelaria fusca* and *Rhodochorton floridulum* reach here the northern limit of their area of distribution. This may be called the *Rhodochorton floridulum* line.

The Strait of Dover, too, forms such a boundary line, although the latter is not determined by the presence or absence of E_3 species. The Algae that do not penetrate any further in the North Sea, are:

Scinaia furcellata	E_2 (also in the Oslo Fjord)
Gelidium pusillum	E_2 (up to N. Scotland)
Gymnogongrus norvegicus	E_2 (up to N. Scotland)
Lomentaria articulata	E_1 (up to N. Norway)
Rhodymenia palmata	B_2
Polyneura gmelini	E_2 (up to N. Scotland)
Griffithsia flosculosa	E_1 (up to the Faeroes)

A very characteristic sea anemone, viz. *Anemonia sulcata* (E_3), is another example of an organism that reaches here the northern limit of its area of distribution. The species which did as yet not succeed in establishing themselves north of this boundary line, which we will call the *Anemonia* line, are all slowly spreading ones. It is noteworthy that some of them are occasionally washed ashore in the Netherlands, *Lomentaria articulata* even rather often.

A very important biogeographic boundary line in the English Channel is the line which connects the Cotentin peninsula with the Isle of Wight. Crisp and Southward (1958), too, emphasize the significance of this boundary, which we will call the *Chthamalus* line. *Chthamalus stellatus* is the barnacle which predominates west of this line; it is doubtless one of the best known representatives of this group of species. The number of algal species that are not found to the east of this line, is very considerable. A selection of them is brought together in the following list.

Monostroma obscurum	E_3	
Elachista scutellata	D	
Alaria esculenta	D	(Dizerbo, 1947)
Saccorhiza polyschides	E_2	
Bifurcaria bifurcata *)	E_3	(Borel, 1954)
Himanthalia elongata	D	
Cystoseira baccata	E_3	
Asparagopsis armata	E_3	
Dudresnaya verticillata	E_2	
Grateloupia filicina	E_3	
Gastroclonium ovatum	E_3	
Ptilothamnion pluma	E_3	
Bornetia secundiflora	E_3	
Halurus equisetifolius	E_3	
Antithamnion sarniense	E_3	

A certain number of species has spread somewhat further to the east, viz. to Dieppe, e.g. *Cladostephus verticillatus* (E_2), *Padina pavonia* (E_3) and *Dictyopteris membranacea* (E_3).

More to the west the boundary lines become less sharp, and here they are not united in groups.

That the boundary of the area of distribution of one group of species is separated by a wide gap from that of another group, is ascribed by us to the presence of a barrier of some kind. The East Scheldt, for instance, forms an extraordinary favourable habitat for quite a number of species; the next favourable habitat to the north is the "Waddenzee", but the distance between these two habitats, is circ. 200 km, and this means that the difference in the environmental conditions prevailing in them is so large that some of the species of the East Scheldt are unable to live in the "Waddenzee".

Along the western part of the coast of Brittany, on the other hand, the rocks on which the Algae are growing, are separated from each other by but short stretches of sand, and there is therefore no marked difference in the edaphic conditions; the boundary of the area of

---

*) Ross (1958) has shown convincingly that the names *Bifurcaria tuberculata* (Huds.) Stackh. and *B. rotunda* (Huds.) Papenf. are illegitimate, and that the correct name for this species is *B. bifurcata* (Velley) Ross.

distribution is here apparently determined by climatic factors, and as the different species will be affected by the latter in a different way, their boundaries do not coincide.

That in the English Channel and in the southern part of the North Sea the boundaries of several species do coincide, and that these species therefore form definite groups, must accordingly be due to the presence of discontinuities in the edaphic conditions of the shore.

It is worth while to draw attention to one other noteworthy feature, viz. the presence in the Netherlands of a number of species with predominantly southern distribution which do not occur on the coast of "le Boulonnais" or at least have not been recorded from there by Debray (1899) and were not collected by myself.

Giffordia mitchellae	E_3	
Sphacelaria plumigera	E_2	
Acrochaetium codii	E_3	W
Antithamnion cruciatum	E_2	W
Chondria dasyphylla	E_2	
Chondria tenuissima	E_3	
Dasya pedicellata	E_2	
Griffithsia barbata	E_3	
Griffithsia devoniensis	E_3	
Polysiphonia denudata	E_3	W

The presence of these species in the Scaldian sub-district is doubtless a remarkable feature. In the English Channel they disappear already along the Normandian coast. Only three of them occur in the "Waddenzee", too (W).

Dasya pedicellata occupies a particular position among these species. This alga occurs in subtropical and tropical waters (Mediterranean Sea, Canary Islands, Gold Coast, American coast from Florida to Massachusetts, West Indies, California). Until a short time ago it was on the west coast of Europe not known north of Cadiz. Then it was collected in the Zuid-Beveland Canal (Zeeland), and slightly later on the west coast of Sweden. Neither from the English nor from the French coast this magnificent alga is known so far. *Giffordia mitchellae*, too, is a predominantly tropical species.

Griffithsia devoniensis presents a quite different picture. It is a rare species, although very common in the East Scheldt, and its area of distribution is very small, for it is confined to the English Channel and the waters of Zeeland; a single floating specimen was collected in Denmark.

The group of the warm-boreal species is therefore very heterogeneous; it comprises species with a mainly tropical distribution, but also mediterranean-lusitanic, lusitanic and even endemic ones.

3.III. The R:P quotient

In 1938 Feldmann has calculated by the aid of species lists found in the literature the percentages of Chlorophyceae, Phaeophyceae and Rhodophyceae occurring in that part of the Atlantic Ocean which is situated north of the equator. By comparison of the results obtained for various parts of this area, the percentage of Chlorophyceae was found to be fairly constant, although it was in the arctic-subarctic as well as in the tropical waters higher than in those of the temperate zone. The percentage of Rhodophyceae, on the other hand, appeared to increase form north to south, whereas the percentage of Phaeophyceae showed at the same time a decrease. The ratio of the two, indicated as the R: P quotient, therefore increases from north to south. In the arctic zone it has a value of 1.1, in the tropical West Indies it amounts to ± 4.5. For the coast of the Netherlands FELDMANN calculated the R: P quotient by means of the data supplied by VAN GOOR (1923), and found 1.3. If we use the data of the most recent, as yet unpublished species list, we find a value of 1.6. In this figure all species that are known from the Netherlands, the autochthonic ones as well as those that are washed ashore, are included. However, in this way we obtain a false impression of the composition of the algal flora. If the species that are known only from specimens that were washed ashore, are left out of consideration, we find a value of 1.1.

The low value of the R: P quotient calculated for the Netherlands, which agrees with that found for the algal vegetation of the arctic and subarctic waters, is to be ascribed to

1°. the absence of a suitable substrate at greater depths, i.e. at more than 1—1.5 m below M.L.W.S., and accordingly of the algal vegetation that is characteristic for the deeper zone;

2°. the low degree of salinity found in a large part of the waters in the neighbourhood of the coast ("Waddenzee" district, the greater part of the deltaic district), which explains why only euryhaline Rhodophyceae and Phaeophyceae occur;

3°. historical factors, which explain why a part of the algal communities occurring in the Netherlands have not yet reached their complete spectrum of species.

The two first-named factors explain at the same time the high percentage of Chlorophyceae.

TABLE III

Number of marine algal species known from the Netherlands, those belonging to the Chlorophyceae, the Phaeophyceae and the Rhodophyceae expressed as a percentage of the total number, and R:P quotient; calculations based on data collected by VAN GOOR and DEN HARTOG (unpublished); a. including the species that are known only from specimens that are washed ashore; b. autochthonic species.

Author	Number of Species	Chlorophyceae	Phaeophyceae	Rhodophyceae	R:P quotient
VAN GOOR	162 (a)	30.2	30.2	39.5	1.3
DEN HARTOG	281 (a)	26.0	28.5	45.6	1.6
idem	174 (b)	33.9	31.3	35.1	1.1

SUMMARY

From the standpoint of physical geography as well as from that of biogeography the coasts of the Netherlands may be divided in three districts, viz. 1°. the "Waddenzee" district (polyhaline, sheltered, poor in species with a predominantly southern distribution), 2°. the beach district (euhaline, exposed, by nature unsuitable to

algal growth), and 3°. the deltaic district. The last-named district is not fully homogeneous, and is provisionally subdivided in a euhaline Scaldian subdistrict, rich in species with a predominantly southern distribution, and a polyhaline estuarine subdistrict, which is poor in species. Further inland we find a mesohaline area and a fresh-water area which is still subjected to the influence of the tides. The extent of these areas has as yet not been sufficiently determined.

As the algal vegetation on the coasts of the Netherlands is confined to the slopes of dikes, to breakwaters, and to other structures erected by the hand of man, i.e. to habitats of very recent origin, we extended the field of our study to vegetations found in parts of the coast where natural rocks are present; to this end we chose the coast of "le Boulonnais" and that of Heligoland. The results of this study have been summarized.

Many warm-boreal species reach the North Sea from two different sides, viz. by rounding Scotland and by way of the Strait of Dover. Another group can reach the North Sea only along the latter route; however, the area of several representatives of this group does not extend beyond the English Channel or the Irish Sea. On account of these findings the subdivision of the warm-boreal species given by BØRGESEN and JONSSON (1905) could be emended. A noteworthy feature is that the northern limit of the area of distribution of various species appears to be found at definite points in the English Channel and in the southern part of the North Sea, e.g. in the East Scheldt and near Terschelling. This discontinuity in the distribution of the Algae must in the first place be due to discontinuities in the structure of the coast, although climatological factors and accessibility will also have played a part.

When the species that are known only from specimens that are washed ashore, are left out of consideration, the R: P quotient, i.e. the ratio between the number of species belonging to the Rhodophyceae and the number of species belonging to the Phaeophyceae, appears to be still less favourable for the coast of the Netherlands than it was found by VAN GOOR (1923), for it appears to be the same as that found in the arctic waters. This must be ascribed to the absence of suitable substrates at a greater depth than 1.5 m below M.L.W.S., to the circumstance that a large part of the coastal waters are brackish, and to historical factors.

CHAPTER III

THE ENVIRONMENT

We will discuss the influence exercised by the environment here under four different headings, viz.

1°. physical factors;
2°. chemical factors;
3°. biotic factors;
4°. historical factors and accessibility.

This division is not ideal, but it seems hardly justified to spend time on attempts to arrive at a more precise one, as the various ways in which the environment acts on the organism, influence each other to such a degree that a complete separation of their action must be regarded as excluded. In this field our knowledge is still very restricted, and it is, for instance, as yet impossible to give a satisfactory explanation of such an ubiquitous phenomenon as the "intertidal zonation", although the latter has drawn the attention of many phycologists, and although it has been studied already for a hundred years. In the following paragraphs we will discuss the most important features of the environment to which the Algae of the Netherlands coast are subjected.

1. PHYSICAL FACTORS

1.I. Substrate

The chemical nature of the substrate is hardly of importance to algal growth. We often find the same species on wood, concrete, granite, limestone and basalt. This indifference to the chemical nature of the substrate rests on the way in which the marine Algae absorb their mineral food; the latter is fundamentally different from that in which most of the land plants obtain it. The land plants absorb by means of their roots, their nutrients in a watery solution from the soil, and it is comprehensible, therefore, that these plants are very sensitive to the chemical composition of the latter, its Ca-content, the presence of humic acid, etc. The marine Algae, on the other hand, absorb their nutrients from the surrounding medium, and the soil is to them merely a solid base which serves them as anchorage.

Good examples of the indifference shown by the marine Algae for the chemical nature of the substrate are

1°. that we find on the Mediterranean seacoast between Nice and Cape Dramont the same algal communities on limestone, and on blue and red porphyry, and
2°. that we find calcareous Algae as well on limestone as on granite.

There are nevertheless some exceptions. *Dictyopteris membranacea* and the *Desmarestia* species are almost always free from epiphytes, because they secrete poisonous substances. There are also examples of obligate epiphytism, e.g. in the Mediterranean Sea that of *Feldmannia paradoxa* on *Cystoseira mediterranea.* The boring endolithic Algae occur exclusively on limestone and in the shells of barnacles. The eulittoral Mediterranean Rhodophycea *Rissoella verruculosa* is, according to a recent communication of MOLINIER and PICARD (1953), calcifugal; however, I found it on limestones at Nice.

The physical structure of the substrate is of much greater importance, as this often decides whether a species will be able to establish itself. The size of the component parts (rock, boulders, smaller stones, shingle, sand, mud), the nature of the surface (smooth or with various degrees of roughness), and the degree of hardness are all of them important factors. Especially in the tidal zone their influence is clearly visible. The black and compact basalt dries far more rapidly and becomes much hotter than the porous limestone from Vilvorde. Wood and concrete too retain their moisture much longer. The influence of the substrate is often recognizable in the position of the successive zones. A definite algal zone will occupy on limestone a higher position with regard to M.S.L. than it does on basalt.

At Strijenham on the island Tholen I could collect interesting data with regard to this effect. The slope of the dike is here partly covered with basalt, partly with limestone of Vilvorde, and a few hundreds of meters furtheron with granite. The slope amounts to circ. 25°.

The limestone of Vilvorde was laid down in 1935, the granite in 1936, whereas the basalt, too, was laid down before 1940. Where basalt was applied, the covering consists at the bottom of the Vilvorde limestone. The latter bears an open *Ascophyllum* community with a degree of covering varying between 40 and 45 %; between the *Ascophyllum* plants we found a fair number of specimens of *Fucus vesiculosus*. The basalt is bare. Where the slope is covered entirely by the Vilvordian limestone, we see an entirely different picture. The algal vegetation extends for another 1.5 m on the slope, and the upper zone is not formed by *Ascophyllum* but by *Pelvetia*, and between the two we find a zone of *Fucus spiralis*. This shifting of the vegetation towards a higher level because of the sudden change in the nature of the substrate is easily visible in fig. 4. Further eastward the limestone is replaced by granite, and here the upper limit of the vegetation has shifted to a lower level, but the *Pelvetia* zone and the *Fucus spiralis* zone are nevertheless intact, although their width has somewhat decreased (fig. 5).

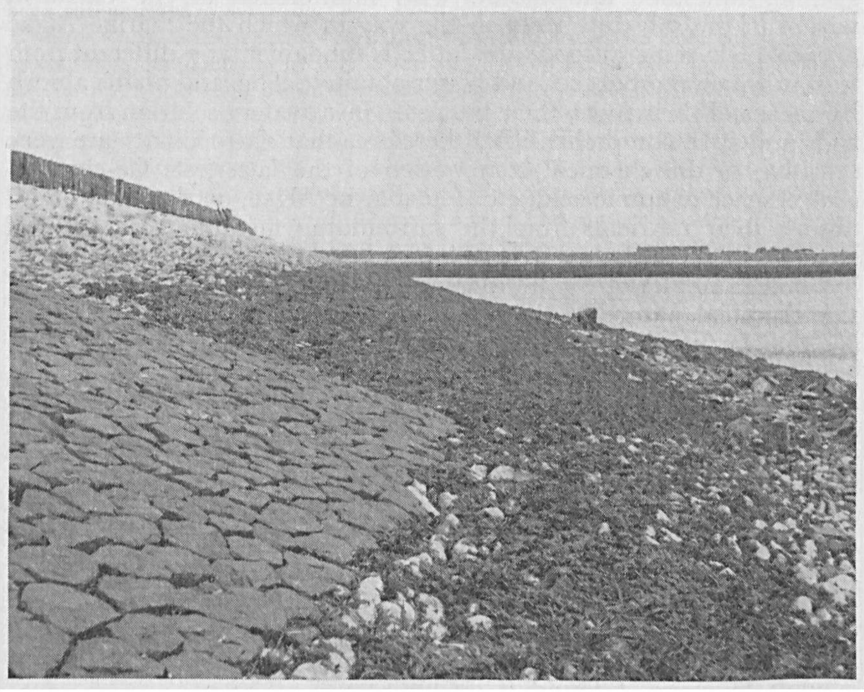


Fig. 4. Influence of substrate on algal zonation. To the left in front basalt, in the background Vilvordian limestone. The algal belts are raised on the latter substrate to a much higher level. Strijenham (Tholen). August 1955.

These observations show that the boundary line between two associations found at one place needs not to occupy the same position as that between the same two associations found at another place; only if the substrate in the two localities is the same, it may be expected that the boundary lines will coincide. Especially some English authors have made the mistake to leave the substrate out of consideration in their attempts to determine the position of such boundary lines. Fig. 5 clearly shows that the lower limit of the *Pelvetia* zone on limestone lies at a higher level than the upper limit of the corresponding zone on granite. For this reason the upper and lower boundary lines of the zone occupied by a definite association can be indicated only approximatively by means of hydrological levels; the position of these lines varies according to the nature of the substrate and also, as we will see, according to the more or less exposed position of the locality.

Where sand is deposited on a solid substrate, a remarkable group of species makes its appearance, viz. a combination of *Sphacelaria fusca*, *Cladostephus spongiosus* and *Rhodochorton floridulum*. The last-named species has not yet been found in the Netherlands as an autochthonous element; on the coast of "le Boulonnais" it determines the character of the vegetation in the undergrowth of the *Fucetum serrati*. On the sandy terraces of Heligoland and on the promontories along the coast of "le Boulonnais" the species quoted above sometimes form communities of their own.

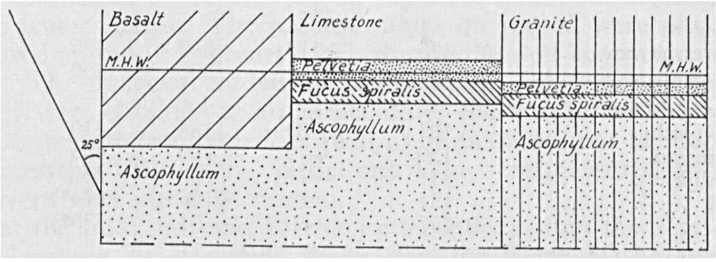


Fig. 5. Diagram of zonation of Fucaceae, near Strijenham (Tholen). On the limestone the algal belts are raised much more than on granite boulders; the basalt remains nearly bare (see also text on p. 30).

1.II. WATER MOVEMENTS

a. *Tidal movements*

The difference between high and low tide varies considerably along the coast of the Netherlands. In the direction south to north it shows a continuous decrease until it reaches its lowest value at Den Helder. East of the latter it increases again. In the estuaries of the rivers which traverse the deltaic district the difference shows towards the interior at first a considerable increase, but higher on it gradually decreases. However, at Vreeswijk, Culemborg, Zaltbommel and Hedel it is still clearly recognizable. In Table IV a survey is given of the tidal differences along the principal waterways and along the coast of the Netherlands. The figures for the tides indicate the average height above or below N.A.P. (new Amsterdam "peil", which is the standard

TABLE IV

Mean values for high and low tide and their difference, maxima for high tide and minima for low tide, all in cm, for various places along the principal waterways and along the coast of the Netherlands

	M.H.W.	M.L.W.	Diff.	Max.	Min.
West Scheldt:					
Flushing	190	—184	374	455	—326
Breskens	198	—186	384	480	—354
Terneuzen	206	—200	406	496	—350
Hansweert	218	—214	432	507	—350
Bath	243	—208	451	560	—371
East Scheldt:					
Westkapelle	171	—163	334	435	—306
Zieriksee	140	—148	288	432	—305
Wemeldinge	167	—169	336	468	—318
Grevelingen:					
Brouwershaven . . .	125	—117	242	425	—273
Bruinisse	148	—154	302	450	—303
Haringvliet-Meuse:					
Hellevoetsluis	104	—80	184	410	—226
Willemstad	130	—79	209	435	—225
Moerdijk	131	—77	208	410	—230
Hedel	131	25	106	574*)	—95
Lith	157	66	91	775*)	—97
New Waterway-Lek:					
Hook of Holland . .	90	—66	156	385	—214
Maassluis	92	—60	152	375	—192
Vlaardingen	101	—60	161	371	—200
Rotterdam	111	—60	171	375	—195
Krimpen o/t Lek . .	121	—53	174	371	—195
Schoonhoven	134	—1	135	382	—150
Vreeswijk	168	94	74	579*)	—55
Culemborg	223	192	31	693*)	—25
Scheveningen	92	—63	155	397	—
IJmuiden	84	—76	160	385	—250
Den Helder	50	—84	134	325	—236
Den Oever	62	—92	154	370	—256
Kornwerderzand. . . .	79	—93	172	373	—255
Harlingen	83	—97	180	366	—218
Terschelling	77	—97	174	318	—255
Holwerd	90	—139	229	—	—
Oostmahorn	96	—144	240	420	—290
Schiermonnikoog (West)	96	—134	230	400	—
Delfzijl	119	—155	274	460	—348

*) Measured when the rivers were strongly swollen.

level used in the Netherlands); they were taken from the "Getijtafels voor Nederland, 1957", the maxima and minima from the "Tienjarig Overzicht 1941—1950 der Waterhoogten" (Wemelsfelder, 1954), a publication of the "Rijkswaterstaat".

Deviations of the average values may have different causes. FELDMANN (1938) showed, for instance, that the high water at Banyuls is influenced by the height of the barometric pressure; a high barometric pressure causes a decrease of the height of the high tide. In the Mediterranean Sea, where the tidal differences are but small, the normal alternation is sometimes entirely obscured by the effect produced by changes in the barometric pressure. On the coast of the Netherlands this influence is also noticeable, but it remains small in comparison with the normal difference between the tides.

Extremely low values may be measured in the event the wind keeps blowing for a long time from the east, especially in winter and in spring. In 1929 at Flushing a height of 3.26 m below N.A.P. was measured, whereas the average value for ebb is —1.84. Winds from the west or from the northwest, on the other hand, cause an increase of the water height. The highest values on record were almost all measured on the 1st February 1953, during the well-known calamitous storm. The figures recorded for Oostmahorn, Schiermonnikoog and Delfzijl were obtained at an earlier date, viz. for the first two places in 1906, for the last-named in 1825. The maxima that are recorded for Vreeswijk, Culemborg, Hedel and Lith were measured at a time the rivers were strongly swollen.

That the tidal movements exercise an influence on the algal vegetation, cannot be doubted. Every day the Algae of the eulittoral region are twice submerged and twice laid dry. The nightly high tides are on the average higher than the daily ones, and the low tides are at night on the average lower than in the day-time. The average value found in a number of places for the inequality between the nightly and daily high tides as well as those for the inequality between the nightly and daily low tides are given in Table v; these data, too, have been taken from the "Getijtafels voor Nederland, 1957".

TABLE V

Average inequality in cm between the nightly and daily high tides and between the nightly and daily low tides along the coast of the Netherlands

	High-tide inequality	Low-tide inequality
Flushing	8	16
Hook of Holland	14	18
IJmuiden	12	16
Den Helder	26	6
Harlingen	28	4
Delfzijl	22	6

Because of these daily returning differences in the height of the high as well as of the low tides, the uppermost and the lowermost part of the eulittoral region differ from the rest of the latter. The uppermost part is formed by a narrow strip which is but once in every twenty-four hours submerged, the lowermost part is formed by a narrow strip which emerges but once in every twenty-four hours out of the water; all the rest of the region is twice submerged and twice laid dry. As the higher high tides and the lower low tides fall either

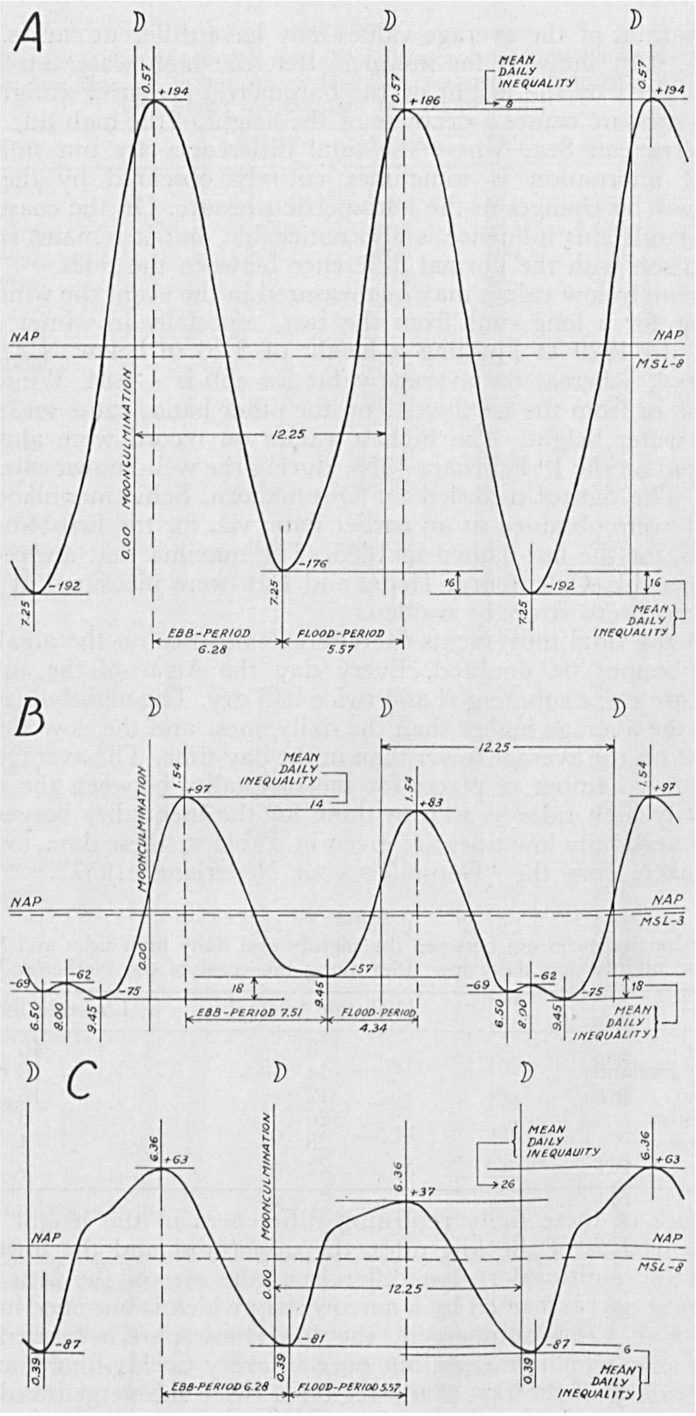


Fig. 6. Tidal curves of some stations along the coast of the Netherlands. A. Flushing. B. Hook of Holland. C. Den Helder. (after "Getijtafels voor Nederland, 1957"). M.S.L. = mean sea level.

in the night or in the early morning when there is no insolation, the desiccating effect of the period of emergence is reduced to zero at the bottom of the eulittoral region, and reaches its maximum at the top of the latter. The maximum values for the high tide and the minimum values for the low tide are found during spring tides, the minimum values for the high tide and the maximum values for the low tide during neap tides. It is possible, therefore, to distinguish a number of "critical levels", at which the hydrological conditions suddenly change. According to DOTY (1946) these abrupt changes would be responsible for the sharp boundary lines observed between the algal zones in the tidal belt.

Apart from the differences noted between the tides falling in the night and those falling in the day, there are still other particularities in the course of the tides that affect the algal vegetation. The average tidal period, i.e. the time which elapses between one high tide and the next, lasts on the coast of the Netherlands 12 hours and 25 minutes. The average lengths of the ebb-period as well as that of the flood period appear to differ considerably at different points of the coast. This is shown in Table VI, which is based on data found in the "Getijtafels voor Nederland, 1957".

TABLE VI

Average length in hours of the ebb periods and flood periods at various points on the coast of the Netherlands

	Ebb-period	Flood-period
Flushing	6.28	5.57
Hook of Holland	7.51	4.34
IJmuiden	8.03	4.22
Den Helder	6.28	5.57
Harlingen	7.14	5.11
Delfzijl	6.34	5.51

Another feature, which deserves the attention, is the rate at which the water rises or falls.

In Flushing high tide is followed by a rapid fall of the water, and after low tide there is an even more rapid rise. The curves representing the tidal movements at Harlingen and Delfzijl show a similar trend, although the rise and fall in the neighbourhood of the tops is somewhat less steep.

The tidal curve of Den Helder shows an entirely different aspect. When high tide is over, the water falls at first slowly and then with gradually increasing rapidity, but in the neighbourhood of the low-tide level the rate of fall once more slows down; then, when the low tide is over, there is a rapid rise to 10—25 cm above N.A.P., after which the last part of the rise takes place at a very slow rate.

At Hook of Holland and at IJmuiden the water rises at a very rapid rate; only at the beginning the rate is somewhat less rapid. The fall shows at IJmuiden in the middle a marked retardation. At Hook of Holland it takes place in two different ways. During day-time it begins slowly, but the rate increases gradually until a point about 10 cm from the lowest level is reached; then the fall is interrupted for two hours, and when it is resumed, it takes another hour to cover the last stretch. At night the initial stages of the fall are the same; in this way in 4 hours and 56 minutes a level of 69 cm below N.A.P. is reached; after that the water begins once more to rise and after 1 hour and 10 minutes it has reached a level of 62 cm below N.A.P.; then once more a fall sets in, and now in 1 hour and 45 minutes at 75 cm below N.A.P. the lowest level is reached. The interruption of the fall by a rise, which is called "agger", occurs in 95 % of the spring tides and in 35 % of the neap tides.

These additional bends in the tidal curves of Den Helder, IJmuiden and Hook of Holland indicate that locally still other critical tidal levels may be present, i.e. tidal levels which exercise a marked influence on the zonation of the Algal vegetations. They cause important changes in the environment. The correlation between the critical levels and the boundary lines between the algal zones is, however, not a linear one, but shows a more intricate pattern. The influence of the insolation and of the accompanying rise in temperature, the action of the surf, which is strongest on those parts of the coast where the rate at which the water rises and falls is but slow, the physical structure of the substrate, the fluctuations in the salinity, etc. make that there is but rarely an exact coincidence between the boundary lines of the associations and the critical tidal levels. This was pointed out already by Delf (1942) and by Doty (1946), but several authors have nevertheless tried to identify the boundary lines of the algal zones with hydrological lines.

b. *Currents*

The most conspicuous effects of tidal currents were observed by me on Heligoland. The tracks through the *Laminaria* fields followed by the currents are at once recognizable by the almost complete absence of *Laminariae.* The latter are in these tracks replaced by *Desmarestia aculeata,* locally also by *Halidrys siliquosa.* Occasionally very large specimens of *Laminaria digitata* were found in the tracks of the currents; these specimens proved to be pressed against the substrate; in such cases the track is probably a new one which owes its origin to a shift in the direction of an older current. In Zeeland we found *Halidrys siliquosa* at the head of a pier which was strongly exposed to tidal currents. In the eulittoral belt the zonation may be disturbed by the action of the tidal currents; under such circumstances the Fucaceae show no longer an orderly arrangement.

c. *Wave action*

The influence exercised on the algal vegetation by waves should not be underestimated. It is generally known that Algae are relatively scarce on exposed coasts, but that the supralittoral communities are in such places better developed than in sheltered spots.

The strength of the waves was so far regarded by most of the authors as a direct result of exposition and of wind force, but it is impossible to explain in this way the enormous force of the surf persisting along the ocean coast even after a calm of several days. According to CRISP and SOUTHWARD (1958) the effect of the wave action depends upon the nature of the coast (slope, lithological composition, presence of bays and promontories) and upon the depth of the water off shore. According to these authors the wind would merely exercise a modifying effect. That there exists a correlation between the depth of the water off shore and the distribution of some algal species, was shown already by FISCHER-PIETTE (1936). He found that *Alaria esculenta* was present only in localities where the water off shore reached a depth of at least 100 m; *Himanthalia elongata* was found only in the neighbourhood of the 50 m line, and *Bifurcaria bifurcata* only in that of the 20 m line.

The influence exercised by the waves is of two kinds, viz. 1° by moistening the Algae, on softly sloping coasts by wash, on steep and rugged coasts by splash, and in both instances by spray, and 2° by a mechanical action, viz. by scouring the surface of the Algae by means of suspended particles, and by the continual shifting of water masses, in which enormous forces may be involved.

CONWAY (1954) described how along the British coast the various Fucaceae disappear with increasing exposure. *Ascophyllum nodosum* is the first to disappear, and the next is the form of *Fucus vesiculosus* which is characterized by the presence of air bladders. The latter is replaced by the form without air bladders, f. *linearis* (= f. *evesiculosus*), which maintains itself even after *Fucus serratus* and then *Pelvetia canaliculata* have disappeared. On very strongly exposed coasts only *Fucus spiralis* f. *nana* (= f. *limitaneus*) and on the north atlantic coasts also *Fucus distichus* *) ssp. *anceps* (= *F. inflatus* f. *distichus* = *F. inflatus* f. *exposita* = *F. anceps*) are left.

BURROWS, CONWAY, LODGE and POWELL (1954) noted on Fair Island a shifting of the algal zones in an upward direction under the influence of the surf. The height to which the Algae occur, depends upon the height of the belt which receives sufficient moisture from the oceanic swell, storm waves and splash. The humidity of the atmosphere, too, plays an important part on Fair Island; fog, rain and low clouds are here the normal features of the weather. During the period in which the Algae emerge above the water, they retain therefore their moisture. BURROWS et al. point out that the environment on this coast can by no means be regarded as ideal to the development of the Fucaceae; *F. spiralis* f. *nana* and *F. distichus* ssp. *anceps* are regarded by them as depauperated forms.

Such a shifting of the algal zones in an upward direction was mentioned already by BRENNER (1916) and afterwards also by DU RIETZ (1940, 1947). DU RIETZ (1940) even expressed this in a law which he called the "Law of WIDAR BRENNER". According to this

---

*) POWELL (1957) has shown that the name *Fucus inflatus* L. can not be applied to this species, and that it has to be replaced by *Fucus distichus* L. emend. Powell. Of the latter he described four subspecies, of which two, viz. ssp. *anceps* and ssp. *evanescens* occur in the waters of northern Europe.

law the high-water line of the sheltered coast would not correspond to the high-water line of an exposed one, but to the upper limit reached on the latter by the storm waves. According to Burrows et al. this law is but an incomplete expression of the actual situation,

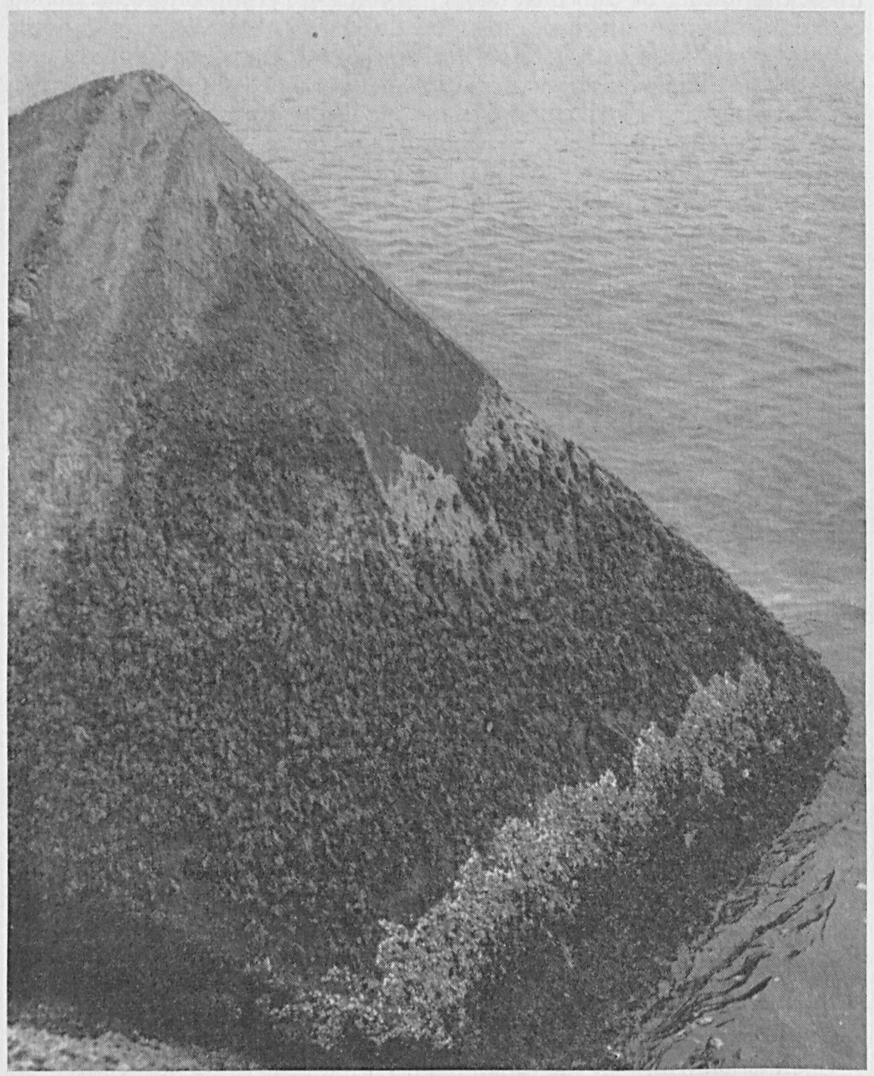


Fig. 7. IJmuiden, southern mole. Raising of the level of the algal vegetation by strong wave action. Above the white belt of barnacles (*Balanus balanoides* and *Elminius modestus*) a nearly pure *Porphyra umbilicalis* zone is seen with *Blidingia minima* at its upper limit; in a more sheltered habitat this community occurs at a considerably lower level. Above the *Porphyra* belt the *Bangieto-Urosporetum* occurs. *Bangia* is dark coloured; "*Urospora*" and *Ulothrix* are light; the two latter are visible at the top of the block of concrete. Below the barnacle belt a girdle of *Mytilus edulis* extends in a downward direction. 14th July 1955.

in which the humidity of the atmosphere also plays a part. I should like to add that the insolation, too, should be taken into account; the effect of the latter is opposite to that of the waves and of the humidity of the atmosphere.

Entirely irreconcilable with the conclusions reached by the aforenamed authors are the observations of SOUTHWARD and ORTON (1954), who studied the effect of the wave action on some Algae and animals living on the Plymouth breakwater. On the exposed southern side of the breakwater the wash reaches a height up to ten times as high as the one it reaches on the sheltered northern side. Most species show at the northern side a greater abundance and form a wider belt with the exception of the Algae *Himanthalia elongata* and *Rhodymenia palmata*, which occur on both sides in about equal numbers, and of the lichen *Lichina pygmaea*, which is more common on the southern side. On the southern side of the breakwater they noted a smaller width of the zones, which, moreover, ascended less high. They ascribed these phenomena to the action of the waves, but this conclusion can not be regarded as justified. We may certainly not leave the insolation out of consideration, whose effect is on the southern side much larger than on the northern one. Moreover, there is also a difference in the nature of the substrate; the southern side of the breakwater consists of granite blocks, the northern side of limestone. In this case the antagonistic influence exercised by the insolation and by the difference in substrate is apparently stronger than the influence exercised by the waves.

That the *Bangieto-Urosporetum* occurs on exposed places throughout the year, is, in my opinion, to be ascribed to the action of the waves. In more sheltered parts of the coast it develops only during the winter months.

1.III. TEMPERATURE

The principal climatic factor is doubtless the temperature, for the latter determines in the main the geographic distribution of the algal species. In the various parts of the area, on the other hand, the distribution is determined by other factors, such as the nature of the substrate, the water movement, insolation, salinity, and above all accessibility.

The temperature of the sea water and that of the air should be considered separately. The temperature of the sea water exercises its influence in the sublittoral region and during the period that the Algae are submerged also in the eulittoral region; the air temperature is of importance in the supralittoral region and during the time that the Algae emerge from the water, in the eulittoral region too.

a. *Temperature of the sea water*

Although I cannot prove it by measurements of the daily fluctuations in the temperature of the sea water, it can not be doubted that I am right in saying that these fluctuations are considerably smaller than those of the air temperature. For this reason the temperature of the sublittoral region is very uniform. Table VII gives the mean monthly temperatures of the surface water at Den Helder and in the East Scheldt. Dr H. POSTMA kindly gave me the data relating to Den Helder, whereas those with regard to the East Scheldt were derived from KORRINGA (1940).

TABLE VII

Average monthly temperatures of the sea water at Den Helder and in the East Scheldt in centigrades

	Den Helder	East Scheldt
January	4.3	3.0
February	3.1	2.9
March	4.5	4.9
April	7.4	8.5
May	11.2	13.3
June	14.9	16.9
July	16.8	19.1
August	17.4	18.8
September	15.7	16.7
October	12.2	12.1
November	8.3	7.1
December	5.2	3.6

At Den Helder the average yearly fluctuation of the temperature is 14.3° C. During the summer months the temperature rises but rarely above 20° C; in the first days of August 1947 20.5° C was recorded. During the winter months the temperature falls but rarely so low that the sea becomes covered with ice; this happened in the winter of 1946/47.

In the East Scheldt the average yearly fluctuation of the temperature is larger than in the Marsdiep at Den Helder, where the water because of the strong tidal currents is continuously replaced, and here is reaches a value of 16.2° C. In winter, if it keeps freezing for some time, already fairly soon a crust of ice is formed. During the summer months, on the other hand, the temperature rises much more rapidly than in the Marsdiep, and reaches a higher maximum. Especially in July and August if often exceeds 20° C; KORRINGA mentions even average temperatures of 22° C for these months in some years. This is due to the small depth of the basin and to the fact that the tidal currents merely shift the water to and fro and do not cause an exchange. It are especially these factors which make the East Scheldt an ideal habitat for the oyster culture (KORRINGA, 1940).

In the high temperatures prevailing during the summer months we must doubtless see the explanation of the presence of a group of species with predominantly southern distribution (*Hypoglossum woodwardii*, *Griffithsia devoniensis*, *Giffordia mitchellae*, etc.). With the exception of *Chondria dasyphylla*, *Ch. tenuissima* and *Hypoglossum woodwardii* they are present only during the summer months, and disappear almost completely before the end of October. They all produce their reproductive organs during the summer months.

b. *Air temperature*

Table VIII gives the average monthly air temperatures at Den Helder and at Goes. These data were received from Dr H. TEN KATE of the K.N.M.I. (the meteorological institute) at De Bilt. The values recorded for Den Helder were calculated from data covering the period 1921/50, those recorded for Goes from data covering the years 1901/30.

TABLE VIII

Average monthly air temperatures at Den Helder and at Goes in centigrades

	Den Helder	Goes
January	2.7	2.9
February	2.5	3.2
March	4.4	5.2
April	7.5	7.9
May	11.2	12.4
June	14.3	14.5
July	16.8	16.7
August	17.0	16.4
September	15.1	14.1
October	11.1	10.4
November	6.7	5.7
December	3.8	3.6

The daily fluctuations in the temperature are not to be neglected. The difference between day and night temperature often exceeds 10° C. During day-time the temperatures are, on the whole, higher than the mean value indicated in the table, and during the night they are lower. The general trend of the temperature curve at Den Helder and at Goes is the same. It is clear, therefore, that the supralittoral and the eulittoral region, the latter during the period of emergence, are subjected to greater differences in temperature than the continuously submerged sublittoral region.

On sunny days, besides the temperature of the air, radiant heat plays an important part. During the period of emergence the algal vegetation may, because of the insolation, undergo a strong rise in temperature, and consequently a strong desiccation.

Because of the immediate vicinity of the sea the temperature of the air is influenced by that of the latter. If it is lower than that of the sea, it will be warmed; if it is higher, it will be cooled. The temperatures that are measured in the eulittoral and supralittoral vegetation will show therefore but little resemblance with the meteorological data; especially during the winter months they will be less extreme.

It is noteworthy that the average temperatures of the air and the sea differ but slightly at Den Helder, whereas in the shallow basin of the East Scheldt during the summer months the average temperature of the water exceeds that of the air.

c. *Frost damage*

By frost damage we mean the disadvantageous changes which are the result of the interaction of a number of factors among which low temperatures occupy the central position. Low temperatures may influence the algal growth in various ways.

Freezing to death. The algae are killed by the direct action of the low temperature.

Destruction by frost. This phenomenon is often observed with the larger eulittoral Algae, especially with the Fucaceae, if the frost continues for some time. Such periods of frost are in the Netherlands often accompanied by an east wind which carries relatively dry air with it, and under these circumstances the transpiration of the Algae is enhanced, and their thallus accordingly desiccates. The remaining moisture may freeze. Both influences tend to make the thallus brittle. In situations where the Algae are continually exposed to the spray, the drops of water on the thallus may freeze, too, and they will in the end form thick crusts of ice. Under the weight of the latter the brittle thallus finally succumbs. Especially the high-littoral algal vegetations are in this way often severely damaged. The parts by which the Algae are anchored to the substrate, are the only ones that are left, but in the next spring the latter, as a rule, appear to be able to grow out into a new thallus, be it one of a more or less deviating shape.

Freezing in. This happens if the spray on the thalli freezes, and encloses them in a crust extending over the whole substrate. We see this mainly in places that are exposed to the surf. A strong snowfall, however, may cause the development of such an ice crust also in sheltered places. I have noticed this phenomenon only with the communities of filamentous Algae that are found in the supralittoral region and which are pressed flat against the substrate, and with the eulittoral *Blidingia* and *Enteromorpha-Porphyra* associations. These communities are, on the whole, well able to withstand such an event; *Enteromorpha compressa*, however, did not survive it, but this fast-growing species needs but a short time to regain its former development.

Floating ice. In severe winters large masses of ice come floating down the rivers or reach the sea by way of the "Waddenzee"; only when the temperature is very low, ice is formed in the sea itself. The blocks of ice scour along the algal vegetation of the eulittoral region and also of the upper part of the sublittoral one which, on account of the fall of the water level caused by the persistent east wind, behaves as a part of the eulittoral belt, and destroy this vegetation. The Algae that are growing in fissures and in cavities, are the only ones that escape the destruction by the drifting ice. In the year 1947 at Den Helder nearly all Fucaceae and Laminariaceae were swept away in this manner. The holdfasts of the Fucaceae which remained behind on the stones, grew out in the next spring to new thalli. Drifting ice may cause a shifting of material, but with regard to the latter I have no data. In their study of Nova Scotia and Prince Edward Island T. A. and A. STEPHENSON (1954) give interesting details on the action of drifting ice on the algal vegetation.

With regard to the regeneration of the algal vegetation it is of great importance to know how the main animal species withstand the frost. The two kinds of periwinkle, *Littorina saxatilis rudis* and *L.*

littorea, stood the severe cold of 1947 very well, and at Den Helder they were at the end of that winter still present in fairly large numbers. They had spent the period of cold in cavities and fissures, and their rapacity subsequently prevented the establishment of new algal vegetations on certain parts of the dike for a comparatively long period.

The barnacles and mussels die almost all in a severe winter, with the exception of the individuals that have settled in fissures. The eggs of the barnacles are not damaged by the frost. A slight increase of the temperature is sufficient for the nauplii to emerge from the eggs. It is noteworthy that a severe winter is followed by a strong spat fall.

As we have mentioned already, the damage caused by the frost does not depend exclusively on the air temperature, but also on other aspects of the weather. A moderate frost in combination with sunny weather (radiating heat!) and a low wind force is less damaging to the flora and fauna of the eulittoral and supralittoral region than a light frost accompanied by heavy gales; the cooling action of the wind should not be underestimated. Other important features are the moment at which the frost period begins, and the time it lasts, the lowest temperature that is reached, and above all the rapidity with which the temperature falls. A sudden start of the frost period causes the greatest number of victims among the flora as well as among the fauna. By taking these points in consideration we arrive at the following classification.

Ice-winters. A period of cold lasting several months; moderate to severe frost; ice formation in the sea; complete destruction of the littoral vegetation. Example: 1946/47.

Severe winters. A frost period which suddenly sets in and lasts 2—4 weeks, in which, moreover, a strong wind is blowing from the north-east or east, and in which very low temperatures are reached; ice formation only in sheltered bays and sea arms; fatal to a large number or individual Algae and animals, but the algal zones are not wiped out as a whole. Examples: 1953/54; 1955/56.

Moderate winters. A frost period which lasts more or less long but in which no very low temperatures are reached, and which is accompanied by sunny weather and sometimes by a good deal of snow; the sea does not freeze, and there is but little frost damage. Example: 1957/58.

Changeable winters. Short periods of moderate to light frost alternating with short frost-free periods; changeable weather with rain, snow, hail and relatively little sun-shine; the sea does not freeze, but there are nevertheless a fairly considerable number of victims. Example: 1954/55.

Mild winters. A short period with light to moderate frost, sunny weather and little wind. Example: 1956/57.

Ice-free winters. There are at the most but a few, scattered days on which the average day-temperature sinks beneath the freezing point. Examples: 1948/49; 1958/59.

The data with regard to frost damage were obtained by inspecting the coast before and after the period of frost as well as during the latter. In future this subject will have to be studied by the aid of more exact methods, e.g. by the study of permanent plots in which by counting or estimating the number of individuals at various moments of the year a good idea may be obtained of the changes in abundance and in the degree of covering which the principal species undergo. In the same way the influence which a heat wave exercises on the intertidal communities, might be studied.

As frost is a normal feature of the winter along the coast of the Netherlands, it is interesting to consider the influence of an ice-free winter on the intertidal communities.

Especially thermophilic species which normally are decimated by the frost, pass such winters without trouble, and are in the next summer extremely well-represented. This applies e.g. to *Zostera marina* var. *stenophylla*, which occurs on the mud flats. To other species the absence of a period of cold appears to be injurious. With *Balanus balanoides* the production of eggs is stimulated by a period of frost, and it is a striking fact that the latter is but moderate when the winter has been mild (see also SOUTHWARD and CRISP, 1952, 1954, 1956).

I.IV. LIGHT

Light is indispensible to the photosynthesis of the Algae, and algal growth is confined therefore to the zone in which a sufficient amount of light penetrates. The lowermost limit of the latter depends largely on the clearness of the water, i.e. on the amounts of suspended material like plankton and mud particles. The greatest depths from which Algae have been recorded, are to be found in the Mediterrenean Sea in the vicinity of the Balearic Isles, where they were collected by RODRIGUEZ at a depth of 180 m (SAUVAGEAU, 1912), and in the Atlantic Ocean near the Canary Islands, where they occur, according to BØRGESEN (1938), even down to 200 m. However, the greatest depth at which they have been found in the English Channel, is said to be 35 m (HAMEL, 1923). In turbid water the depth reached by the Algae, is but very slight.

The distance from the surface determines not only the intensity of the light, but also the length of the period during which it is available, and its quality; it is a well-known fact that blue and violet rays penetrate much farther than the red ones. The influence on the vegetation of the last-named factor cannot be studied in the coastal waters of the Netherlands because of the shallowness of the latter, the large amount of suspended material, and the almost total absence of suitable substrates for the growth of Algae at greater depths.

In the eulittoral region direct light (insolation) as well as diffuse light exercise a quite conspicuous influence. In the case of insolation the algal vegetation is not only exposed to light of high intensity but also to the action of heat rays, which enhance the temperature of the substrate as well as that of the Algae themselves, and which cause during the period of emergence an increase of the transpiration. Especially the species living in the higher part of the eulittoral region, like *Pelvetia canaliculata*, *Fucus spiralis*, *Porphyra umbilicalis*, *Blidingia* *minima*, *Rhizoclonium riparium*, and the supralittoral Prasiolaceae, too, can stand a very strong desiccation. The latter I have found in a condition in which they could be pulverized between the fingers; it appeared that they had nevertheless retained their vitality.

It is noteworthy that in the eulittoral region some communities occur only in fissures and dark angles, and in other places in which they are protected against insolation. In this way the *Callithamnietum scopulorum* is at Den Helder confined to the north side and the east side of the pales on the sea dike. On the coast of "le Boulonnais" the *Lomentarieto-Plumarietum* was found exclusively in rock fissures and on the north side of large boulders. The same applies to the *Callithamnion tetricum* vegetation along the coast of Brittany. It is, however, by no means certain that these vegetations are photophobous. It looks more probable that it is the sensitivity to desiccation which binds them to shaded habitats. If this preference for shaded places really was due to an aversion from high light intensities, these Algae would also occur in the undergrowth of the communities consisting of Fucaceae, but this is not so.

A real preference for habitats with a low light intensity, however, is present in the *Rhodochorton-Waerniella* community, which is confined to supralittoral and eulittoral caves. *Waerniella lucifuga*, a species that so far has not been found in the Netherlands, is a very characteristic constituent of this community. The latter was described by WAERN (1952) from the coasts of Sweden, and could be studied by me near St. Enogat (I. et V.) in Brittany where it is found in the "*Waerniella* cave-fissure" which was already described by LAMI (1940). *Rhodochorton purpureum* *) is less selective, and is found sometimes in fairly well lighted habitats. Along the coast of the Netherlands it is fairly common in the undergrowth of the Fucaceae communities, and occurs there often in large numbers. On Heligoland it is often found on the stalks of the sublittoral *Laminaria hyperborea*. Along the French and Scandinavian coasts it occurs as a distinct vegetation unit in the eulittoral and supralittoral caves, often in company of *Waerniella*. At Flushing I once found this species on a dark spot against a wall, out of the reach of the spray, but exposed to the influence of the sea wind; this habitat therefore was adlittoral. *Rhodochorton* accordingly can live even as an aerophyte.

The most outspoken sciaphilous association in this region is the *Hildenbrandtieto-Verrucarietum mucosae*. The latter penetrates farthest in the littoral caves, and is in the Netherlands a very conspicuous constituent of the undergrowth of the *Fucus* formation.

I.V. OTHER PHYSICAL FACTORS

In this section I will refer to a few factors which in the preceding pages were mentioned but incidentally, and on which we are as yet but badly informed.

---

*) *Rhodochorton purpureum* (Lightf.) Rosenv. is the correct name for the species which appears in the "Checklist" of PARKE (1953) as *Rh. rothii* (Turt.) Näg.

A very important feature of the topographical position is the **exposition.** Where the coast is turned towards the south, the insolation is much stronger than where it faces the northern sky. In the latter localities the angle of the slope, too, is of considerable importance, as is depends upon the size of this angle whether the locality will receive a part of the sun rays or not. Places with a western or south-western exposition are sheltered against the relatively dry east and north-east winds, which the whole year round are accompanied by temperature extremes. That this is a factor of considerable importance, follows from the recent work of CRISP and SOUTHWARD (1958), who saw a direct relation between changes in exposition and irregularities in the outline shown by the area of distribution of some littoral animal species.

Another important aspect is the **depth** at which the Algae occur. Along the coast of the Netherlands the increase in pressure with increasing depth may be neglected, because of the slight differences in depth shown by the localities in which the Algae here occur. The shallowness of the water, however, causes considerable fluctuations in its temperature. This applies especially to the water of the "Waddenzee" and of the deltaic district.

2. CHEMICAL FACTORS

2.1. SALINITY

That the salinity exercises an enormous influence on the algal vegetation, has been known for a long time. It is one of the most principal, perhaps even the most principal, of the factors which determine the local distribution of the algal communities.

In Table IX the average monthly values for the salinity at Den Helder and in the East Scheldt are given. The figures for the Marsdiep at Den Helder were received from Dr H. POSTMA, who calculated them from unpublished estimations made at intervals of ten days by the "Rijksinstituut voor Visserij-onderzoek" during the years 1933—1951. The figures for the East Scheldt were taken from a publication by KORRINGA (1940).

TABLE IX

Average monthly salinity in $^0/_{00}$ Cl′ at Den Helder and in the East Scheldt

	Den Helder	East Scheldt
January	16.2	15.2
February	15.9	14.9
March	15.8	15.0
April	16.3	15.1
May	16.7	15.2
June	16.9	15.3
July	17.0	15.5
August	16.9	15.8
September	17.1	15.8
October	17.0	15.8
November	16.9	15.5
December	16.4	15.4

On the fluctuations in the degree of salinity in the "Waddenzee" we are well informed by the hydrographic investigations of Postma (1950, 1954) and of Postma and Verwey (1950). In the western part of the "Waddenzee" the largest amounts of fresh water are received from the sluices at Den Oever and at Kornwerderzand and from the draining mill at Roptazijl; the largest influx takes place during the winter months. A clear picture of the way in which the fresh water spreads into the basin, was given by Postma. It appeared that the isohalines form concentric arcs round the points of entrance. He adds that the isohalines determined for various dates show considerable diversity, but that "the general pattern is always more or less the same".

With regard to the salinity of the waters of Zeeland we are less well informed. Korringa (1940) published data relating to the East Scheldt. He noted a clear correlation between periods of low salinity in the East Scheldt and periods during which the Rhine was swollen. At such times the salinity decreased to 14.5 $^0/_{00}$ Cl′. As the East Scheldt does not function as an estuary, it is clear that in sea arms like Grevelingen-Volkerak and Haringvliet the salinity will undergo a far stronger decrease in such periods. Postma (1957) recorded for the Volkerak north of St. Philipsland 10.0 $^0/_{00}$ Cl′, for the Haringvliet near Hellevoetsluis 2.0 $^0/_{00}$ Cl′. In the West Scheldt the salinity is considerably higher, as the amount of fresh water that is discharged by the Scheldt is but small. The 14.0 $^0/_{00}$ Cl′ isohaline runs more or less from Hansweert to Perkpolder.

The salinity at high and at low tide may differ considerably in the same place, especially in the deltaic district. During the period of high tide the isohalines shift towards the east, during the period of low tide towards the west.

A study of the hydrography of the deltaic district has already been started by the Hydrobiological Institute, div. Delta Research. The program of the investigation was published by Postma (1957).

A good idea of the relation existing between salinity and the composition of the algal vegetation is obtained by studying the distribution of some of the species. We see then that in the "Waddenzee" *Fucus serratus* is confined to the most western part, Den Helder, Oude Schild on the island Texel, and the coast between Ewijcksluis and Wieringen, i.e. to that part where there is at high tide an influx of salt water. Some other species, like *Codium fragile*, *Bryopsis plumosa* and *Laminaria saccharina*, appear to be concentrated round the sea gates, where the highest salinities are measured.

The decrease in the number of species that is observed in the direction from west to east, does not depend entirely on the decrease in salinity, but also on the low temperatures that prevail during the winter months and on the strong sedimentation, which is especially noticeable where salt water comes into contact with fresh water.

Brackish water is recognizable by a strong increase of the number of *Enteromorpha* species, which form here closed, well-characterized communities, viz. the *Monostrometo-Porphyretum leucostictae* and the

Enteromorphetum prolifero-intestinalis, and by a strong decrease of the number of Rhodophyceae.

The amount of precipitation does not influence the degree of salinity. KORRINGA (1940) already reported from the East Scheldt that he saw no correlation between salinity and precipitation. I can confirm this for the part of the "Waddenzee" near Den Helder. Table x gives the average amounts of precipitation near this place, calculated from observations made in the period 1921—1950. These figures were received from Dr H. TEN KATE of the Meteorological Institute at De Bilt.

TABLE X

Average monthly precipitation in mm at Den Helder

January	57	July	60
February	40	August	68
March	34	September	75
April	43	October	85
May	41	November	79
June	39	December	60

When we compare the figures given in Table IX with those of this table, we do not find the slightest agreement. Ecologically the amount of precipitation may nevertheless be of paramount importance, viz. for the eulittoral communities. As the latter emerge at low tide from the water, the salinity may be lowered considerably for them by rain; by insolation, on the other hand, the salinity may be increased. In the supralittoral region the influence of rain and sunshine is, of course, still more pronounced. The whole amount of salt may be washed away if it keeps raining long enough, and then the species occurring in this region will have to live temporarily under "fresh-water conditions". During a long spell of sunny weather a large part of the water may disappear by evaporation, and under these circumstances salt may even crystallize on the Algae and on the substrate. These considerations make it comprehensible that some of the euryhaline supralittoral Algae also occur on the shore of fresh-water lakes and on river banks, e.g. *Rhizoclonium riparium*, *Bangia atropurpurea* f. *fuscopurpurea*, *Rosenvingiella polyrhiza*, *Vaucheria compacta* and *Blidingia minima*. *Rhizoclonium riparium* and *Bangia atropurpurea* f. *fuscopurpurea* were found by me along the Meuse-Waal Canal near Nymegen and in the Meuse near Brumagne (Belgium, province of Namur); they also occur along the IJsselmeer and in a large number of ponds and lakes in the western and northern parts of the Netherlands. *Rosenvingiella polyrhiza* was recorded from the "Mooie Nel", a watercourse near Haarlem, whereas *Vaucheria compacta* and *Blidingia minima* have been collected along the shores of the IJsselmeer and along the lower course of the rivers.

2.II. POLLUTION OF THE WATER

The influence exercised by pollution of the water on the algal flora has as yet not been studied in the Netherlands. The data which

I myself have collected on this subject, are in good agreement with the observations published by HAYRÉN (1910), COTTON (1911), SUNDENE (1953) and GRENAGER (1957). Along the coast of the Netherlands pollution of the water occurs only at the mouths of rivers and of canals, in harbours and near the draining mills that discharge eutrophic polder-water. The pollution is often accompanied with a decrease in the degree of salinity. Especially the *Enteromorpha* species and *Ulva lactuca* profit by the influx of such water, whereas some other species are very sensitive to pollution, and disappear at once. GRENAGER (1957), who studied the influence of the sewer water of Oslo on the distribution of the Algae, gives interesting details on this subject.

Prasiola stipitata occurs along the coast of the Netherlands only there on sheltered places, where the water is strongly polluted with nitrates and organic substances, therefore especially in harbours and on places where much urine is discharged. On the dike at Den Helder *Prasiola stipitata* and *Rosenvingiella polyrhiza* were especially found in the runlets along which the rain water flows off, and which traverse the *Caloplaca marina* belt. This rain water has become markedly eutrophic, because it flows over the rotting refuse that is thrown on the dike.

WAERN (1952) regards *Bangia atropurpurea* f. *fuscopurpurea* and *Capsosiphon fulvescens* as eutrophic species. *Bangia*, indeed, is in the Netherlands, at least in sheltered places, exclusively found in polluted water, and *Capsosiphon*, which has not been collected so far in the Netherlands, was found in the harbour of Antwerp in Belgium, in company of *Enteromorpha prolifera*, in strongly polluted water.

3. BIOTIC FACTORS

3.I. INFLUENCES EXERCISED BY ANIMALS

The littoral fauna exercises its influence on the algal vegetation mainly in two ways, viz.

1°. by competing with it for the available space, in this field the sedentary and but slightly moving animals play the main part; and

2°. by feeding on it.

Among the animals that compete with the Algae for space, we may reckon various Hydrozoa, Anthozoa, Bryozoa, Ascidia, sponges, further several kinds of worms, barnacles, mussels, etc. Nearly all these groups are very common in the sublittoral region; in the intertidal belt most of them are represented by a few species only. Extensive colonies are found in that part of the sublittoral region where the light is too weak to allow the development of an algal vegetation or at least of a closed algal growth. In the upper part of this region, where the Algae are still well-developed, the animals are found in the undergrowth, where they are often very numerous, or else as epiphytes. The Algae themselves often form a suitable substrate for them; the holdfasts of the Laminariaceae, for instance, offer a home to a large number of animals, and this applies also to swollen base of the stipe of *Saccorhiza polyschides* (COLMAN, 1933, 1940).

In the intertidal belt the animals are found in dark fissures, in caves, between and under stones, but also under Algae and even upon the latter. What part the competition for space will play in the development of the algal growth, depends for a good deal on the light intensity. So long as the latter suffices for the development of the Algae, it plays, in the eulittoral region as well as in the upper part of the sublittoral one, a predominant part in the selection, and then the animal communities are banished to the darker spots where a normal algal growth is no longer possible. This, however, does not mean that these animals are unable to endure light, the algal growth deprives them of the space they need in order to form colonies. A few examples may serve to illustrate these relations.

In the *Ascophyllum* and in the *Fucus vesiculosus* communities of the intertidal belt we often meet *Clava multicornis* f. *squamata*, which forms colonies in their undergrowth, but which also lives in great numbers on the thalli of these Fucaceae. In the room between the sluice-gates at "de Bol" (Texel), where but little light penetrates, TULP found a circ. 40 cm wide belt that was coloured pink by a colony of this beautiful Hydrozoon.

A somewhat similar behaviour is observed in another hydrozoon of the littoral belt, viz. *Dynamena pumila*. In the intertidal belt below M.S.L. the latter is very common on as well as under the Fucaceae. In dark cavities on the French coast we noticed at the same level pure colonies of this species and sometimes also communities in which it was accompanied by the bryozoon *Electra pilosa*; the latter, too, occurs also in the Fucaceae communities. In the undergrowth of the *Laminaria* community in the sublittoral region we meet these two species once more.

In the sublittoral region, too, I found in dark spots pure colonies of animals. Before the harbour of Den Helder was locked up, the timber rafts in the latter bore dense colonies of *Metridium senile*. On the hull of ships that for a long time had stayed in the harbour, I found also large numbers of *Metridium*, and in addition colourful colonies of *Tubularia larynx* and of *Botryllus schlosseri*. On pontoons at Flushing I noticed a coenosium consisting of Bryozoa, sponges (*Haliclona*, *Halichondria*), Hydrozoa and Anthozoa. Coenological studies of these animal communities have not yet been carried out in the Netherlands. On the coast of "le Boulonnais" in dark spots an interesting community was met with, in which *Dendrodoa grossularia* and *Grantia compressa* were the most conspicuous partners.

Light, however, is not the only factor that plays a part in the struggle for space between Algae and animals. Exposition to surf, too, is of importance. In exposed spots, e.g. on the piers jutting out from the beach, we find enormous masses of barnacles in full light. Once they have established themselves, the latter sift the plankton so thoroughly out that the Algae practically do not get a chance to obtain a foothold. Moreover, as there live large numbers of periwinkles between the barnacles, and as these periwinkles show a great liking for the young Algae, it is clear that such colonies of barnacles will remain almost entirely free from algal growth. However, as soon as the barnacles are removed from a stretch of sufficient extent, the Algae at once reappear. This proves that barnacles and Algae are indeed competing for room. The predominance of the barnacles is perhaps often a question of first arrival.

If during a severe winter the algal growth in the littoral region is entirely destroyed by floating ice, in the spring of the next year the stones are so densely covered by young barnacles that they assume a white colour. Young Algae may establish themselves at the same time, but as the barnacles grow very fast, and as they need ever more room, the young Algae are compressed in too narrow a space and give up. Only when in the course of time (after one or two years) gaps appear in the covering of barnacles, the establishment of an algal vegetation becomes possible. However, in very strongly exposed habitats, the algal growth is almost entirely suppressed, and in such localities the barnacles form an uninterrupted belt.

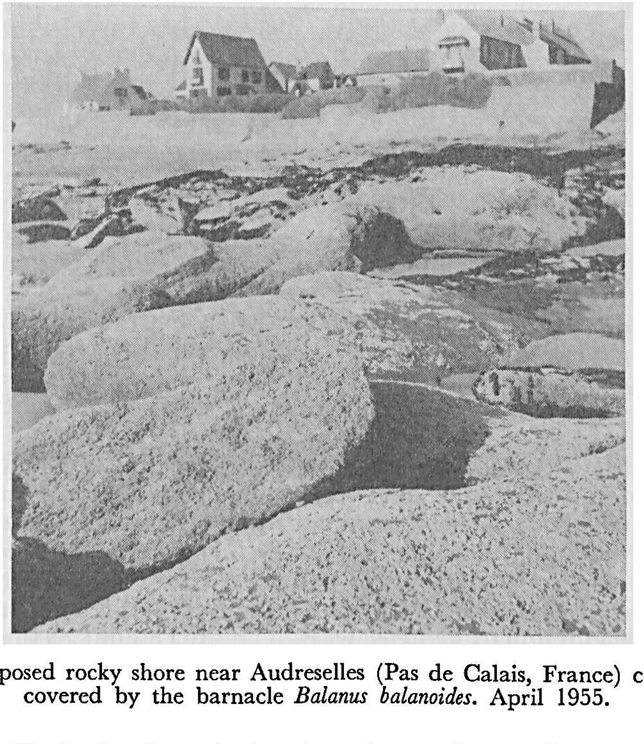


Fig. 8. Exposed rocky shore near Audreselles (Pas de Calais, France) completely covered by the barnacle *Balanus balanoides*. April 1955.

In the Netherlands and elsewhere in north-west Europe this belt is formed by *Balanus balanoides*, which reaches its optimum development in the uppermost part of the eulittoral region. The upper limit of this belt coincides more or less with M.H.W. This barnacle is also very common in the undergrowth of the *Enteromorpha-Porphyra* community and in the various vegetations of Fucaceae. Below M.S.L. it becomes less numerous, and cedes its dominant position to *Balanus crenatus*; the latter occurs in the sublittoral region also in large numbers. As a rule, the *Balanus crenatus* belt remains hidden under the algal covering; only in dark spots it forms pure colonies. In exposed positions, where moreover a considerable difference between high and low tide is found, the *Balanus balanoides* colonies may cover enormous stretches. Since 1945 a barnacle introduced either from New Zealand or from south-eastern Australia, viz. *Elminius modestus*, is spreading with great rapidity along the coasts of western Europe. It has invaded mainly the territory of *Balanus balanoides*, and occasionally the latter has even been completely supplanted by the new-comer (DEN HARTOG, 1953, 1956; BISHOP, 1954; KÜHL, 1954; CRISP, 1958).

On the coasts of Brittany and of south-west England the *Balanus balanoides* belt is replaced by a belt of *Chthamalus stellatus*, which is also found along the lusitanic and mediterranean coasts.

FELDMANN (1938) describes an "association à *Brachytrichia balani* et *Entophysalis granulosa*" which occurs on the shells of *Chthamalus*, and consists of epilithic and endolithic Algae. It is very common in the Mediterranean Sea. As the most characteristic species of this association are widely distributed, it is not impossible that it will prove to be represented in western Europe, too. PARKE and MOORE (1935) wrote an interesting paper on the infection of the shells of *Balanus balanoides* by endolithic Algae; the latter were partly the same as those mentioned by FELDMANN. In the Netherlands the Algae which live on barnacle shells, were studied by VAN DEN HOEK (1958). As species which bore into the shells, he mentions *Gloeocapsa crepidinum* (under the name *Entophysalis deusta*), *Plectonema terebrans*, *Gomontia polyrhiza*, *Entocladia* sp. and the *Conchocelis* stage of *Porphyra umbilicalis*. The first-named species also occurs on the surface of the shells, where it lives in company of *Plectonema battersii*, *Phormidium fragile*, "*Pseudulvella*" (probably the early stage of *Blidingia minima*), *Ralfsia verrucosa*, *Oscillatoria nigro-viridis* and some less common and more accidentally occurring species. The material was collected in all parts of the eulittoral region on barnacles (of which the name is not mentioned) occurring in the undergrowth of the algal vegetations. Unfortunately no material was studied from barnacle communities occurring on exposed places, i.e. from habitats in which the larger Algae are scarce or absent.

In exposed spots the mussels (*Mytilus edulis*), too, occur in belts. They cover the stones in the form of a thick carpet in which almost no full-grown individuals are met with. The upper limit of this belt lies considerably lower than that of the *Balanus balanoides* colonies. Barnacles may live epizoically on the mussels, viz. *Balanus crenatus* and *Elminius modestus*, and in the upper part of the mussel belt also *Balanus balanoides*; in brackish water *B. crenatus* may be replaced by *B. improvisus*. The number of Algae that occur on mussels, is but small; it concerns in the main species belonging to the *Enteromorpha-Porphyra* community, and at the low-water line also *Chondrus crispus*, but, as a rule, the mussel belt is free from algal growth. An exception form the mussels that are found in the small pools in the intertidal region;

these mussels are often overgrown by *Enteromorpha* and *Ulva*, and during spring also by the *Monostroma-Dumontia* association.

The polychaete *Polydora ciliata*, which is very common on the dike at Den Helder, exercises an entirely different influence on the algal vegetation. This animal occurs in enormous numbers in the zone between M.L.W.N. and M.L.W.S., where it bores holes in the calciferous stone. On these stones mud is deposited, and the latter is glued together by the worm to numerous small tubes. The stones often bear a layer of mud 1 to 2 cm thick. It is clear that this will cause a change in the composition of the algal vegetation, especially in that of the *Polysiphonieto-Chaetomorphetum*. Several species avoid the stones that are covered with this "*Polydora*" mud, e.g. *Phyllophora membranifolia*, *Chaetomorpha aerea* and *Ahnfeltia plicata*, whereas *Polysiphonia urceolata* is less well represented. Other species, however, exhibit a preference for "*Polydora* mud", e.g. *Acrosiphonia centralis*, *Petalonia fascia* and *Ulva lactuca*. Near the low-water line the first and second species occur almost exclusively on this substrate.

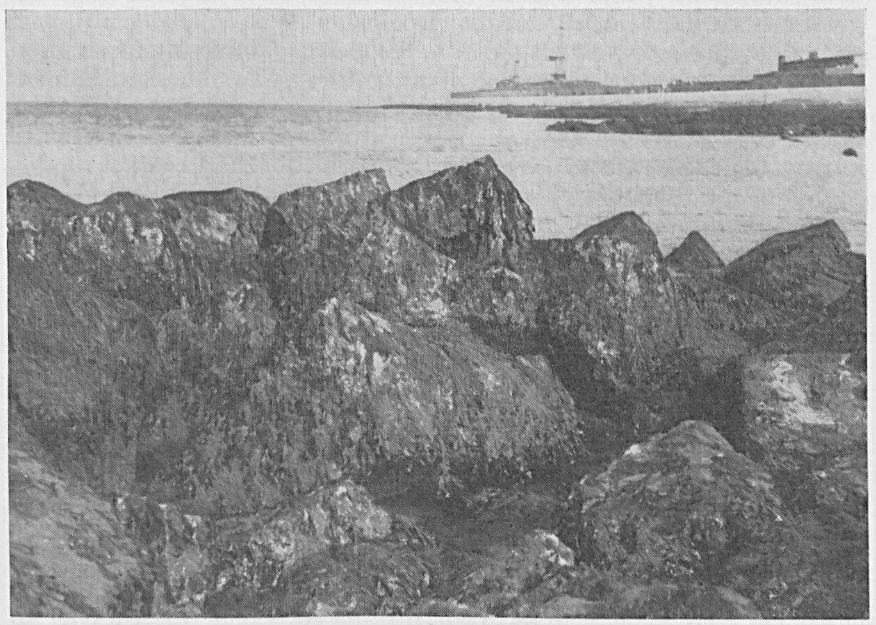


Fig. 9. Den Helder, seadike. Stone-blocks covered by the *Enteromorpha-Porphyra* association, with young plants of *Fucus vesiculosus*. On the blocks near the waterlevel "*Polydora* mud" is visible. 6th September 1956.

Phycophagous animals may exercise a drastic influence on the algal vegetation. However, only common species and species that under certain circumstances may occur in large numbers, act in this way. The greater part of the phycophagous animals does not cause conspicuous damage. The more important representatives of this group will be considered.

Littorina saxatilis rudis, which lives in very large numbers in the lower supralittoral region and in the uppermost part of the eulittoral region, may become disastrous to the algal growth. On new substrates it can detain the establishment of an algal vegetation for a long time; especially in exposed spots, where the establishment of a new algal vegetation is already difficult, it may prevent its establishment entirely. In the barnacle community it destroys every young Alga which succeeds in obtaining a holdfast. Especially young plants of *Enteromorpha*, *Ulothrix*, etc. are relished by this little snail.

Littorina littorea is confined to the eulittoral region, but it behaves in a similar way, and is even more noxious, as it devores also full-grown Fucaceae; under certain circumstances it may destroy even a well-established algal vegetation. Especially along muddy shores, where the continuous deposition of mud often makes the establishment and the development of young Algae difficult, the presence of *Littorina littorea* may have fatal consequences, e.g. if by a change in the course of a current the rate of sedimentation is locally increased; a rejuvenation of the vegetation may in this way be made impossible. Under such circumstances the periwinkles may devore the old plants, too, sparing only the hardened nerves of the Fucaceae, *Verrucaria mucosa* and *Hildenbrandtia prototypus*, or reserving them to the last. Along the "Waddenzee" we often see parts of a dike that are inhabited by an enormous number of periwinkles, and that are completely deprived of their algal growth (Balgzand, the enclosing dike of the former "Zuyderzee", Lauwerszee, Wilhelshaven).

These periwinkles are but slightly affected by the cold. After the severe winter of 1946/47 they were still fairly numerous on the dike at Den Helder. During several years they have prevented there in some parts the regeneration of the algal vegetation.

Interesting observations on the manner in which this species maintains its position in the littoral region, are to be found in the work of NEWELL (1958).

Littorina obtusata littoralis feeds mainly on Fucaceae. In the Netherlands this species is not sufficiently numerous and also too sensitive to all kinds of environmental factors to become noxious (BARKMAN, 1955).

Littorina neritoides petraea is a species with a southern distribution; it does not belong to the permanent fauna of the southern part of the North Sea (STOCK, 1950), although in some years the currents in the English Channel transport eggs and free-swimming larvae which settle along the coasts of the North Sea; these individuals may maintain themselves there for several years. It inhabits the supralittoral region, and as the latter has but a poor algal vegetation, it may destroy here a good deal of the young plants. Its habitats on the coast of the Mediterranean Sea and near Roscoff proved to be nearly entirely devoid of vegetation. On the coast of "le Boulonnais" and on that of the Netherlands it was found in the *Bangia-Urospora* community and above the latter. On Heligoland, too, we found it between the desiccated rests of this community.

Patella vulgata is too rare in the Netherlands to influence the algal vegetation, but on the French coast I had ample opportunity to observe how disastrous the activities of this animal may be. In July 1951 I noticed on the rocks of the littoral region at Audreselles a beautiful mosaic formed by the shells of these molluscs, which appeared to be covered either with *Rhodymenia palmata* or with *Laurencia pinnatifida*. The rocks to which they were attached, bore a few large specimens of *Rhodymenia* and *Laurencia*, some barnacles and a thin green sheet of young Algae traversed in every direction by the tracks along which the *Patellae* had moved and in which the Algae had been shorn off completely. When I visited this spot again in August 1954, it appeared that *Balanus balanoides* had succeeded in colonizing these bare rock surfaces, and that the *Patellae* were often completely embedded between the barnacles; the few large specimens of *Rhodymenia* and *Laurencia* were still there. In April 1955 the situation was still the same.

Southward (1956) has made interesting observations with regard to the influence exercised by the feeding *Patellae* on the algal vegetation of the Isle of Man. On sloping rocks exposed to the surf and covered with *Balanus balanoides* he put out two transects extending from the high-water to the low-water line, and removed in the latter the Fucaceae as well as the *Patellae*. Within a year the following seral stages were noted, viz. diatoms and filamentous Algae → *Enteromorpha-Porphyra* association → establishment of Fucaceae. Two to three years after the beginning of the experiment the Fucaceae once more formed a closed vegetation. Young *Patellae* arrived at the same time as the Fucaceae, and it appeared that they were six times as numerous as before the clearance. They showed a rapid growth, and prohibited the establishment of more Algae. As there was therefore no rejuvenation of the Fucaceae vegetation, the number of the plant individuals gradually declined. Older specimens, often attached to barnacle shells, were wiped away by wave-action, of fell a victim to the *Patellae*; the latter feed especially on the stipes and on the holdfasts. A year after the Fucaceae had reached their fullest expansion, the *Patellae* reached their maximum abundance. After that their number showed a continuous decrease, which therefore ran parallel with the decrease in the amount of food. Two or three years later the Fucaceae had almost completely disappeared. So long as the *Fucus* covering was intact, the number of barnacles was but small, as the covering made it difficult for them to reach the rock surface, but when the Fucaceae vegetation began to decline, *Balanus balanoides* was once more in a position to establish itself and to develop into dense colonies. A similar cycle was also observed by Burrows and Lodge (1950).

In the Netherlands no closed vegetations of Fucaceae occur in exposed situations, notwithstanding the fact that *Patella vulgata* is but rare. The part which elsewhere is played by this limpet, is here presumably taken over by *Littorina littorea*, but this is a question to which a special study should be devoted.

In April 1955 we noted on the coast of "le Boulonnais" that *Lacuna parva* had attacked nearly all the specimens of *Rhodymenia*. In August 1955 it appeared on Heligoland that *Lacuna vincta* is even more noxious; hardly any Alga was safe for its appetite. *Ulva* as well as *Chondrus*, *Enteromorpha*, *Fucus* and *Laminaria* were devored by these animals, which covered them in hundreds. Why this mollusc, which in Heligoland as well as on the coast of "le Boulonnais" is very common, does no longer occur in the Netherlands, is unknown. Formerly it was found in the grass-wrack fields, but with *Zostera marina* this mollusc, too, disappeared.

On the mud flats a similar part is played by *Hydrobia ulvae* and *H. stagnalis*, which feed especially on *Ulva*, *Enteromorpha* and *Chaetomorpha*, but which occasionally attack other species, too.

Some other animals of which it is known that they feed on Algae, like the amphipods *Gammarus locusta* and *Hyale prevostii* and the isopods of the genus *Idotea*, do not seem to cause real damage; this also applies to some small molluscs, like *Rissoa parva* and *Skenia planorbis*. The damage caused by the phycophagous Nudibranchiata, too, is usually negligeable; in the Isefjord (Seeland, Denmark), however, I once noted that *Elysia viridis* had caused real damage, especially to *Chaetomorpha aerea* and *Cladophora fracta* (September 1955).

An entirely different kind of damage is caused by the amphipod *Jassa falcata*; it is not impossible that this animal feeds on Algae, but of this I am not sure. The damage, however, is caused by the tubes of mud particles which it builds on the thalli of the Algae; as these animals are very numerous, the Algae are often entirely covered with these tubes, and this becomes disastrous to them. Near Den Helder and on the island Schouwen in Zeeland *Jassa* is very common in the *Polysiphonia-Chaetomorpha* association, and so it is also on the coast of "le Boulonnais" (1951).

The relation between the animal and the Alga is nearly always referable to a preference of the animal for a definite kind of food, and if the animal feeds on but one species or one genus of Algae, it will, of course, be found exclusively in company of the latter. A few examples may serve to illustrate this relation.

Littorina obtusata littoralis is in the Netherlands bound to the Fucaceae, and shows, moreover, a preference for *Fucus serratus*; on other Algae this species is found less often (BARKMAN, 1955).

On salt marshes the saccoglossan slugs *Alderia modesta* and *Limapontia depressa* are always found on *Vaucheria* species (ENGEL, GEERTS and VAN REGTEREN ALTENA, 1940; DEN HARTOG and SWENNEN, 1952). Experiments have shown that *Alderia* feeds exclusively on *Vaucheria*, but that *Limapontia depressa* may be satisfied with *Cladophora* and *Rhizoclonium*, but only if *Vaucheria* is not available. In its natural surroundings I have found *Limapontia* but once on *Rhizoclonium riparium*. The connection between *Alderia* and *Vaucheria* might be called obligate, that between *Limapontia* and *Vaucheria* preferential.

With other phycophagous slugs, too, we find such bindings. *Actaeonia corrugata* feeds exclusively on *Cladophora* species; *Placida dendritica* lives only on *Codium*; *Hermaea bifida* feeds on Rhodophyceae, especially on *Griffithsia flosculosa*. *Elysia viridis*, on the other hand, feeds on Rhodophyceae as well as on Chlorophyceae.

That organisms are found in each others company, however, does not necessarily mean that the one feeds on the other. COLMAN (1940, 1942) mentions the rich fauna that is found on the English coast between the branches of the high-littoral to supralittoral lichen *Lichina pygmaea*. Here are found large numbers of the isopod *Campecopea hirsuta* and of the small lamellibranchiate *Lasaea rubra*. In this belt one would certainly not expect to find a rich fauna, and the fauna of all other communities that we meet in this belt, is indeed less rich in the number of individuals. An explanation for this preference has not yet been detected. An additional peculiarity is that these two animal species are scarce or absent in other kinds of vegetation. In Roscoff I observed the same binding, so that the latter cannot be regarded as a particularity of COLMAN's special area of study. *Lasaea rubra* is also found on the coast of the Mediterranean Sea, where *Lichina pygmaea* is absent; it lives there in large numbers in the "trottoir à *Tenerea tortuosa*" (Nice). MORTON, BONEY and CORNER (1957) collected interesting data on the ecology of *Lasaea rubra*, which may perhaps contain the explanation of its presence in the high-littoral region.

Cecidia caused by small-organisms have also been described from marine Algae. In 1892 DE MAN found in the waters of Zeeland a parasitic nematode, viz. *Halenchus* (= *Tylenchus*) *fucicola*, which forms cecidia on *Ascophyllum nodosum*. A short time ago COLES (1958) studied the cecidia which in southern England are found on Fucaceae, and noticed that apart from *Halenchus fucicola*, which is confined to *Ascophyllum*, a second species is present, viz. *H. dumnonicus*, which occurs only on *Fucus vesiculosus* and *F. serratus*. HARDING (1954) described the life cycle of the copepod *Thelastris rhodymeniae*, which forms cecidia on *Rhodymenia palmata*.

Finally I wish to draw attention to some endozoic and epizoic Algae.

Rhodochorton membranaceum, a small Rhodophycea which in the Netherlands is very rare, lives endozoically in the hydranths of *Sertularia cupressina*, *Abietinaria abietina* and *Hydralmania falcata*, by the latter species sometimes also in the coenosarc. So far this Alga has been collected only on Schouwen (Zeeland). On the coast of "le Boulonnais" it was very common in the three Hydrozoa mentioned above, but I saw the latter only washed ashore; they live at a greater depth than I could reach. In the Netherlands they occur in the "Waddenzee", where they form the so-called "sea-moss fields", and there the presence of *Rhodochorton* is therefore to be expected, too.

In the periostracum of *Littorina obtusata littoralis* the Chlorophyceae *Tellamia contorta* and *T. intricata* are not rarely met with. Both species appear to be confined to this periwinkle. Some other Algae were also found on *Littorina obtusata*, e.g. *Giraudia sphacelaroides*, but the latter was observed by LUND (1947) also on the fins of sticklebacks.

The presence of endolithic species in the shells of barnacles has already been mentioned.

3.II. INFLUENCES DUE TO THE PRESENCE OF OTHER ALGAE AND OF FUNGI

The competition between the Algae for room and light which leads to what we call the algal communities, is doubtless of an exceedingly complicated nature, and the factors that play a part in this competition and by which the mutual relations between the various species are determined, are still entirely unknown. The sequence in which the algal communities succeed each other, can be followed step by step, but the reason why one community is replaced by another, remains dark. Before we can seriously think of attempting to disentangle the mutual relations between the various species, a good deal more autecological research will have to be carried out on the latter. We are still far away from a complete knowledge of the life cycle of the various species, and there are but few species of which we know approximatively what the conditions are for the further development of the spores, for optimum growth in the various stages of development, for the production of sporangia and gametangia, for the fusion of the gametes, the conditions, in short, that are required for a normal unfolding of the vital functions throughout the whole life cycle. CHAPMAN (1957), too, emphasizes in his review the necessity of widening our phycological knowledge by autecological research.

Conspicuous examples of mutual relations are no doubt epiphytism, endophytism and parasitism. These relations were described in detail by FELDMANN (1938); I will confine myself here to a few examples observed in the Netherlands.

In the case of epiphytism there is occasionally an obligate binding to a definite host. *Ulonema rhizophorum*, for instance, was found by me exclusively on *Dumontia incrassata*; this binding was noted also in various spots on the Atlantic coast. The Rhodophycea *Acrochaetium codii* occurs exclusively on *Codium* species; it is provided with colourless filaments which penetrate very deeply between the filaments of the *Codium* thallus, and is therefore sometimes erroneously regarded as an endophyte. A true transition to the endophytes is *Chlorochytrium willei*, a minute Alga which lives halfway submerged in the thallus of *Blidingia minima*. *Polysiphonia lanosa*, which is often found on *Ascophyllum nodosum*, is regarded as a parasite. It does not occur exclusively on *Ascophyllum*; I have also seen it, though rarely, on *Fucus vesiculosus*.

To the parasites also belong the marine Fungi, to which in the Netherlands so far no attention has been paid, but which undoubtedly will occur there, too. The marine Phycomycetes were studied mainly by PETERSEN (1905), SPARROW (1943), ALEEM (1953) and J. and G. FELDMANN (1956). They infect as parasites diatoms, Cyanophyceae, Chlorophyceae, Phaeophyceae and Rhodophyceae.

3.II. INFLUENCES EXERCISED BY MAN

We have already alluded several times to the influence which man exercises on the algal vegetation. On the coast of the Netherlands suitable substrates for the epilithic Algae were created by man when the latter began to construct moles, dikes, piers and harbours. But this was not the end, for all these works must be kept in repair, and measures like the dumping of stones, the renovation of piles, and the bituminizing of dikes exercise an influence that is not to be neglected. Existing vegetations are destroyed in this way, with the result that pioneer communities consisting of a small number of species take their place. The most harmful measure is the bituminization. This causes a persistent depauperation; the original vegetation is unable to regain its lost position. On the bitumen no Algae are able to establish themselves with the exception of *Enteromorpha*, *Porphyra*, *Ulothrix* and *Blidingia*; lateron the latter are joined by dendritic Algae. On the bituminized northern mole of the harbour of Harlingen, for instance, *Ceramium deslongchampii* has become the dominant species. There is, however, no growth of Fucaceae, and if occasionally a *Fucus* specimen succeeds in obtaining a foothold, it remains a mere stripling. To the fauna, too, the bituminization is fatal; the animals die before the end of the summer.

In the Netherlands exploitation of Algae for economic purposes is not profitable. In Zeeland there was for a short time an industry which used Fucaceae, especially *Ascophyllum nodosum*, as raw material. The Algae were cut on the dikes, but this did not cause a lasting damage; in a few years the algal growth was completely regenerated.

4. HISTORY OF THE MARINE ALGAE IN THE NETHERLANDS

4.I. HISTORY OF THE SUBSTRATE

The history of the marine algal flora in the Netherlands is closely interwoven with that of the North Sea. During the last Würm Glacial period the level of the sea was 50—60 m lower than it is now. As the North Sea was at its northern end dammed in by a huge barrier of ice, it was difficult for the large rivers to discharge their waters in that direction. We may assume therefore that a large reservoir was formed, and that the latter forced an outlet for its waters through the Strait of Dover. At the beginning of the Holocene, i.e. circ. 18.000 B.C., the sea once more rose to a higher level, and a connection between north and south was established by way of the Silver Deep and the Deepwater Channel, but this connection remained as yet but narrow. The southern part of the present North Sea was still mostly land. At the beginning of the Atlantic period, i.e. circ. 5000 B.C., the level of the sea rose to 7 m below the present one (*Littorina* period). According to TESCH (1942) this meant that the North Sea obtained its present form, and that the Strait of Dover was definitely opened. The further rise of its level caused no fundamental changes in the form of its coasts.

During the Atlantic period along the coast of the Netherlands banks were formed on which the dunes arose; behind the latter a lagune was found in which gradually a brackish-water marsh developed. Afterwards the protecting ridge was broken up, and this led to the origin of the "Waddenzee" and still later of the "Zuyderzee". In this development man had nothing to say.

What substrates were available to the Algae since the Atlantic period?

The coast of the Netherlands was a sandy beach, locally covered with some moraine material (Texel). This moraine material may have borne an algal vegetation, but this is not fully certain, as it consists mostly of stones which are rolled to and fro under the influence of the surf and of currents. It is nevertheless not impossible that such places as the Texel Stones and the Borkum Reef bore an algal vegetation in the earlier part of the history of the North Sea.

In the beginning of the Christian era the vegetation in these waters will probably have been confined to that of the mudflats; this vegetation consists of *Zostera marina* with its rich flora of epiphytes, *Zostera nana*, and in sheltered spots with brackish water *Ruppia*, *Zannichellia* and *Potamogeton pectinatus*; and then there were the epilithic Algae which are found on mussel banks as well as on isolated shells, and finally the undergrowth of the salt marsh vegetation.

The algal vegetation will have consisted on the whole of euryhaline species with moderate demands on the environment and able to withstand some hardships. To this group belong *Ulva lactuca*, *Enteromorpha* spp., *Polysiphonia nigrescens*, *P. elongata*, *Ectocarpus siliculosus*, *Chorda filum*, *Ceramium rubrum*, an occasional *Fucus*, *Rhizoclonium* spp., *Vaucheria* spp., etc.

In the "Waddenzee", where the ecological conditions have remained more or less the same, the vegetation would now have reached its ultimate structure, if the grass-wrack *Zostera marina* by the notorious epidemic of 1932 had not wiped out almost entirely. With the grass-wrack its rich epiphytic flora, too, disappeared, and this meant a considerable curtailment of the algal flora in this area. *Zostera marina* is at present a very rare plant, and is found only in creeks, which are traversing the salt marshes in Terschelling and in Schiermonnikoog, and in the inland pools of brackish water that occur at "de Bol" in Texel. The works of VAN GOOR (1919, 1921, 1923) contain excellent descriptions of this vegetation, and give us a good picture of what was lost.

The algal vegetations of the mud flats and the salt marshes are therefore to be regarded as the most ancient entirely natural algal vegetations that are found in the Netherlands. The epilithic algal vegetations appeared much latter on these coasts, viz. when man began to protect the land against the sea by the construction of dikes. The oldest ones were built from grass-wrack that was washed ashore or that to this end was mown; these were the so-called "wierdikes", of which in the northern part of North Holland still several remnants have been preserved. The method of construction which was applied in the middle ages, was gradually improved by using besides *Zostera* clay and by erecting palissades. About 1700 a beginning was made with the construction of a mantle of stone on the slopes of the dikes; to this end use was made of basalt, granite, shale and Vilvoorde limestone. This new type of embankment served a number of Algae as a substitute for the rocks that are their natural habitat, and in this way many species that require a solid substrate, could settle on the coast of the Netherlands.

Apart from the different kinds of natural stone mentioned above, at present also blocks of concrete are used, e.g. at IJmuiden; since the second world war tiles and bitumen, too, have been applied. Bitumen appeared to be very disastrous to the algal vegetation, and absolutely fatal to the fauna; as in summer on account of the high temperatures the bitumen softens, the sessile animals are unable to live through this season. Barnacles, mussels, sea-anemones and similar animals are no where to be seen on such a substrate. In spring, however, Hydrozoa are sometimes very numerous; this applies e.g. to *Coryne sarsii* and *Laomedea* species (Harlingen). The pioneer vegetations consisting of *Enteromorpha*, *Porphyra*, *Bangia* and *Ulothrix* have no difficulty in maintaining themselves; in the lower part of the littoral region, moreover, the *Ceramium deslongchampii* sociation is found, but the Fucaceae are represented only by *Fucus spiralis* in a rather wretched condition.

The vegetations which in the Netherlands are found on the slopes of the dikes are therefore of recent date, and if we compare them with corresponding vegetations abroad, it appears that several of them have not yet reached their final composition. VAN GOOR (1923) nevertheless could state that since 1870, the year in which SURINGAR's list was published, the number of algal species known from the Netherlands had increased; he himself could study the settling of some immigrants in the "Waddenzee". Now, 35 years later, we are able to state that there has been a further increase. This is not merely due to a better knowledge of the flora in the waters of Zeeland, for even in the comparatively well-known western part of the "Waddenzee" several new indigenes were collected.

A further increase, however, is not to be expected. On account of the methods now used in the construction of dikes and on account of the use of bitumen especially those species which live in the fissures between the stones, will undergo a decrease. Moreover, in the next 25 years, on account of the closing of the sea-gates in the south-western part of the Netherlands, which forms part of the "Delta-plan", a comparatively large number of species will disappear, e.g. the species with a predominantly southern distribution which reach the northern limit of their area in the East Scheldt.

4.II. IMMIGRATION ROUTES

According to CARRUTHERS (1925) a current which reaches the North Sea from the English Channel by way of the Strait of Dover, runs along the coast of the Netherlands in a northern direction. A second current runs along the east coast of England in a southern direction, but at the entrance of the North Sea funnel the main part turns towards the east, joins the Channel current, and continues its course together with the latter along the West Frisian Islands. A branch of this second current proceeds along the English east coast, and only turns eastwards at the mouth of the Thames; this branch, too, joins the Channel current.

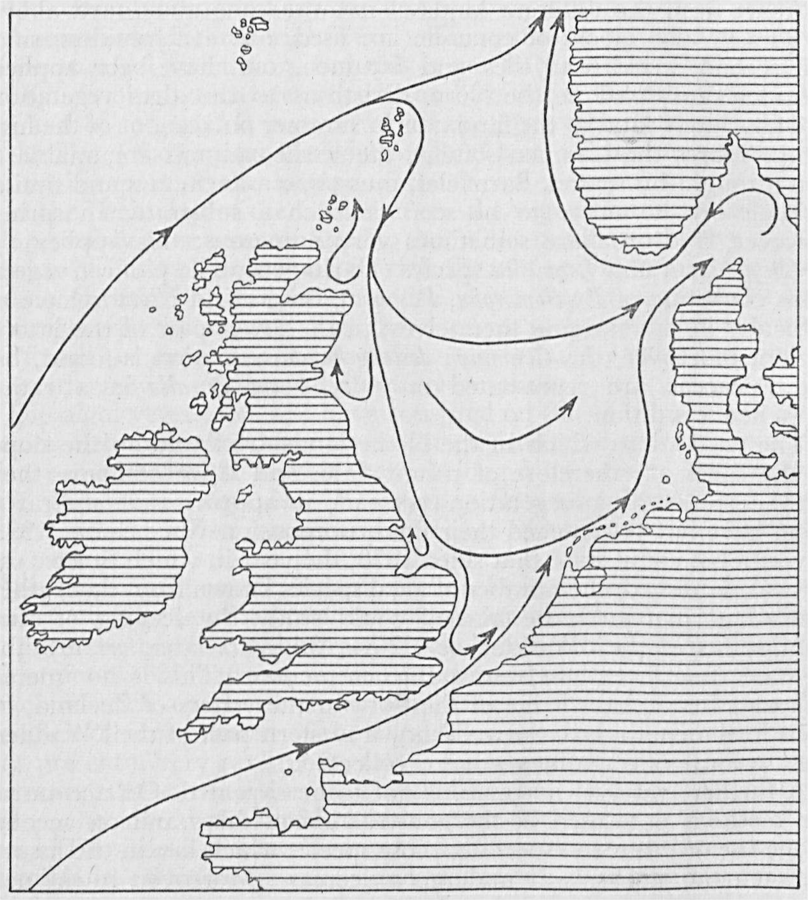


Fig. 10. System of currents in the North Sea (highly simplified). For more details may be referred to map 5057 (North Sea currents), edited by the Hydrographic Department of the Admiralty, London.

As the wind exercises a considerable influence on the direction in which the surface water moves, and as on the coast of the Netherlands south-western winds prevail, it is clear that the Channel current will play the most important part. Large amounts of Algae that have been swept from their anchorage by storms, are transported by this current in a northern direction and over large distances. Where they will be washed ashore, depends in the main on the direction of the wind. If there is a sudden change, the masses of Algae that are thrown on the shore, may be enormous. They consist mainly of the larger Phaeophyceae, viz. *Fucus* species, *Ascophyllum nodosum*, *Himanthalia elongata*, *Halidrys siliquosa*, and in smaller numbers, species of *Laminaria* and of *Cystoseira*. The thalli of these Algae are often richly covered by epiphytes. The latter consist for the greater part of young individuals, but older ones with mature reproduction organs may also be present. The larger Phaeophyceae, too, are often richly provided with reproductive cells. LUCAS (1950) devoted an extensive study to the Algae that are washed ashore with floating objects. He lists no less than 171 species that reached the coast of the Netherlands in this way, and to this list we could now add a comparatively large number of new names. Similar lists have been drawn up for molluscs (BLOKLANDER and BROUWER, 1946/47) and for amphipods (STOCK and BLOKLANDER, 1952).

The transports of Algae are very instructive because they comprise not only species that live on our own coast, but also numerous species of which no autochthonic specimens have ever been found in the Netherlands, and the latter may give us some indications with regard to the country of origin of the floats. Among the Algae that are washed ashore we meet, for instance, a large number of species that have never been found as autochthones north of the English Channel. The same applies to the animals which are transported on the Algae. They indicate therefore a southern origin of the material.

Occasionally parts of the substrate are carried along by the Algae, and such stones are, of course, also of great importance as indicators of the country of origin. IJZERMAN (1937) noted that the fragments which he could study, were derived from rocks on the coast of Normandy and of southern England. Material from the coast of Brittany may also be washed ashore.

Among the objects of southern origin that are washed ashore on the coast of the Netherlands, are also bunches of corks. The latter are used by French fishermen in order to mark the spots where they have put out their lobster-pots.

Other substrates on which many species of Algae reach the coast of the Netherlands, are the bunches of eggs of *Buccinum undatum*, the egg capsules of rays and skates, and the dorsal shell of the cuttlefish *Sepia officinalis*. These objects may reach these coasts by way of the English Channel as well as from the north.

The Algae and animals of which it cannot be doubted that they are of southern origin, are listed below. The list is partly based on my own observations, and partly on data derived from VAN BENTHEM JUTTING (1952), HOLTHUIS (1949, 1952, 1956), LUCAS (1950, 1954), STOCK (1952, 1954, 1955), STOCK and BLOKLANDER (1952), DEN HARTOG and LUCAS (1958) and VAN DEN OORD and HOLTHUIS (1959).

Phaeophyceae:
Bifurcaria bifurcata
Cystoseira baccata
,, *foeniculacea*
,, *tamariscifolia*
Dictyopteris membranacea
Padina pavonia
Sargassum natans

Rhodophyceae:
Antithamnion sarniense
Asparagopsis armata
st. *falkenbergiae*
Bornetia secundiflora
Gastroclonium clavatum
,, *ovatum*
Gigartina acicularis
,, *pistillata*
,, *teedii*
Grateloupia filicina
Halopitys incurvus
Halurus equisetifolius
Spyridia filamentosa

Mollusca:
Acanthochiton communis
Alvania lactea
Bankia fimbriatula
Cantharidus exasperatus
Diodora apertura
Emarginula conica
Gibbula umbilicalis
Haliotus tuberculata
Lutraria magna
Modiolus barbatus
Mytilus galloprovincialis
Neoteredo reynii
Paphia aurea
Patella athletica (= *P. aspera*)
Patella depressa
Tricolia pullus pictus
Trivia monacha

Crustacea:
Amphithoe vaillanti
Apseudes talpa
Balanus amphitrite
,, *perforatus*
Biancola cuniculus
Caprella acutifrons
,, *tuberculata*
Dynamene bidentata
Gnathia maxillaris
Jassa ocia
Lepas pectinata
Leptochelia dubia
Lysianassa ceratina
Naesa bidentata
Planes minutus
Stenothoe spinimana

Pantopoda:
Anoplodactylus virescens
Callipallene emaciata ssp. *tiberi*
Endeis spinosa

Bryozoa:
Stephanosella biaperta

Polychaeta:
Eunice harrasii
Marphysa sanguinea
Nematonereis unicornis

Anthozoa:
Anemonia sulcata
Cereus pedunculatus.

Of *Sargassum natans*, one of the dominant species in the floating algal vegetation of the Sargasso sea, a few specimens reach the shore of western Europe. They must have been transported by the waters of the Gulf-stream. However, as the latter splits already to the west of Ireland into two branches, one which passes Scotland and the Faeroes, and another one which is diverted towards the English Channel, these specimens may have reached the coast of the Netherlands as well along the northern route as along the southern one. The same applies to the West-Indian ship-worms *Bankia fimbriatula* and *Neoteredo reynii*, which have occasionally been washed ashore in the Netherlands with driftwood. The crab *Planes minutus* is an inhabitant of the Sargasso Sea.

Material of northern origin is but rarely washed ashore. However, in the autumn of 1955 some of this drift material became available for study. Noteworthy was the large number of individuals of *Chordaria flagelliformis*, which, however, is not characteristic, further the enormous number of egg capsules of *Raia radiata*, a northern kind of ray which does not occur in the English Channel, the finding of the little crab *Pirimela denticulata* and of the mussel *Modiolus modiolus*, and, on the other hand, the total absence of species with a predominantly southern distribution. These peculiarities form a sufficient ground for regarding this drift material as of "northern" origin.

The number of species that may be used as indicators of a northern origin of the material, is much smaller than that of the indicators for a southern origin. This difference is doubtless due to the fact that much less drift material of northern origin has as yet been studied. The following species, however, may be accepted as indicators for a northern origin:

Rhodophyceae:
Ptilota plumosa
Mollusca:
Astarte montaqui
Lacuna crassior
Malletia obtusa
Trophon truncatus
Crustacea:
Caprella septentrionalis
Gnathia dentata.

Bloklander et al. called the organisms that are washed ashore with floating objects, "natural adventives" in order to distinguish them from the species that are introduced, and sometimes more generally distributed, by man, like the slipper limpet *Crepidula fornicata* (Korringa, 1942), the barnacle *Elminius modestus* (Den Hartog, 1953) and *Codium fragile.* Stock (1955) proposed that to all new arrivals the name "allochthons" should be applied, no matter whether they are washed ashore or introduced by man.

The species that are regularly washed ashore, will doubtless have played an important part in the colonization of our sea-dikes. The *Fucus* species and *Ascophyllum nodosum* that are now quite common, will almost certainly have arrived in this way. Species that are less often washed ashore, could establish themselves in but a few localities, and are even now rather rare. As an example of this group we may quote *Cystoclonium purpureum*, which is found at Flushing, on Tholen, Schouwen and Texel, and formerly also at Den Helder. In spite of the embankments, harbour moles and piers, the coast of the Netherlands remains a very unfavourable habitat for the Algae because of the force of the surf and because of the washing with sand, and the number of algal species increases therefore but slowly. The species with modest demands on the environment and those that are very frequently washed ashore, will have established themselves within a few years, but after that the increase in the number of species will have proceeded but slowly. There are even species which are regularly washed ashore, often provided with mature reproductive cells, and which nevertheless have never succeeded in obtaining a foothold, e.g. *Himanthalia elongata.* In this special case its failure has been ascribed to the salt concentration of our coastal waters, which is lower than that in the English Channel and in the Atlantic Ocean. Others see in the pollution of our coastal waters a possible cause. The following explanation, however, looks to me more plausible. According to

FISCHER-PIETTE (1936) *Himanthalia* is found only in localities where the 50 m depth-line runs in a very small distance from the coast, and such localities are not present in the southern part of the North Sea. The presence of deep water in the near vicinity of the rocks on which this Alga grows, has important consequences to the latter. In the first place it causes an uncommonly strong surf, and on this account the fluctuations of the temperature to which the Algae are exposed, are very small. Because of the great depth the water, moreover, contains but little solid material; it is therefore very clear and its rinsing effect is moreover extremely small.

Apart from the species that have been able to establish themselves in the Netherlands because they were washed ashore, there are also some species which have been introduced by man. It seems that *Codium fragile* was brought here by ship. Some of the Algae in the oyster-beds have perhaps been introduced from abroad with oyster seed. However, as the earlier history of the biocoenoses in Zeeland is but imperfectly known, it will probably be impossible to obtain certainty on this point. The slipper limpet, *Crepidula fornicata*, proves at any rate that with the oysters foreign organisms may be introduced.

The third group is formed by the euryhaline species which lived already long ago on the shells and on the mussel banks in the "Waddenzee" and in the river mouths. It comprises species like *Ulva lactuca*, *Enteromorpha* species, *Ceramium rubrum*, etc.

Finally there is a group of species of which it is unknown in what way they arrived in the Netherlands, but which are now well-established. One of these species is *Gigartina stellata*, which I have never found among the material that is washed ashore, which does not grow on the shells of the "Waddenzee", and which was already known to occur in the Netherlands before the oyster culture was started.

SUMMARY

In this chapter the influence of the principal environmental factors is discussed.

Physical factors. The influence exercised by the substrate is demonstrated by means of observations made on Tholen (Zeeland). The level reached by the algal vegetation appears to be somewhat higher on Vilvordian limestone than it is on basalt; on granite it appears to be intermediate. The influence of the tidal movements is discussed, and by the use of tidal curves (mean daily inequality, difference between the levels reached at neap tides and at spring tides) the existence of so-called "critical levels" is demonstrated; the correlation between the latter and the boundary lines of the algal zones is, however, not a linear one. Some observations on the influence of tidal currents are briefly mentioned. Wave-action causes an increase in height of the level at which the algal vegetation is found; it does this by wash, splash and spray, and also mechanically (grinding by means of suspended particles, water replacement). This action is enhanced when the air has a high degree of humidity, but it is counteracted by insolation. The temperature of the water as well as that of the air exercise a marked influence on the algal vegetation, the first in the sublittoral and in the eulittoral region, the second in the eulittoral and in the supralittoral one. Especially the extreme values are of importance; the presence of the large group of species with a predominantly southern distribution in the East Scheldt is ascribed to the high temperatures reached by the water in the summer months. Much attention is paid to the damage caused by frost;

a distinction is made between freezing to death, destruction by frost, freezing in, and damages caused by floating ice; the winters themselves are classified according to the prevailing kind of weather and the length of the period of frost. The influence of light cannot be studied on these coasts. The sciaphilous algal communities are but partly photophobous; the others prefer shaded spots because they are unable to stand the heat caused by insolation. The effects of exposition, inclination and depth are also discussed.

Chemical factors. Salinity is one of the most important factors which determine the distribution of the Algae. The fluctuations in the degree of salinity are not correlated to the distribution of the precipitation. It is noteworthy that part of the high-littoral and supralittoral Algae also occur on the shores of lakes and rivers. Pollution of the water causes an increase of such Chlorophyceae as *Enteromorpha, Ulva* and *Prasiola.*

Biotic factors. The faune exercises an influence on the algal vegetation by competing with it for the available space, and by feeding on it. As examples of competition for space the barnacle communities, the mussel populations, the growth of Bryozoa, Hydrozoa, tunicates and sea anemones, and the deposition of mud by the worm *Polydora ciliata* are discussed. The observations made on the *Littorina* species, *Patella vulgata* and some other snails reveal how enormous the influence may be which these animals, because of the large numbers in which they are present, exercise by their voracity on the algal vegetation. Hardly anything is known as yet of the way in which Algae infll uence each other. Of the most striking forms in which the relations existing between them may appear, viz. epiphytism, endophytism and parasitism, some examples are given.

Historical factors. A sketch is given of the changes which the coast of the Netherlands has undergone since the Würm Glacial Period, and then the substrates are discussed which have become available since that time. The establishment of epilithic Algae became possible when in the eightteenth century a beginning was made with the strengthening of the dike slopes by means of a mantle of stones. Since then the number of algal species has ever increased. Because of the new methods for the construction of dikes and also because of the execution of the "Delta plan" in future a marked decrease in the number of species is to be expected. The algal flora on the coast of the Netherlands is probably for the greater part of southern origin. This may be concluded from the fact that the material which is washed ashore, mostly contains species which may be regarded as indicating such an origin because they reach the northern limit of their area of distribution either in the English Channel or to the south of the latter. Species of northern origin are but rarely washed ashore.

CHAPTER IV

CLASSIFICATION OF THE ALGAL COMMUNITIES

A system for the classification of the algal communities occurring along the coast of the Netherlands was proposed by the author in 1955. It was based on the physiognomy, stratification, zonation and succession of the vegetation. However, as since that paper was written, several more observations were made, in the Netherlands as well as abroad, various additions and emendations were necessary. It appeared, moreover, that our system of classification is not the only one that can be based on the four aspects of the vegetation mentioned above. Before entering into a discussion of the various possibilities, it seems desirable to turn our attention for a moment to the method of analysis and to the way in which the vegetation units should be characterized.

1. METHOD OF ANALYSIS

For analysing the floristic composition of the different vegetation types the survey-method of BRAUN-BLANQUET was used. In an area with a homogeneous vegetation all species were listed, and their abundance and dominance estimated; these estimations were expressed by means of the scales proposed by BRAUN-BLANQUET *). In some instances the sociability, too, was noted.

For species of microscopic dimensions, e.g. for the smaller epiphytes this method is inaccurate, for if they are rare, they easily escape the attention. In case they are numerous, they often cover the substrate with a kind of mist, and are in this way easily detected. In each survey-plot we collected a number of Algae in order to study by means of the microscope the epiphytic species by which they are accompanied.

The size of the survey-plot was always chosen as large as possible, or at any rate, in such a way there could be no doubt that it exceeded the minimum area required for the community to which it was thought to belong.

The results of such surveys by direct inspection have already been published by KORNAŚ and MEDWECKA-KORNAŚ (1950), WAERN **) (1952), SUNDENE **) (1953), MOLINIER and PICARD (1953) and DEN HARTOG (1953, 1955). In the waters of the Netherlands no further expedients are required, as the algal vegetation, as a rule, does not descend beyond a depth of about 1.5 m below mean low-water; at a greater depth no suitable substrates are present, and in such habitats only a few solitary individuals are met with (VAN GOOR, 1923). In seas where the Algae reach a greater depth, the vegetation of these deeper zones has to be studied either by diving (WAERN, KORNAŚ, ERNST) or by dredging (FELDMANN, 1938); in the latter case the results have to be treated statistically. Diving deserves preference, as by direct observation a much better impression of the submarine vegetation is obtained than by the study of material collected by means of a

---

*) With the estimating method of BRAUN-BLANQUET first a complete list is made of the species occurring in the sample-plot; then the abundance and the area covered by each species are estimated. The abundance is expressed by means of one of the figures of the following scale:
+ = a few specimens only
1 = a good number of specimens
2 = many specimens or a covering of 5—25 % of the sample-plot
3 = covering 25—50 % of the sample-plot
4 = covering 50—75 % of the sample-plot
5 = covering 75—100 % of the sample plot.
In some instances a second figure is added. This expresses the sociability of the species according to the following scale:
1 = single
2 = in tufts
3 = in large groups
4 = in large carpets, but not in a closed vegetation
5 = in a homogeneously closed vegetation.

**) WAERN and SUNDENE used the scale of HULT, SERNANDER and DU RIETZ.

dredge, as with the latter we can never be certain that it represents but a single community.

With regard to the difficulty we referred to at the end of the preceding paragraph, we wish to emphasize the necessity of ascertaining whether the substrate of the survey-plot is homogeneous or not. Is the substrate not homogeneous, e.g. if it consists partly of rock and partly of sediment, it may easily happen that we investigate a mixture of two communities, even if the vegetation at first sight looks rather homogeneous. An example of such a mixture is the *Fuceto-Furcellarietum* described by KORNAŚ and MEDWECKA-KORNAŚ (1950) from the Gulf of Gdańsk (Danzig). They themselves make the following remark "Sur le fond pierreux domine *Fucus vesiculosus,* sans se mêler aux Phanérogames, sur le fond sablonneux-vaseux *Zostera marina* et *Potamogeton pectinatus* se développent et jouent un grand rôle". Actually we have here a mixture of the Baltic *Fucus vesiculosus* community with vegetations belonging to the *Ruppion maritimae* (*Zosteretum marinae, Potameto-Zannichellietum*). Mixtures of this kind I have seen myself in the Ringkøbing Fjord; there the *Cladophoreto-Polysiphonietum* and the *Potameto-Zannichellietum* occur together. On pebbly soils, however, it is, as a rule, not possible to make a distinction between these algal communities and the phanerogamic ones. In the *Cystoseira* vegetations at Roscoff *Zostera marina* is actually represented and in the mediterranean vegetations of *Posidonia oceanica* and *Cymodocea nodosa* many epilithic Algae occur.

2. VEGETATION UNITS

Vegetation units are in the field easily recognizable by the dominant species. They differ therefore in physiognomy, and they form, moreover, zones whose boundary lines are often very sharp. The distinguishing characters that are found in the floristic composition of a vegetation, are established by comparing surveys made in different localities.

In my paper of 1955 these units of vegetation were called sociations, because they were characterized by the presence of at least one dominant species (DU RIETZ, 1930; WESTHOFF, 1951). It was at the same time pointed out that some of these sociations possess a set of characteristic species, and may therefore be regarded as associations in the sense of BRAUN-BLANQUET (WESTHOFF, 1951). As in the paper of 1955 no descriptions of the units were given, their allocation to different ranks would have looked arbitrary, and for this reason they were all listed as sociations. Now, however, it seems worth while to discuss these concepts as there is as yet no complete agreement with regard to their delimitation; this is the more desirable as there are several algal communities which according to the present definitions may just as well be regarded as sociations as classified as associations.

WESTHOFF (1951) defined these concepts in the following way:

Sociation: community containing at least one constant species, and consisting of one or more layers with one dominant in each layer.

Association: community with a more or less constant floristic composition and with a specific assemblage (i.e. the characteristic species joined with the constant companion species of the community).

It appears from these definitions that the sociation as well as the association must possess at least one constant species. The sociation has, according to the definition, at least one dominant species or, if it consists of more than one stratum, one dominant species in each stratum. In the definition of the association no dominants are mentioned; the latter, therefore, may be present or absent. The only essential difference between the sociation and the association is therefore the absence of characteristic species in the first and their presence in the latter.

In phytocoenology the conviction that the presence of characteristic species is not so important as originally was assumed, and that attributes like the constancy of the floristic composition and the structure of the vegetation are more valuable, has gradually gained ground. According to DOING KRAFT (1956) the so-called characteristic species are, as a rule, confined to a definite community in areas of limited extent only, and there is therefore no reason to attribute more weight to their presence than to other criteria. In the outer part of their area of distribution many species appear to be confined to a single biotope, whereas they show no such preference in the central part. In the Netherlands *Bostrychia scorpioides* is found almost exclusively in the *Halimonietum portulacoides*; in Brittany it occurs in all parts of the salt marshes, and further in the undergrowth of the *Pelvetietum canaliculatae* and of the *Fucetum spiralis* (DEN HARTOG, 1955, 1956; see also p. 187). There is therefore no sharp difference between the sociation and the association; they are units of a similar status.

Some algal communities appear to possess a set of species that may be regarded as characteristic, although none of the constituent species of this set is in itself characteristic; such communities, therefore, possess neither dominants nor characteristic species. In spite of the absence of the latter I wish to regard these communities as associations. As an example I may quote the *Enteromorpheto-Porphyretum umbilicalis.*

In the present paper we will confine the use of the term sociation to vegetation units that are not sufficiently characterized by the dominant species and possess no characteristic species either, but which occupy a well-definḋ position in the zonation.

In order to obtain a better survey of the various communities, they have to be united into groups of a higher rank. In general phytocoenology associations and sociations are united into alliances (NORDHAGEN, 1936) according to the pattern of their floristic composition. However, an attempt to base the classification of the vegetation units in phycocoenology, too, on this principle would be premature, as we possess as yet no complete descriptions of algal communities from the various parts of a sufficiently extensive region. For this reason they have been grouped in formations, i.e. units that are not based on floristic composition but on physiognomy and stratification, and partly also on their position in the successional series and on the place they occupy in the zonation. For the time being in algal coenology these formations will have to serve as the units of higher rank.

3. PHYSIOGNOMY

Among the attributes on which a classification of the algal vegetations is to be based, physiognomy and structure play a very important part. Many authors based their communities exclusively on physiognomic characters, and left the floristic composition out of consideration (KJELLMAN, 1878; BØRGESEN, 1905; KYLIN, 1907; JONSSON, 1912; VAN GOOR, 1923; a.o.); the most conspicuous species were the only ones that were mentioned. Their descriptions, nevertheless, give a good idea of the communities. This is not surprising, since in the Algae the diversity in form is much greater than it is in the phanerogams. We meet among them gigantic Laminariaceae and robust Fucaceae, but also delicate filamentous Algae and minute unicellular forms. On the other hand, quite similar life forms may occur in taxonomically distant groups; *Ectocarpus* in the Phaeophyceae, *Cladophora* in the Chlorophyceae, and *Callithamnion* in the Rhodophyceae, for instance, represent the same life form. OLTMANNS (1922—23), FUNK (1927), NIENBURG (1930) and others considered these life forms to be ecological adaptations, and used them for the elaboration of a classification. In a somewhat changed form their system is used here, too.

For the Netherlands the most important life forms 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 that are closely attached to the substrate: *Hildenbrandtia*, *Lithothamnion*, *Melobesia*, *Ralfsia*, *Lithoderma*;
6. Filiform Algae (**Ulothrix** type), monosiphonous and polysiphonous, simple filaments, sometimes provided with rhizoids: *Ulothrix*, *Rosenvingiella*, *Rhizoclonium*, *Bangia*, *Percursaria*, "*Urospora*";
7. Tubular Algae (**Enteromorpha** type), Algae with long, simple or ramified, hollow fronds: *Enteromorpha*, *Blidingia*, *Asperococcus*, *Dumontia*, *Scytosiphon*;
8. Membranaceous Algae (**Ulva** type), with irregular flat membranes: *Ulva*, *Monostroma*, *Porphyra*, *Petalonia*;
9. Dendritic Algae (**Cladophora** type), forming branched tufts: *Cladophora*, *Bryopsis*, *Ectocarpus*, *Sphacelaria*, *Callithamnion*, *Ceramium*, *Cystoclonium*;
10. Fruticose Algae (**Chondrus** type), with flat, branched, ribbon-like or leafy fronds: *Chondrus*, *Gigartina*, *Dictyota*, *Delesseria*, *Rhodophyllis*;
11. Gelatinous Algae (**Nemalion** type), with every gelatinous branched fronds: *Nemalion*, *Mesogloia*, *Scinaia*;
12. Coralline Algae (**Corallina** type), tufted fronds encrusted with lime: *Corallina*, *Jania*;
13. Pulvinate Algae (**Vaucheria** type), forming cushion-like masses: *Vaucheria*, *Rhodochorton*;
14. Microscopical Algae, Algae smaller than 2 mm, and occurring single. This group comprises many epiphytes, endophytes and parasites.

The circumstance that the species which belong to the same life form, do not, as a rule, occur as single individuals but collectively, makes it possible to characterize the vegetation units by means of the dominant life from, i.e. by means of the growth form which determines its physiognomy.

KJELLMANN (1878) was the first to use the term "formation" for such physiognomically determined vegetation units. He wrote "Unter einer Algenformation sollte folglich ein Abschnitt der ganzen Algenvegetation verstanden werden, der durch ein eigentümliches Vegetationsgepräge ausgezeichnet ist. Im Allgemeinen erhalten diese Abschnitte dadurch dieses Gepräge, dass eine oder einige Algenarten die Hauptmasse ihrer Bestandteile ausmachen."

This definition is rather vague, and may be applied to vegetation units of different rank. According to it, we may speak of a *Pelvetia* formation, because the vegetation unit in which *Pelvetia canaliculata* occurs, receives from the latter a definite aspect, but the larger vegetation unit to which the latter belongs, and in which also other Fucaceae are present, would have to be called Fucaceae formation, because it receives its physiognomic aspect from the whole group of the latter; and so the higher as well as the lower unit would have to be classified as a formation.

In 1905 BØRGESEN proposed to call the less comprehensive groups "associations". "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, and from the way in which he expresses himself, it is not always clear whether he means a formation or an association. KYLIN (1907) criticized this inconsistency, and he himself called all his units "formations".

COTTON (1912) had a completely different conception of the units to which the term "formation" should be applied. He reserved it "for communities which occur together in a definite type of habitat". He distinguished in this way a rocky-shore formation, a sandy-mud formation and a salt marsh formation. In this sense the formation is not a phytocoenological unit but a pedological one.

The way in which the term "formation" was applied by O. C. SCHMIDT (1931) differs also from that in which it was used by KJELLMANN and by BØRGESEN. He used it for KJELLMANN's "regions", and spoke of an epilittoral, a littoral and a sublittoral formation.

JONSSON (1912) avoided the use of the term formation, because he was of opinion that the other phycologists had used it in a wrong way. He accepted the term association, and remarked with regard to his associations "Where I think they are closely allied, I combine them into communities". He named these „communities" after the 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) reserved the term formation for the more comprehensive vegetation units that are characterized by a dominating life form, i.e. in the sense of JONSSON's communities. In this sense it will be used in this work, too. This, however, makes it desirable to give KJELLMANN's original definition a more precise form. I define it in the following way: An algal formation is a part of the algal vegetation whose aspect is determined by the dominance of a definite life form or by the joint dominance of some such life forms.

4. STRATIFICATION

The dominant life form is usually accompanied by other life forms; the latter form the undergrowth of the vegetation and the epiphytes. The joint presence of different life forms in the same community causes a kind of stratification, which may be of a definite type. Thus we can distinguish in the *Fucus* formation three layers, viz. 1° a stratum consisting of crustaceous Algae, 2° a stratum consisting of dendritic and fruticose Algae, and 3° the *Fucus* stratum; in addition epiphytic species are present, which are found on the Fucaceae as well as on the dendritic and fruticose Algae. One of these strata may be absent, but potentially the *Fucus* formation is three-layered. One-layered (*Hildenbrandtia* formation), two-layered (*Cladophora* formation) and four-layered formations (*Laminaria* formation) also occur along the European coasts. Each formation has a potential stratification which is characteristic for it.

5. ZONATION

5.I. GENERAL CONSIDERATIONS

During the last hundred years several authors have given their views on the way in which the coast should be divided in belts, and this has repeatedly led to heated discussions on the delimitation of the latter and even on the desirability of maintaining some of them. A large number of difficulties had to be overcome before a more or less universally accepted system was arrived at. Among these difficulties we may mention the presence or absence of tidal movements, the influence of the surf and that of climatological differences, and the differences in the degree of salinity. It is not my intention to give here a survey of all the systems that have been proposed; I will confine myself to the more important publications on this subject.

In an article on the algal flora of the Murmansk Sea published in 1877 KJELLMAN divided the coast in three belt-like superposed "Gebiete". In 1878 he replaced the term "Gebiet" by "Region". This new appellation has almost generally been accepted. FELDMANN (1938) proposed the term "étage", but as this term is often used by phycocoenologists for the various strata of which the vegetation usually consists, its use in FELDMANN's sense cannot be recommended. The term "zone" is also used, e.g. by T. A. and A. STEPHENSON (1949), but as this word has a much more varied significance than the term "region", its use should be avoided in a system of classification of the coastal belts.

Kjellman distinguished three regions. viz. the littoral, the sublittoral and the elittoral region. Lorenz, moreover, had already in 1863 distinguished a supralittoral region. All these names are still in use, but their delimitation has in most cases been changed, and they are now better defined.

In the following pages I will discuss this various regions.

1. The **supralittoral** region is the belt which from below to above is exposed to the surf; it is included therefore between the physiological upper limit of the surf and the physiological high-water line (litus line), which in general lies somewhat above the average high-water line (M.H.W.).

This belt is not homogeneous, and Sjøstedt (1928) rightly divides it in his system in an upper supralittoral belt and a lower one; the latter is the true surf belt ("swell-zone"), which is continuously exposed to the spray and which bears a vegetation consisting of Algae, crustaceous lichens and a few salt-tolerant phanerogams. The upper supralittoral belt is only during storms exposed to the saltish spray, and is characterized by the presence of halophilous phanerogams, dendritic and foliaceous lichens and some mosses. The width of the two belts depends upon the intensity of the surf.

The name supralittoral is almost universally accepted; some Swedish investigators, however, use a different terminology. Du Rietz (1940) calls this region the "Geo-amphibiontenstufe", whereas Waern (1952) uses the word "geolittoral". In his paper on the algal vegetation of the Azores O. C. Schmidt (1931) used the term "epilittoral".

The upper limit of the supralittoral region is extremely irregular; it is in a large measure dependent upon the force of the surf. The humidity of the air and irradiation, however, are also important factors. In the tropics the supralittoral region is but rarely well developed. The chilly and humid climate of the Faeroes, on the other hand, offers the supralittoral Algae very favourable conditions for their development. On the arctic coasts the supralittoral vegetation is once more in an unfavourable position, as they are here exposed to low temperatures and to the action of the ice. The most suitable upper limit of the supralittoral region is therefore the line above which the spray of the surf does not exercise its influence on the vegetation; this is the "physiological surf-limit".

The position of the boundary-line between the supralittoral and the eulittoral region has for a long time remained a point of controversy. Kjellman did not distinguish a supralittoral region, but he regarded the upper limit of the tidal zone nevertheless as the upper limit of his eulittoral region.

Rosenvinge (1899) disagreed with Kjellman's definition of the upper limit of the eulittoral region. According to him the upper limit should be located where the algal vegetation begins, and this may be several meters above the high-water line. Børgesen, Kylin, Jonsson and COTTON were of the same opinion. The acceptance of ROSENVINGE's upper limit nevertheless appears to have a distinct disadvantage; an eulittoral region defined in this way varies considerably in extent. According to BØRGESEN the upper limit coincides in sheltered spots with the upper high-water line, whereas in exposed positions it may be found at a height of 30 m or more above the latter.

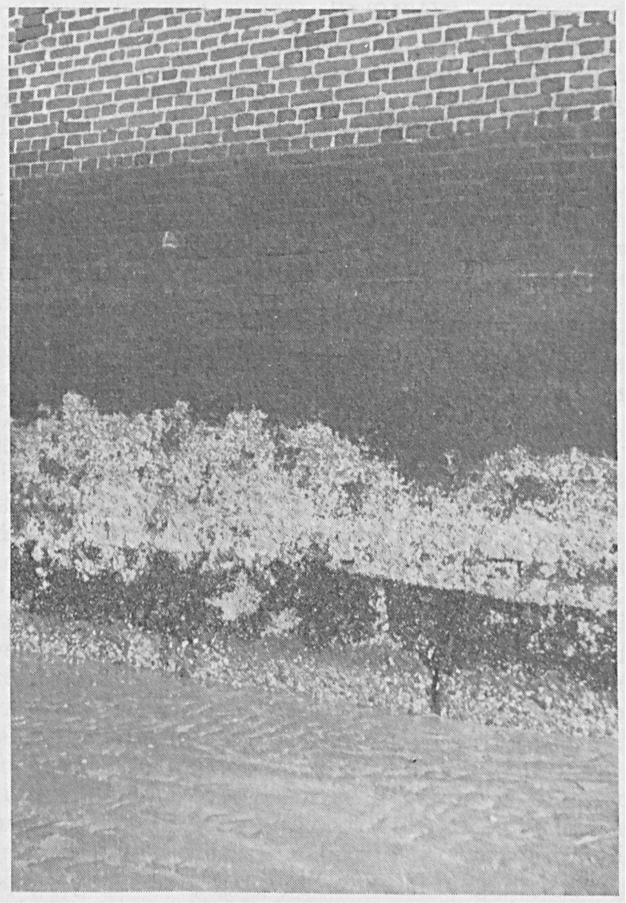


Fig. 11. Zonation on the southern mole at IJmuiden. From the top downward the following belts can be observed: 1. a black belt of *Calothrix scopulorum* with in the lower part *Blidingia minima* and a few *Porphyra* specimens. The light spot to the left is due to voracious activity of a colony of *Littorina saxatilis.* 2. a white belt formed by the barnacles *Balanus balanoides* and *Elminius modestus.* 3. a dark belt of mussels, *Mytilus edulis,* with barnacle colonies in open spots. 4. a belt without life, in consequence of the scouring effect of the sand. 30th November 1955.

SERNANDER (1917) chose the mean high-water line (M.H.W.) as the upper limit, and called the vegetation found above this line supralittoral. This purely physical delimitation of the eulittoral region is unnatural, and was therefore severely criticized. However, SERNANDER's idea that a distinction should be made between a region that is exposed to the waves and one that is exposed to the spray, was generally accepted; the criticism was mainly directed to SERNANDER's choice of the boundary line.

According to KYLIN (1918) the upper limit of the littoral algal vegetation is determined by the high-water line, wave-action and desiccation on account of irradiation; it was called by him the "physiological high-water line". SJØSTEDT (1928) proposed for this upper limit the term "litus line". FELDMANN, (1938) too, accepted a boundary line of this kind, and the latter is now generally in use.

2. The **(Eu)-littoral** region is the belt between the litus line defined in the preceding paragraph, and a lower limit. On coasts without tidal movements the latter is the line below which the water, as a rule, does not sink. Where tidal movements are present, it coincides more or less with the mean low-water line at spring-tide (M.L.W.S.). The eulittoral region therefore is characterized by the presence of a fluctuating water level, but it is of no importance whether the fluctuations are caused by the tides or by the wind. The French definition "zone de la balancement de la mer" is therefore well-chosen (FISCHER-PIETTE).

Although the eulittoral region cannot be regarded as fully homogeneous, a subdivision does not seem desirable, as the local differences are so large that it would have no general applicability. These local differences would make it difficult to apply the terms that would have to be introduced in connection with such a subdivision, and a misapplication of these terms would lead to further complications.

The term "eu-littoral" has been accepted by nearly all phycologists, but some other terms are nevertheless also in use. DU RIETZ (1940) speaks of the "Hydroamphibiontenstufe", WAERN (1952) uses the term "hydrolittoral", whereas MOLINIER and PICARD (1953, 1954) apply the term "mesolittoral". The term "tidal zone", which is often used, is not fully synonymous with the term "eulittoral".

The boundary line between the eulittoral and the sublittoral region is, according to KJELLMAN, formed by the upper limit of the *Laminaria* formation. According to BØRGESEN (1905) it lies slightly above the lowest low-water line, but where no tidal movements are present, its position is difficult to determine, and for this reason he is of opinion that the situation on such a coast is not comparable to that found on a coast of the other type. JONNSON (1912) draws the boundary line between the eulittoral region and the sublittoral one at the place where during the spring tides the low-water line is found (M.L.W.S.).

KYLIN (1907) accepts with KJELLMAN the *Laminaria* formation as the uppermost part of the sublittoral region. In Bohuslan on the Swedish west coast, which is not exposed to the tides, this boundary line is found at a depth of 3—4 m, and in Halland even at a depth of 5 m.

GRAN (1893) was of opinion that in south Norway the boundary line was to be drawn at a depth of 0.5 m, i.e. at the place where the association of *Ahnfeltia* and *Chondrus* reaches its upper limit. This line coincides more or less with the line below which the water, as a rule, does not sink. GRAN chose this line because he thought that he would obtain in this way a better agreement with the mean low-water line at spring tides (M.L.W.S.) of the coasts that are exposed to the tides. His example was followed by SERNANDER (1917), KYLIN (1918), SJØSTEDT (1928), GISLEN (1930), DU RIETZ (1922, 1932, 1940), FELDMANN (1938) and WAERN (1952). LEVRING (1940), on the other hand, accepts the highest low-water level (M.L.W.N.) as the boundary line. For coasts without tidal movements GRAN's line, which corresponds to the M.L.W.S. of the coasts that are exposed to the tides, is now generally accepted.

3. The **sublittoral** region is the belt between the line discussed in the preceding paragraphs and that below which no algal growth is possible. With the exception of the uppermost part, which occasionally viz. at an extremely low spring-tide, falls dry, though for a short time only, this belt is permanently submerged.

The sublittoral region, too, is not homogeneous. FELDMANN (1938) distinguished two belts, an "étage infralittoral supérieur" with vegetations consisting of photophilous Algae, and an "étage infralittoral inférieur" with vegetations consisting of sciaphilous Algae. At Banyuls the boundary line between these two subdivisions is found at a depth of 5—10 m; it is not always sharply differentiated, as below overhanging cliffs and in caves the sciaphilous Algae may extend up to the surface. MOLINIER and PICARD (1953, 1954) indicated these two subdivisions as the "infralittoral photophile" and the "infralittoral sciaphile".

A similar subdivision is also present at the Atlantic coasts, but the two belts that were distinguished by WAERN (1952) in the sublittoral region of the Baltic coast, are of a different kind. In the Baltic Sea the vertical salt gradient plays an important part.

Other names for the sublittoral region are the term "infralittoral" which was proposed by FELDMANN (1938), but which must be regarded as superfluous, and "Euhydrobiontenstufe" used by DU RIETZ (1940).

The boundary line between the sublittoral region and the elittoral one was indicated by KJELLMAN as the 20-fathom line. ROSENVINGE (1898) pointed out that the position of this boundary line varies according to circumstances, and that we ought to confine ourselves to the statement that the elittoral region begins where the algal vegetation stops. BØRGESEN and KYLIN agreed with him, and since then this standpoint has generally been accepted.

4. The **elittoral** region is characterized by the absence of algal growth. A subdivision of this region may perhaps be based on differences in the composition of the fauna.

Some authors accept in addition an **"epilittoral"** or **"adlittoral"** region; this is the belt which undergoes an influence of the vicinity of the sea, e.g. on account of the salt seawind. It has a considerable extent, and coincides more or less with the maritime zone of phyto-geography. In the Netherlands we may regard the region of the dunes as belonging to this belt, and also that part of the polders where we meet the well-known wind-swept trees with their dissymmetrical crowns pointing inland, e.g. in the northern part of North Holland. As the vegetation of this region is not halophilous, it can, strictly speaking, not be called a part of the coast.

It is not always easy to determine the exact position of the boundary lines between the various regions by means of the criteria given in the preceding paragraphs. In order to determine the mean value of the lower and upper level reached by the tides, we need a series of observations extending, if possible, over several years. It is therefore no wonder that attempts have been made to correlate these evasive boundary lines with lines that are directly recognizable, like the upper and the lower limit of the area occupied by an association or by an individual species. These attempts were not unsuccessful. The boundary line between the supralittoral region and the eulittoral one, the physiological high-water line, appeared to coincide with the lower limit of the *Verrucaria maura* association *). This was found out by KYLIN (1918) for the west coast of Sweden, and was subsequently confirmed by SJØSTEDT (1928) and by LEVRING also for the west coast of Norway (1937) and for the Baltic Sea (1940). In water that is sufficiently salt, the upper limit of the zone occupied by *Balanus balanoides* forms, according to SJØSTEDT, another sharp line which corresponds to the physiological high-water line *). LEVRING (1937) confirmed this observation for the west coast of Norway, where the lower limit of *Verrucaria maura* and the upper limit of *Balanus balanoides* practically coincide. A similar boundary line was found by FELDMANN (1938) on the coast of the Mediterranean Sea. Here the litus line proved to coincide with the upper limit of *Chthamalus stellatus* and with the lower limit of *Verrucaria symbalana.*

As *Verrucaria maura* is not always present, SJØSTEDT tried to find another association which might serve as indicator of the litus line. According to him the upper limit of the association of *Calothrix fasciculata* and *Lyngbya lutea* would satisfy this demand, but this was denied by LINDSTEDT (1943). According to the latter *Calothrix fasciculata* is merely a form of *C. scopulorum,* which occurs in the upper part of the eulittoral region in the form of closed vegetations, but which is found also in the supralittoral region. Another boundary line indicated by SJØSTEDT is the lower limit of the spring association of *Urospora mirabilis* (= *Codiolum penicelliforme* st. *urosporae*), but he himself already remarked that this line can only be used when the water level fluctuates but slightly, as "*Urospora*", on account of its rapid growth and of its short vegetation period, is able to "follow" the changes in the water level. This boundary line is therefore of little use.

The boundary line between the sublittoral region and the eulittoral one is formed, according to KJELLMAN (1877), by the upper limit of the *Laminaria* formation. This appeared to be so on all the coasts of western Europe in so far as they are exposed to the tides. The *Laminaria* line is therefore generally accepted. In the Mediterranean Sea at Banyuls the upper limit of the *Cystoseira mediterranea* association may

---

*) Below the litus line *Verrucaria maura* occurs but sporadically and in the form of a few isolated individuals; above the litus line the same applies to *Balanus balanoides.*

be used for this purpose (FELDMANN, 1938). Some other *Cystoseira* communities, e.g. at Nice and at Antibes the *Cystoseira stricta* association, fulfill the same function. In south-western Europe, too, the boundary line between the eulittoral region and the sublittoral one can be determined by means of *Cystoseira* communities, especially when *Laminaria* is absent. In Zeeland (the Netherlands) DEN HARTOG (1955) accepted the upper limit of the *Codieto-Hypoglossetum* as the boundary line between the two regions.

The *Laminaria* line appeared to be unsuitable for the coasts of the Skagerrak, the Kattegat and the Baltic Sea, where there are no tidal movements. However, it proved possible to correlate the lowest level to which the water subsides with definite boundary lines in the vegetation, although the validity of these lines appeared to be restricted to areas of a comparatively small extent. So is, according to SJØSTEDT, along the west coast of Sweden as far as Kullaberg the upper limit of the sublittoral region determined by the upper limit of the *Fucus serratus* community. At Kullaberg the influence of the surface water of the Baltic Sea becomes predominant, and then the upper limit of a Rhodophyceae vegetation with *Polysiphonia urceolata, P. nigrescens* and *Ceramium rubrum* serves the same purpose. South of Kullaberg this function is taken over by the Baltic *Ceramium* community with *C. diaphanum* and *C. strictum.* However, it can only be used between June and the time at which the sea becomes covered with ice. The ice sweeps the upper part of the algal vegetation away, and then it is not before June that the latter is restored.

According to LEVRING (1940) in the Baltic Sea the boundary line between the sublittoral region and the eulittoral one coincides with the upper limit of the *Fucus vesiculosus - Pylaiella rupincola* association, and it is at the same time the line above which no perennial Algae are found. However, it is not fully certain that this biological boundary line really corresponds to the line below which the water, as a rule, does not sink, as the possibility that the upper part of the vegetation of the sublittoral region may be destroyed by the ice, has been left out of consideration by LEVRING.

The correlation established in one area between the boundary lines of definite vegetation units and those of the altitudinal regions, is not necessarily valid in another area. The species in that other area may show an entirely different behaviour. In this respect I may refer to the differences in the behaviour of the Laminariaceae and of the Fucaceae in the Skagerrak, the Kattegat and the Baltic Sea. Although the sequence of the species in the zonation remains the same, they gradually shift to a greater depth. First *Fucus serratus,* and then *F. vesiculosus* pass into the sublittoral region. In the Öregrund Archipelago WAERN (1952) found *Fucus vesiculosus* down to a depth of 11.5 m. T. A. and A. STEPHENSON (1954) describe in their study of Nova Scotia and Prince Edward Island how on the north coast of the island *Fucus vesiculosus* descends into the sublittoral region. On the south coast of Prince Edward Island and of Caribou Island they found rich vegetations of *F. vesiculosus* and of *F. serratus* in the last-named region.

A delimitation of the regions by means of the "tidal levels" is impossible. The relation between the latter and the vegetation units and the individual species is to this end not sufficiently simple. This was already pointed out by KYLIN (1918), and it induced him to introduce the "physiological high-water line". Apart from the factors to which he drew attention, viz. wave action and insolation, the physical nature of the substrate should be mentioned as a factor with a considerable influence on the position of the boundary lines of the areas occupied by the vegetation units or by the individual species.

5.II. THE SYSTEM OF THE STEPHENSON'S

The division in regions discussed in the preceding section, is used by the majority of the European phycologists. In 1949, however, another "zonation" system was proposed by T. A. and A. STEPHENSON. In the elaboration of this system, which in their opinion is universally applicable, they certainly proceeded very cautiously. They studied the tidal zone for more than thirty years, and investigated large parts of the coast of Great Britain, of South Africa, of the Indian Ocean, of the Red Sea, and of the Great Barrier Reef, and the Atlantic as well as the Pacific Coast of North America. They noted that all these coasts have a number of traits in common, and they used the latter for the construction of their system. The result is a division of the coast in five belts which may be characterized in the following way:

1. The supralittoral zone is defined by the STEPHENSONS as "the maritime belt lying near the sea, above tide-marks, but subject to some maritime influence (e.g. to finely divided spray in rough weather). The lower limit of this zone is the same as the upper limit of the one below".

2. The supralittoral fringe is the zone "from the upper limit of barnacles (in quantity) to the nearest convenient landmark above this (e.g. the upper limit of Littorinae or the lower limit of maritime land-lichens or flowering plants). High water or spring tides invade at least the lower part of this zone". As a further particularity they mention the presence of a black belt formed by crustaceous lichens like *Verrucaria maura* and some of its allies, or by incrusted black Cyanophyceae.

3. The midlittoral zone extends "from the upper limit of barnacles (in quantity) down to the upper limit of the zone below. This belt tends to be covered and uncovered every day, at least in part". This zone shows a strong tendency to fall apart into two or more "subzones", but it differs in this respect considerably on the various coasts, and it is for this reason undesirable to develop a universal system for these subzones.

4. The infralittoral fringe is the belt extending "from the upper limit of any convenient dominant organism (e.g. *Laminaria*) to extreme low water level or springtides (E.L.W.S.), or to the lowest level ever visible between waves. This zone uncovers only at the major tides, and sometimes only in calm weather."

5. The infralittoral zone extends "from extreme low water of springs to a depth which has yet to be settled — it may be to the edge of the continental shelf or to the lower limit of seaweed vegetation."

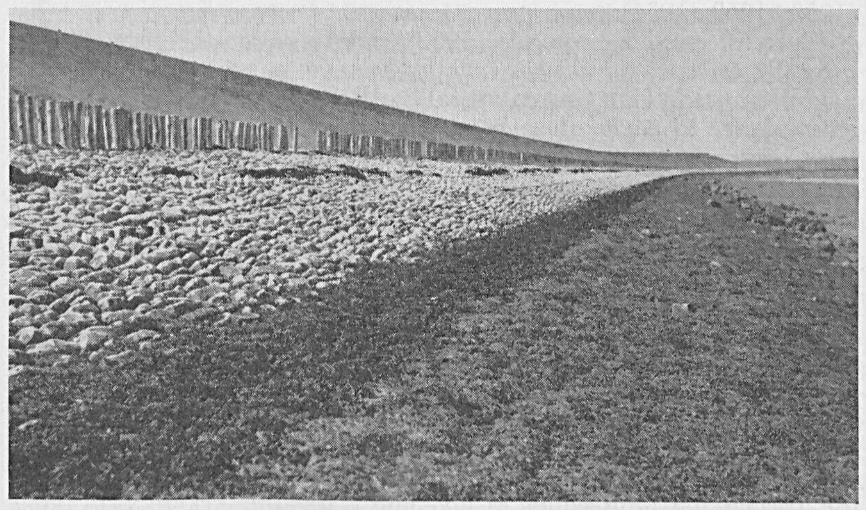


Fig. 12. Fucaceae-zonation near Kattendijke on a dike slope of Vilvordian limestone, from the top downward: 1. *Pelvetia canaliculata*. 2. *Fucus spiralis* and 3. *Ascophyllum nodosum* (light). 14th May 1956.

This classification was very favourably received by a number of investigators, e.g. by CHAPMAN and TREVARTHEN (1953) and by DELLOW (1954), who applied it in New Zealand, by GUILER (1953), who considered it to be suitable for the coast of Tasmania, by LEWIS (1955), who worked with it especially on the west coast of Great Britain, by LAWSON (1954, 1956), who used it in west Africa, and by SOUTHWARD (1958), who discussed it in an elaborate review.

However, criticism, too, did not remain in abeyance. WOMERSLEY and EDMONDS (1952) were of opinion that this classification could not be applied in a satisfactory way to the algal vegetation of the South-Australian coast, and they accordingly proposed some changes. LEWIS (1955), too, adduced some objections.

The principal objections were directed against the terms that were introduced by the STEPHENSON's, and further against the delimitation of the two "fringes" and even against the right of existence of the latter.

WOMERSLEY and EDMONDS (1952) objected against the term "midlittoral", as the latter made it impossible to indicate the subdivisions by the aid of the qualifications "upper", "mid" and "lower"; names like "upper mid-littoral" and "lower-midlittoral" are apt to create confusion, and "mid mid-littoral" even sounds comical. These authors therefore proposed to reintroduce for this belt the name "littoral".

CHAPMAN and TREVARTHEN (1953) disagreed with WOMERSLEY and EDMONDS, and argued that subdivisions of the midlittoral zone may be named after the dominant organisms. The STEPHENSON's themselves had already done this and continue to do this in their studies of the coasts of South Africa (1939, 1942, 1948) and of North America (1950, 1952, 1954).

WOMERSLEY and EDMONDS (1952) rightly reject the term "infralittoral", as "sublittoral" has exactly the same meaning, and has since long been used. That "supralittoral" and "sublittoral" show a certain resemblance to each other, is no sufficient reason to replace one of them, as this resemblance is not so strong that it can lead to confusion.

My own objection against the terminology of the STEPHENSON's is of an entirely different kind. Notwithstanding their remark that they have tried "to choose those words which will be most generally suitable and most widely applicable", their terms have the disadvantage that they are based on typically English expressions, and are therefore not always readily translatable in other languages. A not fully correct translation may, of course, lead to misunderstandings. Difficulties of this nature make the adoption of their terminology less attractive. For this reason I propose to replace the term "midlittoral" by "eulittoral" *), and the term "fringe" by a term of Latin origin, viz. "margin". My objection against the use of the term "zone" in the special meaning which is given to it by the STEPHENSON's, has already been brought forward on p. 73. It seems better to use to this end the term "region".

WOMERSLEY and EDMONDS (1952) questioned the necessity of distinguishing a supralittoral margin and a supralittoral zone. They criticized especially the definition of the upper limit of the supralittoral margin, because on strongly exposed coasts the Littorinids may ascend to a considerable height; they are found there between the maritime Phanerogamae. They also drew the attention towards the influence exercized on the distribution of these snails by the configuration of the rock surface. CHAPMAN and TREVARTHEN (1953) confirmed these observations, but they are of opinion that notwithstanding these irregularities the upper limit of the supralittoral margin remains distinguishable, because it coincides more or less with the upper limit of the belt formed by the yellow lichens, which forms the upper margin of the "black zone".

The lower limit of the supralittoral margin was studied by LEWIS (1955). According to the STEPHENSON's it would be formed by the line above which no barnacles are found in quantity. In his attempts to apply this definition LEWIS was confronted with a noteworthy difficulty.

Along the British east coast and along the coasts of the Irish Sea the lower limit of the supralittoral margin is indicated by the presence of *Balanus balanoides*; this is in agreement with what is found elsewhere

---

*) The term "eulittoral" has for a long time been used by the phycologists of north and west Europe in the same sense as the term "midlittoral" of the STEPHENSONS. The latter seems to be entirely superfluous.

in the cold-temperate part of the northern Atlantic Ocean. However, along the Atlantic west coast of Great Britain the boundary line is indicated by the presence of another barnacle, viz. the tropical-lusitanic *Chthamalus stellatus*. Now it appears that the lines indicated by these two species do not lie at the same level. Along the west coast and in those parts where both species are present but where *Chthalamus* does not become dominant, the latter occupies a position above the belt formed by *Balanus balanoides*. Along the west coast the boundary line between the two belts is not well-marked, but in the other parts it is very conspicuous (EVANS, 1949; SOUTHWARD, 1951, 1953; SOUTHWARD and CRISP, 1952, 1954). Now, if the classification of the STEPHENSON's is rigorously adhered to, a number of species will have to be referred on warmer coasts to the eulittoral region, and on the colder ones to the supralittoral region. This would apply e.g. to *Pelvetia canaliculata*.

A substitute of the barnacle line may be found perhaps in the lower limit of the "black zone". According to LEWIS this boundary line can not be regarded as ideal, as it is not always sharply defined. It sometimes overlaps the barnacle line, but in other places it is separated from the latter by an empty space, so e.g. at Peggy Cove (Nova Scotia), where the STEPHENSON's noted the presence of such an empty space. LEWIS mentions from the literature some analogous cases observed in other parts of the world, but he does not arrive at a decision. It is perhaps noteworthy that the Australian barnacle, *Elminius modestus*, which was introduced in western Europe during the second world war, reaches in several places in the southern part of the North Sea its upper limit at a level which lies circ. 25 cm above that of *Balanus balanoides* (DEN HARTOG, 1953).

The lower limit of the supralittoral margin therefore does not lie on each coast at the same level, although the fluctuations in its position are confined to a definite, rather narrow belt. The STEPHENSON's (in LEWIS, 1955) are of opinion that this needs not to be regarded as an argument against their classification, and they declare that they even had expected such fluctuations. "Again, as any zone is characterized by different species in different parts of the world, there has never been any expectation in our minds that the level at which the upper limit of (for instance) the infralittoral fringe occurs, would be quite the same everywhere, even under comparable environmental conditions."

The belt in which on different coasts the lower limit of the supralittoral region fluctuates, is, in my opinion, the true "supralittoral fringe". The "supralittoral fringe" of the STEPHENSON's corresponds to the "lower supralittoral region" of SJØSTEDT (1928), which was dealt with on p. 74.

The sublittoral margin is the transition belt between the eulittoral region and the sublittoral one. Here the eulittoral species reach the lower limit of their area, the sublittoral ones the upper limit of theirs. The presence in this belt of critical floristic and faunistic levels has been ascertained by various investigators, and may be regarded as fully proved.

WOMERSLEY and EDMONDS (1952) demonstrated the presence of a critical level "some distance above E.L.W.S.", DOTY (1946) one at M.L.W.S., whereas COLMAN (1933) found critical levels between M.L.W.S. and E.L.W.S. and between M.L.W.N. and M.L.W.S. CHAPMAN and TREVARTHEN (1953), too, found a critical level between M.L.W.N. and M.L.W.S., which they regarded as the upper limit of the sublittoral margin. According to the STEPHENSON's the lower limit of the latter coincides with E.L.W.S. However, against this statement WOMERSLEY and EDMONDS (1952) object, because "in actual fact this restricted zone includes only the upper part of a uniform zone which extends down much below E.L.W.S." They observed this in South Australia with *Cystophora* species, and DELLOW (1954) confirmed their observations in the Hauraki Gulf in New Zealand with *Carpophyllum plumosum*, which descends to 7 m below E.L.W.S., and with *Ecklonia radiata*; with the latter the upper part of the thallus often falls dry, but the holdfasts always remain submerged. The STEPHENSON's themselves (1952) described a similar instance from Beaufort (North Carolina), i.e. from the east coast of North America. There on the rocks and immediately below the "low-water level of spring tides" a fine algal vegetation is found of which *Sargassum filipendula*, *Dasya pedicellata* and *Ulva lactuca* are the principal components. "The upper fringe of these rocks (infralittoral fringe strictly speaking) becomes uncovered at the lowest tides, but much of the most luxuriant part of this population lies, even then, just below low water." The *Laminaria* vegetations in the northern part of the Atlantic Ocean, too, are by no means confined to the sublittoral margin, but descend deep into the sublittoral region. This applies as well to the association of *Laminaria digitata* and *L. agardhii* which was described by the STEPHENSON's from Nova Scotia (1954), as to the west-European associations of *L. digitata* and *L. saccharina* and of *Alaria esculenta*. LEWIS (1955) expresses himself in this way. "The height at which the laminarians begin, varies with local conditions, but generally when *Alaria* or *Laminaria digitata* extend up shore (under the influence of surf, for example), the essentially midlittoral species will here be found to have retreated to a higher level." This means that the possibility of passing E.L.W.S. depends for the *Laminariae* on the prevailing ecological conditions. In exposed localities the shifting in an upward direction will be more pronounced than in more or less sheltered spots, and this applies not only to the *Laminaria* zone, but also to the belts of Fucaceae (BURROWS et al., 1954). In such cases the sublittoral margin is therefore an artificial belt which destroys the uniformity of a natural unit.

However, in other instances a special association may actually be present in the sublittoral margin. So WOMERSLEY and EDMONDS (1952) cite from the exposed coast of Kangaroo Island (South Australia) the presence of a *Cystophora intermedia* vegetation which, when there is a heavy swell, may for a moment be entirely uncovered. GUILER (1953, 1955) quotes for Tasmania *Sarcophycus potatorum* and *Lessonia corrugata* as species that are typical for the sublittoral fringe, and according to

Dellow (1954) *Cystophora torulosa*, *Carpophyllum elongatum* and *C. maschalocarpum* are in New Zealand confined to this belt. Finally Lawson (1957) describes *Sargassum vulgare* and *Dictyopteris delicatula* as species that on the Gold Coast are characteristic for the sublittoral margin.

The preceding exposition indicates that the vegetation of the sublittoral region may ascend slightly above E.L.W.S. when special environmental conditions, among which the force of the swell should be emphasized, are present. In many instances the vegetation of the sublittoral margin consists only of the upper part of an association which extends downward to a considerable depth; in other instances this sublittoral margin is occupied by a well characterized community, which deviates from the vegetation at a lower level, i.e. at a level which is continuously submerged. It does not seem necessary to regard the sublittoral margin as a separate region, as proposed by the Stephenson's, as it is clearly no more than the upper part of the sublittoral region.

If we compare the division in regions which was sketched in 5.I. with the classification proposed by the Stephenson's, it appears that there are no fundamental differences. This is proved by the following juxtaposition.

TABLE XI

Comparison between two systems of zonation

European classification	classification of the Stephenson's
upper supralittoral region	supralittoral zone
lower supralittoral region	supralittoral fringe
eulittoral region	midlittoral zone
sublittoral region	infralittoral fringe
	infralittoral zone

5.III. Basic and standard zonation

The classification developed by the Stephenson's derives its significance from the principle on which it is based, viz. on the biological characterization of the various belts and of their limits. They drew attention to a number of universally present biological phenomena by which the zonation is accompanied, and which enable us to compare coasts from all parts of the world. These phenomena are the presence of the supralittoral Littorinids, the "black zone", the barnacle belts, the sublittoral margin, and a few less important ones. Their classification, in fact, is a reflection of this basic zonation. The terminology which they applied in their work on the coasts of South Africa, in which was spoken of a Littorinid zone and of a Balanoid zone, also points in this direction (Stephenson, 1939). The universal character of the basic zonation is not affected by the criticism exercised by Lewis (1955) which is restricted to a point of minor importance, nor by the occasional absence of one of the characteristic features.

The features of the basic zonation come best to the fore in the more exposed parts of the coasts, but besides the features of this main zonation we notice other ones that, although not universally present, are nevertheless characteristic for large parts of the coasts; to the latter belong the Fucaceae zonation, the zonation of the limpets, the presence of Laminariales in the upper margin of the sublittoral region, etc. On less exposed spots these features are often superimposed on the basic zonation. In an area of a definite circumscription we find therefore a characteristic "standard zonation", which consists of the "basic zonation", and superimposed on the latter a local "accessory zonation". In the southern part of the North Sea we find, for instance, the standard zonation shown in table XII.

TABLE XII

Standard zonation in the southern part of the North Sea

region	basic zonation	accessory zonation
upper supralittoral		Ramalina siliquosa
lower supralittoral	Littorina saxatilis Littorina neritoides "black zone" (Verrucaria maura/ Calothrix scopulorum)	"yellow zone" (Xanthoria parietina Caloplaca marina)
eulittoral	Balanus balanoides Elminius modestus Balanus crenatus	Pelvetia canaliculata Fucus spiralis Fucus vesiculosus/ Ascophyllum nodosum Fucus serratus Polysiphonia-Chaetomorpha
sublittoral		Laminaria digitata Laminaria saccharina

This standard zonation shows a striking resemblance to those that were published for the British coast (Stephenson, 1939), the French coast of the English Channel (Davy de Virville, 1932, 1940), the west coast of Norway (Levring, 1937), and the coast of Nova Scotia (Stephenson, 1954), although there are, of course, important differences in the accessory features. We may draw attention e.g. on the presence of various ecotypes of *Fucus distichus* (= *F. inflatus*) in Nova Scotia and northern Europe, the distribution of the *Himanthalia elongata* belt, the substitution of *Laminaria saccharina* by *L. agardhii* in Nova Scotia, the presence of the *Alaria esculenta* community in exposed spots, etc. I will, however, not enter into details. In future it will doubtless be possible to characterize the geographic provinces of the sea coasts by means of such standard zonations.

On account of differences in the environmental factors numerous deviations of the standard zonation described above, are found on the coast of the Netherlands. Light intensity, degree of exposure, nature of the substrate, deposition of mud, overflowing with sand, fluctuations in salinity, etc. exercise their influence on the nature of the communities.

The zonation of the Chlorophyceae which HAMEL (1940, 1942) described from the Basque coast, is doubtless due to sedimentation and to a low degree of salinity. The zonation of the Rhodophyceae which DEN HARTOG (1955) discovered at Flushing, may be ascribed to the low intensity of the insolation prevailing in that habitat. On flat or very slightly sloping rocks the vertical zonation may sometimes be entirely disturbed by horizontal variations. On such spots a vegetation mosaic is found. FELDMANN (1955) described this phenomenon from the coast of Morocco.

I wish to point out here that the vegetations that are found in a definite locality, may often be regarded as stages in the succession. The latter will be discussed in section 6.

5.IV. CAUSES OF THE ZONATION

Although it is not my intention to discuss the causes of the zonation in detail, it seems desirable to pay some attention to this topic.

According to STEPHENSON (1949) and SOUTHWARD (1958) a distinction should be made between the causes by which a zonation is produced, and the causes by which a definite pattern of zonation is created.

Zonation, i.e. a differentiation of the vegetation in successive zones, is a phenomenon that is universally distributed; it is observed even in stagnant water. It is caused by the action of physical factors operating in those parts where the water is in contact with the air (O_2 tension, degree of humidity, temperature changes, etc.).

The special nature of the zonation, its pattern, is caused by quite different, more local factors, which show a gradual change in intensity.

In the sublittoral region light is the principal factor, at least with regard to the vegetation; the decrease in light quantity and in light intensity causes a distinct zonation.

In the supralittoral region the zonation is in the main determined by the amount of spray, and light is here merely a modifying factor.

With regard to the eulittoral region it is generally assumed that the zonation pattern is mainly due to the tidal movements, and to what the latter involve (period of emersion, desiccation, fluctuations in temperature, salinity and pH, differences in the amount of light). In the reviews published by STEPHENSON (1942), CHAPMAN (1942) and SOUTHWARD (1958) numerous arguments are adduced in support of this view. However, although this explanation suffices for many kinds of animals and Algae, there are also phenomena which seem to require another explanation.

In the Skagerrak, the Oslo Fjord and the Kattegat (Bohuslån), where the difference between high and low tide are but small, but where the Baltic surface water does not yet exercise its influence, the zonation pattern of the Fucaceae is the same as on the west coast of Europe, but it is no longer correlated with the length of the period of submergence. At irregular times the wind causes changes in the height of the water level which exceed those that are here due to the tides, and in this way the *Fucus spiralis* zone and, occasionally, a part of the *F. vesiculosus* zone are for a time uncovered; the *F. serratus* belt, however, remains permanently submerged. In this case, therefore, the zonation can only be effected by the gradually decreasing light intensity. If this is true, the Fucaceae zonation on coasts where the tidal movements are more pronounced, might be explained in the same way, as the available light quantity decreases there in a similar way. According to CHAPMAN (1942) the photosynthetic and respiratory activity of the Algae is confined to the periods of submergence. As these activities come to a stop by loss of water during the period of emergence, the large amounts of sunlight that are received during that time, can only be inhibitory. The amounts of light which reach the various belts during the period of submergence, vary according to the thickness of the water layer which they have to traverse. The difference between high and low tide and the transparency of the water may therefore be regarded as modifying agents.

In this connection it is noteworthy that at higher latitudes, where periods with long irradiation times occur, the Fucaceae show a tendency to shift towards a greater depth. T. A. and A. STEPHENSON (1954) describe, for instance, that the *Fucus vesiculosus* zone extends on Prince Edward Island (Nova Scotia) to below the low-water line, and that *Fucus serratus* occurs there in the sublittoral region, findings that are confirmed for the Murmansk coast by GURJANOVA, SACHS and USCHAKOW (1930). From Greenland (LUND, 1954) and Novaya Zemlya (ZINOVA, 1929), too, the shifting of the Fucaceae to a greater depth is reported.

6. SUCCESSION

The terrestrial vegetation units all show a development through various stages towards a final one, the climax, which is reached only at the end of a period of more or less considerable length. After that the vegetation is supposed to be in equilibrium with the climatological and edaphic conditions prevailing in the part in which it occurs. However, in order to reach this stage of equilibrium, the development of the vegetation should be undisturbed, and it should take place under entirely natural circumstances.

The marine vegetation units show a similar development as the terrestrial ones. The edaphic conditions are in their case the physical and chemical properties of the sea water in which they occur.

A bare spot is occupied, first of all, by a "pioneer" community. Under the influence of the latter the environment undergoes a slight change, and now the plants belonging to the next stage in the development of the vegetation, may obtain the opportunity to establish themselves in this place. They supplant the pioneers, but in the course of time they are in their turn crowded out by the representatives of a third stage, and this process goes on until after the elapse of a more or less considerable stretch of time the final stage is reached. This sequence of stages is called the succession. A succession in the direction of the climax is progressive, one in the opposite direction is regressive. As the edaphic and climatological factors differ from one place to another, the climax communities, too, will differ. In a definite area the final stage, therefore, is formed by a swarm of climax types.

The climax may be reached in different ways. In the first place the succession may be of the convergent type. In that case different pioneer communities are seen to develop along entirely or partly different ways towards the same climax. This type of succession is mainly found in terrestrial vegetations.

The second type of succession is the divergent one. Here there is but a single pioneer community, but the latter develops in different directions to a different climax. This is the way in which the littoral algal communities develop.

It is also possible that the succession does not lead to a true climax, but that it first proceeds in one direction and then in the opposite one. This is called cyclic succession. Such a cyclic succession may require some years, but it may also be completed within a single year. In the latter case we speak of seasonal succession. This seasonal succession is met with in the tidal pools on rocky shores, in which we can study in the spring months the *Monostrometo-Dumontietum*. This phenomenon should not be confused with seasonal rhythm. In the case of seasonal rhythm a community assumes in the course of the year different aspects but retains its original composition; in the case of seasonal succession the latter, too, changes.

The succession of the marine communities was discussed for the first time by MOLINIER and PICARD (1953, 1954). They described three successional series from the coast in the western part of the Mediterranean Sea, viz.

1. a "série intercôtidale du trottoir de *Tenarea tortuosa*";
2. a "série photophile de l'herbier de *Posidonia oceanica*"; and
3. a "série sciaphile des fonds coralligènes".

The communities which do not belong to these three series, are

1. the permanent communities (e.g. the association of *Gymnogongrus nicaeensis* and *Phyllophora nervosa*, and the association of *Arthrocladia villosa* and *Sporochnus pedunculatus*), and
2. the nitrophilous communities, which are confined to harbours and to other localities where the water is polluted by human interference.

Along the coast of western Europe, too, succession had already been observed, viz. by HATTON (1938) and by SOUTHWARD (1953, 1956), who studied the development of the algal vegetation on surfaces of rock that had been cleaned. T.A. and A. STEPHENSON (1954) wrote that they regarded the extensive and luxurious vegetations of *Chordaria flagelliformis*, *Ulva lactuca*, *Chorda filum*, etc. in the sublittoral region on the north coast of Prince Edward Island (Nova Scotia), which is strongly exposed to the action of floating ice, as a stage in the development of the association formed by *Laminaria agardhii* and *L. digitata*.

The coast of the Netherlands is eminently suited for studies on the phenomenon of succession, as the vegetation is here destroyed again and again by the activity of man (by the dumping of stones on dikes and breakwaters, by renewing piles, by bituminizing slopes). Independent of the season the same kinds of Algae are seen to colonize the vacant spots in the same way. Stones dumped in the littoral belt are covered within six weeks with *Enteromorpha*, *Porphyra*, *Ulothrix* and *Ulva*, often preceeded by diatoms. Somewhat later various kinds of dendritic Algae settle among them, and soon young Fucaceae begin to appear, too. After some years the whole space is once more occupied by Fucaceae, each species in its own belt. The dendritic algae are still present, but now in the undergrowth only, and of the tubular and membranaceous Algae only a few are left. Occasionally the succession proceeds so rapidly that the dendritic Algae appear only after the Fucaceae have developed into a closed vegetation.

In other localities the establishment of *Fucus* between the *Enteromorpha* vegetation may progress more slowly or not at all. In that case the *Enteromorpheto-Porphyretum* may be succeeded by dendritic and fruticose Algae, and as they are not crowded out by the Fucaceae,

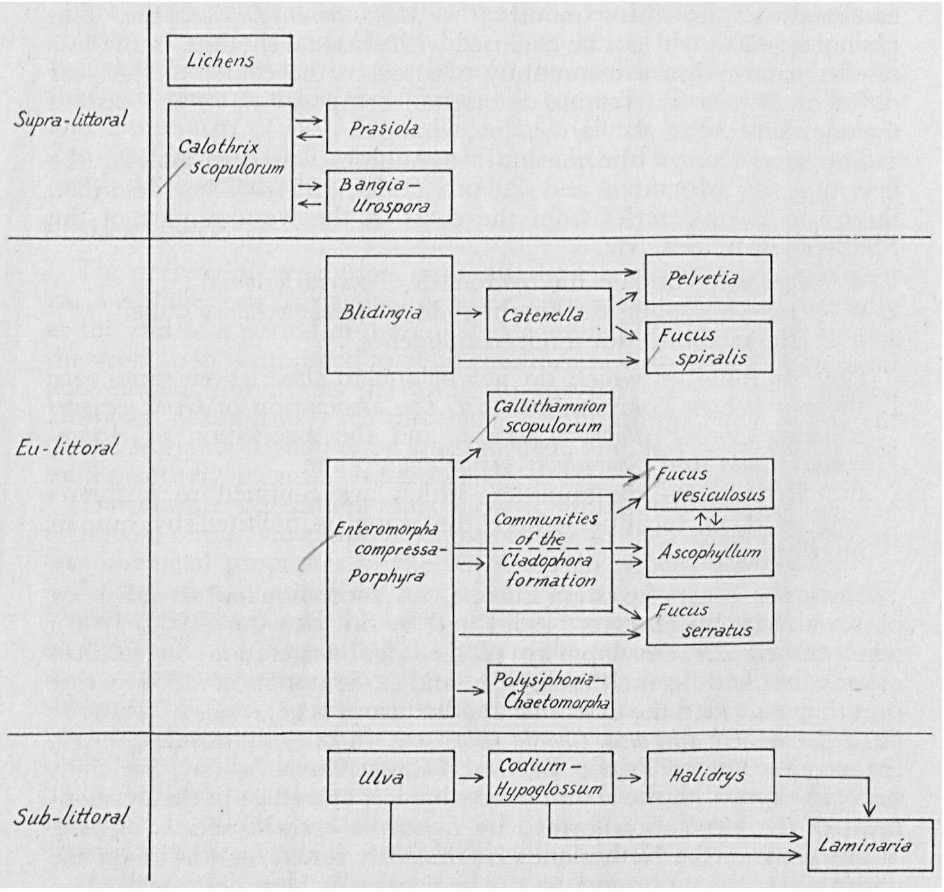


Fig. 13. Survey of the principal succession series in the southern North Sea.

they may develop into a luxurious vegetation. On the bituminized northern mole of Harlingen the *Enteromorpha-Porphyra* association was succeeded by a rich community of *Ceramium deslongchampii*, as Fucaceae do not grow at all or but poorly on bitumen.

The *Enteromorpheto-Porphyretum* maintains itself permanently in localities that are exposed to the surf and that at the same time are strongly overflown with sand, e.g. on breakwaters along the beach.

The divergent succession in the littoral vegetation is a remarkable phenomenon. In the tidal zone only two pioneer communities occur, viz. the *Blidingia* association and the *Enteromorpho-Porphyra* association. The *Blidingia* association occurs in the upper part of the littoral belt, and develops into two different climax communities, the *Pelvetia* association and the *Fucus spiralis* association. The *Enteromorpha-Porphyra* association establishes itself in the lower part of the littoral region, and is the starting point of four different series ending in four different climax communities. It is perhaps worth mentioning that in the course of the year and under the influence of fluctuations in humidity and in insolation the pioneer communities undergo displacements in a vertical direction.

What the final stage will be, is in the eulittoral region mainly determined by the hydrological condition.

In the sublittoral region, too, a succession series occurs; here the *Laminaria* association is the climax.

What climax communities occur on the coast of the Netherlands, is shown in table XIII.

TABLE XIII

Climax communities found on the coast of the Netherlands

Supralittoral	*Verrucaria maura* association *Calothrix scopulorum* association
Eulittoral	*Pelvetia* association *Fucus spiralis* association *Fucus vesiculosus* association *Ascophyllum nodosum* association *Fucus serratus* association *Polysiphonia-Chaetomorpha* association
Sublittoral	*Laminaria* association

The *Polysiphonia-Chaetomorpha* association, which occupies a position between the *Fucus serratus* zone and the *Laminaria* zone, is not a true climax, but a subclimax. Along the coasts of the English Channel (Beauchamp, 1914; Davy de Virville, 1940), in the Faeroes (Børgesen, 1905) along the west coast of Norway (Levring, 1937) at the same level a belt of *Himanthalia elongata* is found. The latter does not grow on the coast of the Netherlands, and the association to which it belongs, is here replaced by the *Polysiphonia-Chaetomorpha* association, which comprises several dendritic and fruticose Algae. This association, therefore, cannot be regarded as a climax; it is only able to maintain itself because the conditions for its replacement by the real climax are not fulfilled.

The algal communities of the supralittoral region are but little differentiated, and show no succession. The pioneer vegetation is also the final stage.

Although the Fucaceae communities are the final stages of the series in the eulittoral region, they do not maintain themselves permanently; they are periodically destroyed, and this happens in two different ways, viz. either by human interference or by floating ice. Destruction by floating ice takes place only in severe winters. The destruction by ice must be regarded as a natural phenomenon, and we might therefore regard the succession as cyclic or as a "cycle évolutive", to use the terminology of MOLINIER and PICARD (1953). It should, however, not be overlooked that the regression is always due to a catastrophe.

The sublittoral *Laminaria* community may also be destroyed by floating ice; I observed this at Den Helder in 1947.

I do not know of what kind the catastrophes are by which the vegetation in deeper water is destroyed, but it cannot be doubted that a considerable decrease in the temperature of the sea as well as changes in the direction of the currents may cause severe damage in the algal vegetation. That in Heligoland *Laminaria hyperborea* is washed ashore in considerable amounts, proves that at the depth at which this species grows, denudating forces make themselves felt.

7. SYSTEMS OF CLASSIFICATION

> "Die Natur wehrt sich einmal gegen die Systeme und es kann keiner, ohne den Verdacht der Anmassung oder Bornirtheit auf sich zu laden, von dem seinigen behaupten, dass es keiner Verbesserung fähig sei."
>
> KÜTZING, 1845 Phyc. germ. p. 34.

7.I. A SYSTEM BASED ON THE LOCALLY PREDOMINATING LIFE FORMS

The system of classification that was published by the author in 1955, was based on the locally predominating life forms. By testing its usefulness on other coasts of western Europe, it could be emended and extended and in this way its applicability was increased.

Our discussion of the phenomena of stratification and of succession has made it clear that the formations are, from a structural point of view, not all fully equivalent. The but slightly differentiated pioneer vegetations are composed of communities consisting of tubular and membranaceous Algae, whereas the final stages are composed of the highly organized Fucaceae associations and of the *Laminaria* association. The communities consisting of dendritic and fruticose Algae are but transitional stages in the succession. It appears therefore that the formations may be classified according to the position they occupy in the series and to the degree of organization they have reached, in other words according to the degree of sociological progression.

In this system of classification zonation is of less importance, but it may be used for the arrangement of the communities inside the formations, e.g. by starting with the uppermost zone.

In the southern part of the North Sea we may distinguish the following littoral formations:

1. The **Caloplaca** formation; this formation consists of foliaceous and fruticose lichens, and occurs in the supralittoral region.

It appears to be more or less heterogeneous, and it is not impossible that it will prove necessary to split it up. On the coast of the Netherlands it is badly developed, and here it has as yet not been studied sufficiently. Descriptions of the supralittoral lichen communities occurring in the Atlantic region were given by WEDDELL (1875), BOULY DE LESDAIN (1910), SERNANDER (1912), HAYRÉN (1914), DU RIETZ (1921, 1925), DES ABBAYES (1934), DAVY DE VIRVILLE (1930, 1932, 1933, 1938, 1939, 1940), DAVY DE VIRVILLE and FISCHER-PIETTE (1931), a.o.

A description of the supralittoral lichen communities occurring on the coast of the Netherlands falls outside the scope of this study. They have been mentioned here for the sake of completeness only.

Communities consisting of bryophytes have also been described from the supralittoral region, viz. by HAYRÉN (1914) and by DU RIETZ (1932).

Another vegetation unit that I wish to mention here, is that of *Asplenium marinum*, which I observed repeatedly along the coast of the English Channel, where it grew in supralittoral rock fissures in strongly shaded spots.

2. The **Hildenbrandtia** formation; this is a one-layered formation consisting of crustaceous Algae; it may develop into formations which show a higher type of organization.

This formation comprises inter alia the *Hildenbrandtia-Verrucaria mucosa* association and the supralittoral "black zone" (T. A. and A. STEPHENSON, 1949); the latter is a belt consisting of nigrescent Cyanophyceae and lichens (e.g. *Verrucaria maura*).

The *Hildenbrandtia* formation is not confined to the sea coast, but occurs also in fresh water. The *Hildenbrandtieto-Verrucarietum rheitrophilae* of the west and central European brooks shows a striking similarity in structure with the marine community.

Vegetations consisting of crustaceous, chalk-incrusted Algae, the "lithothamnia" are perhaps better included in the *Corallina* formation.

3. The **Prasiola** formation; this is a two-layered formation consisting of filiform and of small membranaceous Algae; in the supralittoral region it is confined to stones that are rich in nitrates.

The communities belonging to this formation are not found on the coast only, but they also occur along lake shores, on the stems of trees and on walls that are soiled with excrements, and even on resting places of birds of prey in the alpine zone.

4. The **Bangia** formation; this is a two-layered pioneer formation consisting of filiform Algae; in sheltered spots it is but an ephemerous stage, but in exposed stations in the supralittoral region it forms a permanent vegetation.

The *Bangia* formation occurs in salt, brackish and fresh water.

5. The **Enteromorpha** formation; this is a two-layered pioneer formation consisting of tubular, membranaceous and filiform Algae.

The *Enteromorpha* formation reaches its highest development in brackish water.

The formations 3, 4 and 5 resemble each other in some respects; this explains why the communities included in them have also been classified in other ways. BØRGESEN (1905), for instance, distinguished in the Faeroes 1°. a "*Chlorophyceae* formation", which comprises our *Prasiola* formation and a part of the *Enteromorpha* formation, 2°. a "*Porphyra* association", which is included here in the *Enteromorpha* formation, and 3°. a "*Bangia-Urospora* association". The classification adopted by JONSSON (1912) shows a much closer resemblance to the one proposed here, for he accepted 1°. a "*Prasiola stipitata* association", 2°. a "community of filiform Algae", and 3°. an "*Enteromorpha* association". The "*Porphyra* association", however, was incorporated by him into the community of filiform Algae instead of in the *Enteromorpha* formation; for the rest his community of filiform Algae corresponds with our *Bangia* formation.

6. The **Cladophora** formation; this is a two-layered formation consisting mainly of dendritic and fruticose Algae. It may be regarded as a transitional stage between communities belonging to the *Enteromorpha* formation and the formations formed by the larger Phaeophyceae.

Vegetations belonging to this formation are found on the coast as well as in brackish and fresh water.

Several of the authors who worked on the mediterranean, lusitanic and boreal-atlantic coasts, have distinguished a **Corallina** formation; the latter is characterized by the predominance of coralline Algae (*Corallina, Jania, Amphiroa*) and of "lithothamnia" (*Lithothamnion, Melobesia*), often accompanied by dendritic and fruticose Algae. In the southern part of the North Sea the coralline Algae never occupy a predominant position, and for this reason this formation is here left out of consideration.

7. The **Fucus** formation; this is a three-layered formation consisting of Fucaceae.

The *Fucus* formation is the final stage of the succession in the eulittoral region.

8. The **Sargassum** formation; this is a three-layered formation consisting of Sargassaceae.

The *Sargassum* formation occurs in the sublittoral region.

In the subtropical waters of the Mediterranean Sea (*Cystoseira*) and in tropical seas, too, the *Sargassum* formation is usually the final stage of the succession in the sublittoral region. In the seas of the temperate zone the communities which belong to this formation, are, as a rule, confined to special biotopes or they are an intermediate stage in the development of the *Laminaria* vegetations. In the northern part of the Atlantic waters the *Sargassum* formation is replaced by the **Desmarestia** formation.

9. The **Laminaria** formation; this is potentially a four-layered formation consisting of Laminariaceae.

The *Laminaria* formation is the final stage of the succession in the upper part of the sublittoral region.

Along the coasts of the Netherlands this formation is always three-layered. In the boreal seas, in which it reaches its highest development, it is four-layered, the undergrowth containing a layer consisting of *Desmarestia* species which is absent on the coasts of the Netherlands (BØRGESEN, 1905; KYLIN, 1907; JONSSON, 1912).

Table XIV gives a survey of the algal communities occurring in those parts of the coasts of the Netherlands that are subjected to the tides. The sequence of the communities from left to right indicates their sociological progression.

TABLE XIV

The algal communities occurring on the coast of the Netherlands

supra-littoral	"yellow zone"	Rosenvingiella			
	"black zone"	Prasiola stipitata			
		Bangia-Urospora			
eu-littoral	Hildenbrandtia-Verrucaria	Blidingia	Catenella	Pelvetia	
				Fucus spiralis	
		Enteromorpha compressa-Porphyra + Enteromorpha intestinalis-prolifera	Callithamnion scopulorum	Ascophyllum + Fucus vesiculosus	
			Ceramium deslongchampii + Chondrus	Fucus serratus	
			Polysiphonia-Chaetomorpha		
sub-littoral		Ulva	Codium-Hypoglossum	Halidrys	Laminaria

In general outline this classification is in agreement with the succession, but there are nevertheless some noteworthy differences, e.g. with regard to the position of the *Hildenbrandtia-Verrucaria* association, which may be found in the Netherlands as the last degeneration stage of the Fucaceae communities.

The sequence in the vertical direction indicates the position the communities occupy in the zonation. Sometimes a formation may be represented at a definite level by more than one community; in that case the distribution of these communities is determined by differences in other ecological requirements.

7.II. A SYSTEM BASED ON THE LIFE FORMS WHICH PREDOMINATE IN THE VARIOUS LAYERS

We might have based our system of classification also on another principle, viz. by paying special attention to the stratification of the vegetation. If we do this, it appears that the composition of the subordinate layers is in a large measure independent of that of the main one. The undergrowth of the *Fucus serratus* community, for instance, is the same as that found under *Fucus vesiculosus*, and it may even occur in spots where no *Fucus* layer is present.

The *Hildenbrandtieto-Verrucarietum mucosae* may also be adduced as an illustration. *Hildenbrandtia prototypus*, which is almost everywhere accompanied by *Verrucaria mucosa*, forms in shaded spots, especially on rocks containing silicates, a community of its own. This independent vegetation unit was observed in its most perfect form at Dinard and at Morgat in caves belonging to the eulittoral region. BØRGESEN (1905) found this community in the Faeroes at a high level in the supralittoral region, where it contained four species of *Verrucaria*. But we also meet this community as a crustaceous layer in the Fucaceae communities of the eulittoral region, where the dense canopy formed by the individuals of the *Fucus* species produces a sufficient decrease of the light intensity. In vegetations in which dendritic Algae play a predominant part and which are more "open", and where therefore a higher light intensity prevails, the *Hildenbrandtia-Verrucaria* community is less often met with. BØRGESEN (1905) regarded these *Hildenbrandtia* vegetations, no matter whether they occurred as independent communities or in the form of a definite layer, as belonging to one and the same association, the "*Hildenbrandtia* association".

The classification which was developed in the preceding section, and which is based on the locally predominating life forms, also recognizes a *Hildenbrandtia* community, but the latter is restricted to those local vegetations in which *Hildenbrandtia* is the predominating life form. The *Hildenbrandtia* vegetations which are part of a sociation or an association in which another Alga plays the part of the predominating life form, are in this classification included in these sociations or associations. It is, of course, a drawback of this system of classification that in this way an apparently natural entity is split up in different parts.

If we put ourselves on the standpoint that the various layers of which a vegetation may consist, are independent units, it becomes possible to subdivide the various sociations and associations in a number of one-layered communities, for which the name socions has been introduced. In that case these socions are the smallest vegetation units that can be distinguished. They, too, are characterized by the predominance of a single life form or by the joint predominance of a group of life forms; floristically they are therefore well-characterized. These socions, too, may be combined into higher units, which are more or less comparable to the formations. This system of classification we will indicate as the "socionic life forms system".

Fig. 14 shows a schematic picture of the zonation and stratification which we meet on the dikes of Schouwen (prov. of Zeeland) in sheltered spots. In fig. 14 A the association is taken as the basic unit, whereas in fig. 14 B the socion functions in that way.

The socionic life forms system has, notwithstanding its greater naturalness, some disadvantages that should also be taken into consideration. The first disadvantage is that the socions are not always at once recognizable in their natural habitat, because several of them may be present, so that the one withdraws the other from view. A second drawback is the large number of socions that ought to be distinguished; this makes the classification difficult to survey.

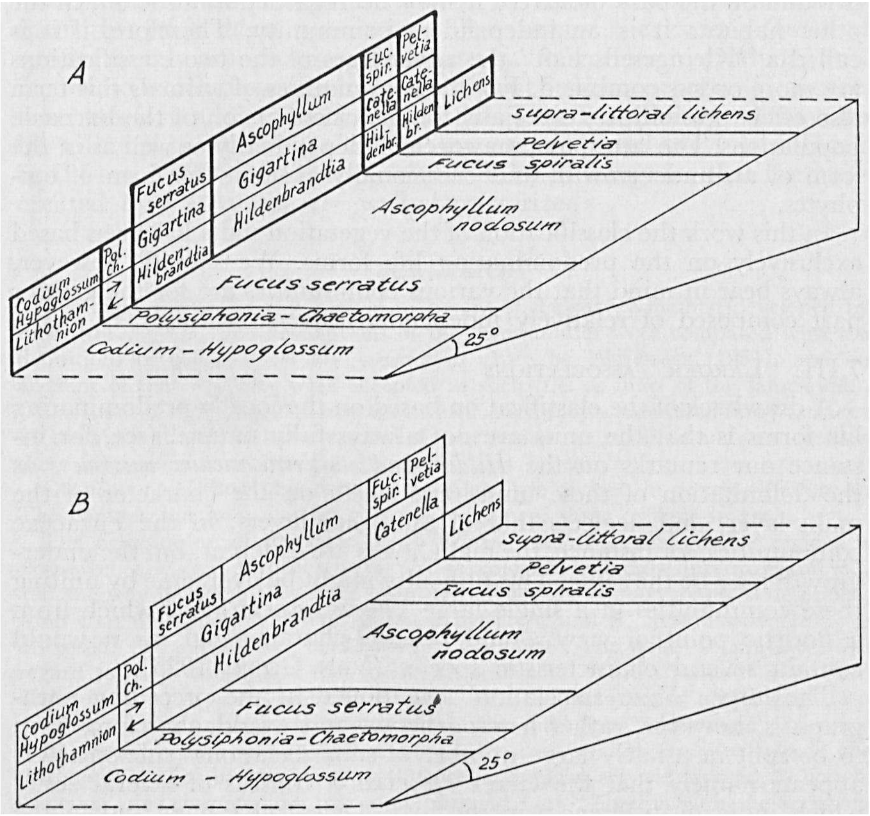


Fig. 14. Diagram of the zonation on a dike slope on the south coast of Schouwen. In diagram A the division of the vegetation according to the system of life forms dominance is given, the units are bordered by heavy lines; in diagram B the division is given according to the socions system of life forms.

In the classification that is based on the locally predominating life forms the vegetation units are in their natural habitat clearly defined; when the predominating life forms are replaced by other ones, this is at once noticed.

It is perhaps not impossible to combine the two systems into one. It would, for instance, be possible to regard the *Hildenbrandtia* community as a "Kleingesellschaft", i.e. as a community with a low degree of organization which, if circumstances are favourable, may also occur within another community. In the terrestrial plant communities a similar part is played, for instance, by several communities of bryophytes. The layer of bryophytes of the dry heath and of the oak-birch woods are in the main of the same kind. Some other communities of small plants are found as well on the bark of trees as on stones and on wooden fences, e.g. that of *Protococcus viridis*. If this algal growth is found on the bark of a tree, it may be regarded as a socion; in the other habitats it is an independent community. Therefore, if it is called a "Kleingesellschaft" the advantages of the two classifications are more or less combined. For the communities of animals this term also offers possibilities, especially for the classification of the barnacle populations. The latter, too, may occur independently as well as in the form of an undergrowth, and occasionally even in the form of epiphytes.

In this work the classification of the vegetation units has been based exclusively on the predominating life forms. We should, however, always bear in mind that the various communities are for the greater part composed of relatively independent layers.

7.III. "LARGER" ASSOCIATIONS

A drawback of the classification based on the locally predominating life forms is that the units are not always fully natural (see, for instance our remarks on the *Hildenbrandtieto-Verrucarietum mucosae*), as the delimitation of these units rests solely on the character of the main layer, and neglects that of the other layers; in the Fucaceae communities, for instance, the main layers are different, but the undergrowth may be the same. This difficulty might be overcome by uniting these communities in a single large "*Fucus* association", which from a floristic point of view would be well-characterized, as it would contain several characteristic species (VAN GOOR, 1923).

The large "*Fucus* association" mentioned in the preceding paragraph is, however, rather heterogeneous, and would, therefore, have to be split in a fairly large number of subassociations (subzones). It appears namely that the larger association consists of several zones which indicate differences in the hydrological character and in the light conditions of the environment, and which cannot replace each other. These subassociations differ from each other in the presence of "differentiating" species, which in this case are at the same time the characteristic species of the subassociations. By splitting the larger "*Fucus* association" in subassociations, we obtain therefore the same units as by basing the classification directly on these differentiating species. The only real advantage gained by the introduction of the larger "*Fucus* association" is that it permits us to regard a few littoral communities now included in the *Cladophora* formation, e.g. the *Chondrus* community and the *Gigartina* community, as stages in the development of this "*Fucus* association". However, as these stages are but sporadically met with, this advantage is of no practical importance.

A number of well-characterized units described by FELDMANN

(1938) from the coasts of the Mediterranean Sea have recently been united by MOLINIER and PICARD (1953) into a single "larger" association. It concerns the *Cystoseira mediterranea* association, the *Cystoseira elegans* association, the association of *Dictyopteris membranacea* and *Phyllaria reniformis*, the association of *Cystoseira discors* and *C. limbata*, and the facies of *Halopteris scoparia* and *Halopitys incurvus*, and the "larger" association in which they are united by these authors, is called by them the *Jania rubens* association. They regard the various *Cystoseira* species merely as indicators of the intensity of various hydrodynamical factors, to which they attach apparently but little importance. However, here, too, it should be realized that this *Jania* association will have to be split up in smaller units. On my excursions to the Côte d'Azur in 1954 and 1956 I had ample opportunity to recognize that the units created by FELDMANN are well-characterized.

SUMMARY

The algal vegetation was studied by means of the survey method developed by BRAUN-BLANQUET. The descriptions of the communities were compared with the definitions of the *sociations* and *associations* given by WESTHOFF (1951), and on account of that test they were accepted as such (i.e. as units of the same rank). On account of their physiognomy and stratification they were united into *formations*. By the aid of the same characters and of their position in zonation and in succession these formations were brought together into a system.

On account of their physiognomy the Algae are divided in groups (life forms). The communities may consist either of one, two, three or four layers.

The delimitation of the *supralittoral*, *eulittoral*, *sublittoral* and *elittoral* regions is extensively discussed. Hydrological as well as biological boundary lines are examined, and the way in which they have been determined on various coasts, is described. After that the zonation system proposed by T. A. and A. STEPHENSON (1949) is discussed. The terminology used by them is criticized, and doubt is expressed with regard to their assumption that a distinct sublittoral "fringe" would be present. These authors, however, must be credited with the discovery of a biological *basic zonation*, which appears to be cosmopolitan (littorinid belt, "black zone", barnacle belt). Besides this basic zonation regionally *accessory zonations* are found; the distinguishing features of the latter (Fucaceae, limpets) are wide-spread, although, of course, not cosmopolitan. By combining the basic zonation with the accessory zonation we obtain the *standard zonation* which is characteristic for a definite area. Differences in the environmental factors may cause local deviations from this standard zonation.

The causes of the zonation should not be confused with the causes which determine the development of a definite pattern of zonation. The opinion of most authors that the latter is due to the tidal movements, does not seem to apply to the zonation of the Fucaceae; the author himself ascribes this to differences in the effective amount of light.

With the algal vegetations of the eulittoral region *divergent* as well as *cyclic* succession occurs. If a single pioneer stage develops into various *"climax" communities*, we have to deal with divergent succession. In case of cyclic succession a *progression* is followed after some time by a *regression*. The "climax" stages are only destroyed by a catastrophe of some sort (floating ice, human interference). No succession at all is found in the supralittoral communities.

The classification of the communities may be carried out in different ways. The system of classification used in this work is based on the life forms which predominate

in the main layer of the vegetation. A disadvantage of this *system of predominating life forms* is that some combinations of Algae may occur as well as an independent community as in the form of an undergrowth in a community of a more complex structure. As the layers of such communities possess a certain degree of independence, it is also possible to base the classification on the combinations of species that are represented in these layers. In this way a large number of small units (layer communities or *socions*) may be distinguished. The latter are in the natural vegetation, as a rule, not at once distinguishable, and this is, of course, a disadvantage of this *socionic life form system*. A third possibility lies in the creation of "*larger*" *associations* (e.g. by uniting all Fucaceae communities into a single association), but this leads inevitably to a division of the larger associations into subassociations determined by hydrological factors (and by the total amount of light), and these subassociations prove to be identical with the associations recognized in the system of predominating life forms.

CHAPTER V

DESCRIPTION OF THE ALGAL COMMUNITIES

1. THE HILDENBRANDTIA FORMATION

The *Hildenbrandtia* formation comprises the plant communities of the simplest structure that are found on the coasts of the Netherlands. These communities are entirely composed of crustaceous Algae and of crustaceous lichens, and they consist of but a single layer. The formation as a whole is extremely heterogeneous in floristic composition. In the supralittoral region it appears in the form of a wide black belt consisting of Cyanophyceae and of black lichens; this is the "black zone" of the STEPHENSON's. In the eulittoral region the red *Hildenbrandtia* itself determines the aspect of the vegetation, and in the sublittoral region the crustaceous vegetation consists mainly of calcareous Algae. The latter, the lithothamnia, may form with some coralline Algae a distinct *Corallina* formation, but the latter does not occur in the southern part of the North Sea. The "black zone" has an almost cosmopolitan distribution.

Along the coast of the Netherlands the *Hildenbrandtia* formation is represented by three communities, viz.

1. the *Verrucarietum maurae*,
2. the *Calothricetum scopulorum*,
3. the *Hildenbrandtieto-Verrucarietum mucosae*.

1.I. The Verrucarietum maurae

The *Verrucaria maura* association, which is here for the first time recorded from the Netherlands, is on our coast but imperfectly developed. *Verrucaria maura*, the only characteristic species, has been found in Zeeland and on the West Frisian Islands, viz. on Texel, Terschelling and Ameland, but it will probably prove to be more generally distributed. On Terschelling *Verrucaria maura* appeared locally in the form of closed vegetations. Other lichens and Algae are but sparsely represented in this community.

In northern Europe the lower limit of this association is regarded as the boundary line between the eulittoral region and the supralittoral one.

The association also occurs in Brittany. On the 16th July 1954 I had the opportunity to study it in some detail at Roscoff. On the numerous blocks of rock at the southern side of the southern mole of the small harbour it proved to be well-developed. *Verrucaria maura* made its first appearance in the *Pelvetia* belt, and from the upper limit of the latter to a level 1.5 m higher on a black zone was noted in which *Verrucaria maura* was by far the most prominent species. In the upper part of this zone, however, some other lichens were represented; the latter were immigrants from the *Caloplaca* zone.

TABLE XV

Verrucarietum maurae

Sample plots	1	2	3	4
Percentage of covering	100	55	95	85
Verrucaria maura	5	4	5	4
Lichina confinis	—	—	+	2
Intruders from the eulittoral region:				
Hildenbrandtia prototypus	1	—	—	—
Verrucaria mucosa	+	—	—	—
Rhodochorton purpureum	+	—	—	—
Pelvetia canaliculata	—	—	+	—
Intruders from the Caloplaca zone:				
"Caloplaca marina"	+	—	+	2
Lecania erysibe var. erysibe	+	—	—	—
Xanthoria parietina	—	—	—	1
Caloplaca cf. murorum	—	—	—	1
Ramalina siliquosa	—	—	—	2

LEGENDA

1. West Terschelling, at the inner side of the "Kom" a 40 cm wide *Verrucaria maura* zone, at the upper margin bordered by an extremely narrow (10—15 cm) *Caloplaca marina* zone; at the lower margin bordering on the *Hildenbrandtieto-Verrucarietum mucosae*; in fissures the latter penetrates into the *Verrucaria maura* zone. Substrate: granite; surface: 3 m² exposition: north-east; inclination: 40°; 10.VI.'58; CH 58011.

2. West Terschelling, on the first part of the "Grote Dam" a circ. 40—50 cm wide *Verrucaria maura* zone, above bordering on a zone in which *Lecania erysibe* predominates, below adjoining the *Hildenbrandtieto-Verrucarietum.* Substrate: granite; surface 2 m²; exposition: north; inclination: 30°; 11.VII.'58; CH 58016.

France:

3. Roscoff (Finistère), on blocks of rock at the southern side of southern mole of the harbour; *Verrucaria maura* predominates; nearly flat piece, circ. 70 cm above the *Pelvetia* zone. Surface: 2 m²; exposition: east; inclination: 5°; 16.VII.'54; CH 54078.

4. Roscoff (Finistère), on the same blocks but 1 m higher. Surface: 0.5 m²; exposition: south-east; inclination 40°; 16.VII'54; CH 54079.

FELDMANN (1938) describes from the coast of the Mediterranean Sea a *Verrucaria symbalana* association.

1.II. The Calothricetum scopulorum

The *Calothrix scopulorum* association, too, is here for the first time recorded from the Netherlands. On the southern mole at the entrance of the North Sea Canal at IJmuiden it forms a 60 cm wide zone, and it is also met with on the northern mole at Hook of Holland.

Calothrix scopulorum is the only characteristic species of this association. In the Netherlands its floristic composition has not yet been studied. For the west coast of Sweden a good floristic description of this association has been given by LINDSTEDT (1943). In the 10 sample plots which he surveyed, *Calothrix scopulorum* and *Phormidium fragile* were always present; *Plectonema battersii* was recorded 9 times and *Gloeocapsa crepidinum* 6 times. These four species are also repeatedly mentioned by VAN DEN HOEK (1958) in his study on the northern mole at Hook of Holland; they form here a supralittoral belt in which *Gloeocapsa crepidinum* predominates. In the sample which I collected on the 30th November 1955 at IJmuiden *Phormidium fragile* was the only one of these four species which was not represented.

The *Calothrix scopulorum* association is widely distributed in the supralittoral region of northern Europe. The black belt which it forms especially on vertical walls, was also observed by me on Heligoland and near Roscoff. In spring it is sometimes covered by a short-living growth consisting of *Bangia atropurpurea* f. *fuscopurpurea* and of the *Urospora* stage of *Codiolum penicelliforme*; this was observed also by VAN DEN HOEK at Hook of Holland. Sometimes it is overgrown by a vegetation of *Prasiola stipitata* or of *Rosenvingiella polyrhiza*, but a covering of this kind persists throughout the year.

1.III. The Hildenbrandtieto-Verrucatietum mucosae

The association of *Hildenbrandtia prototypus* and *Verrucaria mucosa*, too, is here for the first time recorded from the Netherlands. That *Hildenbrandtia prototypus* occurs in the undergrowth of the Fucaceae communities, was, however, since long known.

A *Hildenbrandtia* association was mentioned for the first time by BØRGESEN (1905) in his study of the algal vegetation of the Faeroes. However, he applied this name not only to the association itself, but also to the undergrowth of *Hildenbrandtia* found in the Fucaceae communities.

Hildenbrandtia prototypus and *Verrucaria mucosa* are both strongly sciaphilous species, and both occur throughout the whole eulittoral region. The dense canopy formed by the Fucaceae provides them with enough shade, and under the latter large surfaces accordingly appear to be coloured by this growth. As an independent community the *Hildenbrandtieto-Verrucarietum* is only found in spots where the light intensity is so low that other Algae are unable to grow in them, e.g. in caves in the eulittoral region. From such localities on the coast of the Mediterranean Sea it has been recorded by FELDMANN (1938), on the coast of Brittanny by LAMI (1940); from the Faeroes and the coast of Norway it is also known. In the Netherlands it was found by

Tulp (1953) between Ezumazijl and Oostmahorn, where it originally must have formed the undergrowth of Fucaceae communities; the Fucaceae themselves, however, had disappeared, presumably they had been destroyed by floating ice. The crustaceous Algae now form in this place a very uniform vegetation. Similar vegetations were observed by me on blocks of granite near West Terschelling. Remarkable enough, the community was at that place not confined to spots that were exposed towards the north and the east, but it was also found on the southern slope of the "Grote Dam", where it was exposed to strong insolation. Here, too, it appeared to be what was left of a Fucaceae community, in this case of a *Fucetum vesiculosi*, in which the *Fucus* individuals had been destroyed, here by periwinkles, which were present in large numbers.

TABLE XVI

Hildenbrandtieto-Verrucarietum mucosae

Sample plots	1	2
Percentage of covering	90	5
Hildenbrandtia prototypus	4	1
Verrucaria mucosa	3	1
Fucus vesiculosus	+	—
Gigartina stellata	+	—

LEGENDA

1. West-Terschelling, on the first part of the "Grote Dam"; *Hildenbrandtia-Verrucaria mucosa* growth on blocks of granite. Surface: 0.5 m^2; exposition: south; inclination: 30°; 11.V.'58; CH 58012.

France:

2. Dinard (I. et V.), Plage de St Enogat, in the deepest part of the rock fissure in which *Waerniella* grows. Surface: 0.5 m^2; 27.VII.'54; CH 54104.

Where this community occurs under the canopy of the *Fucus* plants, the percentage of covering often amounts to 70 and more. With regard to the way in which it is to be classified, it is perhaps worth while to repeat that Børgesen's *Hildenbrandtia* association is to be regarded as a quite natural unit, which fits very well into a classification which regards the socions as the basal units. However, as the classification used in this work is based on associations which are characterized by the life forms occurring in the main layer, we include in our association only those *Hildenbrandtia* communities which in the spots where they occur, are themselves the predominating vegetation. We admit that this is not fully satisfactory, but we have to accept this disadvantage because it is a natural consequence of our system of classification.

2. THE PRASIOLA FORMATION

This formation is confined to the supralittoral region, where it forms a more or less wide belt (on the strongly exposed coast of the Faeroes it reaches up to 25 m above sea level) on stones and on rocks, and occasionally also on other substrates, that are rich in nitrates and in organic substances. It consists, as a rule of two layers, of which the upper one is formed by appressed filiform and small membranaceous Chlorophyceae, whereas the lower one, which is not always present, consists of black crusts formed by Cyanophyceae. The formation occurs on all northern Atlantic and northern Pacific coasts. Along the coast of the Netherlands it is represented by two associations, viz. the *Prasioletum stipitatae* and the *Rosenvingielletum polyrhizae*; the latter occurs on a higher level than the first. On the bird islands in the Atlantic Ocean in addition a belt consisting of *Prasiola furfuracea* is found.

Prasiolaceae are not confined to these supralittoral communities; they also occur on lake shores, and take part in some aerophilous communities; the *Prasioletum crispae*, for instance, is found in the Netherlands on the wet side of tree trunks of which the bark has a basic reaction (*Ulmus*, *Populus*).

2.I. **The Prasioletum stipitatae**

The *Prasiola stipitata* association is recorded here for the first time from the coast of the Netherlands. However, although it was discovered but recently, it is by no means rare. Because of the small size of the species of which it consists, it has presumably been overlooked.

LEGENDA (see table XVII)

1. Den Helder, sea-dike, ultimate end of the harbour, at Fort Oostoever. *Prasiola stipitata* vegetation on granite, just above high-water level; surface: 2 m^2; exposition: north-east; inclination: 10—15°; 23.XII.'53; CH-H 1.
2. Den Helder, sea-dike, on wooden pales near the monument, a poor *Prasiola* vegetation, in the supralittorial region, but exposed to a strong surf; surface: 0.04 m^2; 24.VIII.'54; CH 54145.
3. IJmuiden, on the inner side of the southern mole; a well-developed *Prasiola stipitata* vegetation, 0.5—1.5 m above high-water level; surface: 1 m^2; exposition: north; inclination: 90°; 7.VI.'53; CH 53046.
4. IJmuiden, inner breakwater near the lighthouse; *Prasiola stipitata* vegetation on basalt; surface: 10 m^2; 1.V.'55; CH 55028.
5. Wemeldinge, on the inner side of the sluice in the Canal through Zuid-Beveland; well-developed *Prasiola stipitata* vegetation on blocks of basalt; surface: 1 m^2; 28.III.'55; CH 55003.
6. Noord-Beveland, Kamperland; pure *Prasiola stipitata* vegetation without any accompanying species on a breakwater built of basalt blocks; surface: 2 m^2; 29.V.'55; CH 55029.
7. Flushing, near the harbour for the fishing boats; poor *Prasiola stipitata* vegetation on wood; surface: 0.12 m^2; 3.XII.'55; CH 55104.
8. Canal through Zuid-Beveland, at the Post bridge; a 0.2 m wide belt of *Prasiola stipitata* extending just above the *Ulothrix* zone; surface: 1 m^2; exposition: west; inclination: 30°; 14.V.'56; CH 56013.
9. West-Terschelling, on the dike of "de Kom"; luxurious *Prasiola stipitata* vegetation on blocks of granite; surface: 0.25 m^2; exposition: east; inclination: 10°; 9.VI.'58; CH 58005.
10. West-Terschelling, "Grote Dam", at the very beginning of the "Vleugel";

TABLE XVII
Prasioletum stipitatae

Sample plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Percentage of covering	90	100	70	60	80—85	40	20	30—35	70	80	70	20	100	30	80	90	40	70
Prasiola stipitata	5	2	4.4	4	5	3	2	3	4	5	4	2	4	3	5	5	1	4
Rosenvingiella polyrhiza st. submarina	+	+	1.2	+	+	—	—	—	+	—	2	—	+	+	+	+	—	+
Prasiola calophylla	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—
Gloeocapsa crepidinum	—	5	—	—	—	—	—	—	+	—	—	+	5	+	2	+	1	+
Blidingia minima	+	—	+°	+	+	—	—	—	+	—	—	—	—	—	—	—	+	—
Codiolum penicelliforme st. urosporae	—	—	—	+	+	—	—	—	+	—	—	+	—	—	—	—	—	—
Ulothrix subflaccida	—	—	—	—	+	—	—	—	+	—	—	—	—	+	+	—	—	—
Bangia atropurpurea f. fuscopurpurea	+	—	—	—	+	—	—	—	+	—	—	—	—	—	—	—	—	—
Ulothrix flacca	—	+	—	—	+	—	—	—	+	—	—	—	—	—	—	—	—	—
Calothrix scopulorum	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	2	+	—
Verrucaria maura	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	1
Oscillatoria brevis	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	+

Addenda: survey 9: Ulothrix pseudoflacca +, Chlorochytrium willei +, Lyngbya infixa +; survey 10: Hildenbrandtia prototypus +; survey 16: Lyngbya semiplena +; survey 18: Plectonema battersii +.

Prasiola stipitata forms here small vegetations on a resting place of gulls; surface: 1 m²; nearly flat; 11.VI.'58; CH 58015.

Germany

11. Cuxhaven, Alte Liebe, on stones below the landing-place; a well-developed *Prasiola stipitata* vegetation just above the *Blidingia* zone and at its upper margin bordering on a belt of *Rosenvingiella*; surface: 2 m²; 19.VIII.'55; CH 55055.
12. Flensburg, on stones at the shore of the Flensburger Föhrde; poor *Prasiola stipitata* vegetation; surface: 0.12 m²; 10.IX.'55; CH 55098 A.

Denmark

13. Hvide-Sande, at the discharging sluice of the Ringkøbing Fjord; *Prasiola stipitata* vegetation on wooden pales, bordering below on a belt of *Rhizoclonium riparium*; surface: 0.05 m²; exposition: south-west; inclination: 90°; 30.VIII.'55; CH 55082.
14. Saeby, on the Kattegat; on blocks of granite at the outside of the small harbour mole, near the latter's end; small vegetations of *Prasiola stipitata*; surface: 1 m²; exposition: east; inclination: 25°; 1.IX.'55; CH 55084.
15. Frederikshavn; a 20—25 cm wide belt of *Prasiola stipitata* on the sheltered inside of the southern harbour mole; surface: 1 m²; exposition: north; inclination: 30°; 1.IX.'55; CH 55086.

France

16. Roscoff (Finistère), flight of stairs at the small harbour, well-sheltered; *Prasiola stipitata* vegetation above the high-water mark (only the vertical parts of the steps were studied); width of the belt: 60 cm; surface: 1 m²; exposition: north; inclination: 90°; 16.VII.'54; CH 54074.
17. Roscoff (Finistère), southern mole, at the entrance of the harbour on a tread of the stairs; rich *Prasiola stipitata* vegetation; surface: 0.12 m²; 16.VII.'54; CH 54077.
18. Camaret sur Mer (Finistère); *Prasiola stipitata* vegetation on stones that had been polluted with urine, just above high-water mark; at its upper margin bordering on a belt of *Rosenvingiella*; surface: 1 m²; exposition: south; inclination: 10—40°; 18.VIII.'54; CH 54088.

The only characteristic species of the *Prasioletum stipitatae* is *Prasiola stipitata*, a perennial Alga which is very firmly attached to the substrate, and reaches a height of 1 cm. It covers the whole substrate with a dense felt, in which often no other species are represented. Its presence is often ascribed to the influence of birds, who enrich the substrate, by means of their excreta and of the rests of their meals, with organic substances and with nitrates; where such a dressing does not take place, the *Prasiola* vegetation makes but a poor impression. In Sweden *Rosenvingiella constricta* was collected a few times in this association (Waern, 1952), and this Alga may therefore be regarded as possibly a second characteristic species. On the coasts of the Netherlands it has not been found so far.

The number of companion species is but small. The species which is most often met with, is *Rosenvingiella polyrhiza* st. *submarina*, which becomes dominant in the next higher zone. In strongly exposed spots, but also in very quiet ones, the *Prasioletum stipitatae* and the *Rosenvingielletum polyrhizae* are not always sharply separated. In strongly exposed spots the humidity of the air decreases but gradually in the upward direction, and for this reason the two associations are connected with each other by a transitional zone in which *Prasiola* and *Rosenvingiella* occur side by side. This may be seen at IJmuiden, where the *Prasioletum stipitatae* forms a belt between 0.5 and 1.5 m above the mean high-tide level, whereas the *Rosenvingielletum* is found between 2 and 3 m; between 1.5 and 2 m they form a mixture. In very quiet spots the two associations are more or less pressed together into a single unit. As there is but little spray, the environment is unfavourable for their development, and in the most suitable places they compete with each other; this leads to the development of a narrow zone in which the two species occur together; in this narrow zone nevertheless indications may be found for the presence of two zones, but these indications are often indistinct.

Among the companion species there are also some intruders from the communities growing at a lower level. *Bangia atropurpurea* f. *fuscopurpurea*, *Codiolum penicelliforme* st. *urosporae* and *Ulothrix subflaccida* are immigrants from the *Bangieto-Urosporetum*; *Blidingia minima* hails from the *Blidingietum minimae*, and *Ulothrix flacca*, too, comes from a lower level. In strongly exposed spots these species often ascend to a considerable height in the supralittoral region; in very quiet spots they can penetrate into the *Prasioletum*, because in such places the various belts are very close together. A single somewhat higher tide often suffices for the establishment of these intruders. The latter, however, are present in small numbers only, and they do not affect the general aspect of the vegetation (cf. also JONSSON, 1912: 100).

An undergrowth is often absent in the *Prasioletum*, but where it is present, it consists of black crusts formed either by the Cyanophyceae *Gloeocapsa crepidinum* and *Calothrix scopulorum* or, more rarely, by the lichen *Verrucaria maura.*

According to the literature three more Algae may be present as companion species, viz. *Prasiola calpphylla* (KNEBEL, 1936), *P. furfuracea* and *Rhizoclonium riparium* (JONSSON, 1912). The two species of *Prasiola* have not yet been found in the Netherlands, and *Rhizoclonium riparium* was not yet observed in the *Prasioletum*, although it is a common species on our coasts. At IJmuiden it forms a narrow belt between the *Bangieto-Urosporetum* and the *Prasioletum stipitatae.*

SYNECOLOGY

The *Prasioletum stipitatae* is an association which is confined to the supralittoral region; only once a few individuals of *Prasiola stipitata* were found in the eulittoral *Blidingietum minimae*; this happened in spring, but as the *Blidingietum* penetrates during the winter months into the supralittoral region, from which it withdraws again in the first months of the summer, i.e. when the habitat becomes to dry for it, it is not excluded that the two associations may undergo a fusion; such a fusion would be facilitated by the circumstance that the Prasiolaceae are perennials.

As a rule, the *Prasioletum* forms a belt above the *Bangieto-Urosporetum*, but under the influence of the surf and of topographic factors like exposition and inclination, and occasionally on account of the shape of the substrate the two associations may also be united into a single one.

At the upper side the *Prasioletum* often borders on the *Rosenvingielletum polyrhizae*. The width of the belt occupied by the *Prasioletum* depends to a high degree on the way it is exposed to the surf.

According to BØRGESEN (1905) and to JONSSON (1912) the association shows a preference for horizontal or but slightly sloping rock surfaces on which colonies of birds are found. SJØSTEDT (1928), too, reports that it is best developed in localities that are frequented by birds ("bird tops"), which give these spots their eutrophic character. WAERN (1952), too, draws the attention to the importance of bird droppings. On the coasts of the Netherlands no bird rocks are found, and here the association is almost entirely confined to harbour works, where it grows not only on the horizontal surface of the stones, but also on vertical walls like that at the inside of the southern mole at IJmuiden. At this place it is sprayed with the dirty water of the harbour which probably has a similar nutritive value as the bird droppings. On places that are used as a public urinal, e.g. on the flights of stairs, the *Prasiola* vegetation appears to be especially well-developed, with the individual Algae not rarely exceeding a height of 1 cm. At Camaret sur Mer (Finistère) I observed a similar situation. One of the habitats on Terschelling, viz. the one at the end of the harbour mole of West-Terschelling, was centred round a beacon on which continually gulls alighted. Its occurrence on the pales of the sea-dike at Den Helder will probably be due to the same cause.

At Den Helder the association is also found in some places on the slope of the dike, be it in a rather poor condition. At these places the mantle of the dike consists of granite blocks which are cemented together by means of concrete, and the association occurs here in a 0.5 m wide belt, just above the part that is covered with basalt. It shows here a preference for the narrow fissures and pits in the concrete, where it is more or less protected against the sun, and therefore not so much exposed to desiccation. The individual Algae reach but a small size, as they are flooded only during spring tides and storms by the spray and, of course, when it is raining. In the latter case a large part of rain water flows off along the fissures in the concrete.

BØRGESEN, too, (1905) noted that *Prasiola stipitata* shows a preference for places where fresh water runs off. However, it is not so much the fresh water itself, but the substances it dissolves from rotting detritus that is washed ashore, and from the droppings of birds, which are of importance to this Alga.

In the habitat at Den Helder *Prasiola* was sometimes accompanied by *Rosenvingiella polyrhiza* st. *submarina* (see also p. 49).

AREA OF DISTRIBUTION

In the Netherlands the *Prasioletum stipitatae* occurs along the whole length of the coast, usually in the form of vegetations of a restricted extent in which it is sometimes beautifully developed.

The association is widely distributed in the northern part of the Atlantic Ocean. Jonsson (1912) records its presence in Iceland, Foslie (1890) in Finmarken; further it has been described from the Faeroes (Børgesen, 1905), from the west coast of Ireland (Cotton, 1912), from the west coast of Norway (Levring, 1940), from the Oslo Fjord (Sundene, 1953) and from the coasts of the Baltic Sea (Sjøstedt, 1922 and 1928; Waern, 1952). *Prasiola stipitata* itself has been recorded from numerous localities, and we know that its area of distribution extends southwards as far as n.w. Spain. This area was mapped by Knebel (1936). From the east coast of North America only one habitat has been mentioned, viz. Woods Hole, Mass. (Collins, 1916).

2.II. **The Rosenvingielletum polyrhizae**

The *Rosenvingiella polyrhiza* association is, like the *Prasioletum stipitatae*, a community which is here mentioned for the first time from the coast of the Netherlands. It is here not rare, but as it is confined to habitats of an even more restricted extent, it is less conspicuous than the other association.

TABLE XVIII

Rosenvingielletum polyrhizae

Sample plots	1	2	3	4
Percentage of covering	60	80	60	85
Rosenvingiella polyrhiza				
st. submarina	4	5.4	4	5
st. gayellae	—	—		—
Prasiola stipitata	—	1.2	—	—
"Caloplaca marina"	+	—	—	—
Gloeocapsa crepidinum	—	—	+	—
Bangia atropurpurea f. fuscopurpurea	—	—	2	—
Symploca atlantica	—	—	+	—

LEGENDA

1. Den Helder, sea-dike; on the encircling wall, at pale 6; a fairly extensive growth, almost entirely consisting of *Rosenvingiella*; at a considerable height above the high-tide level and in a spot where dogs are used to urinate; surface: 0.25 m^2; exposition: north; inclination: 90°; 13.VI.'53; CH 53048.

2. IJmuiden, southern mole; on the inside against the steep wall; closed vegetation of *Rosenvingiella*, circ. 2—3 m above the high-tide line; surface: 1 m^2; exposition; north; inclination: 90°; 7.VI.'53; CH 53047.

3. Spaarnwoude (to the east of Haarlem), Mooie Nel; on a wooden lining; a habitat of *Rosenvingiella* at a considerable distance from the sea and at a place where the water is oligohaline (0.4—0.5 $^0/_{00}$ Cl'); above the water level; surface: 0.25 m^2; 18.III.'56; CH 56001.

France

4. Camaret sur Mer (Finistère); *Rosenvingiella* vegetation on stones that are polluted with urine, just above the *Prasiola stipitata* belt; surface: 1 m^2; exposition: south; inclination: 10—40°; 18.VII.'54; CH 54088 A.

The only characteristic species of this very uniform association is *Rosenvingiella polyrhiza* *) st. *submarina*, a delicate monosiphonous Alga provided with rhizoids consisting of one to four cells. In the st. *gayellae* the cells divide in all directions so that the filaments become polysiphonous. This stage was only rarely met with; it was collected in the supralittoral region at Zoutkamp, and also in the brackish water of the "Mooie Nel", east of Haarlem. Actually *Rosenvingiella polyrhiza* is the only species, for *Prasiola stipitata* may be regarded as an intruder from a lower level, and "*Caloplaca marina*" grows usually at a greater height. The crustaceous layer is usually absent; if it is present, it consists of *Verrucaria maura* or of *Calothrix scopulorum.*

SYNECOLOGY

Along the coast of the Netherlands the *Rosenvingielletum* is but rarely well-developed. In the zonation it has its place above the *Prasioletum stipitatae,* but it forms only occasionally a true zone; as a rule, it appears in the form of isolated green spots. The only example of a well-developed zone was found on the inside of the southern mole at IJmuiden, where it occurs at a height of 2 to 3 m above the mean high-tide level.

At Den Helder *Rosenvingiella* is found on the sea-dike where it grows on the walls of bunkers dating from the war; it occurs there in the form of green patches at those places where dogs are in the habit of urinating. Only when there blows a strong north or north-west wind, these places are splashed with sea-water; in other circumstances they are outside the reach of the latter. In other localities, too, where this species occurs, a correlation was noted with local pollution by means of urine or of bird droppings; at Delfzijl I only found it round a pale on the harbour mole on which regularly birds were alighting.

That *Rosenvingiella* is not such an outspokenly marine species as *Prasiola stipitata,* appears also from the fact that it was collected about 500 m from the sea on a bunker built on the Noorderleegh, an extended salt marsh in Friesland. The "*Prasiola crispa* f. *radicans*" and "*f. torta*" which were recorded by BRAND (1914) from the inland of Germany, were undoubtedly misidentified forms of *Rosenvingiella polyrhiza.* In the Netherlands this species was found by me along the oligohaline expanse of water called "Mooie Nel", where the st. *submarina* as well as the st. *gayellae* occurred.

AREA OF DISTRIBUTION

The *Rosenvingielletum polyrhizae* occurs in the Netherlands locally along the whole length of the coast. Its distribution in the Atlantic Ocean is not well-known, as *Rosenvingiella polyrhiza* st. *submarina* has often been confused with *Prasiola crispa* st. *hormidii,* and as it has even been misidentified as a species of *Ulothrix.* However, it can not be doubted that this association is commonly distributed in the

---

*) The genus *Rosenvingiella* was originally called *Gayella,* but as this name had already been used for a genus of Phanerogams, SILVA (1957) has introduced for the algal genus the name *Rosenvingiella.*

northern part of the Atlantic Ocean, as it has been found from Greenland (ROSENVINGE, 1893) to Brittany; it has also been recorded from the Baltic Sea (WAERN, 1952). It occurs also on the North-American coast of the Pacific Ocean.

3. THE BANGIA FORMATION

The *Bangia* formation comprises the two-layered communities of filamentous Algae which in exposed spots often form a belt above the mean high-water line. The upper storey consists of filamentous Algae belonging to the genera *Bangia*, *Codiolum* *), *Ulothrix* and *Rhizoclonium*. The lower storey is not always present, but if so, it consists of crusts formed by the Cyanophyceae *Calothrix*, *Gloeocapsa* and *Lyngbya*.

The *Bangia* formation is found in all the seas of the arctic and temperate regions of the northern hemisphere, and may perhaps also occur in the southern hemisphere. Along the coast of the Netherlands it is represented by a single association only, the *Bangieto-Urosporetum*, but in fresh and brackish water a second association occurs, viz. the *Bangieto-Ulothricetum tenerrimae* (DEN HARTOG, 1958). In the mesohalinicum these two communities are connected with each other by transitional stages.

Before entering on a discussion of the *Bangieto-Urosporetum* I wish to make a few remarks on the eulittoral *Ulothrix* vegetations. *Ulothrix flacca* is one of the most important components of the *Enteromorpheto-Porphyretum* and of the *Blidingietum minimae* as well, and often appears in these associations as the dominant or even as the only present species. On account of its life form such a vegetation ought to be included in the *Bangia* formation, but its position in the succession and in the zonation make it more plausible to give it a place in the *Enteromorpha* formation.

3.I. The Bangieto-Urosporetum

From the Netherlands the complete association of *Bangia atropurpurea* f. *fuscopurpurea* and *Codiolum penicelliforme* st. *urosporae* was not yet

---

*) JORDE (1931) discovered that *Codiolum gregarium* and *Urospora mirabilis*, which so far had been regarded as representing two different families, were in reality stages in the life cycle of one and the same Alga. The filaments known as *Urospora mirabilis* first produce zoospores, but at the end also gametes, some of the filaments male ones, others the considerably larger female ones. The zygotes remain inactive for a period of 4 to 5 months, and then develop into the small plants which were known so far as *Codiolum gregarium*. These dwarf plants produce zoospores which in their turn grow out to small plants, but some of the filaments of the latter assume the form known as *Urospora mirabilis*. The reduction division and sexual differentiation takes place in the *Codiolum* stage, viz. at the production of the zoospores.

SILVA (1957) introduced for this species the new combination *Codiolum penicelliforme* (Roth) Silva, which is in agreement with the code of botanical nomenclature. Similarly the names *Urospora wormskioldii* (Mert.) Rosenv. and *U. hartzii* Rosenv. have to be replaced by **Codiolum wormskioldii** (Mert.) den Hartog nov. comb. and **C. hartzii** (Rosenv.) den Hartog nov. comb.

The dimorphic life cycle and the presence of anisogamy make it desirable to create a separate family for the genus *Codiolum*.

Codiolaceae *familia nova Chlorophycearum a Cladophoraceis generationum alternatione dimorpha et cellulis sexualibus dimorphis recedens.*

recorded. Only fragments were described so far, viz. the „*Urospora* Assosiation" found by VAN GOOR (1923) at Stavoren, and the *Ulothrix subflaccida* zone which was mentioned by DEN HARTOG (1953) from the Canal through Zuid-Beveland. KOSTER (1952), however, published a large number of localities on the coast of the Netherlands where *Bangia* had been found, and this justifies the conclusion that this association cannot be rare. At Hook of Holland all its components were met with by VAN DEN HOEK (1958).

TABLE XIX

Bangieto-Urosporetum

Sample plots	1	2	3	4	5	6	7	8	9	10
Percentage of covering	100	95	70	95	80	80	80	70	80	20
Bangia atropurpurea f. fusco-purpurae	2	2	2	3	2	4	5	2	1	+
Codiolum penicelliforme st. urosporae	5	5	4	2	2	1	1	3	+	2
Ulothrix subflaccida	—	—	—	—	1	—	+	—	4	1
Lyngbya semiplena	—	—	—	1	3	2	1	—	—	+
Lyngbya confervoides	—	—	—	2	—	1	—	—	—	—
Ulothrix pseudoflacca	—	—	—	—	—	—	—	+	—	—
Blidingia minima	+	1	2	2	1	3	1	1	+	+
Enteromorpha compressa	+	+	+°	+	—	+	+	+	—	+
Ulothrix flacca	1	+	+	+	1	—	+	1	—	+
Porphyra umbilicalis	—	2	2	2	+	+	+	2	—	—
Gloeocapsa crepidinum	—	1	2	2	1	—	+	—	—	+
Lyngbya aestuarii	—	—	+	1	2	—	—	1	+	+
Fucus vesiculosus	—	+°	+°	+°	—	—	—	—	—	—
Plectonema battersii	—	+	—	1	1	—	—	—	—	—
Rhizoclonium riparium	—	—	—	—	2	—	—	2	—	—
Ralfsia verrucosa	—	—	—	1	—	—	—	1	—	—
Pylaiella litoralis	—	+	—	+	—	—	—	—	—	—
Petalonia zosterifolia	—	+	+	—	—	—	—	+	—	—
Ulva lactuca	—	+°	—	—	—	+°	—	—	—	—
Microcystis reinboldii	—	—	—	—	+	—	—	+	—	—
Chlorochytrium willei	—	—	—	—	—	+	—	+	—	—
Chroococcus turgidus f. submarinus	—	—	—	—	+	—	—	—	—	+
Monostroma oxyspermum	—	—	—	—	—	—	—	—	+	+

Addenda: survey 4: Phormidium valderianum +; survey 5: Caloplaca sp. +; survey 6: Lyngbya infixa +; survey 8: Ectocarpus confervoides +; survey 10: Porphyra leucosticta f. atlantica +, Calothrix pulvinata +.

LEGENDA

1. Harlingen, northern harbour mole; well-developed *Bangia-Urospora* vegetation on a wooden pale at the end of the mole; surface: 1 m^2; 8.IV.'53; CH 53020.
2. Den Helder, sea-dike; *Bangia-Urospora* vegetation on the upper 50 cm of the wooden palisade which some years ago was driven into the body of the dike, between the pales marked 146 and 147; surface: 15 m^2; exposition: north-west; inclination: 90°; 1.IV.'52; CH 52007.
3. Den Helder, sea-dike; *Bangia-Urospora* vegetation on the upper 50 cm of a row of old pales between the pales marked 130 and 132; surface: 10 m^2; exposition: north-west; inclination: 90°; 1.IV.'52; CH 52008.

4. Den Helder, sea-dike; *Bangia* vegetation on the upper 50 cm of a row of wooden pales between the pales marked 147 and 148; surface: 5 m^2; exposition: north-west; inclination: 90°; 6.VII.'52; CH 52074.

5. Den Helder, sea-dike; heterogeneous vegetation consisting of *Bangia* and Cyanophyceae on a row of wooden pales near the Monument (pale marked 64); various patches with their own dominant species; surface: 4 m^2; 24.VIII.'54; CH 54146.

6. Huisduinen, first breakwater; *Bangia-Blidingia* vegetation on bitumen; flat surface with a few shallow depressions filled with water; surface: 10 m^2; 2.XI.'52; CH 52158.

7. Huisduinen, third breakwater at the pale marked 1; *Bangia* vegetation on bitumen; surface: 10 m^2; 2.XI.'52; CH 52159.

8. Hondsbosse Zeewering at Petten, on a palisade; well-developed vegetation consisting of *Bangia* and filamentous Chlorophyceae; surface: 5 m^2; exposition: west; inclination: 90°; 28.VI.'52; CH 52072.

9. Veere, Canal through Walcheren; *Bangia-Ulothrix* zone above the *Enteromorpha* belt; surface: 2 m^2; 3.IV.'54; CH 54002.

10. Canal through Zuid-Beveland near the Vlake bridge (Schore); a circ. 0.5 m wide *Urospora-Ulothrix* zone with occasional patches of *Bangia*; surface: 3 m^2; 6.VI.'54; CH 54045.

The *Bangia-Urospora* association has four characteristic species, viz. *Bangia atropurpurea* f. *fuscopurpurea* (cf. KOSTER, 1952), *Codiolum penicelliforme* st. *urosporae*, *Ulothrix subflaccida* and *U. pseudoflacca*. *Bangia* is best represented in strongly exposed localities; in quiet spots it is much less abundant and often even replaced by one or more of the other species. *Bangia* is also common in harbours on rafts, but always on the emerging parts. Several authors have pointed out that this species shows a preference for eutrophic water. It is at the same time one of the most euryhaline species of our flora (KOSTER, 1952), and occurs not only on the sea coast, but also on the shores of brackish and fresh waters; in such habitats it is associated with other filamentous Chlorophyceae into the *Bangieto-Ulothricetum tenerrimae*.

Along the sea coast *Bangia* is a species which is almost entirely confined to the *Bangieto-Urosporetum*; it penetrates but rarely in the belts that are found above and below the zone occupied by this association. Only in very strongly exposed spots the zonation may be disturbed, and then *Bangia* may be found in vegetations consisting of *Blidingia*, *Enteromorpha* and *Prasiola*.

Codiolum penicelliforme st. *urosporae* reaches its optimum development in the association during spring. In the other seasons it is but sparsely represented. It is also rather often met with in the upper part of the eulittoral region; in this respect it is noteworthy that the st. *codioli* appears to be confined to this habitat; I have never seen it in the *Bangieto-Urosporetum*.

Ulothrix pseudoflacca was found but a few times in this association, but this may perhaps be due to the fact that it shows a very strong resemblance to other species of this genus, and is therefore easily overlooked.

Ulothrix subflaccida occurs especially in sheltered spots, e.g. in the sea-water canals of Zeeland, where it may locally be the dominant species. It penetrates also rather far in brackish water (North-Sea Canal, Amstelmeer), where it is accompanied by fresh-water species. The transition from *Bangieto-Urosporetum* to *Bangieto-Ulothricetum tenerrimae* is a very gradual one.

Apart from the four characteristic species this association may contain some companion species and a few intruders from lower zones. Constant companion species are *Ulothrix flacca*, a filamentous Alga which may be present in considerable numbers, but which is not typical for this association as it also plays a very prominent part in the eulittoral region, and *Porphyra umbilicalis*, which is always present in this association and plays an important part in exposed localities, although it is here never so numerous as in the *Enteromorpheto-Porphyretum*. *Enteromorpha compressa* and *Blidingia* are also frequently met with; *Blidingia* even in very large numbers, but this is probably due to the fluctuations which the upper limit of the area of this species undergoes in the course of the year. *Petalonia zosterifolia* is less common, but reaches its optimum development in this association; it can, however, not be used as a characteristic species, as it also occurs in the eulittoral region, where it shows a preference for open vegetations, e.g. for the *Polysiphonieto-Chaetomorphetum*. Intruders from lower zones which occur but in small numbers in the *Bangieto-Urosporetum*, are *Ulva lactuca*, *Monostroma oxyspermum*, *Fucus vesiculosus*, *Ectocarpus confervoides* and *Pylaiella litoralis*. The Cyanophyceae which were met with in this association, also occur in other supralittoral communities. We may mention here *Lyngbya confervoides*, *L. semiplena*, *L. aestuarii*, *Gloeocapsa crepidinum* and *Plectonema battersii*.

Rhizoclonium riparium occupies a special position. At Den Helder and along the Hondsbosse Zeewering it is an ordinary component of the association, but at the inside of the southern mole at IJmuiden it forms a narrow zone between the true *Bangieto-Urosporetum*, which is here but poorly developed, and the *Prasioletum stipitatae*. This faculty of *Rhizoclonium* to form a zone of its own was also noted on the shore of the IJsselmeer and along the Meuse, where it occurs either in the upper part of the *Bangieto-Ulothricetum tenerrimae* or in a separate zone. Børgesen (1905) mentions from the Faeroes a supralittoral *Rhizoclonium* association which occurs at an even higher level than the *Prasioletum stipitatae*. However, at IJmuiden and at Hvide-Sande (Jutland) I found the *Rhizoclonium* zone immediately below the *Prasiola* zone. It is rather surprising that this species also occurs in the *Callithamnietum scopulorum*, an association in the upper part of the eulittoral region which is regularly submerged at high tide, and that it is locally common in this association. Finally we wish to draw attention to the fact that *Rhizoclonium riparium* is also very common in the algal layer in the undergrowth of the associations of phanerogams that are found on salt marshes which emerge to various heights above the level of the sea; here it occurs in the form which produces but few rhizoids, whereas in the epilithic habitats rhizoids are usually numerous.

SYNECOLOGY

The *Bangieto-Urosporetum* occurs in the lowest part of the supralittoral region, more or less between the mean high-water line (M.H.W.) and the mean high-water line at spring tides (M.H.W.S.), although exceptions to this rule are not rare.

In localities where no tidal movements are present and on the rafts in the harbour of Den Helder, this association occupies but a narrow zone just above the level of the water; occasionally we find it even submerged in such localities, but this is due to a rise of the water level. In very strongly exposed habitats, such as the outside of the moles at IJmuiden, the association may ascend, under the influence of the spray, to a height of several meters above M.H.W. Under such circumstances the boundary line between this association and the *Prasiola* formation may disappear entirely.

The lower margin of the *Bangieto-Urosporetum* borders on the *Blidingietum minimae*. During the winter months *Blidingia* invades the *Bangieto-Urosporetum* in large numbers, and it happens therefore but rarely that the latter is entirely free from *Blidingia*.

Because of the higher degree of humidity prevailing during the winter months, the *Bangieto-Urosporetum* as well as the *Blidingietum* ascend at that time to a higher level. Late in spring this movement is reversed. Almost the whole year round traces of these movements remain recognizable in the supralittoral communities.

The greatest abundance in species is reached in strongly exposed habitats. In more sheltered spots the Chlorophyceae become predominant; this also applies to the *Bangieto-Ulothricetum tenerrimae*.

The *Bangieto-Urosporetum* shows no marked preference for a definite kind of substrate. We found it on wood, concrete, granite, basalt, bitumen and iron.

It is often regarded as a typical spring association, but although it must be admitted that it is most completely developed during the spring months, it can nevertheless be met with throughout the year, especially in exposed localities. In quiet spots, like the Canal through Walcheren and the Canal through Zuid-Beveland, it disappears entirely during the summer months, because the degree of humidity is no longer sufficient; at that time the amount of spray and of rain which the vegetation receives, evaporates too rapidly because of the strong insolation. In exposed localities the width of the zone decreases considerably, as in the higher part the loss of water by evaporation is higher than the amount of water that is received from the spray. In the rest of the zone the water supply suffices.

AREA OF DISTRIBUTION

In the Netherlands this association is to be found along the whole length of the coast. Especially at Den Helder and on the moles at IJmuiden and Hook of Holland it is beautifully developed.

From the coasts of western Europe the association has repeatedly been described, viz. by Gran (1893), Børgesen (1905), Kylin (1907), Cotton (1912), Jonsson (1912), Sjøstedt (1928), Levring (1940), SUNDENE (1953), a.o. Especially the descriptions given by JONSSON and by SUNDENE give interesting details; both authors distinguish in this belt two associations, viz. a *Bangia* association and an association which JONSSON calls the *Ulothrix* association and SUNDENE the *Ulothrix-Urospora* association. These vegetation units, however, are merely different facies of one association, and occur as a rule in each other's company. COTTON (1912) called this association the "*Bangia-Urospora-Ulothrix* association".

It is rather remarkable that *Codiolum penicelliforme* st. *urosporae* also occurs in the Black Sea and in the Aegean Sea, whereas it is not known from the Mediterranean. As the *Ulothrix* species and *Bangia*, too, have been recorded from the Black Sea and from the Aegean Sea, it is not improbable that the *Bangieto-Urosporetum* is represented there, too.

Comparison of the *Bangia* communities observed in the northern part of the Atlantic Ocean shows that they differ according to the degree of latitude on which they occur. On the coast of Greenland and on the east coast of Iceland the Chlorophycea *Monostroma groenlandicum* occurs in communities of this kind, and here as well as elsewhere in the arctic and in the temperate zone we meet *Codiolum penicelliforme* st. *urosporae*, which is absent in the subtropical part of the Atlantic Ocean and also in the Mediterranean Sea. Notwithstanding these differences, the close affinity between these communities cannot be doubted. They resemble each other 1°. by the predominance of the same lifeform, 2° by the position they occupy in the zonation, and 3° by the species they have in common, viz. the representatives of the genus *Ulothrix* and *Bangia atropurpurea* f. *fuscopurpurea*.

Apart from the differences mentioned above, there are in the various parts of the area differences among the intruders, and it seems therefore desirable to distinguish more than one association.

The fullest development is shown by the communities in the northern part of the area; towards the south they show a gradual decline. By using the southern limits of the area of distribution shown by *Monostroma groenlandicum* and by *Codiolum penicelliforme* st. *urosporae* as boundary lines of the associations, we arrive at the following classification.

1. The *Bangieto-Monostrometum*, the arctic association mentioned by ROSENVINGE from Greenland and by JONSSON from Iceland. It is characterized by the presence of *Codiolum hartzii* st. *urosporae* and of *Monostroma groenlandicum*; *Codiolum penicelliforme* st. *urosporae* is also present.
2. The *Bangieto-Urosporetum*, the association which represents the group in the temperate zone of the Atlantic Ocean. It is characterized especially by the presence of *Codiolum penicelliforme* st. *urosporae*.
3. The *Bangieto-Ulothricetum subflaccidae*, the association which is found in the subtropical zone of the Atlantic Ocean and in the Mediterranean Sea (FELDMANN, 1938). It differs from the two other representatives of this group by the complete absence of *Codiolum penicelliforme* st. *urosporae*.

It is rather exceptional that algal associations can be united into an alliance, but with these three vicarious associations this offers no difficulty. In this alliance, which I will call the *Ulothriceto-Bangion* we may also include the *Bangieto-Ulothricetum tenerrimae* of the fresh water.

4. THE ENTEROMORPHA FORMATION

The *Enteromorpha* formation comprises the communities in which tubular and foliaceous Algae play the predominating part. It shows a rather simple kind of stratification, for it consists of a single well-developed layer formed by species of *Enteromorpha*, *Ulva* and *Porphyra*. By way of undergrowth there are sometimes a few crusts formed by Cyanophyceae.

The *Enteromorpha* formation is cosmopolitan, but we are but imperfectly informed on it, because the taxonomic classification of the *Enteromorpha* and *Porphyra* species is still in an unsatisfactory state. For the *Enteromorpha* species I have used, as far as possible, the work of BLIDING (1933—1955).

In the Netherlands I could distinguish the following seven communities, viz.

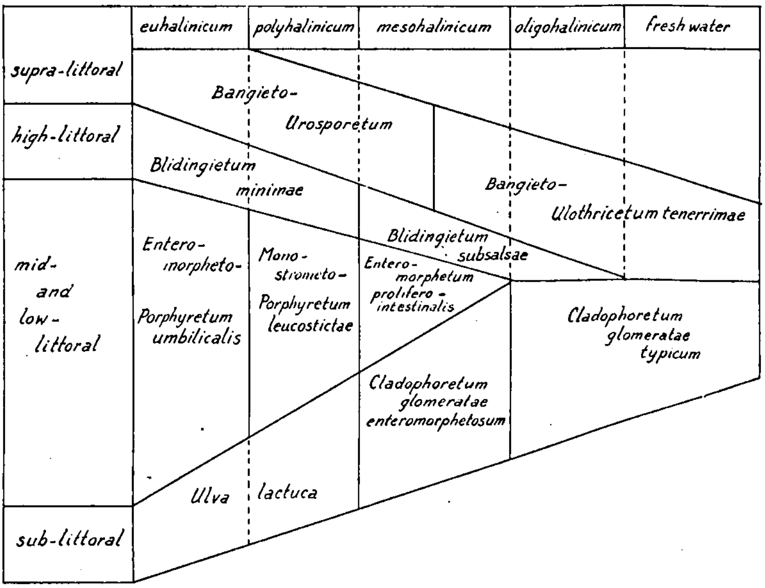
1. the *Blidingietum minimae*,
2. the *Blidingietum subsalsae*,
3. the *Enteromorpheto-Porphyretum umbilicalis*,
4. the *Monostrometo-Porphyretum leucostictae*,
5. the *Enteromorphetum prolifero-intestinalis*,
6. the *Monostrometo-Dumontietum*, and
7. the *Ulva lactuca* sociation.

These communities appear as pioneer vegetations which maintain themselves but for a short time. Only in habitats where the Fucaceae, on account of unfavourable environmental conditions, do not succeed in establishing themselves permanently, the *Enteromorpha* communities may maintain themselves permanently.

Each of the seven communities enumerated above has its own place in the coastal region. The *Blidingietum minimae* occupies the uppermost part of the eulittoral region, and extends from there into mesohaline waters. The *Enteromorpheto-Porphyretum*, on the other hand, is confined to the lower part of the eulittoral region, and only occurs in exposed localities of a coast that is subjected to the influence of the tides, and where the water is euhaline. In quiet spots, no matter whether they are subjected to the tides or not, this community is replaced by the *Enteromorphetum prolifero-intestinalis*, which reaches its optimum development in brackish water. Where sea water is mixed with brackish water we find an association which is nearly related to the last-named one, viz. the *Monostrometo-Porphyretum leucostictae*. The *Ulva lactuca* sociation is a rather unstable vegetation found in the uppermost part of the sublittoral region. The *Monostrometo-Dumontietum* occurs especially in little pools in the eulittoral region.

In table xx I have tried to show how the various communities belonging to the *Enteromorpha* formation gradually decrease in importance when they pass from the euhalinicum by way of the brackish waters into fresh water. It is noteworthy that in brackish waters that are not subjected to the influence of the tides the substitutes of the vegetations occurring in the middle and lower part of the eulittoral region are restricted to the zone with wave action, and that they disappear entirely in the oligohalinicum. In brackish water the vegetation in the upper part of the eulittoral region is bound to the water line, and as it is more euryhaline than the other ones it does not disappear before the water becomes fresh.

TABLE XX



When the salinity decreases, the sublittoral *Ulva* vegetation is replaced by a *Cladophora glomerata* association which in the mesohalinicum is still rich in *Enteromorpha* species.

In the supralittoral region the changes are less conspicuous. Here the marine *Bangieto-Urosporetum* passes gradually into the *Bangieto-Ulothricetum tenerrimae* of the fresh water, but this does not affect the general aspect of the vegetation.

In fresh water the substitutes of the supralittoral and sublittoral vegetations therefore obtain a common border line.

4.1. The Blidingietum minimae

Although the *Blidingia minima* association was not yet mentioned by VAN GOOR (1923), it is nevertheless one of the most common algal communities occurring along the coast of the Netherlands. VAN DEN HOEK (1958) described it from Hook of Holland.

In the brackish waters further inland this association is replaced by the *Blidingietum subsalsae*, in which *Blidingia minima* f. *subsalsa* predominates.

TABLE XXI

Blidingietum minimae

Sample plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Percentage of covering	65	85	100	70	90	85	90	90	90	80	85	100	80	80	100	100	100
Blidingia minima	2	3	3	4	3.2	3.2	3.3	4	5	5	5	5	4	5	5	5	5
Ulothrix flacca	4	4	4	+	3.2	1.3	3.3	1	+	+	+	+	3	—	2	—	—
Porphyra umbilicalis	—	—	—	—	2.2	4.4	3.2/4	1	1	1	—	2	—	—	+	2	2
Codiolum penicelliforme st. codioli	—	—	2	—	—	—	—	3	—	—	—	—	—	—	—	—	—
st. urosporae	—	—	—	—	—	—	—	—	+	—	—	+	—	—	—	—	—
Enteromorpha compressa	—	—	—	+	+	1.2	1.3	2	—	+	—	+	—	+	—	1	—
Fucus spiralis	+	—	—	+	—	—	—	—	—	—	—	+	+	—	( )	—	—
Fucus vesiculosus	—	—	+g	—	1	+	+	—	—	—	—	+	—	—	—	+	—
Hildenbrandtia prototypus	—	—	+	—	+	+	+	+	—	—	—	—	—	—	—	—	+
Ulva lactuca	—	—	—	—	+	1.2	1.3	—	—	—	—	—	—	—	—	—	—
Monostroma oxyspermum	1	—	—	—	—	—	—	—	—	—	—	—	—	+/1	—	—	—
Elachista fucicola	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	+	—
Lyngbya aestuarii	+	—	—	—	—	—	—	—	+	—	+	—	+	—	—	—	—
Plectonema battersii	—	—	—	—	—	—	—	—	+	—	—	—	+	—	—	—	—

Addenda: survey 2: Prasiola stipitata +; survey 6: Fucus serratus +°, Gigartina stellata +; survey 7: Acrochaetium secundatum +; survey 8: Verrucaria mucosa +; survey 9: Calothrix scopulorum +, Gloeocapsa crepidinum +; survey 11: Enteromorpha intestinalis +, Ulothrix pseudoflacca +, Oscillatoria tenuis +; survey 13: Calothrix pulvinata +, survey 14: Rhizoclonium riparium +; survey 16: Phormidium corium +; survey 17: Bangia atropurpurea f. fuscopurpurea +.

LEGENDA

1. Delfzijl, eastern harbour mole, on granite boulders; *Blidingia* community with *Ulothrix flacca* as the dominant species; a circ. 1 m wide zone; surface: 10 m^2; exposition: east; inclination: 15°; 13.IV.'53; CH 53026.

2. Harlingen, on the bituminized slope of the northern mole; *Blidingia-Ulothrix* vegetation; a circ. 2 m wide zone; surface: 20 m^2; exposition: north; inclination: 15°; 8.IV.'53; CH 53015.

3. West-Terschelling, outside of the southern dike of the "Kom"; on granite boulders; closed vegetation of *Ulothrix flacca, Blidingia minima* and *Codiolum penicelliforme*; surface: 10 m^2; exposition: west; inclination: 30°; 2.IX.'54; CH 54173.

4. Oude Schild on Texel, at the high-water line on basalt; *Blidingia minima* community; a 0.5 m wide zone; surface: 4 m^2; exposition: south-east; inclination: 20°; 7.VIII.'54; CH 54143.

5. Den Helder, sea-dike between the pales marked 89 and 90; a 1 m wide zone above the *Fucus vesiculosus* zone; up to the mean high-water line; uniform vegetation consisting of *Blidingia, Ulothrix* and *Porphyra*; on basalt; surface: 25 m^2; 12.VI.'52; CH 52062.

6. Den Helder, sea-dike; on a flat piece of the basalt dike near the pale marked 132; a circ. 2 m wide belt consisting of *Blidingia minima* and *Porphyra umbilicalis*; surface: 30 m^2; 24.VI.'52; CH 52066.

7. Huisduinen, on the crooked breakwater; a circ. 3 m wide belt formed by *Blidingia, Ulothrix* and *Porphyra*; surface: 45 m^2; exposition: north-west; inclination: 10°; 22.V.'52; CH 52045.

8. Huisduinen, on the crooked breakwater; on granite blocks and in the fissures in between; *Blidingia-Codiolum* vegetation; surface: 10 m^2; 24.VIII.'54; CH 54148.

9. IJmuiden, southern side of the southern mole; *Blidingia* vegetation on a concrete wall; a 60 cm wide zone; surface: 0.5 m^2; exposition: south; inclination: 90°; 30.XI.'55; CH 55102.

10. Hook of Holland, at the end of the northern mole; a dense vegetation of young *Blidingia minima* on Vilvordian stone; surface: 1 m^2; 11.IV.'54; CH 54007.

11. Hellevoetsluis, outside the sluice, on granite; *Blidingia minima* community; a 0.5 m wide zone; surface: 5 m^2; exposition: east; inclination: 30°; 4.V.'53; CH 53034.

12. Schouwen, at the entrance of the Canal to Zieriksee; a 3 m wide *Blidingia* zone; on basalt; surface: 30 m^2; exposition: south; inclination: 10—15°; 22.VII.'52; CH 52091.

13. Tholen, Gorishoek, on tiles; *Blidingia-Ulothrix* vegetation; surface: 1 m^2; exposition: west; inclination: 20°; 7.VI.'54; CH 54049.

14. Willemstad, stone-covered slope along the Hollands Deep; *Blidingia* vegetation; surface: 4 m^2; exposition: east; inclination: 10—20°; 13.IX.'58; CH 58035.

France

15. Ambleteuse (Pas de Calais), on blocks of rock at the high-water line; with a slight covering of sand; *Blidingietum minimae*; surface: 4 m^2; 3.VIII.'54; CH 54125.

Germany

16. Heligoland, Düneninsel; *Blidingia* zone on a concrete dam, above the *Fucus vesiculosus* vegetation; surface: 4 m^2; exposition: east; inclination: 90°; 22. VIII. '55; CH 55065.

Denmark

17. Saeby, outside of the harbour mole; closed *Blidingia minima* vegetation with much *Porphyra*, above the water line of the Kattegat; on blocks of granite; surface: 1 m^2; 1.IX.'55; CH 55085.

Blidingia minima, the species after which the association was named, is to be regarded as its principal characteristic species. The hemi-endophytic *Chlorochytrium willei* is a second characteristic species. The other species occurring in this association are also more or less common in other communities.

The *Blidingietum minimae* appears in the form of a closed vegetation. The percentage of covering fluctuates between 65 and 100, the average value being 85.

The aspect of the vegetation is determined mainly by two species. *Blidingia minima*, a small yellowish green tubular Alga is always present in large numbers, but *Ulothrix flacca*, a filamentous Alga, is only rarely absent, and may even be dominant; in some parts of the "Waddenzee" the name "*Ulothrix* zone" would be more appropriate than the name "*Blidingia* zone". Locally *Porphyra umbilicalis* may determine the aspect of the vegetation. Other tubular and membranaceous Algae are less often met with. Nevertheless their number may sometimes be considerable, e.g. that of *Enteromorpha compressa* and *Ulva lactuca*, species which cannot even be regarded as true members of this association. In the autumn *Codiolum penicelliforme* st. *codioli* becomes locally abundant. The presence of young Fucaceae indicates, as a rule, the development of a following stage in the succession. In some instances, however, they develop from the remains of a former Fucaceae vegetation which was destroyed by floating ice or by human interference (works on the dike).

Stratification is hardly noticeable in the *Blidingietum*, and this also applies to the other communities of the *Enteromorpha* formation. Below the layer of tubular and membranaceous Algae we sometimes find a few crusts formed by Cyanophyceae or by *Hildenbrandtia*, but these crusts play but a very unimportant part.

Although the *Blidingietum* consists of a small number of species, it is nevertheless possible to distinguish some variants. The development of these variants appears to be correlated with the degree of salinity, the amount of exposition and the force of the wave action. *Blidingia minima* itself, a species belonging to the upper part of the eulittoral region, tolerates very considerable fluctuations in the degree of salinity, and is not strongly affected by differences in exposition and in wave action either. The companion species, however, show a higher degree of specialization.

In exposed localities in the euhaline coastal waters the *Blidingietum* appears to contain such species as *Porphyra umbilicalis*, *Enteromorpha compressa* and *Ulva lactuca*. The presence of the last two species is very probably due to the action of the surf, as the latter ensures for them a higher degree of humidity during the periods of emersion. Another peculiarity of such sites is that species which elsewhere are confined to the sublittoral region, are ascending here in the eulittoral one.

In the polyhaline water of some estuaries and of the "Waddenzee", the species mentioned in the preceding paragraph are, as a rule, entirely absent. In sheltered spots we find there *Monostroma oxyspermum*.

In the mesohalinicum and even in the oligohalinicum vegetations of *Blidingia minima* are still present, but this Alga appears here in a special form, the thallus being strongly ramified and provided with numerous excrescences; this is the f. *subsalsa*. As it is accompanied by species that are adapted to brackish or fresh water, it seems advisable to regard this variant as a distinct association, the *Blidingietum subsalsae*. A description of the latter falls outside the scope of this work.

SYNECOLOGY

The *Blidingietum minimae* occurs in the upper part of the eulittoral region, above M.S.L., i.e. at the same height as the *Pelvetietum canaliculatae* and the *Fucetum spiralis*. The lower limit lies during the summer months lower than that of the *Fucetum spiralis*, in the winter months higher. The upper limit, too, fluctuates with the seasons. During the summer months it lies immediately below the *Bangieto-Urosporetum*; in the winter months it ascends to a much higher level, and may be found in the *Calothricetum scopulorum*. Although the *Bangieto-Urosporetum* itself also ascends to a higher level in the winter months, it is always rich in *Blidingia*. In exposed localities, e.g. at IJmuiden, the difference between the positions occupied by the upper limit of this association in summer and in winter is easily distinguishable, and fluctuates between 30 and 50 cm. These fluctuations are possible because *Blidingia* is a rapidly growing species which is propagating nearly throughout the year. That it ascends in the autumn to a higher level, is possible because the high tides, too, reach a higher level, and because the sea, on account of the stormy weather, is much more turbulent, which causes an extension of the zone that is affected by the spray. Moreover, because of the lower position of the sun, the desiccation is considerably decreased. In spring the movement of the *Blidingia* vegetation is reversed.

The seasonal migrations mentioned in the preceding paragraph give us a clue to the rather unexpected presence of species like *Calothrix scopulorum* (IJmuiden) and *Prasiola stipitata* (Harlingen), which normally are restricted to the supralittoral region.

In strongly exposed sites *Porphyra umbilicalis* often becomes the dominant species, and in such habitats this species may be found the whole year round to a considerable height in the supralittoral region. This phenomenon has been recorded by BØRGESEN (1905), JONSSON (1912), LEVRING (1937), SUNDENE (1953), COTTON (1912), a.o. On the southern mole at IJmuiden, too, it is clearly illustrated (fig. 11).

SUCCESSION

In the upper part of the eulittoral region the *Blidingietum minimae* is the most prominent pioneer community. On newly dumped stones *Blidingia* and *Ulothrix flacca* are the first settlers. In Zeeland this association is succeeded after a short time by a *Pelvetietum canaliculatae* and by a *Fucetum spiralis*, but the species of the *Blidingietum* succeed in maintaining themselves, be it by a small number of individuals, in these new associations. In the "Waddenzee" only the lower part of the

Blidingietum passes into a *Fucetum spiralis*, whereas the upper part retains its original character.

In various places in Zeeland where a well-developed Fucaceae zonation is found, the undergrowth of the latter ascends in the autumn to a higher level, and this explains why the *Blidingietum* occurs here locally as a winter community.

AREA OF DISTRIBUTION

The *Blidingietum minimae* is common along the whole coast of the Netherlands, and although an independent *Blidingia* association is mentioned by a part of the phycologists only, it is nevertheless represented on a large part of the coast of western Europe. HAMEL (1942) describes from the Basque coast a "ceinture de l'*Enteromorpha minima* et du *Monostroma wittrockii*", which is the variant of the *Blidingietum* that is found in sheltered estuaries (cf. survey 1). SUNDENE (1953) mentions the presence of the association in the Oslo Fjord, LEVRING (1940) from Blekinge in south Sweden. I myself noted its presence everywhere in the southern part of the North Sea (Harwich, coast of "le Boulonnais", of Belgium and the Netherlands, Heligoland, Cuxhaven, Esbjerg) and in the Kattegat (Frederikshavn, Saeby).

4.II. The Enteromorpheto-Porphyretum umbilicalis

The association of *Enteromorpha compressa* and *Porphyra umbilicalis* in which the very common *Porphyra umbilicalis* and *Enteromorpha compressa* are the dominant species, may be regarded as the most common association that is met with on the coasts of the Netherlands. It is therefore rather surprising that it was not mentioned by VAN GOOR (1923). The *Enteromorpha compressa* belt which VAN DEN HOEK (1958) described from the mole at Hook of Holland is doubtless, as appears from the records published by him, an example of the *Enteromorpheto-Porphyretum.*

LEGENDA (see table XXII)

1. West-Terschelling, in rather strongly exposed site on the harbour mole, on basalt; *Enteromorpha-Porphyra* community; surface: 5 m²; exposition: south; inclination: 30°; 2.IX.'54; CH 54174.
2. Texel, Oude Schild, southern dike, on basalt, near the neap-tide high-water line: a 0.5 m wide zone of *Enteromorpha* and *Porphyra*; surface: 10 m²; 14.IV.'52; CH 52020.
3. Texel, Oude Schild, southern dike on basalt; *Enteromorpha-Porphyra* vegetation in the central part of the eulittoral region in the *Fucus serratus* zone; a circ. 1 m wide zone; surface: 4 m²; exposition: east; inclination: 20°; 17.VIII.'54; CH 54144.
4. Den Helder, sea-dike, on the third breakwater from the post office, on basalt; an *Enteromorpha-Porphyra* vegetation with much *Ulva*; surface: 50 m²; exposition: west; inclination: 5°; 26.XII.'51; CH 51-D4.
5. Den Helder, sea-dike, at pale 115; *Enteromorpha-Porphyra* vegetation on the basalt blocks between the *Fucus* zones and the *Polysiphonieto-Chaetomorphetum*; several of the blocks are found at a higher level than the *Fucus* vegetation; a most homogeneous vegetation; surface: 40 m²; 22.V.'52; CH 52044.
6. Den Helder, sea-dike, on top of the breakwater at the monument; (pale 64),

TABLE XXII

Enteromorpheto-Porphyretum umbilicalis

Sample plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Percentage of covering	70	70	70	95	100	100	90	95	95	100	95	90	95	75	90	60	95	90	90
Enteromorpha compressa .	2	4.4	2	2.2	3.2	4	4	4	5.5	5	5	4	3	4	5	2	4	3	5
Porphyra umbilicalis . . .	4	1.2	4⚥	1	2.3	3⚥	2⚥	4⚥	1.2	2	2	4	4	1.1/2	2	3	3	1	2⚥
Ulva lactuca	+	+	1	3.4	5.5	+	+	+	+	+	—	—	—	—	—	+	—	2	1
Ulothrix flacca	—	2	—	—	1.3/4	+	1/2	1	+.2	+	+	+	—	—	+	1	—	—	+
Blidingia minima	+	—	+	—.2	+.2	+	1	1	—	+	—	+	—	—	+	—	+	—	—
Fucus vesiculosus	1	1	—	+	+	1	+	—	—	+	+	+g′	+	+	+	—	+	+°	+
Fucus serratus	—	—	+	2	+	—	—	—	—	+	—	—	+	+	—	+	—	—	—
Pylaiella litoralis	—	+	—	+.2	+.2	+	—	—	—	—	—	—	—	—	—	—	+	—	—
Codiolum penicelliforme st. codioli	—	—	—	—	—	—	2	1	—	—	—	—	—	—	—	—	—	—	—
Elachista fucicola	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—
Gigartina stellata	—	—	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Callithamnion scopulorum	—	—	—	+.2	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ceramium deslongchampii	—	—	—	+.2	1.2	—	—	—	—	—	—	—	—	—	—	—	—	+	—
Polysiphonia urceolata . .	—	—	—	+°	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chondrus crispus	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—
Chaetomorpha aerea . . .	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—
Laminaria digitata	—	—	—	—	+g	—	—	—	—	—	—	—	—	—	—	+	—	—	—
Enteromorpha linza . . .	—	—	—	—	—	—	—	—	1.2	+	—	—	—	—	—	—	—	3	+
Acrochaetium secundatum	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	+	—	—
Enteromorpha prolifera . .	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	2	—

Addenda: survey 4: Hildenbrandtia prototypus 2, Erythrotrichia carnea +.2, Lyngbya semiplena +; Ectocarpus confervoides +; survey 11: Rhodochorton floridulum 1/2; survey 16: Rhodymenia palmata 2, Ceramium rubrum +, Laminaria saccharina 1, Cladophora rupestris +, Scytosiphon lomentaria +; survey 17: Enteromorpha clathrata +, Ralfsia verrucosa +; survey 18: Cladophora nitida +, Phormidium corium 1.

a 2 m wide *Enteromorpha-Porphyra* zone; surface: 10 m^2; exposition: east; inclination: 20°; 16.VIII.'54; CH 54137.

7. Huisduinen, on the crooked breakwater; *Enteromorpha-Porphyra* vegetation on granite, the fissures filled with bitumen; surface: 10 m^2; 24.VIII.'54; CH 54147.

8. Huisduinen, breakwater facing the light house; *Enteromorpha-Porphyra* vegetation on basalt; surface: 12 m^2; 24.VIII.'54; CH 54149.

9. Hondsbosse Zeewering, near Kamperduin, on a flat stretch about three breakwaters south of the wreck; basalt covered with a thin layer of sand, locally with 2—5 cm deep depressions filled with water, a 5 m wide *Enteromorpha-Porphyra* vegetation; surface: 50 m^2; 28.VI.'52; CH 52071.

10. Schouwen, Zieriksee, near the entrance of the canal; *Enteromorpha-Porphyra* vegetation on blocks of stone; surface: 20 m^2; exposition: south; inclination: 10°; 22.VII.'52; CH 52092.

France

11. Ambleteuse (P. de C.); *Enteromorpha-Porphyra* vegetation on limestone in the *Fucus vesiculosus* zone; washed with sand; surface: 10 m^2; 5.IV.'55; CH 55004.

12. Ambleteuse (P. de C.); rocky site near the fort; *Enteromorpha-Porphyra* vegetation, strongly washed with sand; slightly exposed; surface: 10 m^2; 1.VIII.'54; CH 54110.

13. Ambleteuse (P. de C.); rocky site near the fort, on a slightly lower level than the preceding survey; surface: 10 m^2; 1.VIII.'54; CH 54111.

14. Ambleteuse (P. de C.); rocky site near the fort, somewhat more sheltered than the surveys 12 and 13; so much sand that the rock surface is no longer visible; surface: 10 m^2; 1.VIII.'54; CH 54113.

15. Ambleteuse (P. de C.), about 700 m from the fort at the northern end of the village; on stone with a thin covering of sand; surface: 20 m^2; 3.VIII.'54; CH 54117.

16. Ambleteuse (P. de C.), north of the Langue de Chien on Portlandien, a clayey kind of rock; *Enteromorpha-Porphyra* vegetation near the low-water line, with many young plants of *Rhodymenia palmata*; surface: 12 m^2; 3.VIII.'54; CH 54118.

17. Roscoff (Finistère), at the small discharging sluice of the lobsterpark at the Pointe de Bloscon; on muddy boulders; vegetation of *Enteromorpha compressa* and *Porphyra umbilicalis*; surface: 20 m^2; exposition: north; inclination: 5°; 16.VII.'54; CH 54080.

Germany

18. Heligoland, Düneninsel; against the dam at the north-west side of the island; *Enteromorpha* vegetation; surface: 8 m^2; exposition: east; inclination: 90°; 22.VIII.'55; CH 55067.

19. Heligoland, Felseninsel; north-east side, on blocks of rock; *Enteromorpha-Porphyra* vegetation; surface: 10 m^2; 25.VIII.'55; CH 55078.

With this association it is difficult to recognize characteristic species; *Enteromorpha compressa* which reaches here its optimum development, is the only species which might be considered. However, it is perhaps better to recognize a characteristic combination of species, for the joint presence of large amounts of *Enteromorpha compressa* and *Porphyra umbilicalis* accompanied by *Ulva lactuca* and *Ulothrix flacca* is so characteristic for this association that it is at once recognizable by it.

The percentage of covering in this closed vegetation fluctuates rather considerably. As a rule, it varies between 80 and 90, but it may decrease to 40 or rise to 100. Stratification is but rarely present.

The composition of the vegetation is very simple. Apart from the characteristic combination mentioned above, we find in it *Pylaiella* *litoralis*, but mainly in spring. *Codiolum penicelliforme* st. *codioli*, on the other hand, is met with only in late summer. Its period of vegetation is but short, but during that time it is probably very common. In the uppermost part of the zone *Blidingia minima* becomes rather frequent, and there the *Blidingietum* overlaps the *Enteromorpheto-Porphyretum.* Further we meet in this association young plants of the eulittoral Fucaceae, viz. *Fucus vesiculosus*, *Ascophyllum nodosum* and *Fucus serratus.* These species give us an indication of what the next step in the succession will be.

Fig. 15. Close-up of the *Enteromorpheto-Porphyretum.* To the left *Enteromorpha compressa*, in the middle and to the right *Porphyra umbilicalis*; the filiform *Ulothrix flacca* is seen at the top and in the middle. Den Helder, seadike. May 1955.

SYNECOLOGY

The *Enteromorpheto-Porphyretum* is along the whole coast the most common pioneer community. It is found on wood, concrete, basalt, granite, limestone and bitumen, especially in sites where the surf, a slight covering with sand, or the nature of the substrate prevent the Fucaceae from developing into associations; although we may find in such places young *Fucus* plants, we never meet mature individuals.

Especially a regular flooding with sand exercises a very unfavourable influence on the algal vegetation. The Fucaceae are in such circumstances unable to form communities of their own; they are represented only by small individuals, usually with a strongly damaged thallus. If the flooding with sand is accompanied by a strong surf, then there is no *Fucus* development at all. In this case the thalli of the young plants are either buried under the sand or swept away. Only species with a very rapid growth are able to maintain themselves in such sites. This applies to the *Enteromorpha* species which by their particular structure, a tubular thallus enclosed in an elastic membrane, seem to be specially adapted to such habitats. *Enteromorpha linza* even shows a distinct preference for them, as we could observe on the Hondsbosse Zeewering, at Den Helder and on Heligoland. Membranaceous Algae are apparently less well adapted to them, but *Porphyra umbilicalis* nevertheless reaches here, in contrast with *Ulva lactuca* and notwithstanding the fact that its thallus is often severely damaged, very considerable dimensions, viz. a length of 70—80 cm. It is noteworthy that in such habitats often enormous masses of barnacles are found.

During the summer months the *Enteromorpheto-Porphyretum* reaches its optimum development. Although but few observations have been made on the periodicity of its development, it cannot be doubted that this association shows especially in the summer months a very rapid growth, and that it becomes therefore at that time a serious competitor of the other communities. This enables it, for instance, to penetrate into the tidal pools on the beach, where it supplants the *Monostrometo-Dumontietum.* The presence of *Chondrus crispus* and some other species like *Cladophora flexuosa*, *Cl. rupestris* and *Ceramium rubrum*, however, indicates that it is not the original vegetation of such sites. At the same time the components of the *Enteromorpheto-Porphyretum* appear, either epilithically or epiphytically, in other associations. This phenomenon may be called "seasonal vicinism".

The *Enteromorpheto-Porphyretum* occurs from M.L.W.S. up to the *Blidingia* zone, i.e. in the belt in which the *Ascophylletum nodosi*, the *Fucetum vesiculosi*, the *Fucetum serrati* and the *Polysiphonieto-Chaetomorphetum* form the final stages. During the winter months the upper limit of the vegetation zone lies higher than it does in the summer months, and this explains why an intermingling with the *Blidingietum minimae* is no exception at this place. At the lower limit we may meet intruders from lower levels, e.g. *Polysiphonia urceolata*, *Chaetomorpha aerea*, *Ceramium rubrum* and young plants of *Laminaria digitata*. The *Polysiphonieto-Chaetomorphetum*, the association that is met with at the lower limit of the *Enteromorpheto-Porphyretum*, is an open community, and always contains therefore species from the latter.

In sites where the slope is very steep and the light rather weak, the *Enteromorpheto-Porphyretum* may contain much *Callithamnion scopulorum*, often accompanied by *Ceramium deslongchampii*. Where the illumination becomes still weaker, the association is completely replaced by the *Callithamnietum scopulorum*.

The *Enteromorpheto-Porphyretum* is only found in exposed localities in euhaline and in polyhaline water. In quiet spots in polyhaline water *Porphyra umbilicalis* is wanting. In the eastern part of the "Waddenzee" this species is on the whole rare. On account of the fact that the association is bound to a rather narrow range of salinity, there are apparently no variants that can be correlated with differences in the degree of salinity. In sites that are regularly flooded with sand, the *Enteromorpha linza* variant is found. The other deviations of the normal aspect of the vegetation which I observed, proved to be no more than a development in the direction of the following stage in the succession.

SUCCESSION

Where the algal vegetation is destroyed either by floating ice or by human interference (works at the dikes), the *Enteromorpheto-Porphyretum* is the first community to establish itself. The remains of the earlier Fucaceae vegetation may still be present in this community, and young *Fucus* plants may establish themselves, and within a few years, sometimes even within six months, the *Enteromorpheto-Porphyretum* is entirely replaced by the Fucaceae, which means that the climax vegetation is once more restored.

The *Enteromorpheto-Porphyretum* establishes itself very rapidly. In August 1952 at Den Helder stones were dumped on the sea-dike between the anemograph and "Kaap Hoofd", i.e. between the pales marked 100—123. On the 18th October already a closed *Enteromorpheto-Porphyretum* was found, which, however, was still poor in species. *Enteromorpha compressa* and *Ulothrix flacca* were represented by numerous individuals, *Ulva lactuca*, on the other hand, was scarce, and of *Porphyra umbilicalis* a rather large number of individuals were noted, but they were still small; most of them did not exceed a height of 2 cm, and but a few reached 10 cm. On some stones in the higher part *Blidingia minima* was rather well represented. VAN DEN HOEK (1958) describes a similar development from Hook of Holland. The original vegetation was destroyed there by the severe winter of 1954, but very soon *Ulothrix flacca* established itself, after a very short interval followed by *Enteromorpha compressa.*

On breakwaters jutting out from the beach and also on the large moles at IJmuiden large parts often appear to be practically devoid of all algal growth, although such parts appear to satisfy the demands put by the *Enteromorpheto-Porphyretum.* In this case the absence of the Algae is due to the presence of a dense covering of mussels or of barnacles. This is apparently a question of priority. In a severe winter the fauna, too, undoubtedly suffers large losses, but it may happen that the young barnacles nevertheless are able to establish themselves before the Algae appear on the scene. In the spaces between the barnacles the Algae have but little opportunity to grow out, because they are crowded out by the extending shells of the latter. Afterwards they may obtain a foothold on the shells themselves, but the vegetation which develops in this way, is not very dense. The competition between the mussels and the *Enteromorpheto-Porphyretum* is not rarely decided in favour of the mussels. A population of young mussels sieves the water very thoroughly, and the Algae therefore have but little chance to establish themselves.

That the *Enteromorpheto-Porphyretum* is usually succeeded by Fucaceae communities, has already been mentioned. The transition is often rapid and direct, but occasionally the succession proceeds rather slowly, and in such cases an intermediate stage consisting of dendritic and fruticose Algae appeared to be recognizable. This stage may even be the final one, viz. when no young *Fucus* plants establish themselves. I have been able to describe for the middle part of the eulittoral region a stage with *Ceramium deslongchampii* (p. 150) and for the lower part of the latter a stage with *Chondrus* (p. 177).

The differentiation inside the *Enteromorpheto-Porphyretum*, too, deserves our attention. In the course of the succession the new arrivals establish themselves in definite zones. A good example of this development was observed at Den Helder. In 1947 the vegetation on one of the breakwaters had been wiped away completely by floating ice, and here an *Enteromorpheto-Porphyretum* had established itself. This association was but slowly replaced by the Fucaceae. In December 1951 in the upper part the establishment of *Fucus vesiculosus* was noted; the larger middle part showed at that time already well-developed patches of *Fucus serratus*, whereas in the lower part many small Rhodophyceae and Chlorophyceae from the *Polysiphonieto-Chaetomorphetum* had made their appearance.

Our record of survey plot 4 gives an impression of the part of the *Enteromorpheto-Porphyretum* that was recolonized by *Fucus serratus*. On the bluish grey Portlandian clay at Ambleteuse on the coast of "le Boulonnais" a transition from the *Enteromorpheto-Porphyretum* to the *Rhodymenietum palmatae* was observed.

Summarizing we may say that the *Enteromorpheto-Porphyretum* may pass either in the *Ascophylletum nodosi*, in the *Fucetum vesiculosi*, in the *Fucetum serrati*, in the *Polysiphonieto-Chaetomorphetum* or in the *Rhodymenietum palmatae*, and that this may take place either directly or by way of an intermediate stage.

AREA OF DISTRIBUTION

The association occurs along the whole coast of the southern North Sea, and was also found by me near Roscoff (Finistère). It is not improbable that it will appear to be represented along the whole Atlantic coast of Europe, but I have not been able to identify it with certainty from the descriptions of the algal vegetation of other parts of the latter that are to be found in the literature.

4.III. **The Monostrometo-Porphyretum leucostictae**

The association of *Monostroma oxyspermum* and *Porphyra leucosticta* was described by DEN HARTOG (1953) from the Canal through Zuid-Beveland, where it is beautifully developed. In 1955 I published once more a record of this association, this time from the harbour at Nice.

TABLE XXIII

Monostrometo-Porphyretum leucostictae

Sample plots	1	2	3	4	5	6
Percentage of covering	65	70	70	50	70	40
Porphyra leucosticta f. atlantica . . .	+	1	+	+	+	+
Monostroma oxyspermum	1.2	+	—	2	3	1
Enteromorpha compressa	4.4	2	+	+	+	+
Enteromorpha prolifera	+.2	1	—	3	4	3
Enteromorpha intestinalis	—	3	3	—	1	—
Ulva lactuca	+	+	—	—	—	+
Fucus vesiculosus	—	+	—	+	+g	—
Bangia atropurpurea f. fuscopurpurea	—	—	—	+	+	+
Pylaiella litoralis	—	+	+	—	+	—
Ulothrix subflaccida.	+	—	—	—	+	—
Lyngbya semiplena	—	+	—	—	+	+
Oscillatoria brevis	—	—	—	+	+	—

Addenda: survey 2: Enteromorpha linza 1, Codiolum penicelliforme st. urosporae +, Ectocarpus siliculosus +, Pringsheimiella scutata +; survey 3: Ulothrix flacca +, Petalonia fascia +, Callithamnion roseum +; survey 6: Cladophora dalmatica +.

LEGENDA

1. Canal through Zuid-Beveland, eastern bank of the southern part, circ. 50 m from the railway bridge; a 0.5 m wide zone with *Enteromorpha* as dominant; surface: 15 m²; exposition: west; inclination: 15°; depth; 0—20 cm; 25.X.'51; CH 51 ZB-1 (DEN HARTOG, 1953).

2. Same place; surface: 10 m²; 6.VI.'54; CH 54046.

3. Hook of Holland; basin in the Nieuwe Waterweg at the place where the northern mole begins; a 0.5 m wide *Enteromorpha* zone; surface: 5 m²; 11.IV.'54; CH 54006.

4. IJmuiden, inner breakwater at the southern mole; *Enteromorpha-Monostroma* vegetation with much mud deposited among the Algae; also much dead *Enteromorpha*; surface: 1 m²; 30.XI.'55; CH 55103.

5. Den Helder, end of the harbour at Fort Oostoever; an *Enteromorpha-Monostroma* vegetation flooded with sand on blocks of shale; slightly shaded; a 1 m wide zone; surface: 20 m²; exposition: east; inclination: 10°; 6.XII.'54; CH 54183.

France

6. Nice (Alp. Mar.), harbour, at the landing place of the Corsica line; *Enteromorpha* vegetation on wood, at the waterline; surface: 1 m²; 20.IV.'54; CH 54016 (DEN HARTOG, 1955).

In the description which I gave of this association in 1953, I mentioned two characteristic species, viz. *Porphyra leucosticta* f. *atlantica* and *Monostroma oxyspermum* (= *M. wittrockii*). In the Netherlands *Porphyra leucosticta* appears to be entirely confined to this association; *Monostroma oxyspermum*, on the other hand, is also rather often met with in other associations, although it reaches in this one its optimum development. In the *Enteromorphetum prolifero-intestinalis* and in the *Blidingietum minimae* it is not rare. In the last-named association I found it myself at Delfzijl and at Roscoff, whereas HAMEL (1942) mentioned it from the Basque coast. Both species are present throughout the year, although they become very scarce in the summer months, and are then difficult to find. In the winterhalf-year both are at their best.

During the summer months the *Enteromorpha* species reach their optimum development. The vegetation is than more or less closed; in the winter, however, there are a fairly large number of open spaces which are usually occupied by diatoms. The *Enteromorpha* species that are found in the *Monostrometo-Porphyretum leucostictae* are *E. compressa*, *E. prolifera* (incl. *E. tubulosa*), *E. intestinalis* and *E. linza*. The first three species may become dominant; usually it is *E. prolifera* which plays this part. Apart from the fairly common *Pylaiella litoralis* and *Petalonia fascia* all other species occurring in this association may be regarded as intruders. At the upper limit these intruders are *Bangia atropurpurea* f. *fuscopurpurea*, *Codiolum penicelliforme* st. *urosporae* and *Ulothrix subflaccida*, at the lower limit *Ulva lactuca* and *Callithamnion roseum*. The presence of *Fucus vesiculosus* and of *Ascophyllum nodosum* may be regarded as indicating that a new stage in the succession is in the course of development.

SYNECOLOGY

The *Monostrometo-Porphyretum* is found in sheltered sites, where the water is very quiet and preferably somewhat polluted, as it is e.g. in harbours and in salt-water canals. Where no tidal movements take place, it is bound to the wave belt. Its habitat coincides everywhere with the waterline. In waters that are subjected to the influence of the tides, it is found on rafts, buoys, pontoons and other objects that rise and fall with the tides. However, we may also find it in places where brackish water comes into contact with sea water, e.g. at the end of the harbour of Den Helder, at the mouth of the North Sea-Canal outside the large sluices of IJmuiden, and in the harbour of Harlingen. Intermediate between the two last-named types of habitat are the basins at Hook of Holland, where the low dikes become submerged at high tide and emerge at low tide, but where the basin itself remains filled with water; during the period in which the water rises the basin is flooded with sea water during the period in which the water falls with the brackish water from the Nieuwe Waterweg. The vegetation on the low dikes of the basins shows a curious zonation; on top we find the *Blidingietum minimae*, and below the latter the *Enteromorpheto-Porphyretum* with young plants of *Fucus vesiculosus* and of *F. ceranoides*. These two zones emerge from the water during low tide, but below the *Enteromorpheto-Porphyretum* we meet the zones that are persistently submerged. This is the *Monostrometo-Porphyretum* at the low-water line, and then a poorly developed and narrow zone in which *Ceramium rubrum* and *Callithamnion roseum* occur, i.e. the *Callithamnietum rosei*; below the latter there is bare sand.

Differences in salinity find their expression in the presence of the various *Enteromorpha* species. Although *E. prolifera* and *E. intestinalis* reach their maximum abundance in brackish water, they may nevertheless become dominant in this association, but this also applies to *E. compressa*, which prefers a much higher degree of salinity. Which of these species becomes dominant, depends on the conditions which temporarily prevail. The rapidly growing tubular Algae are able to keep pace with the changes in the latter. If we compare the records 1 and 2, we see that *E. compressa,* which in October 1951 was the dominant species in the Canal through Zuid-Beveland, was in June 1954 replaced to a large part by *E. intestinalis.* This indicates that the water was at that time more brackish. To what extent seasonal influences play a part in this change, is not known.

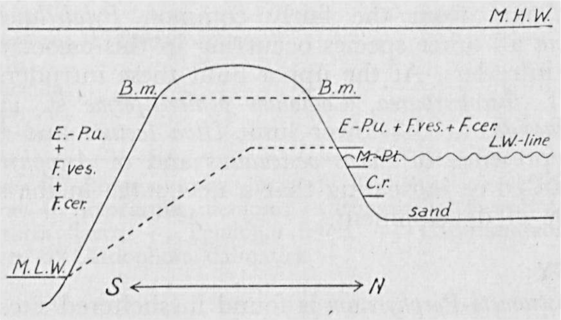


Fig. 16. Zonation on the dike of a basin near Hook of Holland. To the left in the Nieuwe Waterweg normal tidal zonation; in the basin (to the right) only the highest part is subjected to the tidal movement, the lower part of the vegetation is always submerged. B.m. = *Blidingietum minimae*; E.-P.u. = *Enteromorpheto-Porphyretum umbilicalis*; F. ves. = *Fucus vesiculosus*; F. cer. = *Fucus ceranoides*; M.-P.l. *Monostrometo-Porphyretum leucostictae*; C.r. = *Callithamnietum rosei*; M.H.W. = Mean high watermark; M.L.W. = Mean low watermark.

As the characteristic species *Monostroma oxyspermum* also occurs in places where *Porphyra leucosticta* has never been found, e.g. in the Canal through North Holland at Den Helder, in the North Sea-Canal inside the sluices of IJmuiden, and on Texel, it may prove desirable to regard the *Monostrometo-Porphyretum* as a variant of the *Enteromorphetum prolifero-intestinalis.* During the summer months, when the two characteristic species are absent or at least very scarce, it is extremely difficult to distinguish these two associations from each other. However, before such a decision can be taken, the *Enteromorphetum prolifero-intestinalis* will have to be studied in more detail.

In the Canal through Zuid-Beveland *Porphyra leucosticta* is occasionally also found above and below the *Enteromorpha* zone. This was always due to changes in the water level. The same observation was made by LUND in Copenhagen. In a letter to me, he described it in the following terms. "In the harbour of Copenhagen the species is found in the *Enteromorpha* belt, the result being a decided *Enteromorpha-Porphyra leucosticta* association. However, *Porphyra* may also be met with a little above and a little below the *Enteromorphas.* It grows on stones as well as on *Fucus* and on other Algae such as *Ceramium rubrum* and *Scytosiphon.* Furthermore on shells of *Balanus* and on woodwork."

The observations made by HOFFMANN in the Kieler Förde are in good agreement with those mentioned in the preceding paragraph.

In a letter he expresses himself in this way. "*Porphyra atropurpurea* (= *P. leucosticta*) kommt in der Kieler Förde unmittelbar unter der oberen Wassergrenze, also in der Zone des Wellenschlagens, vor. Sie findet sich z.T. mit *Enteromorpha intestinalis* und *compressa* gemischt, geht aber auch in die *Pylaiella*-Assoziation ein. Sie wird stets unterhalb der *Ulothrix* und *Urospora*-Assoziation angetroffen. Nicht selten findet sie sich epiphytisch auf einzelnen *Fucus vesiculosus*-Pflanzen, die der Wassergrenze sehr nahestehen. Wenn wir hier in der Kieler Förde auch keine deutlich sichtbare Gezeitenbewegung finden, so schwankt doch das Wasserniveau unter dem Windeinfluss ausserordentlich stark entsprechend den jeweiligen meteorologischen Bedingungen. Damit dürfte das gelegentliche Heruntergehen der Art bis in die *Fucus*-Assoziation leicht geklärt werden können."

SUCCESSION

It is not impossible that the *Monostrometo-Porphyretum leucostictae* occasionally is succeeded by one of the associations belonging to the *Fucus* formation, and among the latter the *Fucetum vesiculosi* probably makes the best chance. In the Canal through Zuid-Beveland repeatedly young plants of *Fucus vesiculosus* and of *Ascophyllum nodosum* were observed, but after some time these plants seem to succumb, probably because of the protracted lowering of the water level during upkeeping works. According to KOSTER (1954) at an earlier date a *Fucus vesiculosus* zone was observed here by BRAKMAN. In the other habitats in the Netherlands *Fucus vesiculosus* is not rare either; at IJmuiden this species even forms vegetations inside the *Monostrometo-Porphyretum*. *Porphyra leucosticta* also occurs there as an epiphyte on *Fucus*.

In most of the localities occupied by the *Monostrometo-Porphyretum* the *Fucus* plants are unable to maintain themselves because of the continuous deposition of mud, a phenomenon that is observed in all sites where two kinds of water are mixed.

AREA OF DISTRIBUTION

From the communications in the letters of LUND and HOFFMANN that were quoted above, and from the publications of HOFFMANN (1928), ALEEM and SCHULZ (1952) and STEEMANN NIELSEN (1951) it appears that the *Monostrometo-Porphyretum* is not rare on the western part of the German coast of the Baltic Sea and in the Danish waters. Along the coast of the Netherlands it was observed at several places, and finally it was also discovered by DEN HARTOG (1955) in the Mediterranean Sea at Nice. As *Porphyra leucosticta* is often met with on floating objects of southern origin (DEN HARTOG, 1953), it is not improbable that this association will also be represented along the coast of the English Channel.

SUNDENE (1953) described a *Porphyra leucosticta* association from the Oslo Fjord, but this association differs in some important points from the *Monostrometo-Porphyretum*. In the first place is *Porphyra* here dominant with a percentage of covering varying from 25 to 100. The *Enteromorpha* species which in the association described above are predominating, play but a subordinate part. However, as these species reach their predominant position during the summer months, and as SUNDENE does not mention the aspect which his association shows at that time, it is not excluded that there is in this respect no real difference. *Monostroma oxyspermum*, a most conspicuous constituent of the *Monostrometo-Porphyretum*, does not occur in the association described by SUNDENE, but we should realize that this Alga seems to be absent in the whole Oslo Fjord. In its preference for polluted water and in the circumstance that the optimum development is observed in spring, SUNDENE's association agrees very well with the *Monostrometo-Porphyretum*. It is, moreover, described by SUNDENE as usually supralittoral, although occasionally eulittoral, "lying at about the litus line"; in its habitat, the wave-action belt, it also agrees therefore with the *Monostrometo-Porphyretum*.

4.IV. **The Enteromorphetum prolifero-intestinalis**

The "*Enteromorpha*-Association" described by VAN GOOR (1923) is not identical with the association of *Enteromorpha prolifera* and *E. intestinalis* which will be dealt with in this section; it should probably be regarded as a combination of the latter with the *Blidingietum subsalsae*, as VAN GOOR states that *Enteromorpha intestinalis* is the predominant species, and that *E. clathrata* is also very frequent, but that in the upper part of the zone *E. minima* (= *Blidingia minima*) is met with in large numbers.

As we have identified the *Enteromorpha* species by the aid of the works of BLIDING, who has occupied himself for already more than twenty years with the taxonomy of this difficult genus, it is hardly possible to compare the results of our surveys with those of VAN GOOR. In his time these Algae were identified by the aid of the ramification, the arrangement of the ultimate twigs in one or in two rows, and the arrangement of the cells. Nowadays the identification is based mainly on the characters of the cells (size, shape, number of pyrenoids, arrangement, etc.).

The association was briefly described by DEN HARTOG (1958) under the name "*Enteromorpha intestinalis* community". As it is characteristic for the mesohaline inland waters, and as it does not occur on the sea coast itself, we will confine ourselves here to a very short description.

FLORISTIC COMPOSITION

The *Enteromorphetum prolifero-intestinalis* has a large number of characteristic species. *Enteromorpha prolifera* and *E. intestinalis*, both of them often the predominating species, also occur outside this association, e.g. in the *Monostrometo-Porphyretum*; in such cases they may be regarded as indicators of a low degree of salinity. *Enteromorpha ahlneriana* and *E. intermedia* may also occur in large numbers, and these species may be regarded as more exclusively bound to this association. At Antwerp *Capsosiphon fulvescens* is found in it, but this species has not yet been met with in the Netherlands. *Percursaria percursa* may perhaps also be regarded as a characteristic species, although it is also very common on salt marshes. A less frequent companion species is *Enteromorpha compressa*, which is confined to those parts of the area o. distribution where the degree of salinity reaches its highest values *Monostroma oxyspermum* is only met with in sites where sea water if mixed with brackish water. Other companion species are *Ulothrix flacca* and *Enteromorpha linza*, whereas *Ulothrix zonata* is confined to those parts of the area where the degree of salinity is lowest. *Cladophora glomerata* is a very frequent intruder from a lower vegetation belt.

The *Enteromorphetum prolifero-intestinalis* is a closed association; gaps are always completely filled with diatoms.

SYNECOLOGY

The association is common in the stagnant brackish water of such canals as the North Sea-Canal, the Canal through North Holland, the Canal of Harlingen, etc., as well as in waters that are subjected to the tides; it also occurs e.g. in the Hollands Deep. It reaches its optimum development in the mesohalinicum. It also occurs in the polyhalinicum, but there it is often replaced by the *Monostrometo-Porphyretum*; during the summer months these two associations are difficult to distinguish or even indistinguishable. In waters that are not subjected to tidal movements, the *Enteromorphetum* is found in the wave-action belt; in tidal waters it occurs in the middle and in the lower part of the eulittoral region; in this habitat it is much more open.

SUCCESSION

In stagnant brackish water the *Enteromorphetum prolifero-intestinalis* is not succeeded by other stages; Fucaceae are unable to grow there. In brackish waters subjected to tidal movements *Fucus vesiculones* or *F. ceranoides* locally may replace the *Enteromorpha* association.

AREA OF DISTRIBUTION

The association is widely distributed, and has been described under various names. As *Enteromorphetum compressae* it was described by KORNAŚ and MEDWECKA-KORNAŚ (1950) from the Polish coast of the Baltic Sea; as *Enteromorpha intestinalis* association by HANSTEEN (1892) from the coast of Norway and by COTTON (1912) from the Irish coast; and as *Enteromorpha* association by SUNDENE (1953) from the Oslo Fjord. It cannot be doubted that it occurs in all the brackish waters of western Europe.

4.V. The Monostrometo-Dumontietum

The association of *Monostroma grevillei* and *Dumontia incrassata* was not yet described from the Netherlands. It is characteristic for small pools in the tidal belt, but it also occurs in the form of a marginal zone in basins filled with sea water. It reaches its optimum development in the spring months.

TABLE XXIV

Monostrometo-Dumontietum

Sample plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Percentage of covering	70	80	65	60	70	60	25—30	40	85	70	70	20	10	50	80	90	90
Monostroma grevillei	+	—	3.2	2.2	2	2	+	+	+	2	2	+	1.2	3	1.2	2	+
Dumontia incrassata	1.2	2.2/3	1.2	1.2	1	+	—	2	2	2	4	+	( )	1	+	+	2
Petalonia fascia	2.2	1.2	2.2	2.2	2	2	2	1	1	1	1	+	+	1	+	—	—
Scytosiphon lomentaria	+	+	—	+.2	—	+	—	+	+	—	—	—	—	( )	+	—	—
Cladophora flexuosa	1.2	2.2	+	+	1	+	1	—	—	1	+	—	—	+	—	—	—
Ulonema rhizophorum	+	1	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—
Ulva lactuca	+	1.2	2.3	2.3	2	2	2	1	+	+	+	+	+	—	1	—	—
Chondrus crispus	2.2	3.2	+.2	1.2	1	1	—	3.3	4.3	4	2	—	1	+	2.3	1	3
Enteromorpha compressa	+	+	+	—	+	+	1	+	—	—	—	+	+	—	—	—	—
Ceramium rubrum	+	+.2	+	+	+	+	+	+	—	—	—	+	—	—	—	+	—
Ceramium deslongchampii	+	1.2	+	+	+	+	+	—	—	+	+	—	—	—	—	—	—
Verrucaria mucosa	+	+	+	+	+	+	+	+	+	—	—	—	—	—	—	—	—
Hildenbrandtia prototypus	4	3	2	2	3	+	+	—	—	—	—	+	—	—	—	—	—
Fucus vesiculosus	—	—	+	+	—	+	—	1.3	2	+	+	—	+	+	—	—	—
Ralfsia verrucosa	+	+	—	—	+	+	—	+	+	—	—	+	—	+	—	+	—
Fucus serratus	—	+°	+	+	+	—	+/1.3	—	—	—	—	+	+	—	+	+	—
Polysiphonia nigrescens	+	+	—	+	—	—	—	+	—	1	1	—	—	+	—	+	+
Gigartina stellata	+°	1.2	+°	+°	+	—	+	—	—	—	—	—	—	—	—	—	—
Lithothamnion lenormandii	1	1	1	+	+	+	—	—	—	—	—	—	—	—	5	5	5
Chaetomorpha aerea	+	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—	—
Porphyra umbilicalis	—	—	+	+	—	+	+	—	—	—	—	—	—	—	—	—	—
Cladophora rupestris	—	+.2	—	+	+	—	—	—	—	+	—	—	—	—	—	—	—
Polysiphonia urceolata	+	+	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—
Enteromorpha linza	+	+	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—
Ulothrix flacca	—	—	—	—	—	—	—	+	+	—	—	—	+	—	—	—	—
Cladophora refracta	+	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—
Acrochaetium virgatulum	—	+	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—
Ascophyllum nodosum	—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—
Enteromorpha prolifera	—	—	—	—	—	—	—	—	—	—	—	+	1	—	—	—	—
Laurencia pinnatifida	—	—	—	—	—	—	—	—	—	—	—	—	—	+	1	2	+
Corallina officinalis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+.2	2	+
Ectocarpus confervoides	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—

Addenda: survey 2: Callithamnion scopulorum +, Enteromorpha clathrata +; survey 6: Laminaria digitata +g; survey 9: Elachista fucicola +; survey 12: Codium fragile +.

LEGENDA

1. Den Helder, sea-dike, between pale 108 and pale 109; small pool in the tidal belt; 10 cm deep; *Monostrometo-Dumontia* vegetation on mussels and on basalt; surface: 4 m²; 15.V.'52; CH 52037.

2. Den Helder, sea-dike, between pale 106 and pale 107; *Dumontia* vegetation on basalt and on mussels in a 5—15 cm deep pool; surface: 5.5 m²; 21.V.'52; CH 52042.

3. Den Helder, sea-dike, at the pales 105 and 106; on mussels and on basalt in a 10—15 cm deep pool in the tidal belt; surface: 6 m²; 20.III.'53; CH 53001.

4. Den Helder, sea-dike, at pale 107; *Monostroma grevillei* vegetation on basalt and on mussels in a 10—20 cm deep pool; surface: 4 m²; 20.III.'53; CH 53002.

5. Den Helder, sea-dike, at pale 112; *Monostroma-Dumontia* community in a 10—15 cm deep pool; surface: 3 m²; 2.IV.'53; CH 53003.

6. Den Helder, sea-dike, between pale 108 and pale 109, *Monostroma-Petalonia* vegetation in a 10 cm deep pool in the tidal belt; surface: 2 m²; 2.IV.'53; CH 53004.

7. Den Helder, sea-dike, at pale 58; *Petalonia* vegetation on stones and on shells in a little pool on a breakwater; surface: 2.5 m²; 11.V.'53; CH 53037.

8. West-Terschelling, "cascade"; *Monostroma-Dumontia* vegetation in a runlet of sea-water flowing out the of "Kom"; surface: 30 m²; 4.IV.'53; CH 53011.

9. West-Terschelling, "cascade"; same vegetation type as in 8; surface: 20 m²; 4.IV.'53; CH 53012.

10. Harlingen, basin at the southern mole; *Monostroma-Dumontia* vegetation descending to a depth of 20 cm; surface: 5 m²; 2.V.'54; CH 54023.

11. Harlingen, same locality as in 10; surface: 5 m²; 2.V.'54; CH 54024.

12. Yerseke; circ. 10 cm deep pool on mud flat; not very suitable substrate; surface: 15 m²; 28.III.'55; CH 55001.

13. Yerseke; margin of an oyster basin; *Monostroma grevillei* vegetation descending to a depth of 10 cm; surface: 10 m²; 28.III.'55; CH 55002.

France

14. Wimereux (P. de C.), Pointe aux Oies; 10 cm deep rock pool with a *Monostroma-Dumontia* vegetation; surface: 4 m²; 9.IV.'55; CH 55017.

15. Wimereux (P. de C.), Pointe aux Oies; 5—20 cm deep rock pool with *Monostroma grevillei* and *Lithothamnion lenormandii*; surface: 4 m²; 9.IV.'55; CH 55012.

16. Wimereux (P. de C.), Fort de Croy; a circ. 5 cm deep pool with *Monostroma*, *Lithothamnion* and *Corallina*; surface: 20 m²; 10.IV.'55; CH 55021.

17. Wimereux (P. de C.), Pointe aux Oies; *Dumontia-Lithothamnion* vegetation in a 2—20 cm deep rock pool; surface: 10 m²; 9.IV.'55; CH 55016.

The *Monostrometo-Dumontietum* has a rather considerable number of characteristic species. So far I could recognize six.

Monostroma grevillei, an subarctic species, appears in February, and disappears in the middle of May; in March and April it is very numerous, especially in the very shallow little pools in the tidal belt and along the margin of basins filled with sea-water. Locally it may be found in pools on mudflats. So far it was found at Den Helder, Terschelling, Texel, Harlingen, Kats, Canal from Goese Sas to Goes and Yerseke. It is a species which does not occur in other associations.

Dumontia incrassata, a boreal-atlantic species, is in many of the pools the predominant species, and determines, as a rule, the aspect of the vegetation. It grows mainly on mussels. The first individuals appear in the pools in November, but they remain as yet very scarce. When it begins to freeze, growth is stopped, and if the cold continues for a time, they are killed. Early in the next spring the development is resumed, and proceeds then at a very rapid rate. In April and May the optimum is reached, and then they go out, but up to the middle of June some living individuals may be met with.

Dumontia incrassata may be regarded as rather selective. It is found mainly in the small pools in the tidal belt, but I have found it at Roscoff and on Heligoland also in the undergrowth of the Fucaceae communities. It occurs also in pools on mud flats.

Ulonema rhizophorum is an obligate epiphyte on *Dumontia incrassata.* Its vegetation period is very short. In April 1952 at Den Helder not a single *Ulonema* could be detected on the numerous *Dumontia* specimens that were investigated, but in May it appeared to be present in large numbers and so it was in June. It was found at Den Helder as well as at Harlingen.

Petalonia fascia, a boreal-arctic species, determines the aspect of the association in several of the pools. The first individuals appear in October, and in June the last ones disappear. During the winter months the development is stopped. Towards the end of April the colour of the thallus changes from light brown to dark brown; this is the moment at which the development of the spores sets in. Its habit is rather variable; in the pools in the tidal belt we find a form with a wide thallus which is often curled or spirally twisted.

Petalonia fascia is not so faithful to the association as the species mentioned above. However, in no other association it is so frequent and so beautifully developed as in this one. This applies also to the two following species.

Scytosiphon lomentaria, also a boreal-arctic species, is much less common in this community, but where it is present, it is beautifully developed. It is found from March to the end of June. Occasionally it is met with in other associations, too, in spring as well as in the autumn.

Cladophora flexuosa finally is a southern species, which appears already in March, becomes very abundant in May, and remains so till August, after which it gradually disappears. After September I have never found it in these pools. It is also rather common in the vegetation near the low-water line.

Among the companion species a few are of importance because they affect the aspect of the association. This are *Chondrus crispus* and *Ulva lactuca.*

The not very conspicuous crustaceous layer may cover a large part of the substrate. *Hildenbrandtia prototypus* is its most important constituent, although *Lithothamnion lenormandii* may also cover large surfaces. *Verrucaria mucosa* and *Ralfsia verrucosa,* on the other hand, are present in small amounts only.

Other species are, as a rule, present but in small numbers only. It concerns in the main dendritic Algae, viz. *Ceramium rubrum, C. deslongchampii, Polysiphonia nigrescens, P. urceolata, Cladophora rupestris, Cl. refracta* and *Chaetomorpha aerea*; they reach their optimum development at the low-water line. *Gigartina stellata* is also rather often met with, but makes a poor impression, and is to be regarded as an intruder which in these pools is unable to reproduce itself.

Other species occur here only rarely and more or less accidentally. Occasionally, for instance, young plants of *Fucus* and *Laminaria* are met with, but they never reach maturity.

During the summer months *Enteromorpha* species and *Porphyra umbilicalis* play a prominent part in these pools, but this will be discussed hereafter.

The *Monostrometo-Dumontietum* shows a clear stratification. In contrast with what we see in the other associations belonging to the *Enteromorpha* formation, the crust layer is well-developed. The upper layer consists of a mixture of tubular, foliaceous, fruticose and dendritic Algae. This heterogeneous composition raises the question whether it is right to include this association in the *Enteromorpha* formation, as such a composition is more common in the *Cladophora* formation. That I have nevertheless referred it to the *Enteromorpha* formation, rests two arguments, viz. on the fact that most of the characteristic species are either foliaceous or tubular, and on the frequency of *Ulva lactuca* and of *Enteromorpha compressa.* However, it must be admitted that this association occupies a more or less intermediary position between the two formations.

Fig. 17. Small pool near Den Helder, habitat of the *Monostrometo-Dumontietum.* April 1956.

If we compare the records of this formation obtained in the Netherlands with those which in April 1955 were obtained on the coast of "le Boulonnais", we see that the association on the latter comprises a much smaller number of species. The characteristic species were all met with, except *Ulonema rhizophorum* whose presence in the beginning of April was not to be expected, and here, too, *Chondrus crispus* was always present; *Ulva lactuca* appeared to be less common. The crust layer was exceptionally well-developed; *Lithothamnion lenormandii* was here the predominant species and it was accompanied by *Corallina officinalis.*

As companion species only a few ubiquists and some species from the *Cladophora* formation were met with; among the latter the most common one was *Laurencia pinnatifida,* a species which does not occur in the Netherlands.

The presence of *Corallina officinalis* in this association was also recorded from the Faeroes (BØRGESEN, 1905).

SYNECOLOGY

At Den Helder the *Monostrometo-Dumontietum* is best developed in the small, 5—30 cm deep pools between the blocks of basalt in the zones in which *Fucus vesiculosus* and *F. serratus* are found. In these little pools the environment undergoes in the course of the day considerable changes. On account of the slight depth the kind of weather exercises a considerable influence. In sunny weather the temperature will rise rapidly, and at the same time the evaporation will increase, with the result that the salinity increases somewhat. In cold weather the temperature of the pools will show a rapid fall. The temperature extremes are therefore much larger than they are in the sea. During a summer day the temperature of the water in these pools often rises to more than 20° C; a temperature of 30° C is by no means an exception. In the sea at Den Helder temperatures of more than 20° C occur every year on a few days only. The salinity of the water in the pools also depends upon the weather. Bright and windy weather cause an increased evaporation, and rain a dilution. Twice a day the water in the pools is suddenly mixed with sea water of an entirely different temperature and salinity. The Algae living in the pools are responsible for other changes, e.g. in the pH and in the oxygen concentration. The CO_2 which they require for their photosynthesis is in sea water available in small amounts only; most of it is present in the form of carbonates and bicarbonates. The latter, too, may be used by the Algae, but this causes a rise of the pH. Normally the latter fluctuates between 8.0 and 8.1, but according to DAVY DE VIRVILLE (1934—1935), if very actively photosynthesizing Algae like *Ulva lactuca, Enteromorpha* spp. and *Cladophora* spp. are present, a few hours of sunshine suffice to raise the pH to a value of more than 10. During daytime the water is supersaturated with oxygen, but during the night the latter may disappear entirely.

In 1957 a part of the sea-dike at Den Helder was covered with bitumen, but contrary to our expectation, this did not mean the end of the *Monostrometo-Dumontietum.* In 1958 this association appeared to be well-developed in the 2—3 cm deep layer of water which remained behind in the pools on the bitumen at low water. Even in parts of the dike where the association had not been present in the years preceding the bituminization, it appeared to have established itself.

At Harlingen and at Yerseke the *Monostrometo-Dumontietum* is found only along the margin of basins with a greater depth. Here it descends to 25 cm depth; still lower we usually find dendritic Algae or no vegetation at all.

In the harbour of West-Terschelling the situation is entirely different. The water from the "Kom" flows off during the period of ebb via a lower part of the dike, the so-called "cascade". Here in the clay between the shells of mussels and oysters shallow depressions have been formed, in which always water is present. The latter is continually renewed. Because of the small depth of these pools the temperature of the water varies considerably. At this place we find the *Monostrometo-Dumontietum* in the midst of the *Fucetum vesiculosi*.

In May 1958 I found a more or less similar situation near Kats on Noord-Beveland. Here *Monostroma*, *Dumontia*, *Petalonia*, *Scytosiphon* and *Cladophora flexuosa* occurred in a similar runlet on the shells of a mussel population; the association descended here nearly to the low-water line.

In pools on the mussel banks and on the mud flats the association occurs only in the form of fragments.

In "De Bol", a brackish pond situated on the landside of the dike on Texel, BODDEKE found in April 1956 *Monostroma grevillei* and *Dumontia incrassata* together with *Chondrus crispus*.

ANNUAL CYCLE

The annual cycle in the development of the *Monostrometo-Dumontietum* was studied in the little pools on the sea-dike at Den Helder. As all the characteristic species show a marked periodicity, the community may be regarded as a typical example of a seasonal association. In spring, when all the characteristic species are present, it is a colourful, well-characterized community. In the first half of May *Monostroma grevillei* disappears, in June *Scytosiphon lomentaria*, *Petalonia fascia* and *Dumontia incrassata* with the epiphytic *Ulonema rhizophorum* vanish. During the summer months *Cladophora flexuosa* reaches its greatest density, and at the end of the summer it rapidly declines. In May or there about the *Enteromorpha* species (mainly *E. compressa*, but occasionally also *E. intestinalis*, *E. linza* and *E. clathrata*) and *Porphyra umbilicalis* begin to penetrate the little pools from the *Enteromorpheto-Porphyretum* which is the most prominent association on the stones in the neighbourhood of the pools; at the same time *Ulva lactuca* begins to increase in number. When in June the vernal species have gone down, this group of species becomes dominant, and the vegetation might now, at first view, be taken for an *Enteromorpheto-Porphyretum*. However, the presence of persistent species like *Chondrus crispus*, *Ceramium deslongchampii*, *Cladophora rupestris* and *Polysiphonia nigrescens*, and the abundance of crustaceous Algae reveal its entirely different origin.

The phenomenon that the character of an association is changed to a large extent by species which penetrate in it from the surrounding communities, is called vicinism. It is well illustrated by the difference shown by the records 52042 (table xxiv:2) and 52148 (table xxv), which were obtained from the same place but at different dates, the first on 21.V. '52 and the second on 8.IX. '52. In May the group value of the *Enteromorpha* species, *Porphyra* and *Ulva* was 1¾, in September it was 5¾, and at a somewhat earlier date this figure would have been even higher, as *Porphyra umbilicalis* is in September already on the decline. In July the latter is much better represented, but in May it has not yet established itself. When in September the temperature of the sea water begins to fall, the tubular and foliaceous Algae decrease in number.

TABLE XXV

Late-aestival aspect of the Monostrometo-Dumontietum

Den Helder, sea-dike, at pale 106, a circ. 10 cm deep pool in the eulittoral region; surface: 2.5. m^2; substrate: basalt and mussels; 8.IX.'52; CH 52148.

Percentage of covering 80

Chondrus crispus	3.2	Gigartina stellata	+°
Ulva lactuca	2.2	Porphyra umbilicalis	+
Enteromorpha compressa	2	Pylaiella litoralis	+
Enteromorpha linza	1	Chaetomorpha aerea	+
Enteromorpha clathrata	+	Ectocarpus confervoides	+
Enteromorpha intestinalis	+	Fucus vesiculosus	+
Cladophora rupestris	+	Fucus serratus	+
Ceramium rubrum	1.2	Elachista fucicola	+
Cladophora flexuosa	+	Lithothamnion lenormandii	+
Desmotrichum undulatum	+	Ralfsia verrucosa	+
Hildenbrandtia prototypus	2	Verrucaria mucosa	+

On the 18th October 1952 the same little pool was investigated once more. *Cladophora flexuosa*, which in the first half of September was still present, had disappeared completely, and *Enteromorpha*, *Ulva* and *Porphyra* were strongly reduced in number. *Petalonia fascia*, on the other hand, had already returned, be it with a few individuals only. Notwithstanding the period of frost in the beginning of December this species increased continuously in number. *Dumontia incrassata*, which in some of the other pools appeared in November, was for the greater part destroyed in December by the period of frost. In February the development of the association begins to proceed at a very rapid rate. *Dumontia*, *Petalonia* and *Monostroma grevillei* become at that time very numerous, and after a while the other characteristic species follow their example.

This annual cycle of development shows that the various stages can not be regarded as different aspects of a single association. In reality we have here an example of a cyclic succession completed within the course of a year. The *Monostrometo-Dumontietum* is the vernal association, which in time is replaced by the *Enteromorpheto-Porphyretum*, the aestival association, and in the autumn we note the decline of the latter and an attempt to restore the former association. Species like *Petalonia fascia* and *Scytosiphon lomentaria* also occur at the low-water line, but they appear there later than in the small pools of the tidal zone. This is doubtless a question of temperature. In the little pools in spring the amount of heat that is required for the germination of these Algae is probably available at an earlier date than it is at the low-water line, although the fluctuations in the temperature in the pools are much larger. More precise data with regard to the influence of the changes in the environment are urgently needed.

AREA OF DISTRIBUTION

In the Netherlands the association appeared to be well-developed at Harlingen, Yerseke, Goese Sas, Kats, Den Helder and on Terschelling and Texel. At other places only fragments were found.

In the boreal part of the coast of western Europe the association is widely distributed. KJELLMAN (1878) already mentioned the joint presence of *Dumontia incrassata* and *Monostroma grevillei* from a shallow bay on the west coast of Sweden. STEEMANN NIELSEN (1951) reports that these species occur in great numbers in the *Fucus vesiculosus* association of the Isefjord (Denmark). From the Faeroes BØRGESEN (1905) described a *Monostroma grevillei* association in which this species is accompanied by *Dumontia incrassata*, *Petalonia fascia* and *Scytosiphon lomentaria*, but in which *Corallina officinalis*, too, appears as a dominant. From the coast of England, too, the presence of the association has been reported. Whether it also occurs on Heligoland, we could not make out with certainty, but it is not improbable. At the coast of "le Boulonnais" we found it during our spring visit to be very common. Judging from the large amounts of *Monostroma grevillei* found in the material of southern origin that is washed ashore in spring on the coast of the Netherlands we would say that the association cannot be rare along the coasts of the English Channel either.

4.VI. The Ulva lactuca sociation

The *Ulva lactuca* sociation comprises all algal vegetations of the sublittoral region in which *Ulva lactuca*, usually accompanied by *Ceramium rubrum*, occurs as a dominant. These sublittoral *Ulva* vegetations are of a very heterogeneous composition, undoubtedly because they are of very different origin. An *Ulva* community may establish itself as a pioneer vegetation on a new substrate, e.g. on sea-dikes; in this case the community is at first poor in species, but if it is not rapidly replaced by a following stage in the succession, the number of species gradually increases. This happens in sites that are exposed to the surf. In sheltered spots, however, it is succeeded either by the *Codieto-Hypoglossetum* or by the *Laminarietum digitato-saccharinae*. An *Ulva* community may also be formed by degradation of the last-named associations, and in that case it appears to contain crustaceous Algae like *Hildenbrandtia prototypus*, *Lithothamnion lenormandii* and *Corallina officinalis*, and also some slowly growing species like *Ahnfeltia plicata* and *Polyides rotundus* which establish themselves only tardily.

The records from Terschelling were obtained from an *Ulva* sociation in which the succession proceeded at a very slow rate, as the *Codieto-*

Hypoglossetum occurs at that place in an incomplete form only, and as *Laminaria saccharina* is a comparatively new arrival. In the long run here, too, the *Ulva* sociation will be replaced by other communities.

The records from Heligoland show us an *Ulva* sociation which must be regarded as a degeneration stage of the *Laminarietum*. The causes of this degeneration are as yet unknown. The general aspect of the vegetation suggested to us that the development may be of the cyclic type.

One of the most conspicuous companion species is *Chorda filum*. This species occurs in large numbers in the *Ulva* communities found in sheltered sites; in other vegetations it is much more rarely met with. As it is often washed ashore in large amounts, it seems likely that it will occur somewhere in the form of extensive vegetations, but so far I have not been able to discover the whereabouts of the latter.

Once, viz. in 1949 on a breakwater near Callantsoog, an *Ulva lactuca* community was found in which *Petalonia fascia* and *Scytosiphon lomentaria* occurred as companion species.

TABLE XXVI

Ulva lactuca sociation

Sample plots	1	2	3	4
Percentage of covering	30	100	100	100
Ulva lactuca	3	5	4	5
Ceramium rubrum	1	2	2	2/3
Chondrus crispus	+	+	1	1
Chorda filum	1	+	—	+
Laminaria saccharina	—	+	2	1
Polysiphonia nigrescens	+	+	—	—
Porphyra umbilicalis	+	+	—	—
Enteromorpha clathrata	+	+	—	—
Ectocarpus confervoides	+	+	—	—
Fucus serratus	—	—	2	+
Rhodomela confervoides	—	—	+	+
Ahnfeltia plicata	—	—	+	+
Laminaria digitata	—	—	+	1
Corallina officinalis	—	—	+	+
Lithothamnion lenormandii + L. polymorphum	—	—	2	1
Hildenbrandtia prototypus	—	—	+	+
Enteromorpha compressa	1	—	—	+
Callithamnion roseum	1	—	—	—
Codium fragile	+	—	—	—
Fucus vesiculosus [1]	+	—	—	—
Polysiphonia denudata	+	—	—	—
Cladophora utriculosa	—	+	—	—
Cladophora rupestris	—	—	+	—
Halidrys siliquosa	—	—	1	—
Cystoclonium purpureum	—	—	+	—
Polyides rotundus	—	—	+	—
Enteromorpha linza	—	—	—	+
Phyllophora membranifolia	—	—	—	+
Scytosiphon lomentaria	—	—	—	+
Chordaria flagelliformis	—	—	—	+

[1] probably secundar.

LEGENDA

1. West-Terschelling, harbour; stones on black mud; *Ulva* community; the presence of *Fucus vesiculosus* in the survey plot is doubtless a secondary development; surface: 10 m^2; 1.IX.'54; CH 54167.
2. West-Terschelling, along the southern dike of the "Kom", west of the harbour; *Ulva-Ceramium* vegetation; surface: 10 m^2; 1.IX.'54; CH 54169.

Germany

3. Heligoland, Felseninsel; at the sheltered north-east side, in a depression in the sublittoral region; *Ulva* vegetation on small boulders; surface: 10 m^2; 24.VIII.'55; CH 55072.
4. Heligoland, Felseninsel, at the sheltered north-east side; *Ulva* vegetation in the midst of the *Laminarietum*; surface: 25 m^2; 24.VIII.'55; CH 55073.

4.VI.. The vegetation with Desmotrichum undulatum

In September 1954 I found on stones lying at the bottom of the 50—60 cm deep "Kom" at West-Terschelling a rich vegetation consisting of *Enteromorpha* species and *Desmotrichum undulatum.*

The "Kom" at West-Terschelling is a closed basin of which the water is at high tide partly renewed by water from the "Waddenzee"; at low tide it is shut off from the sea. The fluctuations of the temperature and of the degree of salinity are in this basin much larger than they are in the sea.

As we know very little of the ecological conditions in basins of this kind, this aberrant vegetation was provisionally accepted as an independent community.

In April 1958 the "Kom" was once more visited, but this time no *Desmotrichum* was found.

In June of this same year it was found once more in a fairly large number, this time as an epiphyte on *Scytosiphon lomentaria* at a depth of 10—20 cm, i.e. at the same level and even at the same place where in April a well-developed *Monostrometo-Dumontietum* was found, in which *Monostroma grevillei* predominated, and in which *Scytosiphon* and *Petalonia fascia* occurred as companion species, but in which *Dumontia* was not represented.

TABLE XXVII

Vegetation with Desmotrichum undulatum

West-Terschelling, in the "Kom"; surface: 0.25 m^2; 1.IX.'54; CH 54165.

Percentage of covering:	100		
Desmotrichum undulatum	2	Ceramium rubrum	1
Enteromorpha intestinalis	2	Cladophora rupestris	+
Enteromorpha clathrata	+	Polysiphonia nigrescens	+
Enteromorpha compressa	+	Erythrotrichia carnea	+
Enteromorpha linza	1	Ectocarpus confervoides	+
Ulva lactuca	+	Fucus vesiculosus	+
Scytosiphon lomentaria	1		

This development is the more remarkable as I also found *Desmotrichum* in September 1952 in a small pool in the tidal belt at Den Helder where in the spring a rich *Monostrometo-Dumontietum* had been present, (Table xxv). It is possible, therefore, that the *Desmotrichum-Enteromorpha* vegetation is no more than a seasonal variant of the *Monostrometo-Dumontietum*. In order to decide this question, observations in other localities are required.

The floristic composition of the *Desmotrichum* vegetation found on Terschelling is given in table XXVII.

5. THE CLADOPHORA FORMATION

The *Cladophora* formation comprises the numerous communities that are composed of fruticose and dendritic Algae. These communities consist of two layers, viz. 1°. a lower one, in which crustaceous and pulvinate Algae predominate, and 2°. an upper one, which on account of the many different dendritic and fruticose Algae that are represented in it, offers a very colourful aspect.

In the series occurring in the eulittoral and sublittoral region of western Europe these communities appear mostly as transitional stages between the *Enteromorpha* formation and the final stages in which the larger Phaeophyceae play the most important part. Where the latter, because of special edaphic, climatological or other factors, are unable to establish themselves, the fruticose and dendritic Algae often form persistent vegetations which may be very rich in species.

In the Netherlands the following communities may be included in this formation, viz.

1. the *Catenella repens* sociation,
2. the *Callithamnietum scopulorum*,
3. the *Ceramium deslongchampii* sociation,
4. the *Polysiphonieto-Chaetomorphetum*,
5. the *Codieto-Hypoglossetum*,
6. the *Callithamnietum rosei*,
7. the *Cladophoreto-Polysiphonietum*,
8. the community of *Chondrus crispus*, and
9. the community of *Gigartina stellata*.

Some of these communities cannot be regarded as associations, as they possess no characteristic species. They are, however, recognizable by two special features, viz. the presence of a single dominant species and the position they occupy in the zonation. They are here regarded as sociations.

The communities belonging to this formation have on the whole a restricted distribution. Their floristic composition, moreover, is not everywhere the same. Even in such a comparatively small area as the southern part of the North Sea these features are clearly recognizable. On the coast of "le Boulonnais" we find associations which are not present on the coast of the Netherlands, e.g. the *Rhodymenietum palmatae*, the *Lomentarieto-Plumarietum* and the *Polyideto-Gracilarietum*. These associations are here but briefly described. Further to the west, on the north coast of Brittany, the communities are with a single exception totally different from those found in the Netherlands. The same applies to the Scandinavian communities belonging to this formation. In describing the associations occurring on the coast of the Netherlands we will, however, as far as possible draw attention to the points in which they agree with these foreign communities.

5.I. The Catenella repens sociation

This community is mainly characterized by the dominance of *Catenella repens* and by the place it occupies in the zonation. *Catenella* is found exclusively in the upper part of the eulittoral region. The only exception to this rule was noted by me when I examined a cave on the coast at Dinard (Brittany), where this species was also present in the supralittoral region, but this was probably made possible by the high humidity of the air which prevails, as a rule, in habitats of this kind. In the Netherlands *Catenella* is mainly found in fissures between the stones of the dikes and breakwaters and on palisades, where it is protected against a too strong insolation. This sciaphily also explains why *Catenella* is found on the coast of France in large masses in deep rock fissures and in small caves, and that it also finds a suitable habitat in the undergrowth of the *Fucetum spiralis* and of the *Pelvetietum canaliculatae*, more rarely also in the undergrowth of the *Ascophylletum nodosi*.

Catenella does not occur only as an epilithic species, but it is also found on less solid substrates. On salt marshes we find it together with *Bostrychia scorpioides*, *Rhizoclonium riparium*, *Lyngbya aestuarii* and other species in the undergrowth of the halophilous communities of phanerogams, especially in *Halimione* and *Limonium* vegetations, but also in the *Scirpetum maritimi*. In France *Catenella* is in this kind of habitats as common as on solid substrates, but in the Netherlands it is on the salt marshes less often met with.

From what has been said in the preceding paragraph, it will be clear that *Catenella* can certainly not be regarded as a characteristic species for a definite association, but that it is an excellent indicator of a definite region and as such, because of its general occurrence, of practical importance in the mapping of coastal vegetations.

In the succession the *Catenella* community plays but a part of subordinate importance. On new substrates *Catenella* may crowd out *Blidingia minima*, at least if there is enough shade, and in *Catenella* vegetations we sometimes see young individuals of *Fucus spiralis* or of *Pelvetia canaliculata*, but it is an exception that the latter grow out to mature plants.

The floristic composition of the *Catenella* sociation is very simple; it is shown in table XXVIII.

TABLE XXVIII

Catenella sociation

Flushing, Oranjedijk; *Catenella* vegetation on a shaded wooden pale in the upper part of the eulittoral region; surface: 0,16 m^2; exposition: north-east; inclination: 90°; 4.IV.'54; CH 54003.

Percentage of covering :		90
	Catenella repens	5
	Blidingia minima	+
	Fucus spiralis	+ g
	Ulva lactuca	+

5.II. The Callithamnietum scopulorum

The *Callithamnion scopulorum* association which so far was not described from the Netherlands, was mentioned in the classification proposed by DEN HARTOG (1955) under the name "*Callithamnion hookeri*" sociation. VAN DEN HOEK (1958) knew this association from Hook of Holland, where "*Callithamnion polyspermum*" forms a belt on the shade side of the pales on the northern mole. With regard to the ecology of *Callithamnion scopulorum* interesting facts were communicated by BODDEKE (1958).

TABLE XXIX

Callithamnietum scopulorum

Sample plots	1	2	3	4	5
Percentage of covering	95	95	95	90	90
Callithamnion scopulorum	5.5	5.5	5.5	2	2
Pylaiella litoralis	1.2	1.2	+.2	+	1
Ceramium deslongchampii	1.2	2.2	2.2	—	—
Polysiphonia urceolata	+	—	+	—	—
Cladophora flexuosa	—	+	+.2	—	—
Enteromorpha compressa	1	+	+	+	+
Fucus vesiculosus	+	+	+g	+	+
Porphyra umbilicalis	+	+	+	+	—
Blidingia minima	+	+	+.2	+	—
Ulva lactuca	+	+	+	1	+
Ralfsia verrucosa	+	1	1	+	—
Rhizoclonium riparium	—	—	—	—	3
Rhodochorton purpureum	—	—	1	—	—
Fucus spiralis	—	—	—	1	—
Acrochaetium secundatum	—	—	+	—	—
Cladophora rupestris	—	—	+	—	—
Ascophyllum nodosum	—	—	—	+	—
Petalonia fascia	+	—	—	—	—
Cyanophyceae on barnacles	+	+	1	4	3

LEGENDA

1. Den Helder, sea-dike, near pale 132; a dense vegetation of *Callithamnion scopulorum* on wooden pales, exposed to a fairly strong surf; surface: 1.5 m²; exposition: north and east; inclination: 90°; 24.VI.'52; CH 52065.

2. Den Helder, sea-dike; near pale 134; a dense vegetation of *Callithamnion scopulorum* and *Ceramium deslongchampii* on wooden pales, exposed to a fairly strong surf; surface: 1 m²; exposition: east; inclination: 90°; width of the zone: 30 cm; 24.VII.'52; CH 52067.

3. Den Helder, sea-dike, near pale 123; beautifully developed vegetation of *Callithamnion scopulorum* on pales that are exposed to a fairly strong surf; surface: 2 m²; exposition: north, east and west; inclination: 90°; 4.VII.'52; CH 52073.

4. Zieriksee; on palisades at the entrance of the canal to the harbour; vegetation of *Callithamnion scopulorum* on a shaded site; surface: 1 m²; exposition: west; inclination: 90°; width of the zone: 50 cm, 22.VII.'52; CH 52090.

5. Veere, on palisades along the harbour; a dense vegetation of *Callithamnion scopulorum* and *Rhizoclonium riparium* on a shaded place; surface: 1 m²; exposition: north; inclination: 90°; 23.VII.'52; CH 52102.

The association is characterized by the frequency of *Callithamnion scopulorum*, a Rhodophycea which on the whole shows a tendency to form larger groups. As a characteristic species it is nearly perfect, as it occurs outside this association only in the undergrowth of the Fucaceae communities, and there but sporadically and in the form of small individuals which show but little vitality.

Companion species are *Rhizoclonium riparium*, *Ceramium deslongchampii* and *Pylaiella litoralis*, which sometimes are present in large numbers. VAN DEN HOEK (1958) also mentions from Hook of Holland *Sphacelaria brittanica*. *Ralfsia verrucosa* sometimes occurs in considerable amounts in the undergrowth. The other Algae that are found in this association are almost all of them intruders from the *Enteromorpheto-Porphyretum* and from the *Blidingietum minimae*. Young Fucaceae are also occasionally met with. The substrate is often densely covered with barnacles (*Balanus balanoides*) of which the shells are infected with the Cyanophyceae *Plectonema terebrans* and *Entophysalis granulosa*.

SYNECOLOGY

The association shows a marked preference for more or less strongly exposed sites which receive only diffuse light. In the Netherlands it is found mainly on woodwork, no matter whether the latter is covered with barnacles or not, but on stones and blocks of rock it is by no means rare. It is found in the eulittoral region, but the width of the zone it occupies, and the exact position of the latter varies rather considerably. On the pales on the sea-dike at Den Helder it forms a circ. 30 cm wide zone which begins circ. 10 cm beneath the *Bangieto-Urosporetum*. However, along the "Oranjedijk" at Flushing it begins only at the lower limit of the *Catenella repens* sociation. Its own lower limit borders in steep and dark localities on the *Ceramium deslongchampii* sociation, on softly sloping rocks usually on the *Fucetum vesiculosi*.

The association is present throughout the year, although during the summer months it may suffer severely by desiccation. In severe winters the *Callithamnietum* is usually entirely destroyed, and then it takes a long time to recover. Damage by desiccation, too, is but slowly repaired.

SUCCESSION

In sites where it is not exposed to insolation, the *Callithamnion scopulorum* association occupies the lower part of the zone in which usually the *Blidingietum minimae* is found, and the upper part of the zone in which elsewhere the *Enteromorpheto-Porphyretum* occurs. In such habitats it is not succeeded by other communities. If the site receives somewhat more light, a vegetation may develop which is more or less intermediary between this association and one of the two other ones.

On newly dumped blocks on the sea-dike at Den Helder the *Callithamnietum* established itself within six months. Stones that were dumped in August, were very soon covered with a vegetation which belonged to the *Enteromorpha* formation. The darkest fissures between the blocks were, however, in the next spring filled with a well-developed *Callithamnion* vegetation.

AREA OF DISTRIBUTION

The *Callithamnion scopulorum* association occurs in the Netherlands on exposed places in the "Waddenzee", on the large harbour moles along the coast of the North Sea, and locally along the East Scheldt. In France I have seen it at Roscoff, at Dinard and along the coast of "le Boulonnais". On Heligoland I have not been able to find it.

BØRGESEN (1905) describes from the Faeroes a *Callithamnion arbuscula* association. This occurs on the strongly exposed rocks which are covered with *Balanus balanoides* to a height far above the high-water line, whereas it does not overstep this line if the sites are less exposed. *Ceramium acanthonotum* is mentioned as a generally present companion species which in quiet spots may become dominant. Besides these two species a few individuals of *Porphyra umbilicalis* and of *Himanthalia elongata* are sometimes present; those belonging to the last-named species are, however, but rarely fertile. Oher species that may be present, are *Acrosiphonia albescens* (= *A. centralis*), *Polysiphonia urceolata*, *Ceramium rubrum*, *Dumontia incrassata*, *Petalonia zosterifolia*, *Scytosiphon lomentaria*, a few small specimens of *Alaria esculenta*, and in the lowest part of the belt an undergrowth consisting of *Corallina officinalis*.

BØRGESEN says of *Callithamnion scopulorum* that it occurs rather abundantly in caves in the eulittoral region, and that it is found there occasionally in company of the robust *C. arbuscula*.

The description given by BØRGESEN of his *Callithamnion arbuscula* association suggests that it is not homogeneous.

LEVRING (1937) mentions the presence of the *Callithamnion arbuscula* association from the coast of Norway, where it does not overstep the high-water line.

Along the coast of the Netherlands *Callithamnion arbuscula* is unknown, and it is not impossible that its absence has enabled *C. scopulorum* to establish itself in the latter's place. Along the coasts of the Faeroes and of Norway it is unable to compete with *C. arbuscula* on the exposed rocks in the upper part of the eulittoral region, and here it is therefore compelled to withdraw in the dark caves where *C. arbuscula* apparently is in a less favourable position.

5.III. The Ceramium deslongchampii sociation

This community which is characterized by the dominance of *Ceramium deslongchampii*, is found only in places where the Fucaceae for one reason or another are unable to establish themselves. *Ceramium deslongchampii* can hardly be regarded as a characteristic species, as it also occurs in the undergrowth of the *Fucetum vesiculosi*, the *Ascophylletum nodosi* and the *Fucetum serrati* and as it is also very common in the *Callithamnion scopulorum* association and in the *Polysiphonieto-Chaetomorphetum*. Before the harbour of Den Helder was closed, *Ceramium deslongchampii* was also found in the *Callithamnietum rosei* on the wooden rafts just below the water line.

The floristic composition of the *Ceramium deslongchampii* sociation does not differ materially from that of the undergrowth found in the Fucaceae communities. The dominance of *Ceramium deslongchampii* is the only characteristic feature. Another species which may increase considerably in number is *Gigartina stellata.*

The *Ceramium deslongchampii* sociation was found at Harlingen on the bituminized slope of the northern harbour mole, and at Den Helder on shaded stones and pales below the *Callithamnion scopulorum* association. In various places in Zeeland, e.g. at Flushing, Veere and Ellewoutsdijk, it was found rather abundantly on vertical pales; and on the outside of the southern mole at IJmuiden I found it on a strongly exposed site. VAN DEN HOEK (1958) mentions it from Hook of Holland.

In the succession the *Ceramium deslongchampii* stage is found only where the Fucaceae are unable to establish themselves, be it because of lack of light, a too strong surf, a too steep slope or an unsuitable substrate. In the zonation it finds its position between the *Callithamnion scopulorum* association and the *Polysiphonieto-Chaetomorphetum.*

On the coast of "le Boulonnais" we found *Ceramium deslongchampii* mainly in shaded rock fissures and in dark corners, where it occurred together with *Lomentaria articulata, Plumaria elegans, Laurencia pinnatifida, Sphacelaria fusca* and *Lithothamnion lenormandii.* It is not improbable that the *Ceramium deslongchampii* sociation of the coast of the Netherlands is not more than a depauperated variant of the *Lomentarieto-Plumarietum* of the French coast.

On Heligoland we found *Ceramium deslongchampii* in company of *Plumaria elegans* on shaded blocks on the "Lange Anna", the breakwater at the north-western end of the Felseninsel.

TABLE XXX

Ceramium deslongchampii sociation

Harlingen, north side of the northern mole; a dense *Ceramium deslongchampii* vegetation on bitumen, forming a 2 m wide zone; surface: 40 m²; exposition: north; inclination: 10°; 8.IV.'53; CH 53014.

Percentage of covering:	85		
Ceramium deslongchampii	5	Acrosiphonia centralis	+
Ulva lactuca	1	Enteromorpha compressa	+
Callithamnion scopulorum	+	Porphyra umbilicalis	+
Petalonia fascia	+	Fucus spiralis	+
Polysiphonia urceolata	+	Fucus vesiculosus	+
Polysiphonia nigrescens	+	Chondrus crispus	( )
Cladophora rupestris	+		

5.IV. The Polysiphonieto-Chaetomorphetum

This community was called by VAN GOOR (1922, 1923) the "Gemischte *Polysiphonia-Chaetomorpha*-Assoziation". He described it from Den Helder and from Stavoren. With regard to its occurrence at Den Helder he reports: "Sie besetzt die fast horizontale Oberfläche der sich unter dem *Fucus* und über der *Laminaria* vorfindenden Steinen und bietet ein hübsches gemischtes Aussehen von grün und rot, zwischen

TABLE

Polysiphonieto-

Sample plots	1	2	3	4	5	6	7	8	9
Percentage of covering	90	90	90	90	90	100	95	35	90
Polysiphonia urceolata f. roseola	4	1	+.2	2.2	2.3	2	4.4	2.2	4.4
Chaetomorpha aerea	( )	—	+	1	1.1	1	1	+	+.1
Phyllophora membranifolia	+	+—1	—	—	—	2	—	—	+.2
Cystoclonium purpureum	—	+	+	2.2	2.2	1	—	—	—
Cladophora rupestris	( )	—	—	—	+.2	—	+.2	+.2	+.2
Chaetomorpha melagonium	—	+	—	—	—	—	—	—	—
Cladophora refracta	—	—	—	—	—	—	—	—	—
Acrosiphonia centralis	+	—	—	—	—	—	—	+.2	+.2
Codiolum wormskioldii st. urosporae	—	—	+	—	—	—	+	+	+
Ahnfeltia plicata	—	—	—	—	—	—	—	—	—
Polysiphonia nigrescens	2	3	3.3	3.2	2.3	3	1.2	+.2	1.2
Ceramium rubrum	+	2	1.2	2.2	1.2	2	1.2	+.2	1.2
Chondrus crispus	2	3	3.3	2.2	3.2	3	1	1.2	1.2
Ulva lactuca	+	1	1	1	2	+	2—3	2.2	2.3
Enteromorpha compressa	+	+	+	+	+	—	+	1.2	+.2
Fucus serratus	—	+	+	+	+	+	+	+	+
Porphyra umbilicalis	+	+	—	—	+	1	+	+	+
Hildenbrandtia prototypus	—	1	+	—	+	—	—	1	+
Petalonia fascia	+	+	+	+	+	—	+	+	+
Ceramium deslongchampii	2	—	—	—	+.2	+	+	—	—
Acrochaetium virgatulum	+	—	+	—	+	+	+	+	+
Laminaria digitata	—	—	—	—	—	—	1	+	2.2
Gigartina stellata	—	1	+.2	—	—	1	+.2	+.2	+.2
Pylaiella litoralis	—	—	+	+.2	+.2	—	1.2	1.2	1.2
Ectocarpus confervoides	+	—	+	+	—	—	+	—	+
Rhodochorton purpureum	—	—	—	—	—	—	+.2	+.2	+.2
Laminaria saccharina	—	1	+	1.2	1.2	+	—	—	—
Enteromorpha linza	+	—	+.3	+.2	+.2	—	—	+.2	—
Lithothamnion lenormandii	—	—	—	—	—	—	—	+	—
Ulothrix flacca	+	—	+	—	—	—	+	—	—
Cladophora flexuosa	+	—	—	—	—	—	—	—	—
Verrucaria mucosa	—	+	—	—	—	—	—	—	+
Petalonia zosterifolia	—	—	—	—	—	—	+	1.2	—
Giffordia granulosa	—	—	—	—	—	—	—	+	—
Bryopsis plumosa	—	—	—	—	—	—	—	—	—
Lyngbya infixa	—	—	—	—	—	1	—	—	—
Sphacelaria fusca	—	—	—	—	—	+	—	—	—
Erythrotrichia carnea	—	—	—	—	—	+	—	—	—
Hypoglossum woodwardii	—	—	—	—	—	—	—	—	—
Cladophora utriculosa	—	—	—	—	—	+	—	—	—
Ralfsia verrucosa	—	—	—	—	—	—	—	—	—
Fucus vesiculosus	+	—	—	—	—	—	—	—	—
Acrochaetium secundatum	—	—	—	—	—	—	—	+	—
Codium fragile	—	—	—	—	—	—	—	—	—
Ectocarpus crouani	—	—	—	—	—	—	—	—	—
Polysiphonia nigra	—	—	—	—	—	—	—	—	—
Membranoptera alata	—	—	—	—	—	—	—	—	—
Rhodomela confervoides	—	—	—	—	—	—	—	—	—
Chordaria flagelliformis	—	—	—	—	—	—	—	—	—
Dictyosiphon foeniculaceus	—	—	—	—	—	—	—	—	—
Rhodochorton floridulum	—	—	—	—	—	—	—	—	—
Laurencia pinnatifida	—	—	—	—	—	—	—	—	—
Sphacelaria plumigera	—	—	—	—	—	—	—	—	—
Filiform diatoms	3	?	?	?	?	?	?	?	?

Addenda: survey 11: Ectocarpus fasciculatus +; survey 12: Elachista fucicola +; survey 14: sia devoniensis +; survey 21: Callithamnion roseum +, Cladostephus spongiosus scopulorum +, Griffithsia flosculosa +, Lomentaria articulata +, Plocamium coccineum

Note: The filiform diatoms only have been estimated, when they did occur in abundance.

XXXI

Chaetomorphetum

10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
80	95	95	80	85	90	90	90	90	80	80	80	90	90	100	100	40	90
2.2	5	4.5	3	3.4	3	3	4	2	+	—	+	4	4	3	2	+	—
+.2	1.2	1.1	2	+	—	+	—	—	+	—	+	1	+	+	—	+	—
—	1.2	+	—	+	—	—	—	—	1	+	1	+	+	—	+	+	—
—	—	—	—	—	—	—	—	—	—	+	—	2	2	1	1	1	+
—	1.2	1.2	—	2.2	—	—	—	—	1	+	+	—	+	—	—	1	—
—	—	—	+	+	—	—	—	—	+	—	—	+	+	—	+	+	—
—	+	+	+	+	—	—	—	—	—	—	—	+	—	+	—	1	—
—	+.2	—	—	—	3	4	3	4	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	+	+	+	—	—	—	—	—	—	—	—	—
—	+.2	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—
1.2	2.2	1.2	2	2.2	—	+	—	+	+	+	+	2	1	1	2	+	+
4.3	+.2	+	4	+.2	—	—	—	—	4	4	3	1	1	2	3	+	3
1.2	+.2	+.2	1	1	—	—	—	—	1	2	+	1	+	+	+	3	1
2.3	1.2	1.2	1	1.3	2	—	—	—	2	1	1	1	1	3	1	+	1
+	+	+	+	+	2	+	+	+	2	+	+	+	—	—	—	+	+
+	+	+	+	+	—	—	—	—	1	1	+	+	+	+	+	+	+
+	—	—	+	—	1	—	—	—	+	+	+	—	—	—	—	+	—
+	+	2	+	+	—	—	—	—	—	—	+	1	+	+	—	—	+
—	+	—	—	—	2	+	+	+	—	—	—	—	—	—	—	—	—
—	1.2	+.2	+	1.2	—	—	—	+	+	—	—	1	+	—	—	1	—
—	1	+	+	+	—	—	—	—	+	+	—	+	+	—	—	—	—
1	2.2	1.2	1	1	—	—	—	—	—	—	—	1	1	+	+	—	+g
+.2	+.2	+.2	+	+.2	—	—	—	—	—	—	—	—	—	—	—	2	—
1.2	—	—	—	—	—	+	+	1	—	—	+	—	+	—	—	—	—
+	+	+	—	+	—	—	—	—	2	1	—	—	—	—	—	—	—
+.2	+.2	+	+	+.2	—	—	—	—	—	—	—	—	+	—	—	—	—
+	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	+	—	—	—	—	—	1	+	—	—	—	—	—	—	—
+	+	+	—	+	—	—	—	—	—	—	—	—	—	+	+	1	—
—	—	—	—	—	—	1—2	1	1	—	—	—	—	—	—	—	—	—
—	—	—	—	+.2	—	—	—	—	+	—	—	1	+	—	+	—	—
—	—	—	—	+	—	—	—	—	—	—	—	+	+	—	—	—	—
—	—	—	—	—	—	1	+	1	—	—	—	—	—	—	—	—	—
—	—	+	—	+.2	—	—	—	—	+	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	1	+	+	—	—	—	—	1	+
—	—	—	—	—	—	—	—	—	1	+	—	1	1	—	—	—	—
—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—	+
—	—	—	—	+	—	—	—	—	+	+	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	+	+
—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—
—	—	—	+	—	—	—	—	—	—	—	—	—	+	—	—	—	+
—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	+	—
—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	1	—
—	—	—	—	—	—	—	—	—	—	—	—	3	4	3	2	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	+.2	+	+	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	+	1	+	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+
—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—
?	?	?	?	?	3	2	2	3	?	?	4	?	?	?	?	?	?

Myrionema sp. +; survey 19: Giffordia mitchellae +; survey 20: Chondria dasyphylla +, Griffith- +; survey 23: Delesseria sanguinea +; survey 25: Polyides rotundus 1; survey 26: Callithamnion +, Polyneura gmelini +, Rhodymenia palmata +; survey 27: Gymnogongrus norvegicus +.

dem sich bisweilen auch braun und dunkelviolett vorfindet. Sie setzt sich nur aus feinverzweigten Arten zusammen, die während der kurzen Zeit, wenn sie trocken liegen, das Wasser wie ein Badeschwamm zurück halten; über dies wird sie auch dann noch von den Wellen benetzt. Die vier in grösster Zahl in dieser Vegetation vorhandenen Arten sind: *Chaetomorpha aerea*, *Polysiphonia urceolata*, *Ceramium rubrum* und *Cladophora rupestris*, dazwischen finden sich bisweilen noch: *Ceramium deslongchampii*, *Pylaiella litoralis*, *Ectocarpus siliculosus* und *confervoides* und selten auch *Ectocarpus tomentosus* und *Polysiphonia nigrescens*, während in den tieferen Teilen *Chantransia virgatula* auf *Chaetomorpha aerea* und *Cladophora rupestris* ihren roten Anflug bildet."

VAN DEN HOEK (1958) mentions that at the northern side of the mole at Hook of Holland a zone consisting of *Polysiphonia urceolata* and *P. nigrescens* is found; this zone also belongs to the *Polysiphonieto-Chaetomorphetum*.

LEGENDA (see table XXXI)

1. Harlingen, close to the end of the southern mole, south side; a beautifully developed *Polysiphonia urceolata* vegetation near the low-water line; surface: 10 m²; 2.V.'54; CH 54022.

2. Texel, 't Horntje; rich vegetation of *Chondrus crispus*, *Polysiphonia nigrescens* and *Ceramium rubrum* near low-water mark on basalt; substrate locally covered with "*Polydora* mud"; surface: 10 m²; 17.VIII.'58; CH 58033.

3. Texel, Oude Schild, southern dike; dense vegetation of *Chondrus crispus* and *Polysiphonia nigrescens* on granite and basalt at low-water mark; substrate locally covered with "*Polydora* mud"; width of the zone: 3 m; surface: 10 m²; 14.IV.'52; CH 52019.

4. Oude Schild, southern dike; mixed vegetation in which *Polysiphonia nigrescens* is represented by the largest number of individuals, on basalt blocks covered with "*Polydora* mud"; width of the zone: 1 m; surface: 10 m²; 14.IV.'52; CH 52021.

5. Oude Schild, southern dike; mixed vegetation in which *Chondrus crispus* is represented by the largest number of individuals, on basalt blocks covered with "*Polydora* mud"; width of the zone: 1 m; surface: 10 m²; 14.IV.'52; CH 52022.

6. Oude Schild, southern dike; dense vegetation at the low-water line with *Polysiphonia nigrescens* and *Chondrus crispus* as the dominant species; width of the zone: 1 m; surface: 10 m²; 17.VIII.'54; CH 54142.

7. Den Helder, sea-dike, near pale 69; vegetation of *Polysiphonia urceolata* in the 1 m wide zone between the *Laminarietum* and the *Fucetum serrati* and with intruders from both associations; on basalt blocks covered with "*Polydora* mud"; surface: 10 m²; 10.IV.'52; CH 52011.

8. Den Helder, sea-dike, at the end of the small breakwater at pale 58; open vegetation of *Polysiphonia urceolata* and *Ulva lactuca* on basalt blocks that were covered for 80 % with fine mud which had been deposited between the tubes of the worm *Polydora ciliata*; in several spots this layer of mud reached a thickness of nearly 1 cm; surface: 25 m²; 12.IV.'52; CH 52016.

9. Den Helder, sea-dike, at pale 64; dense *Polysiphonia urceolata* vegetation on granite and basalt, locally covered with "*Polydora* mud"; width of the zone: 2 m; surface: 20 m²; 25.IV.'52; CH 52027.

10. Den Helder, sea-dike, at pale 62; closed, 1 m wide zone of *Ceramium rubrum* on basalt covered with a good deal of "*Polydora* mud"; surface: 10 m²; 25.IV.'52; CH 52028.

11. Den Helder, sea-dike, at the pales 106 and 107; very rich vegetation of *Polysiphonia urceolata* on basalt and concrete which at several spots were covered with "*Polydora* mud"; width of the zone: 3 m; surface: 75 m²; 21.V.'52; CH 52043.

12. Den Helder, sea-dike, between the pales 100 and 101; zone of *Polysiphonia urceolata* on basalt and concrete which were here nearly free from "*Polydora* mud"; at the low-water line; width of the zone: 1 m; surface: 10 m²; 22.V.'52; CH 52046.

13. Den Helder, sea-dike, at pale 148; vegetation of *Ceramium rubrum* and *Polysiphonia urceolata* on basalt covered with "*Polydora* mud"; surface: 25 m²; 6.VII.'52; CH 52075.

14. Den Helder, sea-dike, at pale 80; vegetation of *Polysiphonia urceolata, P. nigrescens* and *Cladophora rupestris* on basalt covered with "*Polydora* mud"; surface: 10 m²; 9.VII.'52; CH 52079.

15. IJmuiden, southern mole, almost at the end of the southern side; already declining vegetation of *Acrosiphonia centralis* and *Polysiphonia urceolata* on "*Polydora* mud"; strong surf; surface: 2 m²; exposition: south-west; inclination: 15°; 1.VI.'58; CH 58004.

16. Hook of Holland, northern side of the mole, strongly exposed to the surf; a 2 m wide zone in which *Acrosiphonia centralis* and *Polysiphonia urceolata* are the dominant species; surface: 20 m²; 11.IV.'54; CH 54008.

17. Hook of Holland, northern side of the mole; beautifully developed, 2 m wide zone of *Polysiphonia urceolata* and *Acrosiphonia centralis*; strongly exposed to the surf; surface: 20 m²; 11.IV.'54; CH 54009.

18. Hook of Holland, northern side of the mole; a 2 m wide zone of *Acrosiphonia centralis* and *Polysiphonia urceolata*; strongly exposed to the surf; surface: 20 m²; 11.IV.'54; CH 54010.

19. Schouwen, dike at the entrance of the canal to Zieriksee; vegetation of *Ceramium rubrum* on blocks of stone; surface: 80 m²; 22.VII.'52; CH 52093.

20. Schouwen, along the canal to Zieriksee; beautifully developed, 1 m wide zone of *Ceramium rubrum* on blocks of stone; surface: 50 m²; exposition: west; inclination: 20°; 22.VII.'52; CH 52094.

21. Flushing, Nolledijk, on uncovered peat at the low-water line; a very open vegetation of *Ceramium rubrum* and *Sphacelaria plumigera* on a nearly flat surface, the openings for the greater part filled with filamentous diatoms; surface: 100 m²; 4.IV.'54; CH 54005.

Germany

22. Heligoland, Düneninsel, on the northern side of the island on blocks of rock; a narrow transitional zone between the *Fucetum serrati* and the *Laminarietum* covered with a closed vegetation of *Polysiphonia urceolata* and *Rhodomela confervoides*; surface: 6 m²; 20.VIII.'55; CH 55056.

23. Heligoland, Düneninsel, on blocks of rock on the northern side of the island; a narrow transitional zone with a closed vegetation of *Polysiphonia urceolata* and *Rhodomela confervoides*; surface: 10 m²; 20.VIII.'55; CH 55057.

24. Heligoland, Düneninsel, on blocks of rock at the northern side of the island; a narrow transitional zone with a mixed vegetation in which *Rhodomela confervoides, Ulva lactuca* and *Polysiphonia urceolata* jointly determine the aspect; surface: 4 m²; 20.VIII.'55; CH 55058.

25. Heligoland, Düneninsel, on blocks of rock at the norhern side of the island; a narrow transitional zone in which *Ceramium rubrum* is the dominant species; surface: 4 m²; 20.VIII.'55; CH 55059.

France

26. Cap Gris Nez, on blocks at the most protruding, strongly exposed point of the cape, from the mean low-water line upwards a 70 cm wide, beautifully developed algal zone in which *Chondrus crispus* is the dominant species; surface: 10 m²; 2.VIII.'54; CH 54115.

27. Wimereux, Pointe aux Oies; nearly flat surface in the vicinity of the low-water line, strongly flooded with sand; a poorly developed vegetation in which *Ceramium rubrum* and *Rhodochorton floridulum* are the dominant species; surface: 10 m²; 9.IV.'55; CH 55014.

The *Polysiphonieto-Chaetomorphetum* is an association with a comparatively large number of characteristic species. The latter are not all equally faithful to the community, but without exception they find there their most ideal environment.

Polysiphonia urceolata f. *roseola* is one of the most common of them. It is often dominant, and in that case its warm-red colour determines the aspect of the association. In Zeeland and on the coast of "le Boulonnais" it is, however, rather scarce in this community, and there *Ceramium rubrum* becomes the dominant species. Although *Polysiphonia urceolata* reaches its highest development in the zone which separates the *Laminarietum digitato-saccharinae* from the *Fucetum serrati*, it often occurs in large numbers in the *Laminarietum* itself, partly in the undergrowth and partly epiphytically. For this reason it is to be regarded as a species with a preference for the *Polysiphonieto-Chaetomorphetum*.

Chaetomorpha aerea is almost never absent, but it is much less conspicuous than the preceding species. It does not determine the aspect of the association, and is never dominant; as a rule, it is found only in small numbers. It shows a tendency to form small groups. It is an annual species, which is almost entirely confined to the zone on both sides of the mean low-water line (M.L.W.); sporadically it is also found in the *Monostrometo-Dumontietum* and in the *Laminarietum*. Just like *Polysiphonia urceolata* it is present the whole year round; in spring it is, however, more abundant than in the other seasons.

In the lowermost part of the association a second *Chaetomorpha* species may be present. This is *Ch. melagonium*, which is recognizable by its thicker and more rigid filaments and by its blue-green colour. It is usually found in the form of isolated individuals, rarely in groups, and it is much less common than the other species. I found it only in the summer months. It also occurs occasionally in the *Laminaria* association.

Cladophora rupestris, too, has its main distribution in this association, but is met with also in the undergrowth of the *Fucetum vesiculosi* and of the *Fucetum serrati* and in the *Monostrometo-Dumontietum*. Locally it may form a rather important part of the covering, although rarely a percentage of 20 is exceeded. In contrast to *Cl. refracta*, which we find mainly during the summer months, *Cl. rupestris* is found the whole year round in this association. *Cl. refracta* also occurs sporadically in the *Laminarietum* and in the *Fucetum serrati*.

Acrosiphonia centralis appears as a characteristic species in this association in the course of the winter, usually towards the end of December. In spring it reaches its fullest development, and then it disappears. Its frequency fluctuates considerably from year to year, as I could observe at Den Helder. In 1952, 1955 and 1958 it occurred in rather large numbers. At Hook of Holland, at IJmuiden and in one of the habitats near Den Helder I have seen what effect this species has on the aspect of the association when it becomes dominant, a phenomenon that was very suggestively described by JONSSON (1912: p. 121) from Iceland. In this case *Acrosiphonia* covers the blocks of rock at the low-water line with a closed carpet, which becomes so dense that almost no other species can maintain themselves in it. I found this development only in spots that were more strongly exposed to the surf than the other habitats. In more quiet sites at Harlingen and at Den Helder it forms but small clusters. On the sea-dike at Den Helder it shows a marked preference for flat stones covered with mud; the latter is deposited between the tubes of the boring worm *Polydora ciliata*. On wood, too, it is sometimes found. This preference for somewhat softer substrates may be connected with the presence of the numerous reflexed and rhizoid-like lateral branches by the aid of which it attaches itself. As I have found this Alga but rarely outside this community, I regard it as an exclusive species.

Cystoclonium purpureum is found in this association throughout the year, but it is not common on the coast of the Netherlands. On Texel it grows in large masses, and although it undoubtedly reaches its fullest development in the zone at the low-water line, it may descend into the *Laminarietum.*

In the lowest parts of the zone occupied by the association we may meet *Phyllophora membranifolia*, especially in those sites that receive no direct sunlight. As a rule, it is represented by a few individuals only, but locally it may occur in large masses, and in that case it may exercise an important influence on the aspect of the association, so e.g. on the Nolledijk at Flushing. In the *Laminarietum*, too, it is not very rare. As it is a photophobic species, it is not impossible that it may occur even in deeper water. Provisionally I consider it as a species with a preference for the *Polysiphonieto-Chaetomorphetum.*

At Den Helder *Ahnfeltia plicata* occurs in this association together with *Phyllophora membranifolia* and *Chondrus crispus* on flat stones near the level of the extremely low low-water line reached at spring tides (E.L.L.W.S.). In this part of the coast it may be regarded as a characteristic species, but on Heligoland and along the coast of the English Channel it is also found in large numbers in the *Laminarietum.*

Codiolum wormskoldii st. *urosporae* may probably also be regarded as a characteristic species. So far I have found it only in the zone bordering on the low-water line. Because of its resemblance with *Ulothrix flacca*, a species which may also be found in this zone, it is often overlooked, and for this reason its upper limit could not yet be ascertained.

VAN GOOR (1923) regarded *Ceramium rubrum*, too, as a characteristic species of this association, but this is not correct as this species may occupy a dominant position in vegetations of a very different nature, so e.g. in the *Codieto-Hypoglossetum* and in the undergrowth of the *Laminarietum.* In all those vegetations in the lower part of the eulittoral region and in the sublittoral region which are not too strongly exposed to the surf, it is more or less well-represented.

Species which may reach dominance, but which in opposition to *Polysiphonia urceolata* f. *roseola* and *Acrosiphonia centralis* cannot be regarded as characteristic, are, apart from *Ceramium rubrum*, which has already been mentioned, *Polysiphonia nigrescens*, *Chondrus crispus*, *Ulva lactuca* and in Heligoland also *Rhodomela confervoides*. These constituents are here regarded as dominants if they form at least 30 % of the total mass of the vegetation; in that case they exercise an important influence on the aspect of the latter. Among these species *Ulva lactuca* is the only one which represents a totally different life form.

Ulva lactuca often reaches dominance in the *Enteromorpheto-Porphyretum*, the association which precedes the *Polysiphonieto-Chaetomorphetum* in the succession. Although *Ulva* nearly always passes into the latter, it is there, as a rule, no longer dominant; if it is, this usually indicates a disturbance in the environment, like damage by frost, a sudden flooding with deposits because of a change in the course of a current, or the dumping of a new load of stones.

The other species which may become dominant, may also play a prominent part in other sublittoral communities. *Chondrus crispus*, moreover, may also be met with as the predominant species in the undergrowth of the Fucaceae vegetations in the lower part of the eulittoral region. The factors which determine what species will reach dominance in a definite habitat, are as yet almost entirely unknown. To this problem I will return hereafter.

The floristic composition of the *Polysiphonieto-Chaetomorphetum* is very heterogeneous. This may have various causes, viz.

1°. the recent origin of the "artificial rock coast" which in the Netherlands replaces the natural rocks; this factor is responsible for the fact that several species have not yet reached the sites where they might establish themselves;

2°. the position of this association in the zone where the eulittoral region passes into the sublittoral one; this makes that eulittoral species reach here their lower limit, whereas sublittoral ones which can tolerate a short period of emergence, provided that they remain exposed to the spray and do not suffer from desiccation, reach here their upper limit;

3°. the circumstance that on the dikes almost continuously works are carried out by which the vegetation is disturbed, so that species from the *Enteromorpheto-Porphyretum* obtain a chance to establish themselves;

4°. the very different conditions under which the association may occur, e.g. a more or less strong exposition to the surf, the presence or absence of sedimentation, differences in light intensity, etc.; because of this great difference between the various habitats, locally species which are bound to a special ecological factor, but which show no preference for a definite community, may penetrate into the association;

5°. the fact that some species reach the limit of their area of distribution within the area occupied by the association; this factor, however, is of minor importance, because it does not apply to the characteristic species nor to the dominant ones either.

Eulittoral species found in this association are *Ceramium deslongchampii*, *Gigartina stellata*, *Hildenbrandtia prototypus*, *Ralfsia verrucosa*, *Fucus vesiculosus* and *F. serratus*. They reach their fullest development at a higher level in the eulittoral region, but descend repeatedly in the zone bordering upon the low-water line. Eulittoral species that show no special preference for a definite part of the region, are *Pylaiella litoralis* and the species from the *Enteromorpheto-Porphyretum*.

Sublittoral species which repeatedly penetrate into the association, are *Laminaria digitata* and *L. saccharina*, which, however, never reach maturity in these surroundings. In Zeeland this group of intruders is represented by some more species, viz. *Griffithsia devoniensis*, *Hypoglossum woodwardii*, *Codium fragile* and *Chondria dasyphylla*. Some of the predominantly sublittoral Algae may be regarded as constant companion species, viz. *Petalonia fascia*, *Giffordia granulosa*, *Acrochaetium virgulatum*, *Bryopsis plumosa* and *Erythrotrichia carnea*. With regard to *Petalonia fascia* it is noteworthy that this species undoubtedly reaches its optimum development in the *Monostrometo-Dumontietum* of the tidal pools; however, it is too frequent in the *Polysiphonieto-Chaetomorphetum* to be regarded as no more than an intruder.

Ecological factors may offer some species a chance to establish themselves within the association. This, however, leads but rarely to an important change in the aspect of the latter. So the establishment of *Cladostephus spongiosus*, *Sphacelaria fusca*, *Enteromorpha linza* and of the in the Netherlands absent *Rhodochorton floridulum* is favoured by the deposition of sand. Among these species *Rhodochorton floridulum* is the only one which may put a definite stamp on the aspect of the vegetation; this was noted by me on the coast of "le Boulonnais".

The deposition of mud on stones that are attacked by the boring worm *Polydora ciliata*, is another factor which may cause changes in the aspect of the vegetation. This layer of mud often has a thickness of 1–2(–5) cm. A number of species avoid the stones covered with "*Polydora* mud", perhaps because they are unable to grow on them; this applies, for instance, to the crustaceous Algae and to *Phyllophora membranifolia*, *Chaetomorpha aerea* and *Ahnfeltia plicata*. *Acrosiphonia centralis*, *Petalonia fascia* and *Ulva lactuca*, on the other hand, show a certain preference for these stones. At Den Helder the two first-named species are in this association almost entirely confined to this substrate. In how far mutual competition between the constituents of the association may play a part here, is difficult to decide.

A strong surf may be responsible for the absence of several of the species which prefer quiet water. Other species, however, show a preference for a strong surf, and such species may establish themselves under these circumstances in this association, so e.g. *Petalonia zosterifolia*, an inhabitant of the eulittoral region which, however, if the surf is strong enough, penetrates even into the supralittoral region. In shaded spots, e.g. on inclined blocks of stone and in deep fissures, *Phyllophora membranifolia* increases in number.

According to the way in which the differences in the ecological factors are combined in the various habitats, the association therefore shows a different aspect.

LOCAL DIFFERENCES IN FLORISTIC COMPOSITION

As the floristic composition of the association in the various habitats shows rather conspicuous differences, I will subject these differences here to a closer inspection, paying special attention to the species which determine the aspect of the association and to those that are confined to definite localities but which in such localities are characteristic for the association.

1. At Harlingen the *Polysiphonieto-Chaetomorphetum* is a closed vegetation in which *Polysiphonia urceolata* f. *roseola* is the dominant species, although *P. nigrescens* and *Chondrus crispus* are also very common. *Acrosiphonia centralis*, *Ceramium rubrum* and *Ulva lactuca* are here but sparsely represented.

2. At Oude Schild on Texel *Polysiphonia nigrescens* and *Chondrus crispus* are the dominant species; sometimes they are present in almost equal amounts, whereas in another spot either the one or the other may predominate. *Polysiphonia urceolata* f. *roseola* is fairly well represented, but here it is never dominant. The same applies to *Ceramium rubrum* and to *Ulva lactuca*. *Acrosiphonia centralis* is here very scarce, but characteristic for this variant is the great number of individuals by which *Cystoclonium purpureum* is represented. At "'t Horntje" on Texel the association has almost the same composition, the only difference being that *Ceramium rubrum*, too, becomes dominant.

3. At Den Helder *Polysiphonia urceolata* f. *roseola* becomes dominant in sites that are exposed to the surf, whereas in quiet spots *Ceramium rubrum* predominates. Where *Polysiphonia* predominates, *Ceramium* appears to be but sparsely represented, but where *Ceramium* predominates, *Polysiphonia* is still present in large numbers. In both habitats *Polysiphonia nigrescens*, *Chondrus crispus* and *Ulva lactuca* occur in rather large numbers, but without showing preference for one of them. *Acrosiphonia centralis* is scarce, and occurs only in the habitats in which *Polysiphonia urceolata* predominates, and this also applies to *Ahnfeltia plicata*, which in the Netherlands is known only from Den Helder. VAN GOOR (1923) mentioned in his description that *Cladophora rupestris* and *Chaetomorpha aerea* are very well represented, but these species may here be left out of consideration as they do not become dominant.

4. On the south side of the southern mole at IJmuiden the association is confined to a few spots. For the rest the zone bordering the low-water line is completely controlled by a *Mytilus* population. In the algal association *Polysiphonia urceolata* is throughout the year the predominant species. In the spring months *Acrosiphonia centralis* becomes a very conspicuous constituent, especially on "*Polydora* mud".

5. On the north side of the mole at Hook of Holland the association is characterized by the dominance of *Polysiphonia urceolata* f. *roseola* or, in spring, of the latter and *Acrosiphonia centralis*. Of the species which are, as a rule, rather conspicuous in the other variants, only *Polysiphonia nigrescens* and the characteristic species *Chaetomorpha aerea* are

represented, be it but sparsely. This vegetation was studied by me but once, viz. in April 1954 after a short but cold winter. VAN DEN HOEK (1958) reports that *Polysiphonia urceolata* and *P. nigrescens* are present the whole year round. In the winter of 1953—54 an extensive population of young mussels was wiped out; it was succeeded by epilithic diatoms, which in their turn were replaced by *Acrosiphonia centralis.* In August 1954 the young mussels had returned in great numbers.

6. At Zieriksee the association was studied only in the summer; at that time *Ceramium rubrum* appeared to be the dominant species; it was accompanied by a more or less large number of *Chondrus crispus* and *Ulva lactuca* plants. *Polysiphonia urceolata* and *P. nigrescens* were scarce. The presence of *Cystoclonium purpureum*, *Hypoglossum woodwardii*, *Chondria dasyphylla* and *Griffithsia devoniensis*, of which the last three are to be regarded as intruders from the sublittoral region, give the association a peculiar aspect which probably will prove to be characteristic for the variant occurring in the East Scheldt.

7. Along the Nolledijk at Flushing the association is very open, and here, too, *Ceramium rubrum* is the dominating species; of the species which elsewhere may become dominant *Ulva lactuca* is the only one which is fairly common, whereas *Polysiphonia urceolata*, *P. nigrescens* and *Chondrus crispus* are represented by a few individuals only; *Acrosiphonia centralis* was absent at the time of our visit, which fell in spring. *Sphacelaria plumigera* and *Phyllophora membranifolia* are very prominent constituents, and *Cladostephus spongiosus* is regularly found, although in small numbers.

8. At the coast of "le Boulonnais" the association is but rarely met with; it obviously reaches here the southern limit of its area of distribution. It is replaced by the *Rhodymenietum palmatae*, in which *Rhodymenia palmata* is the dominant species, although *Chondrus crispus* helps in determining the aspect of the vegetation. In the *Polysiphonieto-Chaetomorphetum* itself *Chondrus crispus* and *Ceramium rubrum* are the dominant species. At Cap Gris Nez the aspect of the association is determined by *Chondrus crispus*. *Polysiphonia urceolata*, *P. nigrescens*, *Ceramium rubrum* and *Ulva lactuca* are here but sparsely represented. At Wimereux, where *Ceramium rubrum* is the dominant species and where *Chondrus crispus* is fairly well represented, it is hardly possible to regard the community as belonging to the *Polysiphonieto-Chaetomorphetum*, as *Cystoclonium purpureum* is the only characteristic species of the latter which is represented. However, on the coast of "le Boulonnais" this species is no longer confined to this association; it is also very common in the *Rhodymenietum palmatae.*

9. On Heligoland the association is confined to the Düneninsel. Here we find a joint dominance of some species, especially of *Rhodomela confervoides* and *Polysiphonia urceolata* f. *roseola*. *Ulva lactuca* sometimes acts as co-dominant. Locally, viz. in the most sheltered spots, *Ceramium rubrum* becomes dominant, but in that case *Rhodomela* and *Polysiphonia urceolata* nevertheless remain very numerous. *P. nigrescens* is rather

common, *Chondrus crispus* rather rare. Besides *Rhodomela confervoides* *Chordaria flagelliformis* is represented, and occasionally also *Polyides rotundus*; the two first-named species may be regarded as typical for the Heligoland variant of the association.

SYNECOLOGY

The *Polysiphonieto-Chaetomorphetum* borders on the upper side on the *Fucetum serrati* or, if the latter is absent, on communities in which *Chondrus crispus* or *Ceramium deslongchampii* are the dominant species. In that case the upper limit is difficult to define, as *Chondrus crispus* may also be dominant in the *Polysiphonieto-Chaetomorphetum* itself and as it is always represented in it. However, even in case it is dominant in the association, the difficulty is not insurmountable as the presence of a considerable number of sublittoral species in the latter may be used for determining its upper limit. This limit coincides more or less with the M.L.W.N.

Below the association borders on the *Laminarietum digitato-saccharinae* or, in places where the latter is absent, as it often is in Zeeland, on the *Codieto-Hypoglossetum*. Especially in the latter case this lower limit, which coincides more or less with M.L.W.S., is difficult to determine as the two associations have several species in common. I accept the line below which *Codium fragile* becomes dominant, as the lower limit of the association. Where *Codium fragile* is absent, the disappearance of the eulittoral species and their replacement by the characteristic species of the *Codieto-Hypoglossetum* can be used.

That the upper and lower limit of the zone occupied by the association coincide with definite hydrographic lines, viz. M.L.W.N. and M.L.W.S., is not absolutely true, and under certain circumstances the deviations may even be considerable. On the mole at Hook of Holland, where it is strongly exposed to the surf, it reaches a level far above M.L.W.N. On Heligoland the association is often absent, and then the *Fucetum serrati* borders immediately on the *Laminarietum digitato-saccharinae*.

The association, as has already been stated, is found in very different habitats; the surf may be very strong, but it may also be weak or absent, and salinity, the amount of mud or sand that is deposited, and still other factors vary from place to place. This diversity finds its expression in the fact that the species which reach dominance also vary from place to place.

The factors that play a part in this selection, are still imperfectly known, and will have to be studied in more detail. However, with regard to some of the species I possess ecological data which may give some indications. *Polysiphonia urceolata* f. *roseola*, for instance, prefers sites that are exposed to the surf; in quiet spots it decreases strongly in number. A thin layer of sediment on the substrate exercises a favourable influence on its development, and this is in good agreement with the fact that this species reaches a dominant position at Den Helder and at Hook of Holland. *Ceramium rubrum*, on the other hand, prefers sheltered spots such as are found in quiet bays and between breakwaters. This explains perhaps why this species is the dominant one in the waters of Zeeland. *Acrosiphonia centralis* shows a preference for exposed localities, but only on the sites in which the surf reaches its greatest force, it appears in the form of a closed vegetation. It is not impossible that the temperature may play a part, as the latter remains relatively low at such places, and shows but slight fluctuations. *Ulva lactuca* may also reach dominance, but only in places where the normal development of the vegetation is disturbed by frost, sedimentation or human interference. *Polysiphonia nigrescens* and *Rhodomela confervoides* have their main distribution in the sublittoral region; *Chondrus crispus*, too, but the latter is in the lower part of the eulittoral region still very frequent. Which factors are decisive for the presence or absence of these three species, is not clear. The time of arrival may perhaps play a part. However, so long as we are not better informed with regard to these points, it does not seem desirable to split the admittedly rather heterogeneous *Polysiphonieto-Chaetomorphetum* in local associations or subassociations.

SUCCESSION

The *Enteromorpheto-Porphyretum* is the pioneer vegetation on blocks of stone when the latter are dumped in the eulittoral region. In the zone bordering on the low-water line this association is rich in *Ulva lactuca*. It is succeeded in the course of some years by the *Polysiphonieto-Chaetomorphetum*, and it is therefore not strange that *Ulva lactuca* is in the beginning well-represented in this association, too. The establishment and the multiplication of the fruticose and dendritic Algae proceeds at first at a rapid rate, but several years elapse before the more stenobiontic species make their appearance. This will doubtless have to be regarded as one of the causes that are responsible for the considerable differences in composition which this association shows.

Along the coasts in the southern part of the North Sea the *Polysiphonieto-Chaetomorphetum* is the final stage of the succession, but along the coasts of the English Channel, on the Faeroes and on the west coast of Norway this is probably not so. Here the *Fucetum serrati* is separated from the *Laminarietum* by a zone occupied by a *Himanthalia elongata* or a *Bifurcaria bifurcata* community which appears to be preceded by communities related to the *Polysiphonieto-Chaetomorphetum*. The two characteristic species of these final stages are absent in the southern part of the North Sea. *Bifurcaria bifurcata* reaches the northern limit of its area of distribution in the English Channel; the possible causes for the absence of *Himanthalia* were mentioned on p. 65.

AREA OF DISTRIBUTION

The *Polysiphonieto-Chaetomorphetum* has been found in some sites along the coasts in the southern part of the North Sea. It is not impossible that its area of distribution will prove to be much larger, as from various places in the northern part of the Atlantic Ocean communities have been described which may be identical with this one.

The *Ceramium-Rhodomela* association described by NIENBURG (1930) from Heligoland, is as I have been able to ascertain in August 1955, no more than a variant of the *Polysiphonieto-Chaetomorphetum* which is rich in *Rhodomela.*

The *Acrosiphonia-Polysiphonia* association described by BØRGESEN (1905: p. 171) from the Faeroes shows a very striking resemblance to the variant of the *Polysiphonieto-Chaetomorphetum* which I found at IJmuiden and at Hook of Holland, as appears from the following quotation. "This association which is formed of species of *Acrosiphonia,* especially *A. albescens* (= *A. centralis*), and of *Polysiphonia urceolata* reaches from almost the lowest water mark to a few feet above it. It grows on sloping rocks, which it covers with a very dense matting, generally green at the top and reddish brown at the bottom, these two algae frequently making unmixed facies, an *Acrosiphonia*-facies uppermost and a *Polysiphonia*-facies below it. They may, however, also be found intermingled. On account of their very ample ramification they are both able to retain a great amount of seawater at low tide, which protects them from becoming dried up.

Mingled with the characteristic algae, we find e.g. *Ceramium rubrum, Cladophora rupestris,* and very rarely *Cladostephus spongiosus. Corallina* is usually absent in this association, as the dense growth of both species leaves no room for a subvegetation".

Ceramium rubrum and *Cladophora rupestris,* the two companion species mentioned by BØRGESEN, are absent at Hook of Holland, but elsewhere they are common in the *Polysiphonieto-Chaetomorphetum. Cladostephus spongiosus* is rare in the Netherlands, and that it is absent at Hook of Holland may therefore be accidental. It is rather unfortunate that BØRGESEN does not enlighten us with regard to the force of the surf and to the changes which his community may undergo in the course of the year.

More difficult to interpret are the descriptions given by JONSSON (1912) of communities occurring on the coast of Iceland. He describes (l.c. p. 121) an *Acrosiphonia* association with *Acrosiphonia albescens* (= *A. centralis*) and *A. incurva* (= *A. spinescens*), *Spongomorpha* cf. *vernalis*, *Cladophora sericea* f. and *Cl. rupestris.* This community would be common on the coasts of Iceland and Greenland. A closer inspection of his description reveals that it cannot be regarded as homogeneous, as *Cladophora sericea* f. appears to be characteristic for the tidal pools in that area.

He further describes (l.c. p. 133) a *Polysiphonia urceolata* association from the zone round the low-water line; this association, however, would also be met with at a greater depth, but this is apparently not quite certain, for he remarks "from what I have seen, the stretch of shore just above and somewhat below low-water mark is essentially the home of this association. It usually grows on a rocky substratum and on *Laminaria* stems at no great depth."

Apart from the dominant *Polysiphonia urceolata* two other species, viz. *Cystoclonium purpureum* and *Rhodomela confervoides,* are present in large numbers, which reminds us of the variant of the *Polysiphonieto-Chaeto-*

morphetum we found on Heligoland. This association of JONSSON is not homogeneous either, as the author also mentions besides *Ceramium rubrum C. acanthonotum* and *Callithamnion arbuscula*, species which on the Faeroes and along the west coast of Norway form an association of their own (cf. p. 150).

In studying JONSSON's publication I have got the impression that he has united all Chlorophyceae which show the same life form and which may become dominant, into a single association, and that he paid no attention to the position they occupy in the zonation; the same applies to his associations of Rhodophyceae and of Phaeophyceae. As his *Polysiphonia* association and his *Acrosiphonia* association (when some exceptions are left out of consideration) may be said to occupy the zone bordering on the low-water line, they probably form but a single community, a community which seems to be closely related to BØRGESEN's *Acrosiphonia-Polysiphonia* association. Unfortunately JONSSON, too, gives us no information on the force of the surf and on the seasonal aspect of the vegetations. As neither JONSSON nor BØRGESEN have published complete lists of species, a comparison with our own findings is not fully possible. Nevertheless the high degree of similarity between the vegetations described by these authors and those that are dealt with in this work, indicates doubtless a close sociological relationship.

5.V. The Codieto-Hypoglossetum

The association of *Codium fragile* and *Hypoglossum woodwardii* is here described for the first time. It is beautifully developed in the waters of Zeeland, and is probably confined to this area. In the "Waddenzee" I have occasionally found vegetations which showed some resemblance to this community, but they were imperfectly developed, and it is by no means certain that they may be included in the latter.

In the area that was investigated by me, a considerable number of species appears to be characteristic for this association, and they are, moreover, entirely confined to it. The first of these species is *Codium fragile* ssp. *tomentosoides*, which grows on wood, stones and shells, and which usually is dominant. It is present during the whole year, and is a favoured substrate for epiphytic Algae; especially in the summer months it is often completely covered with the latter. Some individuals of this species penetrate into the eulittoral region, and others, a very few only, are found in the *Callithamnietum rosei*. Some of the epiphytic Algae occur exclusively on *Codium fragile*, viz. *Acrochaetium codii* and *Feldmannia simplex*. *Callithamnion byssoides* and *Antithamnion cruciatum* show a preference for this species, but they may also be found on other Algae and even on stones. *Hypoglossum woodwardii* is found almost as often on Algae as on stones, and this also applies to *Dictyota dichotoma*. The latter is in some years extremely numerous. *Chondria dasyphylla*, *Ch. tenuissima* and *Antithamnion plumula*, on the other hand, are almost entirely confined to non-living substrates.

TABLE XXXII

Codieto - Hypoglossetum

Sample plots	1	2	3	4
Percentage of covering	45	70	70	70
Codium fragile	3	4	4	2
Hypoglossum woodwardii	1	1	2	2
Erythrotrichia investiens	+	+	1 ¹)	—
Dictyota dichotoma	+	1	+	—
Chondria dasyphylla	1	1	—	—
Chondria tenuissima	—	+	—	—
Acrochaetium codii	+	—	—	—
Feldmannia simplex	+	—	—	—
Giffordia mitchellae	1	+	—	—
Ectocarpus crouani	+	—	+	—
Feldmannia irregularis	+	—	—	—
Callithamnion byssoides	+	2	—	—
Polysiphonia denudata	+	+	—	—
Antithamnion cruciatum	—	2	—	—
Goniotrichum elegans	+	+	+	—
Griffithsia devoniensis	1	—	2	—
Giffordia sandriana	—	+	—	—
Ceramium rubrum	1	1	2	4
Chondrus crispus	1	1	2	—
Polysiphonia nigrescens	—	+	+	1
Bryopsis plumosa	+	—	+	+
Ulva lactuca	1	1	1	+
Erythrotrichia carnea	1	+	1	—
Polysiphonia nigra	+	+	+	—
Giffordia granulosa	+	+	+	+
Enteromorpha compressa	+	+	—	+
Lithothamnion lenormandii	—	+	+	—
Acrochaetium virgatulum	+	2	+	—
Lyngbya infixa	1	+	+	—
Sphacelaria fusca	+	—	+	—
Ectocarpus siliculosus	+	—	+	—
Ceramium deslongchampii	—	+	+	—
Cladophora refracta	—	—	+	+
Cladophora utriculosa	+	—	—	—
Gracilaria verrucosa	—	+	—	—
Polysiphonia elongata	—	+	—	—
Polysiphonia urceolata	—	—	+	—
Cystoclonium purpureum	—	—	+	—
Cladostephus spongiosus	—	—	+	—
Erythrocladia subintegra	—	—	+	—
Fucus serratus	—	—	+	—
Porphyra umbilicalis	—	—	+	—
Pylaiella litoralis	—	—	+	—
Hildenbrandtia prototypus	—	—	+	—
Callithamnion roseum	—	+	—	—

¹) perhaps partly E. reflexa

LEGENDA

1. Schouwen, canal to Zieriksee; well-developed vegetation consisting of *Codium fragile* and Rhodophyceae on wood and stones in the sublittoral region; width of the zone; 1 m; surface: 100 m²; 22.VII.'52; CH 52095.

2. Zuid-Beveland, Yerseke; beautifully developed vegetation consisting of *Codium fragile* and Rhodophyceae on wood and stones at the entrance of the harbour; width of the zone: 1 m; surface: 10 m^2; 27.VII.'52; CH 52106.

3. Tholen, Strijenham; a vegetation consisting of *Codium fragile* and Rhodophyceae on large, nearly flat stones below M.L.W.S.; surface: 25 m^2; exposition: south-east; 19.IX.'58; CH 58046.

4. Flushing, outer harbour; a vegetation of *Codium* and *Ceramium* on the steel walls of a permanent SHV pontoon; surface: 15 m^2; exposition: south and east; inclination: 90°; 22.IX.'58; CH 58048.

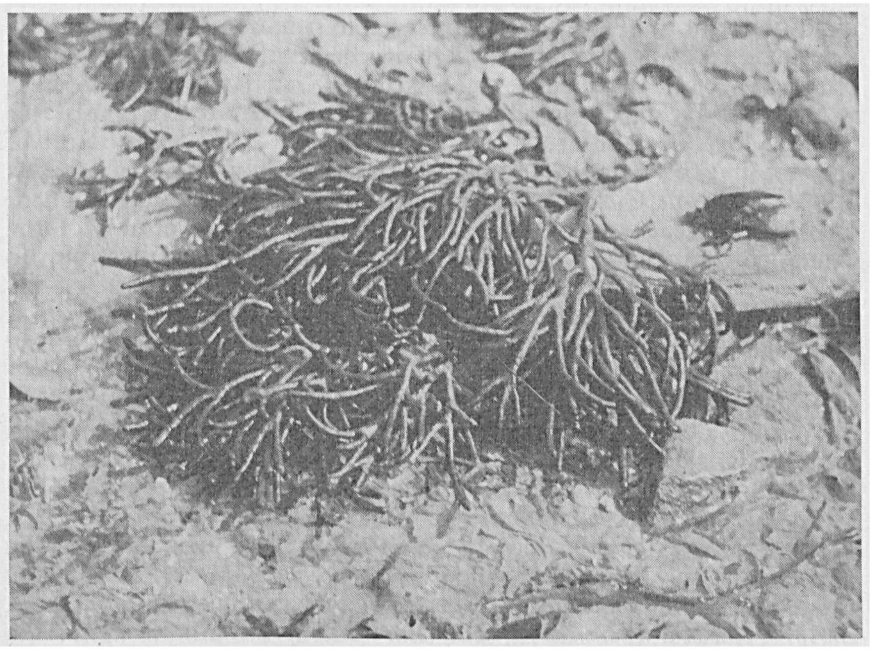


Fig. 18. *Codium fragile* ssp. *tomentosoides*. Yerseke, March 1955.

To the rare characteristic species, i.e. the characteristic species that are found only occasionally, but then often in large amounts, belong *Griffithsia barbata*, *Giffordia mitchellae* and *Taonia atomaria*. The number of these species will probably prove to be still larger, but we have as yet too few data to draw a definite conclusion.

Apart from the characteristic species, among which *Codium fragile*, *Hypoglossum woodwardii*, *Antithamnion cruciatum*, *Dictyota dichotoma* and *Chondria dasyphylla* are often present in very large numbers, a considerable number of less characteristic species are met with, viz. *Bryopsis plumosa*, *Ceramium rubrum*, *Griffithsia devoniensis*, *Polysiphonia nigrescens*, *P. nigra*, *P. denudata*, *Cladostephus spongiosus*, *Sphacelaria plumigera* and *Chondrus crispus*, some of them occurring frequently.

SYNECOLOGY

The association begins immediately below M.L.W.S. and reaches, according to the amount of light that is available, a depth of 1—2 m, and perhaps even more. It is found exclusively in very quiet spots in which it is protected against the surf, and where no Laminariaceae are found. Another condition is that the water must have a high summer temperature. The characteristic species belong all to the classes E_2 and E_3 (cf. p. 21), i.e. to the classes comprising the species with a predominantly southern distribution, and this also applies to many of the companion species. A high degree of salinity is also absolutely necessary.

In the Netherlands the East Scheldt is the only area in which these conditions are fulfilled. Its very favourable situation, on almost every side enclosed by land, ensures a high degree of quietude; a high degree of salinity is safeguarded by the fact that it carries little or no river water; and during the summer months the temperature of the water remains high because of the shallowness of the basin, and because of the fact that the water is only slowly renewed by the tidal movements. In this basin the *Codieto-Hypoglossetum* finds therefore the environment in which it reaches its optimum development. On account of the oyster culture, there is moreover no lack of suitable substrates.

The species which reach the northern limit of their area of distribution on this part of the coast, are almost all represented in this association.

Outside the East Scheldt the association has but rarely been met with. At Flushing it occurs in a much depauperated form, and on Texel and Terschelling fragments of it are found; in the last-named habitats it is soon ousted by the *Laminarietum*. In the East Scheldt *Laminaria saccharina* and *Halidrys siliquosa* are very rare, and here the *Codieto-Hypoglossetum* therefore is perfectly safe.

Where the water is less quiet, *Codium fragile* often loses its dominant position. At the Westbout (Schouwen) it is even scarce, so that here the aspect of the vegetation is determined by *Hypoglossum woodwardii*, *Bryopsis plumosa*, *Cladostephus spongiosus* and *Sphacelaria plumigera*.

The *Codieto-Hypoglossetum* passes through a typical annual cycle of development. During the winter half-year the vegetation is comparatively poor; at that time it consists of *Codium* individuals entirely devoid of epiphytes, a little *Ceramium rubrum*, *Chondrus crispus* and some other perennial species. In the warmer months of the summer half-year they are joined by the short-living species with a predominantly southern distribution, and then the association acquires a colourful and prosperous aspect. These species arrive towards the end of May or in the beginning of June, and reach their fullest development in July and August. At the end of October they have almost completely disappeared, only a few individuals being able to maintain themselves for a somewhat longer period.

The fact that several of these species are in the Netherlands confined to the East Scheldt, and that they are often eastwards of Normandy very rare, might perhaps be ascribed to the oyster culture. It is wel-known that all kinds of foreign organisms have reached the waters of the Netherlands with imported oysters. One of the most striking examples of such an introduction is that of the small mollusk *Crepidula* *fornicata*, a pest which has now spread along the whole coast of the Netherlands. However, it is not probable that the Algae have been imported in this way. The latter are so delicate and so vulnerable that it is hardly to be expected that they would have survived such a transport. One of these Algae, viz. *Griffithsia devoniensis*, was, moreover, already collected in the preceding century by VAN DEN BOSCH, i.e. before a begin was made with the oyster culture (KOSTER, 1952).

It is plausible therefore to assume that these species have reached the Netherlands in a more natural way, e.g. by transport on floating clumps of Algae. Several of the characteristic species of the *Codieto-Hypoglossetum* have repeatedly been observed on such substrates, e.g. *Hypoglossum woodwardii*, *Dictyota dichotoma* and *Chondria dasyphylla*.

The oyster culture, however, is certainly of importance for the development of this association, but in an entirely different way. The roof tiles that are laid out as collectors for the young oysters, as well as the walls of the oyster pits form suitable substrates for these Algae. Especially on places where the *Codieto-Hypoglossetum* establishes itself on the oyster shells, the growth of the *Codium* individuals ensures for the association a certain degree of motility. As soon as the upward pressure exercised by the water on the *Codium* thallus surpasses the weight of the substrate, in this case that of the oyster, a slight movement in the water suffices to set the *Codium* adrift. This explains why it is continually washed ashore along the dikes of Zeeland and occasionally even on the beaches of South and North Holland.

SUCCESSION

In the succession the *Codieto-Hypoglossetum* is preceded by the *Ulva lactuca* sociation, a very heterogeneous community in which *Ulva lactuca* is the dominating species; in addition it contains some other Algae, e.g. *Chorda filum*. The *Codieto-Hypoglossetum*, in its turn, is succeeded by the *Laminarietum* or occasionally by a *Halidrys* vegetation (e.g. at Strijenham, Tholen). These communities are, however, very rare in Zeeland, so that the *Codieto-Hypoglossetum* often forms here a semi-permanent vegetation.

AREA OF DISTRIBUTION

As the very special ecological circumstances which the *Codieto-Hypoglossetum* requires for its development, are realized only in the East Scheldt, the association bears a very local character. In the English Channel its characteristic species are found in all kinds of communities, in tidal pools as well as deep in the sublittoral region, and without any mutual connection. This is another argument in favour of our opinion that the special hydrographic and climatological circumstances in the East Scheldt are the efficient cause of the origin of this community. According to FELDMANN (1954) in the vicinity of Roscoff *Chondria dasyphylla* and *Ch. tenuissima* are found on stones and empty shells lying on a sandy substrate near the low-water line as well as in tidal pools. *Hypoglossum woodwardii* occurs in similar places, but often also on the stipes of *Laminaria hyperborea*. *Giffordia mitchellae* is mentioned by him as an epiphyte growing on *Scytosiphon lomentaria*, on *Nemalion helminthoides*, on *Petrospongium berkeleyi* and on the leaves of *Zostera marina*. *Taonia atomaria* lives in sandy pools in the tidal zone, on rocks below the low-water line, but also on the "maerl", a vegetation of *Lithothamnion calcareum*, which is found in quiet spots at a depth of 20—25 m. *Dictyota dichotoma*, too, descends to great depths. However, a community which would be more or less comparable to the *Codieto-Hypoglossetum* of the East Scheldt, I have seen nowhere along the coasts of the English Channel. The association seems to be related to the *Callithamnietum rosei*, which is found in very quiet water in which the salinity shows considerable fluctuations, although it is usually polyhaline, and in which to some extent a pollution with waste products takes place.

The execution of the Delta works will probably cause a nearly complete disappearance of the *Codieto-Hypoglossetum*. Although none of the constituents of this association will become extinct by the closure of the East Scheldt, this curious association itself will be dissolved in due time, and this means a serious loss to science. *Griffithsia devoniensis*, which reaches its fullest development in the East Scheldt, and which locally may be dominant, will show a considerable decline, as it is in the rest of its area a rarity.

5.VI. The Callithamnietum rosei

The *Callithamnion roseum* association, which is recognized here for the first time as a special community, has been known already for some years. The first description was given by DEN HARTOG (1953: p. 313) in his brief sketch of the sublittoral algal flora which was observed by him in the Canal through Zuid-Beveland. KOSTER (1954: p. 565), who studied the salt water canals of Zeeland, united the vegetation of the Canal through Zuid-Beveland and that of the Canal through Walcheren in a single schema, which led here to combine the *Callithamnietum rosei* of the first canal with the *Cladophoreto-Polysiphonietum* of the second. The vegetation of *Callithamnion roseum* and *Cladophora glaucescens* which in the course of the summer was observed by VAN DEN HOEK (1958) at the entrance to the Nieuwe Waterweg, in the lowermost part of the eulittoral region and in the sublittoral region, belongs undoubtedly to the *Callithamnietum rosei*. Observations on the ecology of *Callithamnion roseum* were published by BODDEKE (1958).

The characteristic species of this association are *Callithamnion roseum*, *Polysiphonia violacea*, *Dasya pedicellata* and *Giffordia sandriana*.

Callithamnion roseum is by no means confined to this association, but on quiet spots where much mud is deposited it also occurs in the *Fucetum vesiculosi*, e.g. in the harbour of West-Terschelling and in the harbour of Den Helder, and further also in the *Codieto-Hypoglossetum*. However, it reaches its fullest development in waters that are not subjected to tidal movements, but where the salinity nevertheless shows considerable fluctuations, and which are to some extent polluted.

TABLE XXXIII

Callithamnietum rosei

Sample plots	1	2	3	4
Percentage of covering	60	25	35	90
Callithamnion roseum	4	3	3	4
Polysiphonia violacea	—	+	2	—
Dasya pedicellata	—	—	+	—
Polysiphonia nigrescens	+.2	2	2	1
Bryopsis plumosa	( )	1	+	2
Ulva lactuca	+	1	1	1
Ceramium rubrum	—	+	+	1/2
Cladophora utriculosa	—	2	+	1
Spirulina subsalsa	2	—	+	—
Enteromorpha compressa	+	+	—	—
Codium fragile	—	—	+	1°
Griffithsia devoniensis	—	—	+	+
Polysiphonia urceolata	—	—	+	+
Enteromorpha ahlneriana	—	—	+	+
Ectocarpus siliculosus	—	+	—	—
Ectocarpus fasciculatus	—	—	—	+
Enteromorpha prolifera	—	—	—	+
Erythrotrichia carnea	—	—	—	+
Acrochaetium virgatulum	—	—	—	+
Polysiphonia elongata	—	—	+	—
Acrosiphonia centralis	( )	—	—	—

LEGENDA

1. Den Helder, harbour; below the water line on the wood of the last raft at the "Koopvaardijsluis"; a large concentration of *Mytilus edulis* with *Mya arenaria* in between; on the shells much *Callithamnion roseum*; width of the zone: 15 cm; below this zone but very little *Callithamnion* and *Spirulina subsalsa*; surface: 1.5 m^2; exposition: north; inclination: 90°; 23.VII.'53; CH 53 H-2.
2. Canal through Zuid-Beveland, near the Vlake bridge (at Schore); a vegetation of *Callithamnion roseum* descending to a depth of 40 cm; surface: 10 m^2; 9.IX.'54; CH 54175.
3. Canal through Zuid-Beveland on a small raft near the sluice at Wemeldinge; on wood; a very rich vegetation of *Callithamnion roseum* and many other Rhodophyceae, descending to a depth of 40 cm; surface: 4 m^2; 9.IX.'54; CH 54177.
4. Same place; 17.X.'58; CH 58056.

BODDEKE (1958) measured at the "Koopvaardijsluis" at Den Helder, where fresh water is discharged into the harbour, a salinity of $2{,}8\,^{0}/_{00}$ Cl'; the *Callithamnion* vegetation was here beautifully developed. In tidal waters, too, it is found; but on sites which fall dry at low water, it is found only in the shade, e.g. on Fucaceae.

Polysiphonia violacea was seen by me almost exclusively in the *Callithamnietum rosei* of the Canal through Zuid-Beveland. On the ecology of this species we are still badly informed.

Dasya pedicellata may probably also be regarded as a characteristic species of this association. It was found from the water line to a depth of 1,5 m, but only in the Canal through Zuid-Beveland. As the vegetation below a depth of 0.5 m has as yet been studied but superficially, and as *Dasya* is found mainly below 0.5 m, for the moment no more can be said. This also applies to *Giffordia sandriana*, which was found by me in the Canal through Zuid-Beveland on *Dasya pedicellata*, but which was collected by BRAKMAN in the Canal through Walcheren, too, (DEN HARTOG, 1954) and which at a later date was also found in a few specimens in the *Codieto-Hypoglossetum*.

The aspect of the *Callithamnietum rosei* is, as a rule, determined by *Callithamnion roseum*, although some other species, too, may play an important part, viz. *Cladophora utriculosa*, *Polysiphonia nigrescens*, *P. violacea*, *Chondrus crispus*, *Griffithsia devoniensis*, *Ulva lactuca* and *Bryopsis plumosa*; these species often form large patches. The floristic composition and accordingly the aspect of the vegetation, too, change from year to year. This may be due to an abnormally low water level, to sudden changes in the salinity and to fluctuations in the temperature in the summer months as well as in winter. On account of these differences in the relations between the various factors which influence the development, some species are in one year much better represented than in another. In 1950 but a single specimen of *Dasya pedicellata* was found; in 1951 this species appeared to be very common; in the following years it was met with in smaller amounts, but the severe winters of 1954 and 1956 were unable to eliminate it. The frequency of *Griffithsia devoniensis* and of *Callithamnion roseum* itself also show considerable fluctuations from year to year.

The number of intruders is but small. From above *Enteromorpha* species sometimes penetrate into the association. From the *Codieto-Hypoglossetum*, which occurs on the outside of the sluices at Wemeldinge, but a few species enter occasionally the Canal through Zuid-Beveland, viz. *Codium fragile* and *Antithamnion cruciatum*.

SYNECOLOGY

This association is almost exclusively found in harbours, where it lives on rafts and against the hull of ships, i.e. on substrates that follow the movements of the tides. Further it occurs in salt-water canals, which are shut off from the open water by sluices, and in which the water level therefore remains rather constant.

In harbours it is only met with if the latter regularly receive a supply of fresh water. In the harbour of Den Helder this happens when the sluices of the Canal through North Holland are opened, and at West-Terschelling it comes from the dunes. The abundance of *Callithamnion roseum* in the basins at Hook of Holland I am inclined to ascribe to a supply of polluted river water from the Nieuwe Waterweg.

A high degree of pollution of the water is no serious obstacle. Even in sites where the water is covered by a film of oil, and where the bottom consists of a stinking black mud, the association appears to be well-developed. The water in the salt-water canals, too, is rather strongly polluted, although not in the same measure as that in the harbours; the Canal through Zuid-Beveland is one of the most frequented waterways of Europe. However, as the sluices at the two ends of the canal are regularly opened, the water is continually renewed by relatively pure sea water. The salinity decreases from north to south, and is in the summer higher than in the winter, as in the latter a larger amount of polder water is discharged into it. In most cases, however, the water remains polyhaline.

The habitats in which I have observed the association, have another feature in common, viz. that they all occur in quiet water.

The *Callithamnietum rosei* is a sublittoral association. On the upper side it borders on the *Monostrometo-Porphyretum leucostictae* or, occasionally, on the *Enteromorphetum prolifero-intestinalis* of which some species penetrate into it. The lower limit is less well known. At Den Helder, where the association occupies a zone with a width of but 15—20 or at the most 25 cm, it borders on a zoocoenose with *Mytilus*, *Mya* and *Laomedea* sp. However, before the harbour was shut off from the sea, *Metridium senile*, *Tubularia larynx* and other Hydrozoa took the place of these zoocoenose. On account of the shutting off the fauna underwent a considerable depauperation, and the *Callithamnietum rosei*, too, lost part of its species. In the Canal through Zuid-Beveland the lower limit has not yet been studied; the *Callithamnietum* occurs at least to a depth of 0.5 m, but the algal vegetation as a whole descends to a depth of 1.5 m. However, whether the remaining part of this vegetation also belongs to the *Callithamnietum*, has not yet been ascertained.

SUCCESSION

Data with regard to the succession of this association are as yet almost entirely wanting. The fact that in similar places often *Ulva* vegetations are found, suggest that the latter may pass into a *Callithamnietum*. A transition of the latter into a more highly developed type of vegetation was never observed.

AREA OF DISTRIBUTION

At this moment the *Callithamnietum rosei* is known only from the Netherlands, but it will undoubtedly be found also elsewhere on the coasts of the North Sea. I myself observed this association at Den Helder, Terschelling, Hook of Holland and in the Canal through Zuid-Beveland. As *Callithamnion roseum* itself has been recorded from a large number of places (Boddeke, 1958), the association cannot be rare in the Netherlands.

5.VII. The Cladophoreto-Polysiphonietum

The association of *Cladophora glomerata* and *Polysiphonia urceolata* f. *formosa* is described here for the first time from the waters of the Netherlands. Although it does not contain a large number of species, and although it is not common, it is nevertheless an interesting object of study, as it occupies an intermediate position between the marine and the brackish-water vegetations.

The *Cladophoreto-Polysiphonietum* has but two characteristic species, viz. *Polysiphonia urceolata* f. *formosa* and *Ceramium diaphanum*.

TABLE XXXIV

Cladophoreto-Polysiphonietum

Sample plots	1	2	3	4
Percentage of covering	90	90	100	100
Polysiphonia urceolata f. formosa	4	3	2/3	3
Ceramium diaphanum	1	4	+	+
Cladophora glomerata	3	+	5	5
Cladophora utriculosa	1	+	—	—
Griffithsia devoniensis	1	+	—	—
Callithamnion roseum	+	—	—	—
Ulva lactuca	+	+	—	—
Enteromorpha intestinalis	1	2	1	—
Enteromorpha prolifera	+	+	+	—
Enteromorpha ahlneriana	+	—	—	—
Enteromorpha linza	—	+	—	—
Oscillatoria spec.	—	—	+	1
Potamogeton pectinatus	—	—	+	2
Zannichellia pedicellata	—	—	1	+
Myriophyllum spicatum	—	—	—	+
Ruppia spiralis	—	—	+	+
Zostera marina	—	—	—	( )
Laomedea loveni	—	—	+	1

LEGENDA

1. Canal through Walcheren, harbour for yachts at Veere; a beautiful vegetation of *Polysiphonia urceolata* f. *formosa* and *Cladophora* descending to a depht of 80 cm; substrate: broken stone; surface: 200 m²; exposition: east; inclination: 20°; 23.VII.'52; CH 52103.

2. Canal through Walcheren, at Veere, but much farther southward than plot 1; a beautiful vegetation of *Polysiphonia urceolata* f. *formosa* and *Ceramium diaphanum*, descending to a depth of 1 m; substrate: broken stone; surface: 120 m²; exposition: east; inclination: 30°; 23.VII.'52; CH 52104.

Denmark

3. Ringkøbing Fjord, on the south-western shore in shallow water on a muddy floor with little shells and gravel; a closed vegetation of *Cladophora glomerata* and *Polysiphonia urceolata* f. *formosa*, also epiphytically on phanerogamic waterplants, and descending to a depth of 20 cm; surface: 10 m²; 30.VIII.'55; CH 55080.

4. Ringkøbing Fjord, on the south-western shore in 50 cm deep water on a muddy floor covered with little shells and gravel; a dense vegetation of *Polysiphonia urceolata* f. *formosa* and *Cladophora glomerata*, also epiphytically on phanerogamic waterplants; surface: 10 m²; 30.VIII.'55; CH 55081.

Polysiphonia urceolata f. *formosa* is a very densely ramified Rhodophycea, which attaches itself to the substrate by means of rhizoids. It forms in this way a flocky carpet which covers the substrate completely. By its entangled growth this species may even succeed in covering substrates which for most of the epilithic Algae would be unfit. Starting from the small pebbles and shells it spreads its branches over the more or less muddy sand floor. However, this is possible only in very quiet water like that in the shallow south-western corner of the Ringkøbing Fjord. In sites where the water is less quiet, it does not succeed in establishing itself, and during storms it may in its normally quiet habitat be severely damaged, because at such times the substrate is disturbed by the moving water. Under ordinary circumstances, however, *Polysiphonia urceolata* is found in the association at all times.

Ceramium diaphanum is also rather often met with, and may locally reach dominance. In very quiet sites it forms large globose clumps which are easily swept away by the waves. In the Canal through Walcheren I found this species during the summer only.

Apart from the two characteristic species *Cladophora glomerata* plays a very important part. It is not rarely even better represented than *Polysiphonia urceolata*, and is the most important dominant. It is decidedly euryhaline, for it occurs in all kinds of water varying between fresh and slightly polyhaline, and it may everywhere reach dominance. It is not improbable that this species comprises several ecotypes, but the polymorphism which this Alga displays in a single habitat, is already so large that it is for a field ecologist impossible to make out what the exact status of these forms is. This would require a special, time-consuming study.

Apart from the three constituents mentioned above, the association may contain some *Enteromorpha* species, but the latter are intruders from communities occurring at a higher level. For the rest the companion species are rare. In the Canal through Walcheren I noted *Griffithsia devoniensis* and *Ulva lactuca.*

SYNECOLOGY

Ecologically the *Cladophoreto-Polysiphonietum* is related to the *Callithamnietum rosei.* It is confined to very quiet water in which there is hardly any movement and where therefore no waves are noticeable. The degree of salinity in which the *Cladophoreto-Polysiphonietum* reaches its fullest development, is somewhat lower than it is for the *Callithamnietum rosei*; it will be found between 3 and 10 ‰ Cl′. The *Cladophoreto-Polysiphonietum* is, however, much more sensitive to pollution.

In the Netherlands the Canal through Walcheren is the only place where this interesting association is well-developed. This canal, which connects the euhaline part of the West Scheldt at Flushing with the euhaline East Scheldt at Veere, is but slightly polyhaline to mesohaline the dilution being due to the fact that much polder water is discharged into it, especially during periods of rain. Under such circumstances the salinity may decrease to 3—4 ‰ Cl′ (5—6 ‰ NaCl; KOSTER, 1954) Another cause of the comparatively low degree of salinity is that there is but little traffic in the canal; the sluices therefore are opened but rarely, so that but comparatively little sea water penetrates into the canal. As a result, the highest salinity is found immediately behind the sluices, and here the *Cladophoreto-Polysiphonietum* reaches its fullest development. That the canal is used by so few ships, makes that the water is comparatively quiet. The periods during which the algal vegetation is subjected to the action of waves caused by a passing ship, are too far apart to damage the *Cladophoreto-Polysiphonietum*, and to stimulate the development of a wide belt of *Enteromorpha* such as is found in the Canal through Zuid-Beveland.

Changes in the level of the water occur but rarely; in spring the water line lies somewhat lower than in the other seasons. The association is rather sensitive to pollution of the water. This is apparently the reason why it is not found at a distance of less than 3 km from Middelburg. In the harbour for yachts at Veere, too, it is for this reason less well-developed.

About 2 km south of Veere the association begins to depauperate, and in the next stretch of about 1 km it gradually passes into a heterogeneous vegetation consisting of isolated individuals of *Enteromorpha* species, which extends from there to a point at the other side of Middelburg.

South of Middelburg the *Cladophoreto-Polysiphonietum* is now almost entirely absent. In 1950, however, it was well-developed, but a subsequent improvement of the dikes which necessitated a renewal of the stones on which the association was found, led to its disappearance, and since then it has not been able to reestablish itself. In 1952 in the vicinity of Flushing locally a poor vegetation of *Polysiphonia urceolata* and *Ceramium diaphanum* was still present, but the new stones on the slope of the dikes were even in 1958 still almost entirely free from Algae.

As I could observe in the south-western part of the Ringkøbing Fjord in Denmark, the association may also occur epiphytically. On small pebbles and shells and on the muddy sand floor on which the latter rest, a carpet is found consisting of *Cladophora glomerata* and *Polysiphonia urceolata* f. *formosa*, a little *Ceramium diaphanum* and occasionally a tuft of *Enteromorpha*, a good example therefore of this association; in the muddy soil, however, a number of aquatic phanerogams are rooting, viz. *Potamogeton pectinatus*, *Zannichellia pedicellata*, *Ruppia spiralis* and *Myriophyllum spicatum*, i.e. the association which has been described from the mesohaline waters of the Netherlands under the name *Potameto-Zannichellietum pedicellatae*, but which probably occurs in the whole of north-western Europe (Den HARTOG, 1958). All these plants were covered with species belonging to the *Cladophoreto-Polysiphonietum* and with the Hydrozoon *Laomedea loveni*. Whether the algal species are found also in the *Zosteretum marinae*, the association which in the Ringkøbing Fjord occurs in deeper water, is as yet unknown.

The *Cladophoreto-Polysiphonietum* occurs from the water line to a depth of 1—1.5 m. At the upper side it borders on the *Enteromorphetum prolifero-intestinalis* or, rarely, on the *Monostrometo-Porphyretum leucostictae*. With regard to the place it occupies in the succession no data area vailable.

AREA OF DISTRIBUTION

So far I have seen this association in its fully developed form only in the Canal through Walcheren and in the Ringkøbing Fjord.

In 1953 I found *Polysiphonia urceolata* f. *formosa* at Den Helder in the Canal through North Holland and near Fort Dircksadmiraal. It was accompanied by *Cladophora glomerata* but not by *Ceramium diaphanum*. Since that time this *Polysiphonia* was not seen again in the vicinity of Den Helder.

In the strongly mesohaline pools at the "Bol" on Texel *Cladophora glomerata*, a mesohaline form of *Chondrus crispus* and *Chaetomorpha linum* are dominant. *Cladophora glomerata* appears here in the same form as in the Ringkøbing Fjord. *Polysiphonia urceolata* f. *formosa* and *Ceramium diaphanum* are both absent, and for this reason it remains dubious whether this community may be regarded as a fragment of the *Cladophoreto-Polysiphonietum.*

In the creek in the Oosterkwelder on Schiermonnikoog I found in 1952 *Polysiphonia urceolata* f. *formosa* together with *Cladophora glomerata, Callithamnion roseum* and a number of small Phaeophyceae on *Zostera* roots, but so long as no more data are available, it would be premature to identify this vegetation with the *Cladophoreto-Polysiphonietum.*

As the association is found only in very quiet, weak polyhaline to mesohaline waters, not subjected to the tides, I would not be surprised when it would prove to have its main distribution in the western part of the Baltic Sea and in the Liimfjorden.

5.VIII. The community of Chondrus crispus

On dikes where, as in the greater part of the "Waddenzee", *Fucus serratus* is absent, *Ceramium deslongchampii* usually is the dominant species. It is more or less sciaphilous, and for this reason it only appears in the form of more or less closed vegetations on dikes of which the slope is facing north or which for some other reason are exposed but for a short time to direct insolation. If, however, the exposition is south or west, then *Chondrus crispus* appears at this level as the dominant species; in the closed vegetation in which this species dominates, *Ceramium deslongchampii* and *Pylaiella litoralis,* too, are present in a large number of individuals, whereas some other species like *Ceramium rubrum, Polysiphonia nigrescens, P. urceolata* and *Petalonia fascia* are also present, though very rare. As *Chondrus* may also become dominant in the *Polysiphonieto-Chaetomorphetum*, which is found below this zone, and even in communities belonging to the sublittoral region, the name of this species cannot be used for indicating a definite vegetation unit. The level at which it occurs, and the fact that this community consists almost entirely of eulittoral species, are the only features which distinguish this *Chondrus* community from other communities in which it may dominate.

TABLE XXXV

Community of Chondrus crispus

Kornwerderzand, on the western side of the eastern breakwater, a *Chondrus crispus* vegetation in the vicinity of the low-water line and in the lower part of the eulittoral region; surface: 10 m^2; 3.IV.'53; CH 53010.

Percentage of covering:	100		
Chondrus crispus	5.5	Ralfsia verrucosa	+
Ceramium deslongchampii . .	1	Hildenbrandtia prototypus . .	+
Ceramium rubrum	+	Ulva lactuca	+
Pylaiella litoralis	2	Fucus vesiculosus	+.2
Polysiphonia nigrescens	+	Petalonia fascia	( )
Enteromorpha compressa . . .	+	Polysiphonia urceolata. . . .	( )

This *Chondrus* community was observed along the southern dike of Texel, where it is slowly replaced by the *Fucetum serrati*, and also on the south coast of Schouwen. At Kornwerderzand on the dike by which the Zuyderzee has been shut off, it was most fully studied.

5.IX. The community of Gigartina stellata

In several places along the coast of the "Waddenzee", e.g. on the dam at Ballum on Ameland, on the "Grote Dam" at West-Terschelling and at 't Horntje on Texel, *Gigartina stellata* was found as a dominant species. In the first-named place it replaces *Fucus vesiculosus*, and in the *Fucetum vesiculosi* at that place it is often even more numerous than *Fucus* itself. At West-Terschelling it forms a zone corresponding to the uppermost part of the *Fucetum vesiculosi*. In the *Fucetum vesiculosi* at the "Grote Dam" two subzones are distinguishable which differ in the composition of the undergrowth, viz. a *Gigartina* subzone and lower down a *Mytilus* subzone. At 't Horntje on Texel it occurs on *Mytilus edulis* and on basalt, and here it is found in all parts of the eulittoral region, in the zone of the *Fucetum vesiculosi* as well as in that of the *Fucetum serrati* and even higher. High in the eulittoral region it assumes a deceptive resemblance to the lichen *Lichina pygmaea*, which is found in the eulittoral region of the English Channel.

These vegetations, which are very poor in species, were found only in sheltered spots where much mud is deposited, but which at the same time are exposed to tidal currents, with the result that the water is very muddy in the period of submergence. When the vegetation is exposed to a stronger current, the *Gigartina* vegetations gradually pass into Fucaceae communities.

BØRGESEN (1905) mentioned the presence of a *Gigartina* association in the Faeroes, but the only point in which the latter agrees with the community described above, is the dominance of *Gigartina stellata*.

5.X. The Rhodymenietum palmatae

The *Rhodymenia palmata* association is characterized by the dominance of the robust, somewhat membranaceous Rhodophycea *Rhodymenia palmata*, which shows along the margin of the thallus a strong proliferation. Another characteristic species is *Acrochaetium daviesii*, which grows in large numbers on the thallus of *Rhodymenia*. It is not impossible that *Gymnogongrus norvegicus* may also be regarded as characteristic. A closer study of this association will probably reveal that there are still other characteristic species.

Species that cannot be regarded as characteristic, but which occur in large numbers, are *Chondrus crispus*, *Ceramium rubrum*, *Laurencia pinnatifida*, *Rhodochorton floridulum*, *Lithothamnion lenormandii* and *Cladostephus spongiosus*.

The association shows a preference for a homogeneous smooth rocky floor which is not too strongly weathered, and it does not occur on boulders and isolated blocks. When sand is deposited on the rock, this leads at once to an increase of *Rhodochorton floridulum*, *Cladostephus spongiosus* and some less often occurring species.

The *Rhodymenietum palmatae* occupies the lowermost part of the eulittoral region in sites that are moderately exposed to the surf, and forms on the coast of "le Boulonnais" a substitute for the *Polysiphonieto-Chaetomorphetum* from the southern part of the North Sea. At other places on the coast of the English Channel, e.g. at

Roscoff, the association may reach a higher zone of the eulittoral region; this happens at the expense of the *Fucetum serrati*.

Only little is known with regard to the succession. Near Ambleteuse (P. de C.) I observed a transition from the *Enteromorpheto-Porphyretum* towards the *Rhodymenietum*. In the eastern part of the English Channel the association is probably the final stage of the succession. It is not impossible that it is succeeded in the western part of the English Channel by a vegetation consisting of the larger Phaeophyceae, but this is so far no more than a supposition.

Our *Rhodymenietum* is not identical with the *Rhodymenia* association described by BØRGESEN (1905) from the Faeroes.

5.XI. The Lomentarieto-Plumarietum

The association of *Lomentaria articulata* and *Plumaria elegans* is a well-defined community with a large number of species. *Lomentaria articulata* is the principal characteristic species, and is usually dominant, but *Plumaria elegans* and *Gelidium pusillum* are also to a high degree typical.

A preference for this community is shown by *Ceramium deslongchampii*, which reaches here its fullest development and which often becomes dominant. Well-represented are also *Laurencia pinnatifida*, *Sphacelaria fusca*, *Lithothamnion lenormandii*, *Rhodochorton floridulum*, *Polysiphonia urceolata* and *Bryopsis plumosa*, whereas *Chondrus crispus*, *Ulva lactuca* and young individuals of *Fucus serratus* are always present in smaller numbers.

The association was found by me on the coast of "le Boulonnais" (Cap Gris Nez, Audreselles, Wimereux), in the lower and in the central part of the eulittoral region, where it occurred in sites that received diffuse light only, e.g. on the north side of blocks of stone, in fissures in the rock and on inclined cliffs. Where the light is weakest, *Lomentaria articulata* and *Ceramium deslongchampii* are the dominant species, but in sites that are for a short time exposed to the sun, *Laurencia pinnatifida* becomes the most important constituent.

On the coast of "le Boulonnais" the association shows a preference for fairly exposed sites.

With regard to its presence elsewhere, little is known so far. On p. 151 I have mentioned already that the *Ceramium deslongchampii* sociation from the coast of the Netherlands may perhaps be regarded as a depauperated form of this association. The same applies to the vegetation of *Ceramium deslongchampii* and *Plumaria elegans* that was met with on Heligoland.

5.XII. The Polyideto-Gracilarietum

The association of *Polyides rotundus* and *Gracilaria verrucosa* is an open community, which covers the substrate but for 20—45 %. It consists of a small number of species only, and its aspect is to a large extent determined by *Polyides rotundus* and *Gracilaria verrucosa*. Both species also occur in other communities, but as they reach here their fullest development, they apparently have a preference for this association. Other characteristic species are *Plocamium coccineum* f. *uncinatum*, *Polysiphonia nigra* and *Spongomorpha lanosa*; especially the first-named species is very faithful to it. The epiphytic *Spongomorpha lanosa* is found on the coast of "le Boulonnais" almost always on *Polyides rotundus*, but elsewhere it also occurs on several other species.

Constant companion species are *Rhodochorton floridulum*, *Chaetomorpha aerea*, *Cladophora* spp., *Ulva lactuca* and *Polysiphonia nigrescens*.

The association was discovered in the lower part of the eulittoral region on the coast of "le Boulonnais", where it occurs in up to 40 cm deep pools on the rocks; the floor of these pools is covered with a thin layer of sand. Especially in the boulder field at Audreselles it was beautifully developed.

Elsewhere this association was not yet met with.

6. THE FUCUS FORMATION

The *Fucus* formation comprises all eulittoral communities in which Fucaceae are dominant. These communities consist of three layers, viz. a crustaceous layer, a layer consisting of dendritic and fruticose Algae, and an upper layer formed by the Fucaceae themselves. In the eulittoral region they represent the final stage in the succession.

The *Fucus* formation is widely distributed on the coasts in the northern part of the Atlantic Ocean, on the European as well as on the American side, and they are also found on the North-American coast of the Pacific.

On the coast of the Netherlands the formation is represented by five associations, viz.

1. the *Pelvetietum canaliculatae*,
2. the *Fucetum spiralis*,
3. the *Ascophylletum nodosi*,
4. the *Fucetum vesiculosi*, and
5. the *Fucetum serrati.*

The first two associations are floristically and sociologically nearly related, more nearly so than either of them is with any of the other three. They have a common origin, viz. from the *Blidingietum minimae*, and they have the region indicator *Catenella repens* in common.

The three other associations, too, agree in some points. They all originate from the *Enteromorpheto-Porphyretum*, and they have the region indicators *Gigartina stellata* and *Ceramium deslongchampii* in common. Furthermore we find in these associations a number of species which also occur in the sublittoral region, e.g. *Chondrus crispus*, *Sphacelaria fusca* and *Ceramium rubrum.*

Some phycologists regard the *Ascophylletum nodosi* and the *Fucetum vesiculosi* as forms of a single association, as they occupy the same place in the zonation, and as *Ascophyllum nodosum* and *Fucus vesiculosus* are sometimes found together. That the two species are sometimes found in each other's company is, however, no convincing argument, as other Fucaceae, too, are often found outside their own association, be it in small numbers only. This is shown in table XXXVI.

TABLE XXXVI

Distribution of the Fucaceae over the Fucus associations

	Pelvetia canaliculata	Fucus spiralis	Ascophyllum nodosum	Fucus vesiculosus	Fucus serratus
Pelvetietum	++	+	—	—	—
Fucetum spiralis . . .	+	++	+	+	—
Ascophylletum	—	+	++	+	+
Fucetum vesiculosi . .	—	+	+	++	+
Fucetum serrati . . .	—	—	+	+	++

(++ = dominant; + = sparsely)

Facts that plead in favour of the distinction of two associations, are that the *Ascophylletum* possesses characteristic species of its own, and that it occupies a zone of greater vertical range.

A sixth community, in which *Fucus ceranoides* is the dominant species, is probably also represented in the Netherlands. *F. ceranoides*, a species which is common on the westcoast of France, is found only at the mouth of rivers and other water courses, i.e. in places were sea water is mixed with fresh water. In such sites it replaces *F. vesiculosus* (HAMEL, 1939), and ascends the rivers to such a distance as the influence of the sea water reaches. Such an environment is found in the Netherlands in the Deltaic District. VAN DEN HOEK (1958) found this species together with *F. vesiculosus* in the mouth of the Nieuwe Waterweg at Hook of Holland. In July 1952 I found at Drimmelen on stones in the Amer some very badly developed *Fucus* specimens; as at this place the presence of *F. vesiculosus* is not to be expected, they must have belonged to *F. ceranoides*. In the Volkerak I found both species, but here they formed separate zones, *F. vesiculosus* the upper zone, and *F. ceranoides* the lower one. Intermediate forms were not observed.

STOMPS (1911) found in the mouth of the Yser (Belgium) various intermediates between *F. vesiculosus*, *F. spiralis* and *F. ceranoides*, and HAMEL reported their presence from the French coast. I myself observed intermediates between *F. vesiculosus* and *F. ceranoides* at Hellevoetsluis.

In the brackish tidal waters of the former Zuyderzee VAN GOOR (1922, 1923) observed intermediates between *F. vesiculosus* and *F. spiralis*, which where the salinity decreased still further, passed into *F. intermedius*.

The studies of STOMPS (1911), KNIEP (1925) and BURROWS and LODGE (1951) show that hybrids between *F. vesiculosus* and *F. spiralis* are not rarely met with on the borderline between the two zones, especially in sites where the vegetation is more or less open. On the sea-dike at Den Helder *F. spiralis* is very rare, but above the *F. vesiculosus* zone, where there is no competition between the various species, an intermediate between *F. vesiculosus* and *F. spiralis* (thallus flat and without visicules; dioecious; receptacles ovate, with sterile rim) is more common. Similar intermediates were found by me along the coasts of the West-Frisian Islands Vlieland and Terschelling. Intermediates between these two species and *F. ceranoides* will also have to be regarded as hybrids. Intermediates between *F. vesiculosus* and *F. serratus* were not found by me in the Netherlands. The rarity of these intermediates may be due, as BURROWS and LODGE (1951) have pointed out, to the fact that these two species do not readily hybridize, as their fruiting periods do not coincide.

F. lutarius, which has been found on the salt marshes in the province of Zeeland (Tholen, Noord-Beveland), is perhaps but a habitat form of *F. vesiculosus*. Intermediates between the two are not rare. In my opinion this form may develop in the following way. Plants of *F. vesiculosus* that are swept away from the slopes of the dikes, are thrown in large numbers on the salt marshes in front of the dikes, the so-called "schorren". If they arrive at a place where the floor remains sufficiently wet during the periods of emergence, as it does in the *Spartinetum strictae*, or where the water stagnates, as it does in the cupshaped depressions that are not rarely met with on the larger salt marshes, then they may remain alive. In that case they form a dense mass of proliferations along the margin of the thallus, which subsequently are set free because the original part of the thallus rots away. They grow out to narrow, strongly contorted thalli, which continue to grow at their top, but which rot away at their base, and which may split off new individuals, viz. if the decay at the base reaches a ramification. In this way in a few years a dense carpet of *F. lutarius* may be formed in the undergrowth of the *Spartinetum strictae* and sometimes also in that of other communities belonging to the *Puccinellio-Salicornion*. In April 1958 I found at the Dellewal on the island Terschelling a large number of specimens of *F. vesiculosus* and of *Ascophyllum nodosum*, which had been washed ashore in a *Scirpetum maritimae*. In June 1958 *Ascophyllum* had almost entirely disappeared, but at the thalli of the *Fucus vesiculosus* plants numerous proliferations had developed. The latter were strongly contorted, and showed a striking resemblance to *F. lutarius*, but they were still attached to the original thallus. If they become detached, they may perhaps help us to solve the riddle of *F. lutarius*.

Data with regard to the habitats of *F. lutarius* along the French coast and with regard to the multiplication of this Alga were given by SAUVAGEAU (1907, 1908), CHEMIN (1925), LAMI (1930, 1931), HAMEL (1939) and DIZERBO (1940, 1953, 1954). Details with regard to the places where it was collected in the Netherlands, were published by KOSTER (1952).

A somewhat similar development as described above was observed in the "Waddenzee". Detached specimens of *F. vesiculosus*, which, as the water fell, were stranded on a mussel bank, were fettered to the latter by the mussels by the aid of their byssus. Under the influence of the environment the thallus of the plants which remained alive, soon underwent a change. The colour became light brown to yellow, the bladders disappeared, the tissue became brittle, and the thallus sometimes became contorted; the habit, moreover, assumed a remarkable uniformity. Just as in the proliferations observed by *F. lutarius*, the thallus grew only at the apex, whereas it rotted away at the base. Proliferations, however, were formed only in specimens which were fastened in a horizontal position, and receptacles appeared but rarely. NIENBURG (1932) found receptacles in specimens of this kind which he observed in some places on the North Frisian Islands, and stated that on top of the latter once more normal vegetative shoots were produced. In the conceptacles he found exclusively oogonia. These peculiarities induced him to describe these specimens as a new species, *F. mytili*. However, my observations in the "Waddenzee" south of Terschelling leave no doubt that *F. mytili* is merely an anomalously developed form of the dioecious *F. vesiculosus*. I found all kinds of transitions between the form described as *F. mytili* and the normally developed *F. vesiculosus*, the most complete series perhaps at the "Vleugel", a lateral extension of the "Grote Dam" at West-Terschelling.

On the "Vangdamwad" at Den Helder I found *F. serratus* fastened in a similar way to the mussel banks, but this species is apparently less plastic, and it soon went down.

For literature on *Fucus* growth on mussel banks I may refer to the publications of NIENBURG (1925, 1932), of WOHLENBERG (1937) and of DEN HARTOG (1958).

6.I. The Pelvetietum canaliculatae

A description of the *Pelvetia canaliculata* association is given here for the first time. In his description of the "*Fucus*-Association" VAN GOOR (1923: p. 148) mentions the presence of *Pelvetia canaliculata*, and in the systematical part of his work he even gives a brief characterization of the habitat in which it occurs, but a full description of the *Pelvetia* zone as a whole is not to be found in his work. The presence of a *Pelvetia* zone is mentioned by KOSTER (1954) from some localities on Schouwen.

LEGENDA (see table XXXVII)

1. Schouwen, Canal to Zieriksee; a 0.5 m wide zone of *Pelvetia* on Vilvordian limestone; surface: 10 m²; exposition: east; inclination: 10°; 21.VII.'52; CH 52085.
2. Schouwen, dike at the "Kistersinlaag"; a 0.5 m wide zone with a sparse vegetation of *Pelvetia* on basalt; surface: 5 m²; exposition: south; inclination: 10°; 22.VII.'52; CH 52098.
3. Schouwen, same locality; a 0.3 m wide zone with a rich *Pelvetia* vegetation on blocks of limestone which but a short time ago had been fastened together by

TABLE XXXVII

Pelvetietum canaliculatae

Sample plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Percentage of covering	40	< 5	60	20	35	25	10	5—10	15	80	50	80	90	85	60	70
Pelvetia canaliculata	3	1	4	2	3	2.3	1	1	2	4.5	3	4	5	5	4	4
Catenella repens	—	—	—	+	1	—	+.2	+	+	+.2	2	4	1	+.2	2	1
Hildenbrandtia prototypus	+	—	1	+	+	1	+	+	+	+	2	1	1	+	+	—
Verrucaria mucosa	+	+	3	1	2	2	+	+	—	—	—	+	1	+	+	—
Fucus spiralis	+	—	1	+	+	+	+	—	+	+	+	+	+	+	+	+
Blidingia minima	—	+	+	—	+	—	+	—	1	2.2	—	—	2	—	1	+
Ralfsia verrucosa	+	+	+	1	—	+	—	+	—	—	—	—	+	—	—	—
Rhizoclonium riparium	—	—	—	—	—	—	—	+	+	—	—	+	—	—	+	+
Monostroma oxyspermum	—	—	—	—	—	—	+	+	+	—	—	—	—	—	—	+
Verrucaria maura	—	—	—	—	—	—	2	—	—	—	1	+	—	2	—	—
Porphyra umbilicalis	—	—	—	—	—	—	+	—	+	+	—	—	—	—	—	—
Rhodochorton purpureum	—	—	—	+	+	—	+	—	—	—	—	—	—	—	—	—
Calothrix pulvinata	—	—	—	—	—	—	—	—	—	—	—	+	+	—	+	—
Dermocarpa prasina	—	—	—	—	—	—	—	—	—	—	—	+	1	—	+	—
Oscillatoria formosa	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—
Ulothrix flacca	—	—	—	—	—	—	+	—	+	—	—	—	—	—	—	—
Microcoleus chthonoplastes	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	+
Bostrychia scorpioides	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	2
Enteromorpha marginata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+
Isactis plana	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—

Addenda: survey 5: Oscillatoria nigroviridis +; survey 9: Ulothrix consociata +, Lyngbya lutea +; survey 13: Prasiola stipitata +, Lichina confinis +, Codiolum penicelliforme st. urosporae +, Gloeocapsa crepidinum +, Lyngbya majuscula +; survey 15: Enteromorpha compressa +; survey 16: Oscillatoria brevis +.

means of concrete; surface: 3 m²; exposition: north-east; inclination: 15°; 22.VII.'52; CH 52099.

4. Schouwen, De Val, south of Zieriksee; a 0.5 m wide zone of *Pelvetia* on Vilvordian limestone; surface: 3 m²; exposition: east; inclination: 15°; 22.VII.'52; CH 52097.

5. Walcheren, Veere; a 0.5 m wide zone of *Pelvetia* on Vilvordian limestone; surface: 5 m²; exposition: east; inclination: 10°; 23.VII.'52; CH 52101.

6. Tholen, on a little dike at Gorishoek (municipality Scherpenisse); a 0.4 m wide, rather open vegetation of *Pelvetia* on Vilvordian limestone with deep fissures between the blocks; exposition: east; inclination: circ. 10°; 28.X.'51; CH Th. 7.

7. Tholen, breakwater at Gorishoek; a poor vegetation of *Pelvetia* on Vilvordian limestone; surface: 1 m²; exposition: east; inclination: 20°; 7.VI.'54; CH 54050.

8. Zuid-Beveland, dike west of Wemeldinge; an almost 1 m wide zone with a poor vegetation of *Pelvetia* on basalt; surface: 10 m²; exposition: north; inclination: 20°; 6.VI.'54; CH 54047.

9. Zuid-Beveland, same locality; a 0.5 m wide zone with a poor vegetation of *Pelvetia* on basalt; surface: 5 m²; exposition: north; inclination: 20°; 6.VI.'54; CH 54048.

France

10. Boulogne sur Mer (P. de C.), at the beginning of the northern mole at Fort de la Crèche; a dense vegetation of *Pelvetia* on blocks of stone; substrate almost flat; surface: 5 m²; 9.VII.'51; CH Fr. 12.

11. Cap Gris Nez (P. de C.); a poor vegetation of *Pelvetia* on blocks of Jurassic limestone near the high-water line; surface: 1 m²; 2.VIII.'54; CH 54114.

12. Anse de Dinard (I. et V.); at the mouth of the Rance; a vegetation of *Pelvetia* on rocks with many fissures and locally covered with a little sand; surface: 4 m²; exposition: east; inclination: less than 5°; 25.VII.'54; CH 54100.

13. Roscoff (Finist.), blocks on the small beach near the harbour; a closed *Pelvetia* community; surface: 5 m²; 16.VII.'54; CH 54075.

14. Roscoff (Finist.), on the north-east side of the Ile Verte on a flat rock floor; surface: 5 m²; 15.VII.'54; CH 54073.

15. Santec (Finist.), at the mouth of the little river l'Horn, on rocks of granite; a *Pelvetia* vegetation strongly flooded with sand and covered with rotting algal remains (*Ulva*, *Enteromorpha*, etc.); surface: 4 m²; 23.VII.'54; CH 54094.

16. Pennelé (Finist.), circ. 4 km north of Morlaix, in the Penzé; a *Pelvetia* vegetation on stones at the shore, the stones covered with a clayey mud; surface: 10 m²; exposition: east; inclination: 50°; 21.VII.'54; CH 54093.

The *Pelvetietum* is an association formed by a small number of species of which but one, viz. *Pelvetia canaliculata* itself, is characteristic; the remaining species are also found in other communities.

The records of this association that were obtained from the coast of the Netherlands, show a striking resemblance to each other. The crustaceous layer is present in all of them, and it is often remarkably well-developed. Its principal species are *Hildenbrandtia prototypus* and the lichen *Verrucaria mucosa*, but *Ralfsia verrucosa* may also be present, and even *Verrucaria maura*, which, as a rule, occurs at a higher level, has been observed. In some localities mud is deposited on the stones, and in that case Cyanophyceae and *Rhizoclonium riparium* appear on the scene.

The dendritic Algae are represented by one species only, viz. by

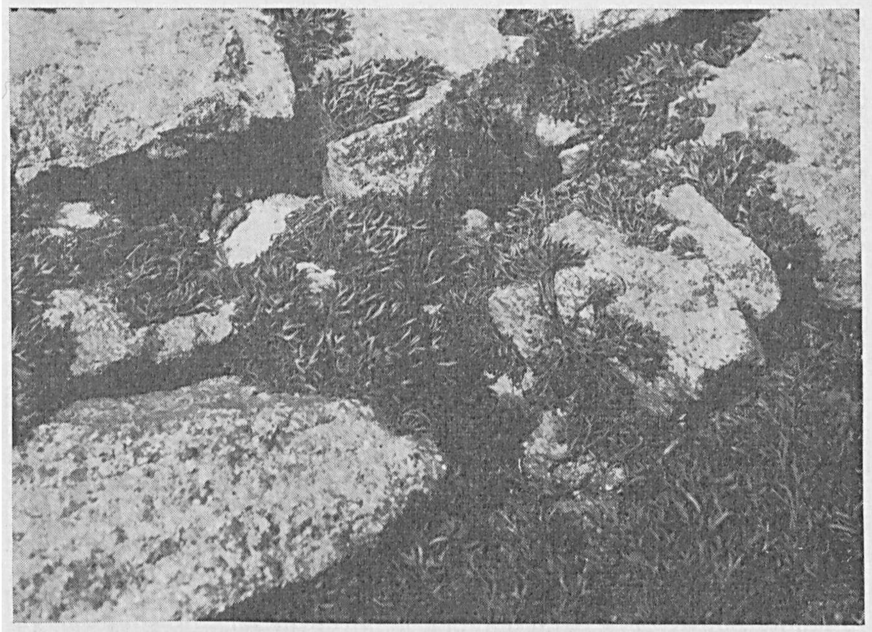


Fig. 19. *Pelvetia canaliculata* association near Kortgene (Noord Beveland). May 1958.

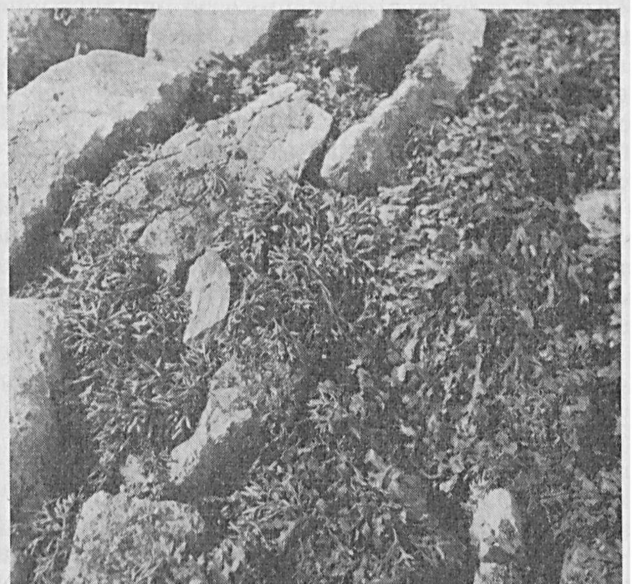


Fig. 20. Zonation near Kattendijke. To the left the *Pelvetietum canaliculatae*, to the right the *Fucetum spiralis*. 14th May 1956.

Catenella repens, a Rhodophycea which is found especially in fissures and under the canopy of the *Pelvetia* clusters.

Blidingia minima, *Porphyra umbilicalis* and *Ulothrix flacca* appear regularly in the *Pelvetietum*, but they do not develop into larger groups. In quiet spots we moreover find *Monostroma oxyspermum*. *Fucus spiralis* often penetrates into it from the adjacent *Fucetum spiralis*.

The records that were obtained from the west coast of France differ but slightly or not at all from those from the coast of the Netherlands. This seems to justify the conclusion that on our coast, too, the association has reached its complete composition. The *Pelvetietum* is nevertheless in the Netherlands not so richly developed as in France, for although it forms a distinct zone, the degree of covering in the survey plots never exceeded 60 %, and the mean value was but 25 %, whereas in France it reached 90 % with a mean value of more than 70 %; in France it is therefore much richer developed. The degree of covering is extremely variable, as *Pelvetia* absorbs a large amount of water during the period in which it is submerged. During the period of emergence this water is gradually given off, and this causes the Algae to shrink to one third of their former size. This explains why the estimations of the degree of covering may vary considerably according to the time elapsed since the last submergence. The records 1, 5 and 10 were obtained shortly after the vegetation fell dry; the records 4, 13 and 14 immediately before they were submerged.

SYNECOLOGY

The *Pelvetietum* is confined to the uppermost part of the eulittoral region. As a rule, it is situated between M.H.W. and M.H.W.S. This rather vague indication of the position which it occupies in the zonation, is necessary, as the latter does not depend only upon the factors that are influenced by the tides, but also upon factors that are entirely independent of the latter, like the nature of the substrate and the degree of exposition. Most instructive in this respect are the observations we collected during our study of the "Kistersinlaag" on Schouwen on 22.VII.'52. On the slope of the dike we found there at a depth of circ. 15 cm a poor *Pelvetia* vegetation on basalt (record 2), whereas a few hundred meters further on upon blocks of Vilvordian limestone which a short time ago had been cemented together by means of concrete, a rich vegetation of the same species was met with; the latter grew on the inside of a small breakwater at a height of 30 cm above the water line (record 3). The two records were obtained on the same day and with an interval of no more than five minutes.

The *Pelvetietum* is often but partly submerged; this depends on the direction of the wind. During storm floods the water may, according to Brakman, rise sometimes to 1 m above the *Pelvetia* zone.

On the lower side the *Pelvetia* zone borders on the *Fucetum spiralis*, on the upper side often on vegetations of lichens in which *Verrucaria maura*, *Xanthorina parietina* and *Caloplaca* species play the most important part, or occasionally on the *Prasioletum stipitatae*. The width of the zone varies between 10 cm and 1 m, according to the tidal difference, the inclination of the substrate, and the exposition. In the Netherlands it is best developed on Vilvordian limestone; on basalt it is found but rarely and then only poorly developed.

THE BOSTRYCHIA VARIANT OF THE PELVETIETUM

In the Penzé, north of Morlaix, the *Pelvetietum* was found in brackish, very quiet water, where it was still fairly well developed. Notwithstanding a large amount of mud was deposited on the substrate, there was an undergrowth consisting of seven species; the crustaceous layer, however, was completely absent. Besides *Catenella repens* *Bostrychia scorpioides* proved to be very common in the undergrowth. On the salt marshes in the neighbourhood these species also occurred in large numbers. Other companion species indicating a high amount of mud are *Rhizoclonium riparium* and *Enteromorpha marginata*. The Phanerogam *Halimione portulacoides*, which had established itself here and there between the stones, points in the same direction.

In the Netherlands the presence of *Bostrychia* in the *Pelvetietum* has but once been reported, viz. by BRAKMAN (KOSTER, 1952: p. 211).

SUCCESSION

With regard to the way in which the *Pelvetietum* is formed, some observations were collected in July 1952 at the "Kistersinlaag" on Schouwen. On the small dike from which record 3 was obtained, the blocks of limestone had been cemented together a short time ago by means of concrete. *Pelvetia* survived this treatment at least partly; however, at the end of the little dike the original vegetation was completely destroyed, and here within a short time its place was occupied by a *Blidingietum minimae*. At the end of July a large number of young *Pelvetia* plants appeared in the latter.

Blidingia is occasionally, especially in rather dark spots, ousted by *Catenella repens*. A transition from the *Catenella* vegetation into a *Pelvetietum* was not noted by me, but the fact that *Catenella* is often found in large numbers in the undergrowth of the latter, as well as the presence of pure *Catenella* vegetations in the uppermost part of the eulittoral region, i.e. in the same zone as the *Pelvetietum*, make the presence of such a succession plausible.

In France the *Pelvetietum* may also develop out of a *Lichina pygmaea* vegetation.

AREA OF DISTRIBUTION

In the Netherlands the *Pelvetietum* is found in the waters of Zeeland where it is not rare. In former years it was also represented at Den Helder, although in a fragmentary condition only, but there it disappeared when works were carried out at the site on which it occurred. The record from IJmuiden has never been confirmed.

The *Pelvetietum* is distributed along the entire west coast of Europe from the Iberian Peninsula to the Murmansk Coast, and is also found on the Faeroes (BØRGESEN, 1905) and on Iceland (JONSSON, 1912); it is absent, however, from nearly the whole southern and eastern part of the North Sea. Along the German and Danish coast of the North Sea it was never met with, not even on Heligoland. Nor does it occur in the Skagerrak, the Kattegat and the Baltic Sea.

6.II. The Fucetum spiralis

The association of *Fucus spiralis* was already mentioned by VAN GOOR (1923) in his description of the "*Fucus*-Association" when he distinguished in the latter a special zone occupied by this species. He says of this zone "Die mittlere Hochwasserlinie wird durch einen nur kaum 2 dm breiten Gürtel von *Fucus platycarpus* angedeutet." Very few details, however, are given. ZANEVELD (1937) studied this zone at Den Helder; KOSTER (1954) found it on Schouwen, but she gives no floristic data.

Just like the *Pelvetietum* the *Fucetum spiralis* has but one characteristic species, viz. *Fucus spiralis* itself. It is not impossible that some of the smaller epiphytes which have not yet been sufficiently studied, will also prove to be characteristic.

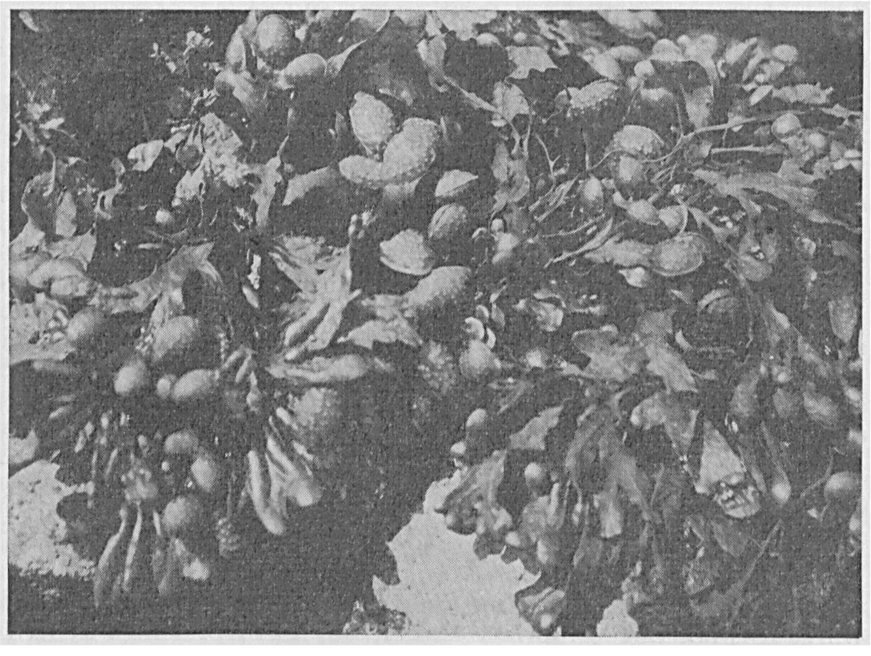


Fig. 21. *Fucus spiralis*. Kortgene (Noord Beveland). May 1958.

In the records from the Netherlands we may distinguish two forms of this association, which, however, are connected with each other by intermediate stages. The first form is characterized by the common

TABLE XXXVIII

Fucetum spiralis

Sample plots	1	2	3	4	5	6	7	8	9	10	11	12	13
Percentage of covering	70	60	35	65	60	80	100	80	95	70	70	100	80
Fucus spiralis	4	4	3	4	4	5	5	5	5	4	4.4	5	5
Blidingia minima	1	+	2	—	2	1	—	—	+	—	—	2.2	1
Catenella repens	—	—	—	—	—	2	—	—	—	+	( )	—	—
Hildenbrandtia prototypus	—	+	+	—	—	—	5	+	+	+	+	1	+
Verrucaria mucosa	—	—	—	—	+	1	1	2	2	+	4	+	—
Ralfsia verrucosa	—	—	—	—	—	—	—	1	+	2	1	1	1
Ascophyllum nodosum	—	—	—	—	+	+	+	+	—	+	+	—	—
Rhodochorton purpureum	+	2	—	—	+	+	—	—	—	+	—	—	—
Enteromorpha compressa	+	+	+	+	—	—	—	—	—	—	—	—	+
Ulothrix flacca	1	+	2	1	—	—	—	—	—	—	—	—	+
Pelvetia canaliculata	—	—	—	—	—	—	—	+	—	+	—	+	—
Porphyra umbilicalis	—	—	+	+	—	—	—	—	—	—	—	+	—
Ulva lactuca	—	+	—	+	—	—	—	—	—	—	—	—	+
Pylaiella litoralis	—	( )	1	—	—	—	—	—	—	—	—	—	+
Fucus vesiculosus	—	—	—	—	—	—	—	—	+	—	—	—	+
Lithothamnion lenormandii	—	—	—	—	—	—	—	—	—	+	—	+	—
Oscillatoria nigroviridis	—	—	—	—	+	+	—	—	—	—	—	—	—
Monostroma oxyspermum	+	—	—	—	—	—	—	—	—	—	—	—	—

Addenda: survey 2: Gigartina stellata +; survey 4: Elachista fucicola +, Petalonia fascia +; survey 5: Oscillatoria formosa +; survey 6: Microcoleus tenerrimus +; survey 13: Ceramium deslongchampii +, Callithamnion scopulorum +, Sphacelaria fusca +, Cladophora sp. +°, Acrochaetium secundatum +, Dermocarpa prasina +.

LEGENDA

1. Delfzijl, eastern harbour mole; a 0.5 m wide zone of *Fucus spiralis* accompanied by *Blidingia minima* and *Monostroma oxyspermum* on granite; surface: 5 m²; exposition: east; inclination: 15°; 13.IV.'53; CH 53027.
2. Ameland, dam at Ballum; vegetation of *Fucus spiralis* on basalt; surface: 1 m²; exposition: east; inclination: 10°; 10.IV.'53; CH 53022.
3. Westhoek (Friesland), circ. 1.5 km east of this hamlet; a 0.5 m wide zone of *Fucus spiralis*; surface: 10 m²; exposition: north; inclination: 10—15°; 9.IV.'53; CH 53021.
4. Harlingen, north side of the northern mole; a *Fucus spiralis* vegetation on bitumen; surface: 20 m²; 8.IV.'53; CH 53013.
5. Walcheren, Veere, outside the sluices of the Canal through Walcheren; a 0.5 m wide zone of *Fucus spiralis* on Vilvordian limestone; surface: 5 m²; exposition: east; inclination: 10°; 23.VII.'52; CH 52100.
6. Southern shore of the West Scheldt, small dam east of Hoofdplaat; a 0.5 m wide zone of *Fucus spiralis* on Vilvordian limestone; surface: 10 m²; exposition: east; inclination: 10°; 26.VII.'52; CH 52105.
7. Oostmahorn (Friesland); poorly developed zone of *Fucus spiralis* with interruptions in which a few *Fucus spiralis* plants are mixed with *Fucus vesiculosus* or with *Ascophyllum nodosum*; substrate granite, nearly flat; surface: 1 m²; 31.V.'52; CH 52047.
8. Zieriksee, in the harbour canal; a 0.3 m wide zone of *Fucus spiralis* on Vilvoordian limestone; surface: 3 m²; exposition: east; inclination: 10°; 22.VII.'52; CH 52086.
9. Zieriksee, at the mouth of the harbour canal; a 0.5 m wide zone of *Fucus spiralis* on basalt; surface: 10 m²; exposition: east; inclination: 10°; 22.VII.'52; CH 52088.
10. Zieriksee, de "Val", south of the town; a 0.5 m wide zone of *Fucus spiralis* on Vilvordian limestone; surface: 5 m²; exposition: south-east; inclination: 10°; 22.VII.'52; CH 52096.
11. Tholen, dike at the Koffiehoek; a 1 m wide, not fully closed zone of *Fucus spiralis* with but few other species on blocks of limestone; surface: 20 m²; exposition: south; inclination: 15°; 27.X.'51; CH Th. 2.

France

12. Boulogne sur Mer (P. de C.); northern mole, at Fort de la Crèche; a completely closed vegetation of *Fucus spiralis* on blocks of rock that are covered with crustaceous Algae; nearly flat substrate; surface: 40 m²; 9.VII.'51; CH Fr. 13.
13. Audreselles (P. de C.); on blocks in the upper part of the beach; vegetation of *Fucus spiralis*; surface: 6m²; exposition: west; inclination: 5°; 3.VII.'54; CH 54124.

occurrence of the tubular Algae *Blidingia minima* and *Enteromorpha compressa*, further of *Ulothrix flacca*, *Ulva lactuca* and *Porphyra umbilicalis*, and locally also of *Monostroma oxyspermum*, whereas *Hildenbrandtia prototypus* is met with but sporadically. The other form possesses a well-developed crustaceous layer consisting of *Hildenbrandtia prototypus*, *Verrucaria mucosa* and *Ralfsia verrucosa*, and in which occasionally *Lithothamnion lenormandii* is found, but the species that we have mentioned as common in the first form, are here almost entirely absent. Both these forms are met with in the "Waddenzee" as well as in the waters of Zeeland. The first form is most easily recognizable in spring, because that is the period in which *Ulothrix flacca* reaches its fullest development; in the summer months it is recognizable by the large amount of tubular Algae and by the absence or the poor development of the crustaceous undergrowth. The differences between the two forms are due to differences in salinity and in the amount of sediment that is deposited in them. A deposit of mud particles retards the development of the crustaceous layer, but it encourages, at least in summer, the development of Cyanophyceae, e.g. of *Oscillatoria nigroviridis*, *O. formosa* and *Microcoleus tenerrimus*. In waters with a rather low salinity, which in the Netherlands are mostly found in sheltered localities *Blidingia minima*, *Ulothrix flacca* and *Monostroma oxyspermum* reach their fullest development. As *Fucus spiralis* itself prefers a higher degree of salinity, its development in such localities is, as a rule, but poor, and the vegetation remains more or less open. This enables a greater expansion of the tubular and the foliaceous Algae. *Porphyra umbilicalis* avoids brackish water, and is therefore rather rare in this form of the *Fucetum spiralis*.

Intruders from other communities are rare in the *Fucetum spiralis*. *Pelvetia canaliculata* may penetrate into it from the zone just above it, *Ascophyllum nodosum* and *Fucus vesiculosus* from the lower zones. *Gigartina stellata*, *Lithothamnion lenormandii*, *Petalonia fascia*, *Ceramium deslongchampii* and *Callithamnion scopulorum* may also be included in the last-named group.

Along the French coast I made only 2 records, what is too few for comparison. However, I have got the impression that the vegetations of *Fucus spiralis* which I saw at Dinard and at Roscoff, but of which I made no records, did not differ very much from those found in the waters of the Netherlands. On Heligoland the *Fucetum spiralis* proved to be very badly developed, and the *Fucus spiralis* vegetations from the Danish waters show a different composition.

A few remarks will have to be made on *Catenella repens*. On the French coast as well as in Zeeland this species is often met with in the *Fucetum spiralis* as well as in the *Pelvetietum canaliculatae*, but as it is absent in the *Fucetum spiralis* found further to the north, it might be used for a subdivision of this association.

Still another variant of this association was found by me in the Penzé north of Morlaix, where it occurred in brackish, very quiet water that appeared to be extremely muddy. It contained a large amount of *Catenella repens* and of *Bostrychia scorpioides*, and also a certain amount of *Monostroma oxyspermum*. In fissures between the stones, moreover, some specimens of *Halimione portulacoides* were found. It may be called the *Bostrychia* variant.

SYNECOLOGY

The *Fucetum spiralis* is on the whole confined to the zone between M.H.W. and a line slightly below M.H.W.N.

The aspect of this association, too, is entirely determined by the characteristic species, i.e. by *Fucus spiralis*. The degree of covering for which this species is responsible, is far more constant than that in the *Pelvetietum*, as *Fucus spiralis* does not shrink so strongly during the period of emergence as *Pelvetia* does. The degree of covering during the period of emergence remains therefore practically the same. The period of submergence is longer than it is in the *Pelvetia* zone, as it occupies a lower position in the zonation.

This association, too, shows a preference for the Vilvordian limestone; it is nevertheless also rather common on granite, but basalt is usually avoided. This preference is accounted for by the difference in the amount of moisture that is retained by these substrates. The porous limestone absorbs much more water than the compact basalt, and granite occupies in this respect an intermediate position (cf. p. 30–31).

The association borders above on the *Pelvetietum canaliculatae*, below on the *Fucetum vesiculosi* or on the *Ascophylletum nodosi*. The width of the zone varies between 10 cm and 1 m; this depends upon the tidal difference, the inclination of the substrate, and the exposition. On the dikes in Zeeland it varies usually between 40 and 50 cm; in the "Waddenzee" it may be much wider.

SUCCESSION

The *Fucetum spiralis* develops out of the *Blidingietum minimae*. Although we possess no direct observations with regard to this succession, it is made plausible by the following arguments, viz. 1°. the common occurrence of *Blidingia minima* between the individuals of *Fucus spiralis*; 2°. the fact that the *Blidingietum minimae* occurs at the same level in the zonation; and 3°. the circumstance that the related *Pelvetietum* could be proved to develop out of the *Blidingietum*. It is not impossible that the succession may take place via an intermediate *Catenella repens* stage, as such a stage was found by me in France.

AREA OF DISTRIBUTION

In the Netherlands the *Fucetum spiralis* occurs along the whole length of the coast; especially in Zeeland it is beautifully developed. On Heligoland *Fucus spiralis* was found but locally, usually on vertical walls, where it was by no means well-developed. On the coast of "le Boulonnais" the *Fucus spiralis* association is in every respect comparable with that of the Netherlands. Elsewhere along the English Channel I found no important differences either. The presence of *Lichina pygmaea* in the *Fucetum spiralis* along the western part of the Channel may be ascribed to a stronger exposition to the surf. On strongly exposed rocks on which the barnacle *Chthamalus stellatus* plays a predominant part, *Lichina* forms an association of its own.

Zones of *Fucus spiralis* also occur in other territories, but in how far they are comparable with the *Fucetum spiralis* described above, can only be decided when full records become available. The vegetations of *Fucus spiralis* from the Skagerrak and the Kattegat are not identical with our *Fucetum spiralis*, as they contain species which on the coasts that are subjected to the influence of the tides, occupy a much lower level.

Fucus spiralis itself is found everywhere along the coasts of the Atlantic Ocean from Morocco, where it still forms, according to FELDMANN (1955) a zone, to Lapland. It also occurs on the Faeroes, on Iceland and along the coast of North America. T. A. and A. STEPHENSON (1954) described a *Fucus spiralis* zone from Peggy Cove (New England), JOHNSON and SKUTCH (1928) one from Mount Desert Island (Maine).

6.III. The Fucetum vesiculosi

The association of *Fucus vesiculosus* is the most common representative of the *Fucus* formation in the Netherlands. It occurs from the most exposed sites to the most quiet waters. VAN GOOR (1923) described the relation between *Fucus vesiculosus* and *Ascophyllum nodosum*, but he did not give a description of the *Fucus vesiculosus* zone. The association was mentioned by ZANEVELD (1937), KOSTER (1954) and VAN DEN HOEK (1958).

Apart from *Fucus vesiculosus* this association has but one characteristic species, viz. the small epiphyte *Elachista fucicola*, which is almost always present on the thalli of *Fucus vesiculosus*, and which shows a preference for this species; it is also found, however, on other Fucaceae, viz. on *Fucus spiralis* (rarely), on *F. serratus* and on *Ascophyllum nodosum*. On *Fucus serratus* it may even occur in great numbers, as I found on Heligoland, but in the Netherlands it shows a marked preference for *F. vesiculosus*.

Fig. 22. *Fucus vesiculosus*, Strijenham (Tholen). 19th September 1958.

LEGENDA (see table XXXIX)

1. Delfzijl, west side of the eastern harbour mole; a *Fucus vesiculosus* association on stones covered with mud; surface: 10 m²; exposition: west; inclination: 15°; 13.IV.'53; CH 53028.

2. Ameland, dam at Ballum; a very open *Fucus vesiculosus* association with in the undergrowth *Gigartina stellata* as the dominant species; on basalt; width of the zone: 1 m; surface: 100 m²; exposition: east; inclination: 15°; 10.IV.'53; CH 53023.

3. Oostmahorn, harbour; a circ. 1 m wide poorly developed and not fully closed zone of *Fucus vesiculosus* on basalt; surface: 10 m²; exposition: north-east; inclination: 30°; 22.VIII.'51; CH 51119 A.

4. Oostmahorn, dike north-west of the harbour, at the place where the road ascends the dike; a 2 m wide zone occupied by a not fully closed vegetation of *Fucus vesiculosus* on granite; surface: 60 m²; exposition: north; inclination: 30°; 22.VIII.'51; CH 51120.

5. West-Terschelling, harbour mole; a *Fucus vesiculosus* vegetation on rather muddy stones; surface: 15 m²; exposition: east; inclination: 30°; 1.IX.'54; CH 54166.

6. Harlingen, at the end of the northern harbour mole; a circ. 2 m wide zone of *Fucus vesiculosus* on basalt; surface: 20 m²; 8.IV.'53; CH 53019.

7. Kornwerderzand, east side of the eastern breakwater; a circ. 2 m wide zone of *Fucus vesiculosus* on blocks of stone; surface: 20 m²; 3.IV.'53; CH 53008.

8. On the dike along the Amsteldiep between Ewijcksluis and Wieringen; a 2 m wide zone of *Fucus vesiculosus* on muddy blocks of basalt; surface: 10 m²; 13.XI.'52; CH 52161.

9. Texel, dike south of Oude Schild; a 3 m wide zone of *Fucus vesiculosus* on blocks of granite and on shells covered with mud; surface: 60 m²; 14.IV.'52; CH 52017.

10. Den Helder, sea-dike at pales 100 and 101; a *Fucus vesiculosus* zone on a nearly horizontal substrate consisting of blocks of basalt and granite and of fragments of concrete; surface: 30 m²; 5.IV.'51; CH 51002.

11. Den Helder, sea-dike at pales 129 and 130; a 3—4 m wide zone of *Fucus vesiculosus* on a nearly horizontal substrate consisting of granite and basalt; surface: 70 m²; 6.IV.'51; CH 51003.

12. Den Helder, sea-dike at pale 60; a not very rich vegetation of *Fucus vesiculosus* on a substrate consisting of basalt blocks covered with mud and with some small pools; width of the zone: 3 m; surface: 30 m²; 12.IV.'52; CH 52014.

13. Den Helder, sea-dike at pale 89; a very dense but not very pure vegetation of *Fucus vesiculosus*; surface: 75 m²; 12.VI.'52; CH 52063.

14. Tholen, dike west of Strijenham; a circ. 4—5 m wide zone of *Fucus vesiculosus* on a mixture of granite and basalt blocks; surface: 20 m²; exposition: south; inclination: 20°; 9.VIII.'55; CH 55051.

15. Kattendijke, outerside of the harbour mole; an open *Fucus vesiculosus* vegetation on loose stones and on basalt; width of the zone: 3 m; surface: 15 m²; exposition: north-east; inclination: 3—5°; 18.IX.'58; CH 58037.

France

16. Ambleteuse (P. de C.), rock formations at the fort; a very poorly developed *Fucus vesiculosus* vegetation, but slightly flooded with sand; surface: 6 m²; 1.VIII.'54; CH 54112.

Germany

17. Heligoland, Düneninsel, on the east side of the dam at the north-west side of the island; a poor vegetation of *Fucus vesiculosus* on concrete; surface: 10 m²; exposition: east; inclination: 90°; 22.VIII.'55; CH 55066.

TABLE XXXIX

Fucetum vesiculosi

Sample plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Percentage of covering	80	60	65	85	100	100	80	60	85	95	95	90	100	100	80	100	90
Fucus vesiculosus	5	3/4	4.4	4.4	4/5	5	5	4	5	5	5	5	5	5	5	5	5
Elachista fucicola	+	+	+	—	2	+	+	+	+	1	+	+	2	1	2	1	2
Gigartina stellata	—	4	—	—	2	—	—	3	3.2	1.2	1	1.2	2.3	—	—	—	—
Chondrus crispus	—	+	—	—	+	—	2.3	1	1.2	—	—	+	—	—	+	+	—
Pylaiella litoralis	—	+	—	—	—	—	1	+	—	+	—	1	+	—	—	—	2
Porphyra umbilicalis	—	+	+	+	2	—	+	+	—	+	+	+	+	—	+	1	1
Enteromorpha compressa	+	—	—	—	+	—	+	1	—	+	+	+	+	+	+g	+	+
Ulva lactuca	—	+	—	—	1	—	+	+	+	+	+	1.2	+.2	—	+°	+	+
Ulothrix flacca	+	+	—	—	—	1	+	—	—	—	—	+	2	+	—	—	—
Hildenbrandtia prototypus	—	1	—	5	+	2	+	—	2	4	5	1	4	1	+	—	—
Verrucaria mucosa	—	—	1	1	+	+	+	—	1	+	+	+	1	2	1	—	—
Ralfsia verrucosa	—	+	—	+	—	+	—	+	+	—	+	+	+	—	1	—	—
Fucus serratus	—	—	—	—	—	—	—	+	—	1	+	+	2.2	+	+	1	—
Ectocarpus confervoides	—	—	—	—	+	—	—	+	+	—	+	+	—	—	—	—	—
Ceramium deslongchampii	—	—	—	—	+	—	+	—	—	+	—	—	+	—	—	—	+
Rhodochorton purpureum	+	+	—	—	—	—	—	+	—	—	1	—	—	—	—	—	—
Blidingia minima	+	—	—	—	—	+	—	—	—	—	—	—	+	—	—	+	1
Petalonia fascia	—	—	—	—	—	—	+	—	—	+	—	+.2	—	—	—	—	—
Ascophyllum nodosum	+	—	—	—	—	—	—	—	—	—	—	—	+.2	—	+	—	—
Chaetomorpha aerea	—	+	—	—	—	—	—	—	—	—	—	+	—	—	—	—	+
Enteromorpha linza	—	—	—	—	+	—	—	—	—	—	—	—	—	+	—	—	—
Cladophora rupestris	—	+	—	—	—	—	—	—	—	—	—	+.2	—	—	—	—	—
Dumontia incrassata	—	+	—	—	—	—	—	—	—	—	—	+.2	—	—	—	—	—
Callithamnion scopulorum	—	—	—	—	—	—	—	—	—	+	—	—	+.2	—	—	—	—
Laminaria digitata	—	—	—	—	—	—	—	—	—	—	—	+°	+°	—	—	—	—

Addenda: survey 2: Fucus spiralis +; survey 5: Callithamnion roseum +, Enteromorpha prolifera 2; survey 9: Polysiphonia nigrescens +; survey 12: Ceramium rubrum +.2; survey 17: Cladophora nitida +, Phormidium corium 2.

Here, too, it is not impossible that a more detailed study of the epiphytical Algae will lead to the recognition of a larger number of characteristic species.

In studying the records we should bear in mind that the latter are not representative for the Netherlands as a whole, but only for the "Waddenzee". On our excursions in Zeeland, we directed our attention in the main on the rarer communities, and paid but little attention to the *Fucus* vegetations. From the data that were obtained, we may conclude, however, that the composition of the *Fucetum vesiculosi* is in Zeeland not richer than it is in the "Waddenzee".

The *Fucetum vesiculosi* is in the "Waddenzee" rather poor, but nevertheless richer than the *Fucetum spiralis*. It is not possible to distinguish definite variants.

Where sedimentation takes place, the crustaceous layer is poorly developed, and the *Fucus* canopy often remains more or less open; on clean stones the crustaceous layer may be completely closed, and then the blocks are coloured wine-red by *Hildenbrandtia prototypus*, speckled with green by *Verrucaria mucosa* and with dark brown by *Ralfsia verrucosa*. *Lithothamnion lenormandii* may also be present in this association, although its name is not found in my records.

The undergrowth consists of dendritic and fruticose Algae, and to some extent of tubular and foliaceous ones. It is often entirely dominated by *Gigartina stellata*, an eulittoral species, which in the "open" *Fucus* vegetation on Ameland fills every gap, so that its degree of covering is there even higher than that of *Fucus vesiculosus* itself (record 2). According to VAN GOOR this species would be present only in the more exposed localities, but this is not so. Its presence at Den Helder, West-Terschelling, Ameland, Oude Schild and on the dike along the Amsteldiep suggests that it has a preference for a fairly high salinity. Even where it occurs in rather brackish water, it is always in sites that are within the reach of the undiluted flood-current from the North Sea (Ameland, Amsteldiep). It is also noteworthy that it is not driven away by sedimentation.

Chondrus crispus is often met with at this level in the zonation, but it is not very numerous. It can stand a lower degree of salinity than *Gigartina stellata*. *Ceramium deslongchampii*, *Callithamnion scopulorum* and *Pylaiella litoralis* are much scarcer. The last-named species usually lives epiphytically. *Enteromorpha compressa*, *Ulva lactuca*, *Porphyra umbilicalis* and *Enteromorpha prolifera* are also often met with in the undergrowth, but they are always scarce. These photophilous species are more often met with as epiphytes. *Ulothrix flacca* is found even mainly as an epiphyte, and as such it is most numerous in spring. Intruders from the communities found at a higher level are not numerous; we find as such *Fucus spiralis* and *Blidingia minima*. The vegetations occurring at a lower level produce a larger number of intruders, and this is easily comprehensible as under the dense canopy of the *Fucus* thalli the humidity is nearly as high as it is at the low-water line. *Chaetomorpha aerea*, *Cladophora rupestris*, *Ceramium rubrum*, *Polysiphonia nigrescens* and young specimens of *Laminaria digitata* belong to this group of intruders. Some less frequent species indicate a special environment. *Dumontia incrassata* and *Petalonia fascia* are found, for instance, only in the often minuscule pools under the *Fucus* canopy; they reach their fullest development in the *Monostrometo-Dumontietum*. *Enteromorpha prolifera* indicates places where fresh water is mixed with sea water, *E. linza* is an indicator of sand or of sandy mud, *Callithamnion roseum* of rather strongly polluted water, which explains its preference for harbours.

Fucus serratus, the dominant species of the vegation in the next lower zone, is found repeatedly and often in fairly large numbers in this association. That the boundary line between these two zones is not very sharp, is mainly due to the circumstance that their ecological amplitudes overlap (ZANEVELD, 1937; BARKMAN, 1950). On the horizontal parts of the sea-dike at Den Helder the two species often form a mixed vegetation.

The presence of *Ascophyllum nodosum* remains confined to sites that are at least fairly well-sheltered. The associations of *Fucus vesiculosus* and of *Ascophyllum nodosum* are bound to the same level in the zonation, and it is therefore often assumed that they are no more than variants of the same association. *Ascophyllum* would become dominant in sheltered sites, *Fucus vesiculosus* in exposed ones; in between mixed vegetations would be found. However, such mixed vegetations were never seen by me. *Ascophyllum* is found only sporadically in the *Fucetum vesiculosi*, and although *Fucus vesiculosus* is usually present in the *Ascophylletum*, its degree of covering exceeds here but rarely 5 %. As the floristic composition of the two vegetations is different, they are here regarded as independent units.

SYNECOLOGY

The association is characteristic for the slopes of dikes that are exposed to the surf, and covers there, as a rule, the entire zone extending from M.H.W.N. to below M.S.L. In quiet sites it is usually replaced by the *Ascophylletum*, which has more or less the same upper limit. In some cases we find a narrow zone of *Fucus vesiculosus* between the *Ascophyllum* zone and the *Fucetum serrati*, but everywhere where I could study such a narrow zone of *Fucus vesiculosus*, there appeared to be a correlation with a sudden change in the composition of the substrate.

The physical structure of the substrate appears to have a considerable influence on the outcome of the competition between these two Phaeophyceae. The zygotes of *Ascophyllum* require a more humid environment for their development than those of *Fucus vesiculosus*. On basalt the *Ascophyllum* zygotes are therefore at a disadvantage, whereas they stand a better chance on the Vilvordian limestone, in which a fair amount of moisture is retained. Another factor which may be decisive for the outcome of the competition between the two species, is the force of the surf; *Fucus vesiculosus* is more resistent against the latter than *Ascophyllum*.

The boundary line between the *Fucetum vesiculosi* and the *Fucetum* *spiralis* or the *Blidingietum minimae* is, as a rule, very sharp; it happens but rarely that the associations merge into each other. On basalt the *Fucetum vesiculosi* is often the highest vegetation of the eulittoral region; in such cases above the *Fucetum vesiculosi* a zone is found in which *Balanus balanoides*, *Elminius modestus* and *Littorina saxatilis* predominate.

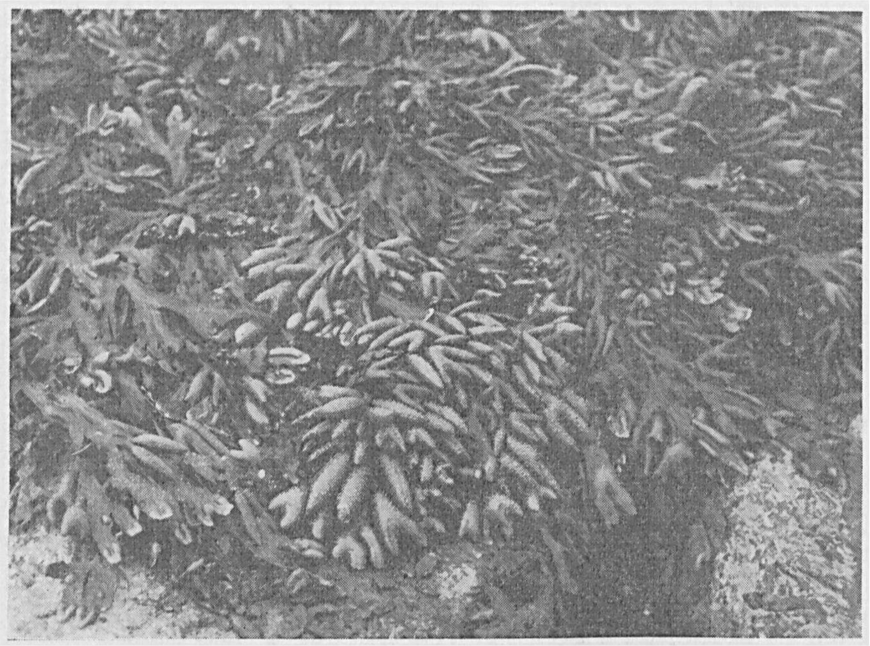


Fig. 23. *Fucus vesiculosus*, form without air-bladders. Den Helder, seadike. May 1955.

SUCCESSION

The *Fucetum vesiculosi* originates almost always in the course of a few years from the *Enteromorpheto-Porphyretum*. This development was observed by me in several places. Sometimes the succession proceeds at a very slow rate, and then several dendritic and fruticose Algae may establish themselves in the *Enteromorpheto-Porphyretum* before *Fucus vesiculosus* becomes dominant; this, however, is only an intermediate stage, for in the long run *Fucus* always succeeds in establishing itself.

A fully developed *Fucetum vesiculosi*, on the other hand, may under certain circumstances degenerate either into a community of dendritic or fruticose Algae, so e.g. on Ameland into a vegetation of *Gigartina*, or even into a pure *Hildenbrandtia-Verrucaria* association, as I noticed in Esbjerg, Oostmahorn, Ezumazijl and West-Terschelling, where it was caused by the gluttony of *Littorina littorea*.

If the association is destroyed by a catastrophe, for instance by floating ice in a severe winter, it may rapidly reestablish itself, and then it may even occupy sites which before the catastrophe were inhabited by other communities. At pale 89 on the sea-dike at Den Helder I could study a good example of such a reestablishment. Before the severe winter of 1946/47 the horizontal part of the dike bore an *Ascophyllum* vegetation. After that winter this vegetation, and the *Fucetum vesiculosi* which had occupied a site in the immediate vicinity, too, proved to be almost completely swept away; only a few specimens of *Ascophyllum* and *Fucus* were left. At first it looked as if *Ascophyllum* would succeed in reoccupying a surface of about one square meter, but via an *Enteromorpheto-Porphyretum* finally the whole area became covered with a *Fucetum vesiculosi*. In 1950 4 *Ascophyllum* plants could still be found, in 1952 (record 13) only 1, and since that year I have seen no more autochthonous *Ascophyllum* plants on this site.

AREA OF DISTRIBUTION

The *Fucetum vesiculosi* is very common along the coast of the southern part of the North Sea, but in how far the *Fucus vesiculosus* vegetations elsewhere agree with the one described in this work, can only be decided when complete records of the floristic composition are available.

The *Fucus vesiculosus* vegetations from the Skagerrak, the Kattegat and the Baltic Sea, waters that are not subjected to the tides, were described by GRAN (1893), SUNDENE (1953), KYLIN (1907, 1918), SJØSTEDT (1928), LEVRING (1940), KORNAŚ and MEDWECKA-KORNAŚ (1950), SVEDELIUS (1901) and WAERN (1952), but prove to have an entirely different floristic composition. The *Fuceto-Furcellarietum*, which was described by KORNAŚ and MEDWECKA-KORNAŚ from the Gulf of Gdańsk (Danzig) probably occurs in a large part of the Baltic Sea, but it is not identical with the *Fucus vesiculosus* vegetation from the Skagerrak and the Kattegat.

Fucus vesiculosus itself is widely distributed, and occurs in the form of vegetations on the European as well as on the North-American coast of the Atlantic Ocean. It reaches its southern limit in Morocco, where it occurs, according to HAMEL (1939), locally in salt marshes but no longer on rocks. In North America the southern limit lies, according to T. A. and A. STEPHENSON (1952), at Beaufort (Carolina). The northern limit lies in the vicinity of the polar circle (Greenland, Iceland, White Sea).

6.IV. **The Ascophylletum nodosi**

The *Ascophyllum nodosum* association is not rare in the Netherlands, and has already been mentioned by VAN GOOR (1923), but the latter did not describe the associations belonging to the *Fucus* formation. It has subsequently been recorded by ZANEVELD (1937) and by KOSTER (1954).

TABLE XL

Ascophylletum nodosi

Sample plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Percentage of covering	100	100	70	100	90	85	80	100	100	100	100	90	90	100
Ascophyllum nodosum	5	5	4	5	5	5	5	5	5	5	5	5	5	5
Polysiphonia lanosa	—	—	—	—	—	—	—	2.2	2.2	2	1	+.2	1	—
Spongonema tomentosa	—	—	—	—	—	—	—	—	—	—	+	—	—	—
Enteromorpha compressa	1	+	+	—	—	+	+	+.2	—	—	+	+°	+	+
Ulva lactuca	—	+	—	—	+	+	—	+.2	+	+	+	+	+	+°
Porphyra umbilicalis	—	—	+	—	+	+	+	+	—	—	+	—	+	—
Chondrus crispus.	—	—	1	2	2	1.2	2.3	+	2.2	1	2	—	—	—
Gigartina stellata	—	—	—	—	1	—	—	+	1.2	—	+	+.2	—	—
Ceramium deslongchampii.	—	—	—	+	+	—	+	1.2	+	+	1	1.2	1	1
Elachista fucicola	1	—	+	+	+	1	+	—	—	—	+	—	—	—
Fucus vesiculosus.	+	+	2	+	+	1	1	+.2	+	+	+	+	+	+
Rhodochorton purpureum	+	3	—	—	—	—	—	1	+.2	—	—	2.2	+	2
Hildenbrandtia prototypus.	—	3	3	4	3	1	+	1	1	1	1	1	2	+
Verrucaria mucosa	—	+	+	1	+	—	+	1	1	1	+	+	1	2
Ralfsia verrucosa.	—	—	1	1	+	+	+	1	+	1	+	2	+	1
Pylaiella litoralis	+	—	—	—	1	+	1	—	—	—	—	—	+	—
Ulothrix flacca	1	+	+	+	+	+.2/3	+	—	—	—	—	—	+	—
Blidingia minima	+	+	+	—	—	—	—	—	—	—	—	—	—	1g
Fucus spiralis	+	+	—	—	—	—	—	—	—	+	—	—	—	—
Cladophora rupestris	—	—	—	—	+	—	—	—	—	—	—	—	+	—
Cladostephus spongiosus	—	—	—	—	—	—	—	+.2	+	+	+	+	—	—
Sphacelaria fusca	—	—	—	—	—	—	—	+	1	+	1	+	+	+
Lithothamnion lenormandii	—	—	—	—	—	—	—	1	3	2	+	+	+	—
Polysiphonia urceolata	—	—	—	—	—	—	—	+	+	—	+	+	+	1
Callithamnion scopulorum	—	—	—	—	—	—	—	—	+	—	+	+	+	—
Cladophora utriculosa	—	—	—	—	—	—	—	+°	+°	—	+°	+°	+°	1°
Erythrotrichia carnea	—	—	—	—	—	—	—	+	+	—	+	—	—	—
Fucus serratus	—	—	—	—	—	—	—	—	+	—	+	—	+	—
Chaetomorpha aerea	—	—	—	—	—	—	—	—	—	—	+°	+°	—	+
Lola implexa	—	—	—	—	—	—	—	—	—	—	+	+	—	+
Catenella repens	—	—	—	—	—	—	—	—	—	—	—	+.2	+°	1

Addenda: survey 5: Petalonia fascia +; survey 9: Phyllophora membranifolia +; survey 11: Ceramium rubrum +, Codium fragile +, Goniotrichum elegans +, Acrochaetium secundatum +; survey 14: Verrucaria spec. +.

LEGENDA

1. Delfzijl, long harbour mole; an *Ascophyllum* vegetation on granite; surface: 50 m²; exposition: east; inclination: 15°; 13.IV.'53; CH 53025.
2. Delfzijl, on the dike east of the harbour; an *Ascophyllum* association on granite; surface: 100 m²; exposition: north; inclination: 15° 13.IV.'53; CH 53029.
3. Harlingen, northern breakwater; a badly developed *Ascophyllum* association on blocks of basalt; surface: 10 m²; 8.IV.'53; CH 53016.
4. Harlingen, northern harbour mole; an *Ascophyllum* vegetation on blocks of stone; surface: 100 m²; 8.IV.'53; CH 53017.
5. Harlingen, same locality; an *Ascophyllum* vegetation on blocks of stone covered with mud; surface: 200 m²; 8.IV.'53; CH 53018.
6. Kornwerderzand, in a quiet corner at the east side of the breakwater east of the sluice; a poorly developed *Ascophyllum* vegetation flooded with mud; surface: 30 m²; 3.IV.'53; CH 53007.
7. Kornwerderzand, on blocks of stone at the west side of the eastern breakwater; a 2 m wide *Ascophyllum* zone on a site that is regularly washed with fresh water from the IJsselmeer; surface: 20 m²; 3.IV.'53; CH 53009.
8. Tholen, Koffiehoek; a circ. 4 m wide *Ascophyllum* zone on Vilvordian limestone; surface: 60 m²; exposition: east; inclination: 30°; 27.X.'51; CH Th. 1.
9. Tholen, Gorishoek; a fine *Ascophyllum* vegetation on a little dam consisting of basalt and broken bricks, which runs through a tidal mud flat and which is submerged at high water; surface: 40 m²; 28.X.'51; CH Th. 8.
10. Tholen, dike west of Strijenham; a 4 m wide zone of *Ascophyllum* on Vilvordian limestone; surface: 40 m²; exposition: south-east; inclination: 20°; 9.VIII.'55; CH 55053.
11. Schouwen; harbour canal at Zieriksee; a beautiful, circ. 4 m wide zone of *Ascophyllum* on Vilvordian limestone; surface: 40 m²; exposition: east; inclination: 15°; 22.VII.'52; CH 52087.
12. Zuid-Beveland, dike east of Yerseke; a closed, 3 m wide zone of *Ascophyllum* on black calcareous shale and on large boulders of granite; surface: 45 m²; 26.X.'51: CH ZB. 2.
13. Flushing, Oranjedijk; an *Ascophyllum* vegetation on boulders of granite; surface: 10 m²; 4.IV.'54; CH 54004.
14. Zuid-Beveland, Hoedekenskerke, ferry-boat harbour, near the pontoon; an *Ascophyllum nodosum* zone on Vilvordian limestone; width of the zone: 2.1 m; surface: 10 m²; exposition: north-east; inclination: 20°; 15.X.'58; CH 58054.

This association has three characteristic species, viz. *Ascophyllum nodosum*, *Polysiphonia lanosa* and *Spongonema tomentosa*, but it is not impossible that further study will reveal the presence of some more.

Polysiphonia lanosa is a Rhodophycea which lives as a parasite on *Ascophyllum*, and which is found but rarely on other Fucaceae. I have seen it once on *Fucus vesiculosus*, viz. on a detached specimen which I found in a large amount of material that had been washed ashore. In the Netherlands *Polysiphonia lanosa* is common in the waters of Zeeland. In the "Waddenzee" it had been recorded, according to VAN GOOR, (1923), only from Den Helder and from Delfzijl, but more recent findings in this part are unknown to me.

Spongonema tomentosa is a rare species, which is found mostly as an epiphyte on *Ascophyllum*, but which is met with occasionally in the undergrowth. It has been collected in the "Waddenzee" as well as in the waters of Zeeland, and may in the Netherlands be regarded as a characteristic species, but not necessarily elsewhere, for in Brittany I found it in other communities, too.

A comparison of the records obtained in the Netherlands reveals that the association is here fairly homogeneous, but it also appears that it contains in Zeeland a larger number of species than in the "Waddenzee". On account of this difference we may distinguish a "Waddenzee" variant without differentiating species and a "Zeeland" variant with at least ten of these species, the most important ones being *Sphacelaria fusca*, *Cladostephus spongiosus*, *Lithothamnion lenormandii* and *Polysiphonia urceolata*. All these species are also found in the "Waddenzee", but they are there never met with in the *Ascophylletum*, whereas they are in Zeeland always present in this association.

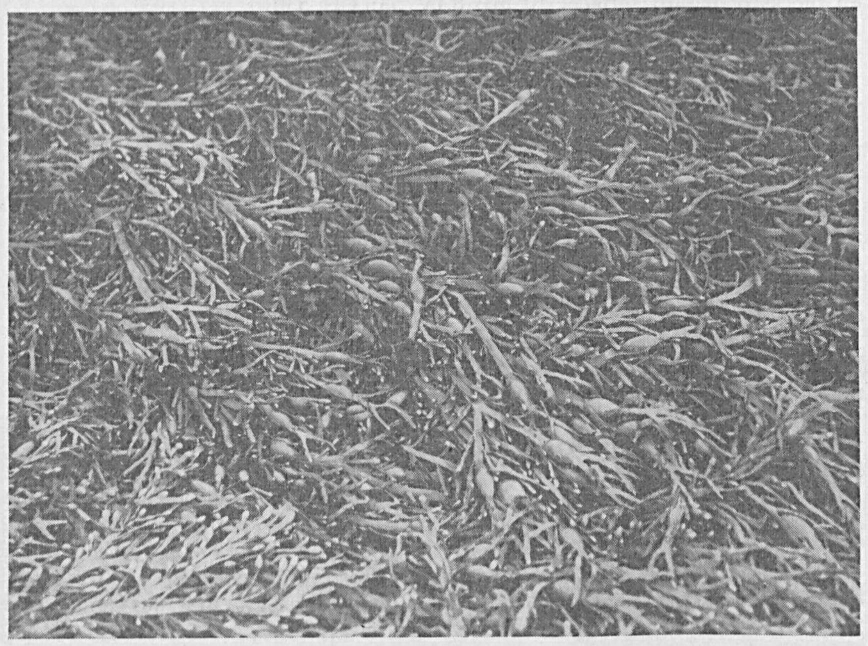


Fig. 24. *Ascophyllum nodosum*. Strijenham (Tholen). 19th September 1958.

In the "Waddenzee" the difference between the *Ascophylletum* and the *Fucetum vesiculosi* is not very striking, as both associations are here poor in species; the difference therefore is confined to a few species and their relative abundance. In Zeeland, on the other hand, the two associations are well characterized.

The crustaceous layer is almost always well-developed in the *Ascophylletum*; in only one of my records it was absent. In the "Waddenzee" it consists mainly of *Hildenbrandtia prototypus*, *Verrucaria mucosa* and *Ralfsia verrucosa*; in Zeeland it contains moreover *Lithothamnion lenormandii*; on Vilvordian limestone the latter often becomes dominant.

In the undergrowth especially *Chondrus crispus* comes to the fore. *Gigartina stellata* is here of less importance than it is in the *Fucetum vesiculosi*; *Ceramium deslongchampii*, on the other hand, is more common, whereas *Rhodochorton purpureum* may cover large stretches with a layer of red velvet. Algae like *Enteromorpha compressa*, *Ulothrix flacca*, *Porphyra umbilicalis* and *Ulva lactuca* are much scarcer; the first three species are, as a rule, entirely absent in the undergrowth, but they may be present as epiphytes.

The dense and often up to 10 cm thick *Ascophyllum* layer retains a high amount of moisture during the period of emergence, and this enables species belonging to associations which occupy a lower position in the zonation to penetrate into this one. This applies e.g. to *Codium fragile*, *Phyllophora membranifolia*, *Ceramium rubrum*, *Erythrotrichia carnea*, *Chaetomorpha aerea*, *Cladophora rupestris*, etc. Sciaphilous species like *Rhodochorton purpureum* and the crustaceous Algae find in this association a most favourable environment. Where in Zeeland the *Ascophylletum* occurs on stones with a rough surface, the latter is often covered with sand or with sandy mud; this deposit is often retained in its place by Algae like *Ceramium deslongchampii*, *Sphacelaria fusca*, *Cladostephus spongiosus*, *Callithamnion scopulorum* and *Polysiphonia urceolata*, which occur only in a diminutive form. *Callithamnion* and *Polysiphonia* were often overlooked so long as no use was made of the microscope, but they are nevertheless, as the records show, always present. *Sphacelaria fusca* and *Polysiphonia* appeared to be much better developed at a lower level, but *Cladostephus* was, except on Schouwen and Tholen, found exclusively in the form of dwarf plants in the *Ascophylletum*. However, notwithstanding the large number of species that are represented in the undergrowth, the latter does not look very flourishing.

SYNECOLOGY

In the Netherlands the *Ascophyllum* association shows a preference for quiet sites like small harbours, the sheltered side of moles and harbour canals. On more exposed sites it is replaced by the *Fucetum vesiculosi*. On the upper side it borders on the *Fucetum spiralis* from where *Catenella repens* sometimes penetrates into it, on the whole it remains somewhat below M.H.W.N. If the association is well-developed, its lower limit lies somewhat below that of the *Fucetum vesiculosi*; in that case, therefore, the *Ascophylletum* has gained some ground on the *Fucetum serrati*, on which it borders at that side, and then the lower limit coincides more or less with M.L.W.N.

The *Ascophylletum* puts no very special demands on the substrate, but on Vilvordian limestone and on the black calcareous shale it grows nevertheless better than on granite and on basalt. SCHMIDT (1928) remarked that *Ascophyllum* showed on Heligoland a strong preference for blocks of granite, and that it was therefore very rare on that island. When after the war the naval harbour was demolished, it multiplied strongly on the ruins. It is possible, therefore, that *Ascophyllum* prefers blocks of stone above an unbroken expanse of rock.

Another possibility is that *Ascophyllum*, which established itself for the first time on Heligoland in the twentieth century, did not succeed in gaining access to the sites occupied by the closed vegetations of *Fucus vesiculosus* and of *F. serratus*, but that the bare surface of the blasted rock offered it an unexpected opportunity. Why *Ascophyllum* established itself on Heligoland so much later than *Fucus vesiculosus* and *F. serratus*, remains as yet unanswered. The fact is the more strange, as *Ascophyllum* floats much better than *Fucus serratus*.

SUCCESSION

The *Ascophylletum nodosi* originates from the *Enteromorpheto-Porphyretum*. This was observed by me at Zieriksee as well as at Veere. Occasionally this association seems to oust the *Fucetum vesiculosi*, for instance when the site becomes less exposed on account of a change in a current. The reverse, i.e. the substitution of the *Ascophylletum* by the *Fucetum vesiculosi*, may also take place, e.g. after a catastrophe, because the latter regenerates more rapidly; this was seen at Den Helder (cf. p. 199).

AREA OF DISTRIBUTION

In the southern part of the North Sea the *Ascophylletum nodosi* is found along all the coasts. At Esbjerg it is poorly developed, on Heligoland it is still young. In the "Waddenzee" the association is but poor in composition; in Zeeland it consists of a considerable number of species; on the coast of "le Boulonnais" it is but poorly developed. The *Ascophyllum* vegetation which I could study at Roscoff, contained a smaller number of species than that found in Zeeland. In the absence of records, a comparison is, however, not well possible. From the descriptions in the literature it follows with certainty that the *Ascophyllum* vegetations from the Skagerrak belong to a different association.

Ascophyllum nodosum itself occurs along the whole west coast of Europe, from Spain to the Arctic Circle, and further on Iceland, on Greenland and on the Atlantic coast of North America. In all these parts it occurs in the form of zones.

6.V. The Fucetum serrati

The *Fucus serratus* association is in the Netherlands much less common than the *Fucetum vesiculosi*, the *Fucetum spiralis* and the *Ascophylletum nodosi*. It was nevertheless already mentioned by VAN GOOR (1923), viz. from Den Helder. ZANEVELD (1937), too, studied it. KOSTER (1954) reports its presence from Schouwen.

Fucus serratus is the only species of which we are quite certain that it is characteristic for this association. *Hecatonema fucicola*, a small epiphyte which I found at Den Helder and along the Amsteldiep on this species, may perhaps also be regarded as characteristic, but as it is very small and in other ways, too, not very conspicuous, it has probably often been overlooked; for this reason it is not quite certain

TABLE XLI

Fucetum serrati

Sample plots	1	2	3	4	5	6	7	8	9	10	11
Percentage of covering	70	95	95	95	90	90	100	100	100	100	100
Fucus serratus	4	5	5	5	5	5	5	5	5	5	5
Hecatonema fucicola	+	—	—	—	—	—	—	—	—	—	—
Ulva lactuca	1	+	+	+.2	1.2	+	1	1	+	1	+
Enteromorpha compressa	+	+	+	+.2	+	—	+	+	—	+	1
Chondrus crispus	2	—	—	—	—	1	2	2	2	2	1
Hildenbrandtia prototypus	+	4	4	4	4	—	—	—	—	+	+
Lithothamnion lenormandii	—	—	—	—	+	+	2	1	4	1	3
Elachista fucicola	—	—	+	+	+	+	2	1	1	+	—
Fucus vesiculosus	+	+	+	—	+	+	—	—	—	—	+
Cladophora rupestris	—	+	+	+	+	—	—	—	+	—	—
Polysiphonia urceolata	—	—	+	+	—	—	+	—	+	1	—
Ceramium rubrum	—	—	—	—	+	1	3	+	+	—	—
Laminaria digitata	—	—	—	+	+	—	+	1	1	—	—
Verrucaria mucosa	—	1	+	+	—	—	—	—	—	—	+
Polysiphonia nigrescens	—	—	—	—	—	+	—	+	—	—	—
Sphacelaria fusca	+	—	—	—	—	2.2	—	—	—	1	—
Cladophora refracta	+	—	—	—	—	—	—	—	—	+	—
Gigartina stellata	1	2.2	1.2/3	1.2	2.2	+	—	—	—	—	—
Ectocarpus confervoides	+	+	+	+	+	—	—	—	—	—	—
Pylaiella litoralis	+	—	+	1.2	+	1	—	—	—	—	—
Rhodochorton purpureum	+	—	+.2	1	—	+.2	—	—	—	—	—
Porphyra umbilicalis	+	—	+	+	+	—	—	—	—	—	—
Ceramium deslonchampii	+	—	+	+	—	+	—	—	—	—	—
Ulothrix flacca	—	—	+	+	+	+	—	—	—	—	—
Ralfsia verrucosa	+	—	+	+	—	—	—	—	—	—	—
Chaetomorpha aerea	—	+	+.2	+	—	—	—	—	—	—	—
Callithamnion roseum	+	—	—	—	—	1	—	—	—	—	—
Acrochaetium secundatum	—	—	—	+	—	+	—	—	—	—	—
Dictyosiphon foeniculaceus	—	—	—	—	—	—	+	+	—	—	—
Corallina officinalis	—	—	—	—	—	—	+	2	2	2	+
Rhodomela confervoides	—	—	—	—	—	—	1	+	1	+	—
Cystoclonium purpureum	—	—	—	—	—	—	+	—	1	—	—
Chordaria flagelliformis	—	—	—	—	—	—	+	+	—	—	—
Dumontia incrassata	—	—	—	—	—	—	—	—	—	+	+

Addenda: survey 1: Giffordia granulosa +; survey 4: Petalonia fascia +, Callithamnion scopulorum +; survey 5: Enteromorpha linza +; survey 6: Ascophyllum nodosum +, Codium fragile +.3, Cladophora utriculosa +, Hypoglossum woodwardii +, Antithamnion plumula +, Antithamnion cruciatum +, Callithamnion corymbosum +, Giffordia mitchellae +, Erythrotrichia carnea +/1, Erythrotrichia investiens +; survey 7: Lyngbya infixa +; survey 8: Lithothamnion polymorphum 1; survey 9: Phyllophora membranifolia +, Ahnfeltia plicata +, Polyides rotundus +, Membranoptera alata +, Polysiphonia nigra +; survey 10: Cladostephus spongiosus +.

LEGENDA

1. Between Ewijcksluis and Wieringen on the dike along the Amsteldiep; a circ. 1 m wide *Fucus serratus* zone on muddy blocks of basalt; surface: 10 m²; 13.XI.'52; CH 52162.

2. Den Helder, sea-dike between the pales 118 and 119; a circ. 5 m wide, very homogeneous vegetation of *Fucus serratus* on blocks of basalt and on a few boulders of granite; surface: 50 m²; 3.IV.'51; CH 51001.

3. Den Helder, sea-dike at pale 55; an up to 4 m wide, homogeneous zone of *Fucus serratus* on blocks of basalt; surface: 75 m²; 5.IV.'52; CH 52009.

4. Den Helder, sea-dike, on a small breakwater near pale 64; a 4 m wide zone of *Fucus serratus* on blocks of basalt; surface: 60 m²; 9.IV.'52; CH 52010.

5. Den Helder, sea-dike, on the fourth of the small breakwaters from the post office; a circ. 3 m wide zone of *Fucus serratus* on basalt blocks; surface: 45 m²; 10.IV.'52; CH 52013.

6. Tholen, Gorishoek, on a dam which juts out into the sea; a circ. 2 m wide, not very homogeneous zone of *Fucus serratus* descending to the low-water line; surface: 30 m²; exposition: south-west; inclination: 10°; 28.X.'51; CH Th. 5.

Germany

7. Heligoland, Hauptinsel, on the terraces at the west side of the island; a very extensive *Fucus serratus* vegetation; surface: 10 m²; 21.VIII.'55; CH 55062.

8. Heligoland, Hauptinsel, on a ridge of the rocks at the west side of the island; an extensive *Fucus serratus* vegetation; surface: 10 m²; 23.VIII.'55; CH 55068.

9. Heligoland, Hauptinsel, similar locality; an extensive *Fucus serratus* vegetation; surface: 6 m²; 23.VIII.'55; CH 55070.

10. Heligoland, Hauptinsel, similar locality; a very large field of *Fucus serratus*, the rock floor covered with sand; surface: 10 m²; 23.VIII.'55; CH 55071.

11. Heligoland, Hauptinsel, at the north-eastern side of the island; uppermost part of a field of *Fucus serratus* of a particularly large size, very sheltered; surface: 10 m²; 24.VIII.'55; CH 55076.

that it is bound to *Fucus serratus*. It is to be expected that a more thorough study will reveal the presence of some other characteristic epiphytes.

Just as in the case of the *Fucetum vesiculosi* my records are not representative for the whole of the Netherlands. There is but one record from Zeeland and five from the northern part of the country, and four of these five were obtained at Den Helder.

Especially in the "Waddenzee" district the *Fucetum serrati* is but sparsely represented. At Den Helder it is well-developed, and at the Amsteldiep also, but on Texel it was met with only in the form of fragments, and other places in the "Waddenzee" where it may be present, are unknown to me. It is at any rate absent in the eastern part of the latter and on Terschelling, and it does not occur on Wieringen, the "Afsluitdijk" and Harlingen. In the waters of Zeeland it is more often met with.

Comparison of the records from the Netherlands reveals a high degree of uniformity, although the record from Zeeland shows the presence of a larger number of species. A well-developed crustaceous layer with *Hildenbrandtia prototypus* and *Verrucaria mucosa* is present, in which *Lithothamnion lenormandii*, too, is found; on Heligoland the last-named species becomes dominant in this layer.

The undergrowth is on the whole rather similar to that of the

Fucetum vesiculosi and that of the *Ascophylletum nodosi*. Here, too, *Gigartina stellata* and *Chondrus crispus* are the dominant species. *Ulva lactuca* and *Ceramium rubrum* are better represented than in the two other associations, and the number of sublittoral species is distinctly higher, and they are moreover represented by a larger number of individuals. As examples of such sublittoral species we may quote *Polysiphonia nigrescens*, *Giffordia granulosa*, *G. mitchellae*, *Antithamnion cruciatum*, *Codium fragile*, *Hypoglossum woodwardii*, *Polysiphonia urceolata*, *Chaetomorpha aerea*, *Laminaria digitata*, *Ceramium rubrum*, etc.

Fig. 25. *Fucus serratus*. Den Helder, seadike. 24th December 1958.

The *Fucetum serrati* of Heligoland appears to differ in some important points from that of the Netherlands. In the first place *Hildenbrandtia* and *Verrucaria mucosa* are replaced as the most important species of the crustaceous layer by *Lithothamnion lenormandii*. Secondly, species like *Ulothrix flacca*, *Pylaiella litoralis*, *Ectocarpus confervoides*, *Ceramium deslongchampii*, *Gigartina stellata* and *Rhodochorton purpureum*, which in the Netherlands are common in this association, are absent. However, some of these species may have been absent on account of the season, the absence of *Ceramium deslongchampii* may have been accidental, and *Gigartina stellata* and *Rhodochorton purpureum* are rare on Heligoland. Thirdly, the presence of a number of species that are absent in the Netherlands, e.g. *Polyides rotundus*, *Corallina officinalis*, *Rhodomela confervoides*, *Lithothamnion polymorphum* and *Membranoptera alata*. In the fourth place, the presence of a group of species which are known from the Netherlands, too, but which do not occur there in the *Fucetum serrati*, viz. *Ahnfeltia plicata*, *Cystoclonium purpureum*, *Cladostephus spongiosus* and *Phyllophora membranifolia*.

Although I have made no records of the *Fucetum serrati* found on the coast of "le Boulonnais", I am convinced that it shows a fairly great resemblance to that of Heligoland, and this leads me to the conclusion that this association has not yet reached its final composition in the Netherlands. In future a subdivision in variants with a definite area of distribution will perhaps be possible, but to this end a larger number of records will be required. In this respect the presence of a large number of species with a predominantly southern distribution in the record from Tholen and their absence in those from Heligoland is noteworthy.

SYNECOLOGY

The *Fucetum serrati* occupies in the Netherlands a lower position in the zonation than the other communities of the *Fucus* formation; it extends, as a rule, from slightly below M.S.L. to M.L.W. Along the upper margin it borders on the *Fucetum vesiculosi* or on the *Ascophylletum nodosi*. The lower limit is in the Netherlands usually determined by the *Polysiphonieto-Chaetomorphetum* or, along the East Scheldt, by the *Codieto-Hypoglossetum*. In the last-named case it extends to M.L.W.S. On Heligoland the *Fucetum serrati* borders almost everywhere directly on the *Laminarietum*; here, too, *Fucus serratus* descends therefore to M.L.W.S. In pools in the eulittoral region, too, I saw that *Fucus serratus* often remains constantly submerged. This was pointed out to me by Prof. BOREL during an excursion in the vicinity of Boulogne. In such pools *Fucus serratus* remains sterile. In Heligoland, too, I have observed this repeatedly, and here I found it even in robust but sterile individuals in the sublittoral region. This phenomenon deserves a special investigation.

SUCCESSION

At Den Helder the *Fucetum serrati* was in the winter of 1946/47 almost entirely swept away, but it recovered rapidly. On some breakwaters I observed how the *Enteromorpha-Porphyra* association with much *Ulva* via a stage of dendritic and fruticose Algae and young *Fucus* plants passed into a *Fucetum serrati*. At Oude Schild on Texel I found in 1948 a *Fucus serratus* zone with but little *Fucus serratus* but with a very dense undergrowth consisting of *Chondrus crispus* and *Gigartina stellata*. In 1950 the number of individuals of *Fucus serratus* had increased, but the covering did not reach 25 %; whereas *Chondrus* and *Gigartina* together showed a covering of more than 80 %. Similar *Chondrus* vegetations with young plants of *Fucus serratus* were observed in Zeeland, too, especially in muddy sites and on mussels.

AREA OF DISTRIBUTION

The *Fucetum serrati* is very beautifully developed on the terraces at the west side and at the north-east side of Heligoland. In the western part of the "Waddenzee" it occurs in a much poorer form. In Zeeland it appears to contain many species with a predominantly southern distribution, and on the coast of "le Boulonnais" it is also a most important type of vegetation.

Whether the *Fucus serratus* vegetations in other territories are comparable with those described in this work, can, as we have pointed out in our discussion of the other associations of this formation, only be decided if records are available, and with regard to the *Fucus serratus* vegetations, too, we find that those that have been described from the the Skagerrak, the Kattegat and the Baltic Sea belong to a different association.

Fucus serratus itself is found along the west coast of Europe from Spain to Spitsbergen and Novaya Zemlya. According to BØRGESEN (1905) it is absent on the Faeroes, but on Iceland it is present. Its occurrence in New England is of recent date.

7. THE COMMUNITY WITH HALIDRYS SILIQUOSA

A well-developed *Sargassum* or *Desmarestia* formation is not recognizable in the sublittoral region of the Netherlands. The dominant constituents of the *Sargassum* formation, the *Cystoseira* species, reach the north-eastern limit of their area of distribution in the English Channel. The northern *Desmarestia* species reach the southern limit of their area in Brittany; the only place in the southern part of the North Sea where they form vegetations, is Heligoland; here they occur in the form of open vegetations in the gaps in the *Laminarietum* which mark the places through which currents pass. In the Netherlands *Desmarestia* was collected but once, viz. in the form of a single individual of *D. viridis*, which grew at Wemeldinge (DEN HARTOG, 1954).

The Sargassacea *Halidrys siliquosa*, which on account of its distribution as well as because of its growth form might better be included in the *Desmarestia* formation, has been found in one place in the Netherlands, viz. at Strijenham on Tholen, and here it occurs in the form of a narrow zone on both sides of a breakwater which is exposed to a strong tidal current. During E.L.L.W.S. the upper parts of the plants become visible.

The floristic composition of this *Halidrys* vegetation proved to be atypical. Not a single of the epiphytes and parasites that are bound to this species could be found. The epiphytic flora as well as the undergrowth consisted of species belonging to the *Codieto-Hypoglossetum*. For this reason I regard this *Halidrys* vegetation merely as a poor fragment of a community that elsewhere reaches a much richer development. On Heligoland, too, a *Halidrys* vegetation was observed, but this one also showed a floristic composition which could not be considered typical.

8. THE LAMINARIA FORMATION

The *Laminaria* formation comprises the algal communities in which the Laminariaceae s.l. form the main part of the vegetation. These communities consist, as a rule, of four layers, viz. a crustaceous layer, a layer consisting of dendritic and fruticose Algae, a layer in which species of the *Cystoseira* or *Desmarestia* type predominate, and finally the layer formed by the Laminariaceae themselves. In some of the communities the third layer is absent.

The Laminariaceae grow very close together, and cover in the sublittoral region large stretches. As the constituents of the upper layer, moreover, reach a considerable size, these extensive vegetations are often called "forests".

The communities of the *Laminaria* formation reach their fullest development in the arctic and subarctic regions, where the number of species, too, is much higher than it is in the temperate zone; this is shown very clearly in table XLII.

TABLE XLII

Distribution of the Laminariaceae s.l. in the northern part of the Atlantic Ocean

	Ecklonia	Phyllaria	Laminaria	Saccorhiza	Alaria	Agarum	
Canary Islands	1	—	1	—	—	—	Børgesen, 1926
Morocco	—	2	1	1	—	—	Dangeard, 1949
Portugal	—	—	1	1	—	—	Hamel and Feldmann, 1928
Brittany	—	—	4	1	1	—	Hamel, 1938
Southern North Sea . .	—	—	3	—	—	—	
Scotland	—	—	3	1	1	—	Børgesen and Jonsson, 1905
West Norway	—	—	3	1	1	—	id.
Faeroes	—	—	4	—	2	—	id.
Finmarken	—	—	5	1	2	—	id.
Iceland	—	—	5	1	2	—	id.
Greenland	—	—	7	1	2	1	id.
Arctic North America .	—	—	1	—	1	1	id.
Murmansk Coast . . .	—	—	5	1	1	—	id.
Siberian Ice Sea . . .	—	—	3	—	3	—	id.

In the southern part of the North Sea the genus *Laminaria* is represented by three species, which are divided over two associations, viz.

1. the *Laminarietum digitato-saccharinae*, and
2. the *Laminarietum hyperboreae.*

Only the first-named one is represented on the coast of the Netherlands.

8.I. The Laminarietum digitato-saccharinae

The association of *Laminaria digitata* and *L. saccharina* was already described, although rather incompletely, by VAN GOOR (1923: p. 155) under the name "*Laminaria* Association" from Den Helder.

Apart from *Laminaria digitata* and *L. saccharina*, which form the principal part of the vegetation, there are in this association three other elements that may be regarded, at least locally, as characteristic, viz. *Ectocarpus confervoides* f. *pygmaea*, *Myrionema corunnae* and *Ectocarpus fasciculatus.*

TABLE XLIII

Laminarietum digitato-saccharinae

Sample plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Percentage of covering	80	85	75	95	90	70	70	60	80	100	100	100	100	100	100	100
Laminaria digitata	4	5	4	5	4.4	4	—	2	2	4	4	1	2	4	2	1
Laminaria saccharina	+	—	—	2	3.4	+	4	4	5	4	4	5	5	4	5	5
Ectocarpus confervoides f. pygmaea	—	—	—	—	—	1	—	—	+	—	1	—	—	—	—	—
Ectocarpus fasciculatus	+	+	—	—	+	—	1	—	—	+	+	—	—	—	—	—
Myrionema corunnae	—	—	—	1	1	+	—	—	—	—	+	—	—	—	—	—
Ceramium rubrum	1.2	1.2	+	+	2.2	1	2	+	+	2	1	2	+	+	1	—
Chondrus crispus	+	+	2	+	+	+	2	1	1	2	+	+	—	1	1	2
Ulva lactuca	+	—	1	+	1	1	2	+	+	+	+	1	—	+	+	+
Polysiphonia nigrescens	+.2	+.2	1	+	+	+	+	+	+	1	—	+	—	—	—	—
Polysiphonia urceolata	1.2	+.2	+	1	1	+	+	—	—	—	2	+	—	+	—	+
Lithothamnion lenormandii	+	—	+	—	—	—	—	1	1	1	2	+	1	2	2	2
Fucus serratus	+	+	+	—	+	+°	—	+	—	+	—	—	—	1	+	+
Hildenbrandtia prototypus	+	+	+	—	—	—	—	—	+	+	+	—	—	+	+	+
Phyllophora membranifolia	—	—	+	—	+	—	+.2	+	+	+	+	—	—	—	+	—
Chaetomorpha melagonium	—	—	+.1	—	+	—	+	—	—	—	+	—	—	—	—	—
Gigartina stellata	+.2	+.2	+°	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhodochorton purpureum	+	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—
Chaetomorpha aerea	—	—	+.2	+	1	—	—	—	—	—	—	—	—	—	—	—
Cladophora rupestris	+.2	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—
Chorda filum	—	—	—	—	—	—	+	—	—	—	—	—	—	—	+	—
Ectocarpus confervoides	+	+	—	—	—	—	+	—	—	+	+	—	—	—	—	—
Acrochaetium virgatulum	—	—	—	—	—	—	+	—	—	—	+	—	—	—	—	—
Lyngbya infixa	—	—	—	—	—	—	+	—	—	—	+	—	—	—	—	—
Lithothamnion polymorphum	—	—	—	—	—	—	—	1	1	1	1	+	+	1	3	2
Cystoclonium purpureum	—	—	—	—	—	—	—	+	+	+	+	+	+	—	+	+
Polyides rotundus	—	—	—	—	—	—	—	+	+	—	+	—	—	—	+	+
Corallina officinalis	—	—	—	—	—	—	—	—	—	+	—	—	—	+	+	+
Ahnfeltia plicata	—	—	—	—	—	—	—	—	+	—	+	—	—	—	+	+
Rhodymenia palmata	—	—	—	—	—	—	—	+	+	+	—	—	—	—	—	—
Griffithsia flosculosa	—	—	—	—	—	—	—	+	+	+	—	—	—	—	—	—
Gymnogongrus norvegicus	—	—	—	—	—	—	—	+	+	+	—	—	—	—	—	—
Rhodochorton floridulum	—	—	—	—	—	—	—	2	2	—	—	—	—	—	—	—
Plocamium coccineum	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—
Rhodomela confervoides	—	—	—	—	—	—	—	—	—	—	2	2	+	+	—	+
Ralfsia sp.	—	—	—	—	—	—	—	—	—	—	+	+	+	+	—	+
Desmarestia aculeata	—	—	—	—	—	—	—	—	—	—	+	—	—	—	+	—
Laminaria hyperborea	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—

Addenda: survey 1: Pylaiella litoralis +, Codiolum wormskioldii st. urosporae +; survey 2: Verrucaria mucosa +; survey 4: Cladophora refracta +; survey 7: Codium fragile +, Acrochaetium codii +, Erythrotrichia carnea +, Giffordia granulosa +, Scytosiphon lomentaria +, Porphyra umbilicalis +, Enteromorpha clathrata +; survey 9: Bryopsis plumosa +, Gracilaria verrucosa +; survey 10: Lomentaria articulata +, Dictyota dichotoma +, Laurencia pinnatifida +; survey 11: Cladophora utriculosa +, Chordaria flagelliformis +, Ceramium deslongchampii +, Polysiphonia nigra +, Ectocarpus cf. parasiticus +; survey 14: Elachista fucicola +, Halidrys siliquosa +.

LEGENDA

1. Den Helder, sea-dike, on the fourth of the small breakwaters on the far side of the post office; a *Laminaria digitata* vegetation; surface: 15 m²; 10.IV.'52; CH 52012.

2. Den Helder, sea-dike, at pale 60 on basalt; *Laminaria digitata* facies; surface: 30 m²; 12.IV.'52; CH 52015.

3. Den Helder, sea-dike, at pale 52; *Laminaria digitata* facies; surface: 15 m²; 7.VII.'52; CH 52076.

4. Den Helder, sea-dike, at pale 149; vegetation with *Laminaria digitata* as dominant; surface: 100 m²; 8.VII.'52; CH 52077.

5. Den Helder, sea-dike, at pale 134; vegetation of which the aspect is determined by *Laminaria digitata* and *L. saccharina* jointly, descending to 1.5 m below M.L.W., flooded with sand; surface: 100 m²; 8.VII.'52; CH 52078.

6. Den Helder, sea-dike, at pale 80; vegetation dominated by *Laminaria digitata*; surface: 20 m²; 9.VII.'52; CH 52080.

7. West-Terschelling, at the end of the harbour mole; open vegetation of *Laminaria saccharina*; surface: 10 m²; 1.IX.'54; CH 54168.

France

8. Ambleteuse (P. de C.), a small but deep bay in the Langue de Chien, very sheltered; vegetation dominated by *Laminaria saccharina*; surface: 10 m²; 7.IV.'55; CH 55009.

9. Ambleteuse (P. de C.), a deep bay in the Langue de Chien, somewhat less sheltered than the preceding locality; vegetation dominated by *Laminaria saccharina*; surface: 10 m²; 7.IV.'55; CH 55010.

10. Wimereux (P. de C.), at the south side of the rock formations at Fort de Croy; joint dominance of *Laminaria digitata* and *L. saccharina*; surface: 20 m²; 11.IV.'55; CH 55024.

Germany

11. Heligoland, Düneninsel, on the terraces at the northern side, circ. 250 m from the beach; extensive vegetations of which the aspect is determined by *Laminaria digitata* and *L. saccharina*; surface: 100 m²; 20.VIII.'55; CH 55061.

12. Heligoland, Düneninsel, on the terraces at the north-west side, circ. 70 m from the beach, fairly sheltered; vegetation dominated by *Laminaria saccharina*; surface: 40 m²; 22.VIII.'55; CH 55063.

13. Heligoland, Düneninsel; on the terraces at the north-west side, circ. 150 m from the beach, fairly sheltered; vegetation dominated by *Laminaria saccharina*; surface: 40 m²; 22.VIII.'55; CH 55064.

14. Heligoland, Felseninsel, in a deep gully between some solid rock ridges at the western side of the island, fairly exposed; vegetation of *Laminaria digitata* and *L. hyperborea*; surface: 10 m²; 23.VIII.'55; CH 55069.

15. Heligoland, Felseninsel, in one of the gullies at the very sheltered north-eastern side of the island; vegetation of which the aspect is determined by *Laminaria saccharina*; surface: 15 m²; 24.VIII.'55; CH 55074.

16. Heligoland, Felseninsel, in one of the gullies at the north-eastern side of the island; vegetation dominated by *Laminaria saccharina*; surface: 40 m²; 24.VIII.'55; CH 55075.

Ectocarpus confervoides f. *pygmaea* was reported by DEN HARTOG (1954: p. 412) as occurring on the stipe and more rarely on the lamina of *Laminaria digitata*. BØRGESEN (1903), JONSSON (1903) and LUND (1941) found it in the same way on the coasts of respectively the Faeroes, Iceland and Denmark. This epiphyte, however, also occurs on *Fucus serratus*, be it as a great exception.

Myrionema corunnae, which until recently was not known from the Netherlands, was found in July 1952 in a fairly large number on the lamina of *Laminaria saccharina*, more rarely on that of *L. digitata*. This species was also mentioned by HAMEL (1931—39), NEWTON (1931) and SUNDENE (1953) as epiphyte of *Laminaria*. The only finding on another host, viz. on *Porphyra umbilicalis*, was reported by FELDMANN (1954).

Ectocarpus fasciculatus may at the most be regarded as a species which locally shows a preference for *Laminaria* species. VAN GOOR (1923: p. 87) already mentions this species as occurring on *Laminaria*, but he also reports it from a buoy in the harbour of Den Helder. HAMEL (1931—39) also reports its occurrence on *Laminaria*, but according to him it is also found on *Chorda filum* and on *Himanthalia elongata*. LUND (1941), too, mentions its occurrence on other species, and SUNESON (1939) found it even on the fins of fishes. At Den Helder, however, it shows a quite distinct preference for the lamina of the *Laminaria* species.

A more detailed study of the small epi- and endophytes will perhaps lead to the recognition of some more characteristic species, but this is laboratory work; in their natural habitat these microscopical Algae are recognizable only when they are present in large masses.

A comparison of the records obtained in the Netherlands, shows that the association is here fairly homogeneous, and that it almost contains no elements that are typical for the eulittoral region; *Fucus serratus* is the only eulittoral species that is regularly represented, but it is noteworthy that it always remains sterile at this level. *Gigartina stellata* is sometimes present, but usually in a rather poor condition. *Hildenbrandtia prototypus* occurs but in a small number of individuals.

The main constituents of the layer of dendritic and fruticose Algae are *Ceramium rubrum*, *Polysiphonia urceolata*, *P. nigrescens* and *Chondrus crispus*, whereas *Ulva lactuca*, too, is always present. *Ceramium rubrum*, *Polysiphonia urceolata* and *Ulva lactuca* are not confined to this layer. but are also found on *Laminaria*, just as *Giffordia granulosa*, which is much more common than one would be inclined to assume from the records. *Phyllophora membranifolia*, *Chaetomorpha aerea*, *Ch. melagonium*, *Cladophora rupestris* and *Cl. refracta* are less regularly met with; these species reach their fullest development in the *Polysiphonieto-Chaetomorphetum*, the association which occupies the next higher position in the zonation.

A crustaceous layer is hardly developed. *Lithothamnion lenormandii* and *Hildenbrandtia prototypus* are its only constituents, and even these species are scarce.

The records reveal that *Laminaria digitata* is sometimes better represented than *L. saccharina*, that the two species may occur in nearly the same number, and that *L. saccharina*, too, may be the dominant species. In the literature it has often been said that *L. digitata* shows a preference for more exposed sites, and *L. saccharina* one for sheltered ones, but the solution of the problem appears to be less simple. The sea-dike at Den Helder is an exposed site, and here

L. digitata is the dominant species. This is therefore in accordance with the generally accepted rule. However, the situation was formerly different. VAN DEN BOSCH (1853) records in the "Prodromus Florae Batavae" for Den Helder *L. saccharina* only, and the first record of *L. digitata* dates from 1871. VAN GOOR (1923) wrote "Ueberall besteht diese Vegetation aus zwei Arten, *L. digitata* und *L. saccharina*", and there is not the slightest indication in his description that one of these two species was at that time more common than the other. Since then, however, there occurred a sudden change. In the severe winter of 1946/47 the *Laminaria* vegetation at Den Helder was completely destroyed by floating ice. In the summer of 1947 not a single *Laminaria* plant could be found on this site, but in 1948 *L. digitata* already appeared to have recovered fairly well. *L. saccharina*, however, is since that time much less common than *L. digitata*, and it seems doubtful whether it will ever regain the position it occupied before the catastrophe.

In 1884 *L. saccharina* was recorded for the first time from Texel, but it is not known whether it was there at that time autochthonous. In 1950 a vegetation of this species was found at Oude Schild on a site where it had not been seen in April 1948. In West-Terschelling *L. saccharina* was for the first time observed in the summer of 1952; in July 1950 on this site a fragment of the *Codieto-Hypoglossetum* was found. In 1954 *Laminaria saccharina* was present in a much larger number of individuals, but it formed as yet no closed vegetation, and the *Codieto-Hypoglossetum* was not yet completely replaced by it. In April and June 1958 at West-Terschelling a beautifully developed, closed zone of *L. saccharina* was found along the harbour mole as well as along the "Grote Dam".

A comparison of the records from the Netherlands with those from the coast of "le Boulonnais" and of Heligoland shows that the association consists in the last-named places of a larger number of species. These additional species are partly the same in the two habitats, so e.g. *Cystoclonium purpureum* (in the Netherlands present in the *Laminarietum* on Texel, which has not yet been analysed), *Polyides rotundus*, *Corallina officinalis* and *Ahnfeltia plicata* (perhaps also present in the *Laminarietum* at Den Helder). On the coast of "le Boulonnais" the *Laminarietum* appeared to contain moreover *Rhodymenia palmata*, *Griffithsia flosculosa* and *Gymnogongrus norvegicus*, on Heligoland *Desmarestia aculeata* and *Rhodomela confervoides*. A second difference is found in the better development of the crustaceous layer, especially on Heligoland.

The greater richness of the association on the coast of "le Boulonnais" and on that of Heligoland is undoubtedly due to the greater age of the vegetation in these sites. We may assume that they have reached there their final composition, whereas this is not so in the Netherlands where it has existed but little more than a hundred years. Here it is therefore still open to new immigrants. The practical absence of the crustaceous layer, and perhaps also the absence of some of the other constituents, in the *Laminarietum* of the Netherlands is doubtless due to a stronger sedimentation, i.e. to the presence of a thin layer of sand or mud on the solid substrate.

The differences between the *Laminarietum* from the coast of „le Boulonnais" and that from Heligoland which were mentioned above, are not of geographic importance. The presence of *Griffithsia flosculosa* and of *Gymnogongrus norvegicus* may perhaps be regarded as a reflection of the more southern position of "le Boulonnais", these species are too scarce and also too little typical to justify such a geographic subdivision. The same applies to *Desmarestia aculeata*, might be taken as indicating a more northern type of the vegetation found on Heligoland.

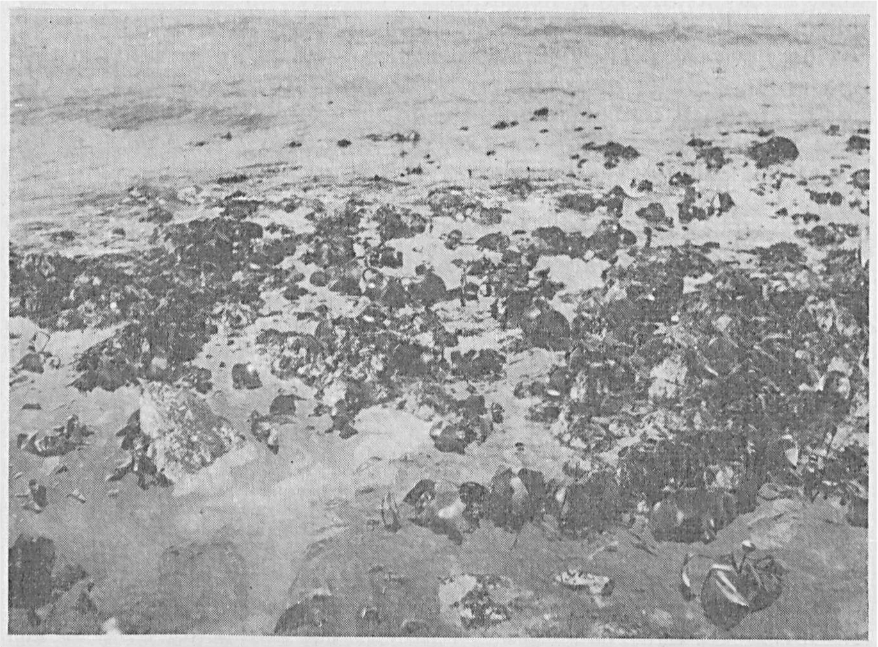


Fig. 26. *Laminarietum digitato-saccharinae* on the Langue de Chien (Ambleteuse, Pas de Calais, France). *Laminaria digitata* partly emerged, to the left submerged *L. saccharina* also visible. April 1955.

SYNECOLOGY

In the Netherlands the *Laminaria* association is found in the uppermost part of the sublittoral region. The upper limit coincides more or less with M.L.W.S. It is nevertheless often difficult to separate it from the *Polysiphonieto-Chaetomorphetum*, which occupies the next higher position in the zonation, as especially *Laminaria digitata* establishes itself easily above M.L.W.S. However, at that level it is unable to survive severe winters; the individual plants, moreover, remain much smaller, which indicates that this species has reached here the limit of its possibilities. Moreover, the two associations have a number of species in common. Well-represented in each of them are e.g. *Polysiphonia urceolata, P. nigrescens, Chondrus crispus* and *Ulva lactuca.*

The lower limit of the *Laminarietum* is usually determined by the place where the mantle of stones on the slope of the dike stops, sometimes also by a covering of the lower part of this mantle with sand or mud. For this reason the *Laminarietum* descends in the Netherlands rarely to a depth of more than 1 m below M.L.W.S., although locally it has been met with at a depth of 1.5 or of 2 m.

At Den Helder, as mentioned above, *Laminaria digitata* reaches a higher level than *L. saccharina.* On the coast of "le Boulonnais", too, I noticed this, but on Heligoland the two species reach their upper limit nearly at the same height, so that each of them falls partly dry during each low spring tide.

How deep the *Laminarietum* descends on the coast of "le Boulonnais" and of Heligoland, could not be made out with certainty, but it cannot be doubted that it reaches in the first-named site a depth of at least 1.5 m, and on Heligoland one of more than 2 m. At that depth it passes gradually in the *Laminarietum hyperboreae.*

THE LAMINARIETUM ON HELIGOLAND

The *Laminaria* vegetations in the Netherlands are not very extensive, and those on the coast of "le Boulonnais" are difficult of access. An ideal place for the study of this association is Heligoland, where at spring tides on the cliffs and on the terraces that are exposed to the surf large stretches covered with this vegetation are within easy reach.

Fig. 27. *Laminaria saccharina* facies of the *Laminarietum digitato-saccharinae*, emerged during spring-ebb. Heligoland, Düneninsel. August 1955.

These fields are hundreds of square meters in extent, and are separated from each other by narrow, up to 1.5 m deep gullies in which sedimentation or tidal currents form an obstacle for the establishment of the *Laminaria* plants. In these fields the two species form such a dense mass that other Algae can hardly maintain themselves (records 12 and 13), so that the association often becomes very poor in species.

In the gullies where sand is deposited, the lower limit of the *Laminarietum* is indicated by a vegetation consisting of *Ulva lactuca*, *Enteromorpha linza*, *Cladophora refracta*, *Ceramium rubrum* and *Rhodomela confervoides*. Other gullies possess a floor which is covered with pebbles, and the latter are mainly covered with *Lithothamnion polymorphum*, and to a smaller part with *L. lenormandii*, *Ulva lactuca* and small *Laminaria* plants. Larger boulders are mainly covered with *Laminaria* and with *Desmarestia aculeata*. In the gullies through which a rather strong current passes, we find an entirely different situation, viz. an open vegetation with gigantic, up to 1.5 m high plants of *Desmarestia aculeata*, *Ulva lactuca*, *Chorda filum*, *Ceramium rubrum*, *Chordaria flagelliformis*, some isolated individuals of *Laminaria saccharina* and a few other less numerous Algae. On the ridges and on the flats the two *Laminaria* species are, however, uncontested dominants; *L. digitata* reaches here a height of 2 m, *L. saccharina* even one of 3—4 m. These observations were made on the north side of the Düneninsel.

On the exposed terraces at the western side of the Felseninsel the ridges run parallel to the coast. Consequently at low water many elongated, 0.5—1.5 m deep pools are cut off from the sea, and as this coast is rather exposed, sedimentation is confined to the pools that are farthest from the sea. Nearer to the sea the sedimentation is less, and the sediment is often swept away by the current which sets in when the water begins to fall. In these pools the *Laminarietum* is remarkably well developed, especially in the deeper ones. In the latter *Laminaria hyperborea*, a species that finds its true habitat at a still greater depth (record 14), is rather often met with and further *Plocamium coccineum*, *Halidrys siliquosa* and *Delesseria sanguinea*.

In the north-eastern part of the island the ridges are, just as on the Düneninsel, directed at a right angle to the coast, but as this part occupies a much more sheltered position than the north side of the Düneninsel, there is sedimentation, with the result that the gullies often bear *Laminaria saccharina* vegetations which are rather rich in *Ulva*. The development as well as the degeneration of the *Laminaria* vegetation could be studied here in a very satisfactory way.

SUCCESSION AND DEGENERATION

The series of stages through which a *Laminarietum* developing on a new substrate has to pass, are: a vegetation in which *Ulva* is the dominant species → the *Codieto-Hypoglossetum* or some other vegetation of dendritic Algae → the *Halidrys* vegetation (sometimes *Desmarestia aculeata*) → the *Laminarietum digitato-saccharinae*. This series is the ideal one, as in the area studied by us the *Halidrys* vegetation is only exceptionally present, and as sometimes even a second intermediate stage may be absent. However, at the north-eastern side of the Felseninsel at Heligoland all these stages were found. Open spaces are in this place due to the enormous masses of Algae that are sometimes washed ashore, and which may suffocate the vegetation and kill it. After the rotting remains have been swept away, the site is at once reoccupied, and then we note the following succession: *Ulva* → *Ceramium rubrum* → (*Halidrys*) → *Laminaria*. In gullies with very quiet water in which much rotting detritus is left behind, the reestablishment of the *Laminarietum* proceeds at a slower rate or not at all. In that case the development stops at one of the intermediate stages.

A reversion of the normal sequence is not excluded. On Heligoland I saw at a few places gigantic *Laminariae* which had toppled over and were extended flat against the floor; young plants were not present, but *Halidrys siliquosa* and *Ceramium rubrum* were very abundant; the first-named species even determined the aspect of the vegetation. This degeneration I ascribe to a diversion of a current.

Our data with regard to the natural rejuvenation of the vegetation are as yet but incomplete. At Den Helder the whole year round plants of all possible dimensions are present, but on Heligoland I have seen several plots which consisted exclusively of very large, mature specimens, and where not a single young plant could be found. It looks as if these vegetations will in the end die of age or that they will be destroyed by some catastrophe, and that only then a new one may develop.

AREA OF DISTRIBUTION

In the Netherlands completely developed vegetations belonging to the *Laminarietum digitato-saccharinae* are common at Den Helder, whereas the *Laminaria saccharina* facies of this association has been found on Texel (Oude Schild, 't Horntje), at West-Terschelling and at Kattendijke (Zuid-Beveland).

Heligoland is the only place on the German part of the North Sea coast where the association is found, and on the coast of "le Boulonnais" it is common from Cap Gris Nez to Le Portel. HAMEL (1938) mentions the presence of the two *Laminaria* species from Dunkirk.

Although the area of distribution of this association is doubtless larger, as the area of distribution of the two dominating species extends far beyond these limits, I am unable to give any positive data, as no records of the floristic composition of these vegetations are available. So much is certain that the *Laminaria saccharina* association and the *Laminaria digitata* association described by SUNDENE (1953) from the Oslo Fjord are not fully identical with the *Laminaria* association described above. The two associations described by SUNDENE differ only in the dominant species; they contain a number of species that do not occur in the *Laminarietum digitato-saccharinae* from the southern part of the North Sea, and their ecology, too, is different from that of the latter. Although doubtless nearly related, they cannot be regarded as identical with the association described above.

8.II. The Laminarietum hyperboreae

The *Laminaria hyperborea* association extends in the sublittoral region of Heligoland over enormous distances, occasionally kilometers wide, but this area can unfortunately not be reached from the beach. It begins at a depth of circ. 2 m below M.L.W.S. and reaches a depth of 6 m. Although no records could be obtained from this vegetation, some idea of it could be formed from what was washed ashore. The scabrous stipes of *L. hyperborea* proved to be covered with a large number of epiphytes like *Delesseria sanguinea*, *Membranoptera alata*, *Phycodrys rubens*, *Polysiphonia urceolata*, *Desmarestia aculeata*, *Rhodomela confervoides*, *Corallina officinalis*, *Ulva lactuca*, *Ceramium rubrum*, *Phyllophora membranifolia* and *Rhodochorton purpureum*.

SUMMARY

In this chapter descriptions are given of all epilithic algal communities that so far could be recognized in the Netherlands. These descriptions are based on observations in the natural habitats and on data found in the literature. For the discussion of the floristic composition of these communities use has been made of survey records; the *Enteromorphetum prolifero-intestinalis*, an association confined to brackish water, is the only one of which no such records were available. Some related communities that were found on the coast of "le Boulonnais" and on Heligoland, are briefly described, but of these communities, too, no records are given.

The communities were divided over 8 formations; the number of associations that could be distinguished is 22, most of which are here recorded for the first time for the Netherlands. Further 3 sociations are described and 4 communities of which the position remains uncertain.

GENERAL SUMMARY

This work contains a survey of the epilithic algal vegetations found on the coast of the Netherlands. The substrates on which these vegetations occur, are of recent origin; they all owe their existence to human activity (reinforced dikes, breakwaters, harbour works).

The coast is divided in three geographical districts, viz. the "Waddenzee" district, the beach district, and the deltaic district. The latter is split in an euhaline Scaldian subdistrict and a polyhaline estuarian subdistrict. The algal vegetation of the nearest natural rock coasts, viz. that of Heligoland and that of "le Boulonnais" in the English Channel are taken into consideration for comparison.

In a following chapter the influence of the main factors operating in the environment is sketched. Then the delimitation of the supralittoral, the eulittoral and the sublittoral regions as well as the concepts basic and standard zonation are discussed.

After that the communities are defined on account of their floristic composition, and combined into formations on account of the life form of their main constituents and their stratification. The formations themselves are classified according to their physiognomy and stratification and to the position they occupy in the zonation as well as in the succession. On the base of these criteria two systems of classification are possible, viz. one in which the community is regarded as consisting of several layers and in which emphasis is laid on the life form of the main consituents of the principal layer, and one in which the various layers are regarded as independent communities (socions). However, in this work the classification is not based on the socions, but on communities of the first-mentioned category.

In the last chapter the various vegetation units are described by the aid of records containing qualitative as well as quantitative data. This enables us to compare them with vegetations occurring on other coasts. Most of the associations had not yet been recorded from the Netherlands.

The study of the various species also led to the recognition of a new family of the Cladophorales, viz. the *Codiolaceae.* For two species so far included in *Urospora* the new combinations *Codiolum hartzii* (Rosenv.) and *C. wormskoldii* (Mert.) are made.

At the end of each of the five chapters a partial summary is given.

REFERENCES

Abbayes, H. des, 1934. La végétation lichenique du Massif armoricain. Étude chorologique et écologique. 267 p.

Aleem, A. A., 1950. A fungus in Ectocarpus granulosus C. Agardh near Plymouth. Nature. **165**: 119.

Aleem, A. A., 1950. Some new records of marine algae from the Mediterranean Sea. Medd. fr. Göteborgs Bot. Trädgård. **18**: 275—288.

Aleem, A. A., 1950. Some Cyanophyceae from the Eastern Mediterranean. Medd. fr. Göteborgs Bot. Trädgård. **18**: 303—307.

Aleem, A. A., 1951. Algues marines de profondeur des environs d'Alexandrie (Egypte). Bull. Soc. Bot. Fr. **98**: 249—252.

Aleem, A. A., 1953. Marine fungi from the West-Coast of Sweden. Ark. f. Bot. ser. 2, **3**: 1—33.

Aleem, A. A., 1955. Structure and evolution of the seagrass communities Posidonia and Cymodocea in the Southeastern Mediterranean. Essays in the Natural Sciences in honor of Captain Allan Hancock: 279—298.

Aleem, A. A. and E. Schulz, 1952. Über Zonierung von Algengemeinschaften. Ökologische Untersuchungen im Nord-Ostsee-Kanal I. Kieler Meeresforsch. **9**: 70—76.

Ambler, M. P. and V. J. Chapman, 1950. A quantitative study of some factors affecting tide pools. Trans. Roy. Soc. New Zeal. **78**: 394—409.

Anand, P. L., 1937. An ecological study of the algae of the British Chalk-Cliffs. Journ. Ecol. **25**: 153—188, 344—367.

Arwidsson, Th., 1937. Meeresalgen aus Vestagder und Rogaland. Nytt Mag. f. Naturvid. **76**: 85—149.

Barkman, J. J., 1950. Wierzonering in het littoraal. Vakbl. v. Biol. **30**: 1—14.

Barkman, J. J., 1955. On the distribution and ecology of Littorina obtusata (L.) and its subspecific units. Arch. Néerl. Zool. **11**: 22—86.

Baster, J., 1765. Van de zee-rui of strandwier. Natuurkundige uitspanningen, behelzende eenige waarneemingen, over sommige Zeeplanten en Zee-insecten, benevens derzelver zaadhuisjes en eijernesten. 2^3: 129—141.

Batters, E. A. L., 1902. A catalogue of the British marine algae. Journ. of Bot. *suppl.*: 1—107.

Beauchamp, P. de, 1914. Les grèves de Roscoff. Étude sur la répartition des êtres dans la zone de marées. Paris.

Bennett, I. and E. C. Pope, 1953. Intertidal zonation of the exposed rocky shores of Victoria, together with a re-arrangement of the biogeographic provinces of temperate Australian shores. Austr. J. Mar. and Fresh water Res. **4**: 105—159.

Benthem Jutting, W. S. S. van, 1952. On Bankia fimbriatula Moll & Roch in driftwood washed ashore on the Dutch coast. Basteria. **16**: 37—39.

Berner, L., 1931. Contribution à l'étude sociologique des algues marines du Golfe de Marseille. Ann. Mus. Hist. nat. Marseille. **24**: 1—84.

Bishop, M. W. H., 1947. Establishment of an immigrant barnacle in British coastal waters. Nature. **159**: 501.

Bishop, M. W. H., 1954. Elminius modestus in France. Nature. **173**: 1145.

Blackler, H., 1954. Observations on the phenology of the reproductive organs of certain algae. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 130—132.

Bliding, C., 1933. Sexualität und Entwicklung bei Enteromorpha. Sv. Bot. Tidskr. **27**: 233—256.

Bliding, C., 1938. Studien über die Entwicklung und Systematik in Enteromorpha. I. Bot. Not. Lund: 83—90.

Bliding, C., 1939. idem II. Bot. Not. Lund: 134—144.

Bliding, C., 1944. Zur Systematik der schwedischen Enteromorphen. Bot. Not. Lund: 331—356.

BLIDING, C., 1948. Uber Enteromorpha intestinalis und compressa. Bot. Not. Lund: 123—136.

BLIDING, C., 1949. Enteromorpha kylinii, eine neue Art aus der schwedischen Westküste. K. Fys. Sällsk. Lund Förh. **18**^{14}: 1—6.

BLIDING, C., 1955. Enteromorpha intermedia, a new species from the coasts of Sweden, England and Wales. Bot. Not. Lund. **108**: 253—262.

BLIDING, C., 1957. Studies in Rhizoclonium. I. Life history of two species. Bot. Not. Lund. **110**: 271—275.

BLOKLANDER, A. E. M. H., 1949. Eiernesten van de Wulk als importeurs. Lev. Natuur. **52**: 14—17.

BLOKLANDER, A. E. M. H. and J. BROUWER, 1946. De natuurlijke adventieve Loricata, Gastropoda en Lamellibranchiata van het Nederlandsche strand. I. Basteria. **10**: 49—64.

BLOKLANDER, A. E. M. H. and J. BROUWER, 1947. idem. II. Basteria. **11**: 89—112.

BOALCH, G. T., 1957. Marine algal zonation and substratum in Beer Bay, Southeast Devon. Journ. Mar. Biol. Ass. **36**: 519—528.

BODDEKE, R., 1958. The genus Callithamnion Lyngb. in the Netherlands. Act. Bot. Neerl. **7**: 589—604.

BOREL, A., 1954. La répartition de Bifurcaria tuberculata Stackh. C-R, Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 58—60.

BØRGESEN, F., 1900. A contribution to the knowledge of the marine algal vegetation on the coast of the Danish West Indian islands. Bot. Tidsskr. **23**: 49—60.

BØRGESEN, F., 1903. The marine algae of the Shetlands. Journ. of Bot. **41**: 300—306.

BØRGESEN, F., 1903. Marine Algae. Bot. Faeröes. **2**: 339—532.

BØRGESEN, F., 1905. The Algae Vegetation of the Faeröese Coasts, with remarks on the phyto-geography. Bot. Faeröes. **2**: 683—834.

BØRGESEN, F., 1909. Fucus spiralis, Linné, or Fucus platycarpus Thuret, a question of nomenclature. Journ. Linn. Soc. Bot. **39**: 105—119.

BØRGESEN, F., 1911. The algal vegetation of the lagoons in the Danish West Indies. Biolog. Arbejder t. E. Warming: 41—46.

BØRGESEN, F., 1913. The marine algae of the Danish West Indies I. Chlorophyceae. Dansk Bot. Ark. **1**^{4}: 1—160.

BØRGESEN, F., 1914. Idem II. Phaeophyceae. Dansk. Bot. Ark. **2**^{2}: 1—68.

BØRGESEN, F., 1914. The species of Sargassum found along the coasts of the Danish West Indies with remarks upon the floating forms of the Sargasso Sea. Mindeskrift f. Jap. Steenstrup.: 1—20.

BØRGESEN, F., 1916—20. The marine algae of the Danish West Indies III. Rhodophyceae. Dansk Bot. Ark. **3**: 1—504.

BØRGESEN, F., 1925. Marine Algae from the Canary Islands. I. Chlorophyceae. Kgl. Danske Vid. Sellsk. Biol. **5**^{3}: 1—123.

BØRGESEN, F., 1926. Idem II. Phaenophyceae. Kgl. Danske Vid. Sellsk. Biol. **6**^{2}: 1—112.

BØRGESEN, F., 1927—30. Idem III. Rhodophyceae. Kgl. Danske Vid. Sellsk. Biol. **6**^{6}: 1—97; **8**^{1}: 1—97; **9**^{1}: 1—159.

BØRGESEN, F., 1928. On Rosenvingea stellata, a new Indian alga, and on an interesting littoral algal vegetation in which this species is a characteristic constituent. Dansk Bot. Ark. **5**^{2}: 1—11.

BØRGESEN, F., 1938. Sur une collection d'algues marines receuillis à une profondeur remarquable près des îles Canaries. Rev. Alg. **11**: 225—230.

BØRGESEN, F. and H. JONSSON, 1905. The distribution of the marine algae in the Arctic Sea and of the Northernmost part of the Atlantic. Bot. Faeröes **3**: 1—28.

BOSCH, R. B. VAN DEN, 1846. Enumeratio plantarum zeelandiae belgicae. Ned. Kruidk. Arch. **1**: 84—104.

BOSCH, R. B. VAN DEN, 1846. Bijdrage tot de Algologische Flora van Nederland. Ned. Kruidk. Arch. **1**: 280—291.

Bosch, R. B. van den, 1851. Tweede bijdrage tot de Algologische flora van Nederland. Ned. Kruidk. Arch. **2**: 202—227.

Bosch, R. B. van den, 1853. Algae. Prodr. Flor. Bat. **2**^{2}: 169—281.

Bouly de Lesdain, M., 1910. Recherches sur les lichens des environs de Dunkerque. 310 p.

Boye, P., 1895. Bidrag til kundskaben om algvegetationen ved norges vestkyst. Bergens Mus. Aarbok. **16**.

Boye-Petersen, J., 1928. The aerial algae of Iceland. Bot. Iceland. **2**: 328—447.

Braun-Blanquet, J., 1951. Pflanzensoziologie. 2e ed. Vienna.

Braun-Blanquet, J., 1951. Pflanzensoziologische Einheiten und ihre Klassifizierung. Vegetatio. **3**: 126—133.

Broek, A. N. Ch. ten and P. Kaas, 1939. Aantekeningen over het transport van zeemollusken door drijvende voorwerpen. Lev. Natuur. **44**: 147—158.

Burrows, E. M., 1954. The culture of Fucus hybrids in relation to problems of shore ecology. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 136—138.

Burrows, E. M., E. Conway, S. M. Lodge and H. T. Powell, 1954. The raising of intertidal algal zones on Fair Isle. Journ. Ecol. **42**: 283—288.

Burrows, E. M. and Sh. Lodge, 1951. Autecology and the species problem in Fucus. Journ. Mar. Biol. Ass. **30**: 161—176.

Carruthers, J. N., 1925. The water movements in the southern North Sea I. The surface drift. Min. Agric. and Fisheries. Fish. Invest. ser. 2, **8**.

Carruthers, J. N., 1925. The water movements in the neighbourhood of the English Channel — North Sea Junction. Drift Bottle Experiments. Journ. Mar. Biol. Ass. **13**: 665—669.

Cedergren, G. R., 1939. Aërofila Alger. Bot. Not. Lund: 97—111.

Chalon, J., 1905. Liste des algues marines observées jusqu'à ce jour entre l'embouchure de l'Escaut et la Corogne.

Chalon, J., 1909. Liste des algues marines qui ont été recoltées dans les environs de Roscoff. Bull. Soc. Roy. Bot. Belgique. **46**: 240—249.

Chalon, J., 1910. Additions à la florule algologique de Roscoff. Bull. Soc. Roy. Bot. Belgique. **46**: 377—380.

Chapman, V. J., 1942. Zonation of marine algae on the sea shore. Proc. Linn. Soc. Bot. **154**: 239—253.

Chapman, V. J., 1944. Methods of surveying Laminaria beds. Journ. Mar. Biol. Ass. **26**: 37—60.

Chapman, V. J., 1946. Marine Algal Ecology. Bot. Rev. **12**: 628—672.

Chapman, V. J., 1946. Algal zonation in the West Indies. Ecology. **27**: 91—93.

Chapman, V. J., 1950. The marine algal communities of Stanmore Bay. New Zealand Pacif. Sc. **4**: 63—68.

Chapman, V. J., 1957. Marine Algal Ecology. Bot. Rev. **23**: 320—350.

Chapman, V. J., 1957. The marine algae of New Zealand. Journ. Linn. Soc. Bot. **55**: 333—501.

Chapman, V. J. and C. B. Trevarthen, 1953. General schemes of classification in relation to marine coastal zonation. Journ. Ecol. **41**: 198—204.

Chemin, E., 1925. Le Fucus vasicole de la baie de Terrénès. Rev. Alg. **2**: 146—157.

Chemin, E., 1928. Multiplication végétative et dissémination chez quelques algues floridées. Trav. Stat. Biol. Roscoff **7**: 1—61.

Christensen, T., 1947. Om Griffithsia devoniensis Harv. Bot. Tidsskr. **48**: 163—172.

Christensen, T., 1952. Studies on the genus Vaucheria I. Bot. Tidsskr. **49**: 171—188.

Christensen, T., 1955. Some additions to the Danish flora of marine algae. Bot. Tidsskr. **52**: 158—162.

Christensen, T., 1956. Studies on the genus Vaucheria III. Bot. Not. Lund. **109**: 275—280.

Christensen, T., 1957. Chaetomorpha linum in the attached state. Bot. Tidsskr. **53**: 311—316.

COLES, J. W., 1958. Nematodes parasitic on seaweeds of the genera Ascophyllum and Fucus. Journ. Mar. Biol. Ass. **37**: 145—156.

COLLINS, F. S., 1903. The Ulvaceae of North America. Rhodora. **5**.

COLLINS, F. S., 1909. The green algae of North America. Tufts College Stud. **2**^{3}.

COLLINS, F. S., 1916. Notes from the Woods Hole Laboratory 1915 I. Prasiola stipitata Suhr. Rhodora. **18**.

COLMAN, J., 1933. The nature of the intertidal zonation of plants and animals. Journ. Mar. Biol. Ass. **18**: 435—476.

COLMAN, J., 1940. On the faunas inhabiting intertidal seaweeds. Journ. Mar. Biol. Ass. **24**: 129—183.

COLMAN, J., 1942. Some intertidal enigmas. Proc. Linn. Soc. Bot. **154**: 232—234.

COLMAN, J., 1953. The nature of intertidal zonation of plants and animals. Journ. Mar. Biol. Ass. **18**: 435—476.

CONWAY, E., 1954. The modification and raising of intertidal algal zones on exposed rocky coasts of the British isles, with special reference to the zonation of Fucaceae. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 133—134.

COOPER, L. H. N., 1958. Sea temperatures in Plymouth Sound. Journ. Mar. Biol. Ass. **37**: 1—3.

COTTON, A. D., 1911. On the growth of Ulva latissima L. in water polluted by sewage. Kew Bull.: 15—19.

COTTON, A. D., 1912. Clare Island Survey 15. Marine Algae. Proc. Roy. Irish Ac. **31**: 1—178.

CRANWELL, L. M. and L. B. MOORE, 1938. Intertidal communities of Poor Knight Islands. Trans. Proc. Roy. Soc. New Zealand. **67**: 375—407.

CRIBB, A. B., 1954. Macrocystis pyrifera (L.) Ag. in Tasmanian waters. Austr. Journ. Mar. and Freshwater Res. **5**: 1—34.

CRISP, D. J., 1958. The spread of Elminius modestus Darwin in north-west Europe. Journ. Mar. Biol. Ass. **37**: 483—520.

CRISP, D. J. and A. J. SOUTHWARD, 1958. The distribution of intertidal organisms along the coasts of the English Channel. Journ. Mar. Biol. Ass. **37**: 157—208.

DANGEARD, P., 1949. Les algues marines de la côte occidentale du Maroc. Le Botaniste. **34**: 89—189.

DANGEARD, P., 1951. Sur une espèce nouvelle d'Ulva de nos côtes atlantiques (U. olivacea n. sp.). Le Botaniste. **35**: 27—34.

DANGEARD, P., 1951. Les espèces de Fucus et leur variabilité. Le Botaniste. **35**: 245—255.

DANGEARD, P., 1952. Algues de la presqu'île du Cap Vert (Dakar) et de ses environs. Le Botaniste. **36**: 193—392.

DAVID, H. M., 1943. Studies in the autecology of Ascophyllum nodosum LeJol. Journ. Ecol. **31**: 178—198.

DAVY DE VIRVILLE, A., 1930. Existence d'une zone de végétation inédite sur le littoral du Massif armoricain: la zone à Caloplaca marina Weddell. C-R. Ac. Sc. **191**: 577—578.

DAVY DE VIRVILLE, A., 1930. Sur la répartition en zone du Rivularia bullata. C-R. Ac. Sc. **191**: 1021—1023.

DAVY DE VIRVILLE, A., 1932. Les zones de Lichens sur le littoral atlantique. Bull. Mayenne-Sc. 1931—32: 35—66.

DAVY DE VIRVILLE, A., 1933. Contribution à l'étude de la répartition des zones de lichens sur le littoral du Portugal. C-R. Ac. Sc. **136**: 1921—1922.

DAVY DE VIRVILLE, A., 1934—35. Recherches écologiques sur la flora des flaques du littoral de l'Océan Atlantique et de la Manche. Rev. gén. Bot. **46**: 705—721; **47**: 26—43, 96—114, 160—177, 230—243, 308—323.

DAVY DE VIRVILLE, A., 1938. Étude de la répartition des zones de lichens le long du littoral portugais. C-R. Soc. Biogéogr. **15**: 21—23.

Davy de Viriville, A., 1938. Les zones de lichens sur les côtes du Portugal. Boll. Soc. Broteriana. ser. 2, **13**: 123—176.

Davy de Virville, A., 1939. Contributions a l'étude des zones de végétation sur le littoral atlantique. C-R.. Soc. Biogeogr. **16**: 29—33.

Davy de Virville, A., 1940. Les zones de végétation sur le littoral atlantique. Mém. Soc. Biogéogr. **7**: 205—251.

Davy de Virville, A., 1954. Sur un project de cartographie des algues marines des côtes de France. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 142—144.

Davy de Virville, A. and E. Fischer-piette, 1931. La zone du Caloplaca marina. Rev. gén. Bot. **43**: 337—360.

Dawson, E. Y., 1944. The marine algae of the Gulf of California. Allan Hancock Pacific Exped. **3**: 189—454.

Dawson, E. Y., 1946. A guide to the literature and distribution of the marine algae of the Pacific Coast of North America. Mem. South Californ. Acad. Sc. **3**.

Dawson, E. Y., 1954. Marine plants in the vicinity of the Institut Océanographique de Nha Trang, Viêt Nam. Pacific Sc. **8**: 373—469.

Debray, F., 1899. Florule des algues marines du Nord de la France. Bull. Sc. Fr. et Belg. **32**: 1—193.

Delf, E. M., 1942. The significance of the exposure factor in relation to zonation. Proc. Linn. Soc. Bot. **154**: 234—239.

Dellow, V., 1955. Marine algal ecology of the Hauraki Gulf, New Zealand. Trans. Roy. Soc. New Zealand. **83**: 1—91.

Diannelides, T., 1954. Aperçu sur la flore marine de la Grece. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 146—148.

Dizerbo, A., 1940. Une nouvelle station de Fucus lutarius Kütz. sur les côtes de France, dans l'estuaire de l'Aulne. Bull. Lab. Mar. Dinard. **22**: 44—46.

Dizerbo, A., 1947. La répartition et la zone de végétation dans le Massif armoricain d'Alaria esculenta (L.) Grev. Bull. Soc. Sc. Bretagne. **22**: 113—117.

Dizerbo, A., 1950. La végétation des algues marine de l'Aulne (Finistère). Bull. Soc. Sc. Bretagne. **25**: 85—92.

Dizerbo, A., 1950. Les algues de la vallée marine de l'Odet (Finistère) et leur répartition. Bull. Soc. Sc. Bretagne. **25**: 93—98.

Dizerbo, A., 1952. Quelques aspects de la végétation marine d'Ouessant. Bull. Soc. Sc. nat. Ouest France. ser. 6, **2**: 3—5.

Dizerbo, A., 1952. Nouvelles stations de Fucus vasicoles du Massif armoricain. Bull. Soc. Sc. Bretagne. **27**: 74—76.

Dizerbo, A., 1953. La végétation d'un couloir rocheux dans les falaises du Portzic en Crozon (Finistère). Bull. Soc. Sc. Bretagne. **28**: 83—93.

Dizerbo, A., 1954. Les Fucus vasicoles dans le Massif armoricain. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 213—214.

Dizerbo, A., 1954. La flore algologique de Vila Nova de Milfontes (Baixa Alentejo, Portugal). Portug. Act. Biol. (B). **4**: 324—330.

Doing Kraft, H., 1956. De tegenwoordige opvattingen omtrent het associatiebegrip en de systematiek van plantengemeenschappen volgens de methode van Braun-Blanquet. Vakbl. v. Biol. **36**: 1—13.

Doty, M. S., 1946. Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast. Ecology. **27**: 315—328.

Doty, M. S., 1947. The marine algae of Oregon 1. Chlorophyta and Phaeophyta. Farlowia. **3**: 1—67.

Doty, M. S. and J. Archer, 1950. An experimental test of the tide factor hypothesis. Amer. Journn. Bot. **37**: 458.

Drew, K. M., 1928. A revision of the genera Chantransia, Rhodochorton and Acrochaetium. Univ. California Publ. Bot. **14**: 139—224.

DREW, K. M., 1949. In situ Development of carpospores of Bonnemaisonia asparagoides. Nature. **163**: 253.

DREW, K. M., 1949. Conchocelis-Phase in the Life-history of Porphyra umbilicalis (L.) Kütz. Nature. **164**: 748—749.

DREW, K. M., 1952. Studies in the Bangioideae 1. Observations on Bangia fuscopurea (Dillw.) Lyngb. in culture. Phytomorphology. **2**: 38—51.

DREW, K. M., 1954. Studies in the Bangioideae III. The life-history of Porphyra umbilicalis (L.) Kütz. var. laciniata (Lightf.) J. Ag. A. The Conchocelis-phase in culture. Ann. Bot. **18**: 183—211.

DREW, K. M., 1954. Life-histories in the algae. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 50—57.

DREW, K. M., 1954. The organization and interrelationships of the carposporophytes of living Florideae. Phytomorphology. **4**: 55—69.

DREW, K. M., 1955. Life histories in the algae, with special reference to the Chlorophyta, Phaeophyta and Rhodophyta. Biol. Rev. **30**: 343—390.

DREW, K. M., 1956. Conferva ceramicola Lyngb. Bot. Tidsskr. **53**: 67—74.

DREW, K. M., 1958. The typification of Polyides and Furcellaria. Journ. Linn. Soc. Bot. **55**: 744—752.

DREW, K. M. and K. S. RICHARDS, 1953. Studies in the Bangioideae II. The Conchocelis-phase of Porphyra sp. in Polliceps cornucopia Leach at Roscoff. Journ. Linn. Soc. Bot. **55**: 84—87.

DROUET, F. and W. A. DAILY, 1948. Nomenclatural transfer among coccoid algae. Lloydia. **11**: 77—79.

DROUET, F. and W. A. DAILY, 1956. Revision of the coccoid Myxophyceae. Butler Univ. Stud. **12**.

EKMAN, S., 1932. Die biologische Geschichte der Nord- und Ostsee. Tierwelt Nord- und Ostsee. **1 b**: 1—40.

ENGEL, H., S. J. GEERTS and C. O. VAN REGTEREN ALTENA, 1940. Alderia modesta (Lovén) and Limapontia depressa Alder & Hancock in the brackish waters of the Dutch coast. Basteria. **5**: 6—34.

ERCEGOVIĆ, A., 1954. Sur quelques traits caractéristiques de la flore benthique de l'Adriatique. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 145—146.

ERNST, J., 1955. Sur la végétation de la Manche d'après des observations en scaphandre autonome. C-R. Ac. Sc. **241**: 1066—1068.

EVANS, R. G., 1947. The intertidal ecology of selected localities in the Plymouth neighbourhood. Journ. Mar. Biol. Assoc. **27**: 173—218.

EVANS, R. G., 1949. The intertidal ecology of rocky shores in South Pembrokeshire. Journ. Ecol. **37**: 120—139.

EVANS, R. G., 1953. Studies on the biology of British limpets. The genus Patella on the south coast of England. Proc. Zool. Soc. Lond. **123**: 357—376.

EVANS, R. G., 1957. The intertidal ecology of some localities on the Atlantic coast of France. Journ. Ecol. **45**: 245—272.

FABER, F. J., 1947—48. Geologie van Nederland. **1-2**. Algemeene Geologie, Historische Geographie, 3e ed. **3**. Nederlandse Landschappen, 2e ed.

FAEGRI, K., 1938. Trekk av Lichina-artenes utbredelse i Norden. Nytt Mag. Naturvid. **78**: 141—151.

FAEGRI, K. and E. MOSS, 1952. On the occurrence of the genus Codium along the Scandinavian coasts. Blyttia. **10**: 108—113.

FARLOW, G. W., 1881. The Marine algae of New England. Rep. U.S. Comm. Fish and Fisheries 1879. *Appendix* **A-1**: 1—210.

FELDMANN, G., 1956. Développement d'une Plasmodiophorale marine: Plasmodiophora bicaudata J. Feldm., parasite du Zostera nana Roth. Rev. gén. Bot. **63**: 390—420.

FELDMANN, G. and J. FELDMANN, 1954. Sur l'origine des Floridées parasites. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 110—112.

Feldmann, J., 1937—1942. Les algues marines de la côte des Albères. I—III. Cyanophycées, Chlorophycées, Phéophycées. Rev. Alg. **9**: 141—335, IV. Rhodophycées. Rev. Alg. **11**: 247—330; Rev. Alg. **12**: 77—100; Trav. Alg. **1**: 29—113.

Feldmann, J., 1938. Recherches sur la végétation marine de la Méditerranée. La côte des Albères. Rev. Alg. **10**: 1—339.

Feldmann, J., 1950. Sur l'existence d'une alternance de générations entre l'Halicystis parvula Schmitz et le Derbesia tenuissima (De Not.) Crouan. C-R. Ac. Sc. **230**: 292—295.

Feldmann, J., 1951. Ecology of marine algae, in G. M. Smith: Manual of Phycology - an Introduction to the Algae and their Biology: 313—334.

Feldmann, J., 1954. Inventaire de la flore marine de Roscoff. Trav. Stat. Biol. *suppl.* **6**: 1—152.

Feldmann, J., Sur la classification des Chlorophycées siphonées. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 96—97.

Feldmann, J., 1955. La zonation des algues sur la côte atlantique du Maroc. Bull. Soc. Sc. Nat. Phys. du Maroc. **35**: 9—17.

Feldmann, J. and A. Davy de Virville, 1933. Les conditions physiques de la végétation des flaques littorales de la côte des Alberès. Rev. gén. Bot. **45**: 621—655.

Feldmann, J. and G. Feldmann, 1941. Un nouveau type d'alternance de générations chez les Rhodophycées; les Bonnemaisoniacées. Chron. Botan. **6**: 313—314.

Feldmann, J. and G. Feldmann, 1942. Recherches sur les Bonnemaisoniacées et leur alternance de générations. Ann. Sc. Nat. Bot. ser. 2, **3**: 75—115.

Feldmann, J. and G. Feldmann, 1946. A propos d'un travail récent du Prof. H. Kylin sur l'alternance de générations du Bonnemaisonia asparagoides. Bull. Soc. Hist. Nat. de l'Afr. du Nord. **37**: 35—38.

Feldmann, J. and G. Feldmann, 1952. Nouvelles recherches sur le cycle des Bonnemaisoniacées; le développement des tétraspores du Falkenbergia rufolanosa (Harv.) Schmitz. Rev. Gén. Bot. **59**: 313—323.

Feldmann, J. and G. Feldmann, 1956. Observations sur quelques Phycomycètes marins nouveaux ou peu connus. Rev. Mycologie. **20**: 231—251.

Feldmann, J. and G. Hamel, 1934. Observations sur quelques Gélidiacées. Rev. gén. Bot. **46**: 528—549.

Feldmann, J. and G. Mazoyer, 1937. Sur l'identité de l'Hymenoclonium serpens (Crouan) Batters avec le protonéma du Bonnemaisonia asparagoides (Woodw.) C. Ag. C-R. Ac. Sc. **205**: 1085—1086.

Feldmann-Mazoyer, G., 1940. Recherches sur les Céramiacées de la Méditerranée occidentale: 1—510.

Fischer-Piette, E., 1932. Répartition des principales espèces fixées sur les rochers battus des côtes et des îles de la Manche, de Lannion a Fécamp. Ann. Int. Océan. **22**.

Fischer-Piette, E., 1936. Études sur la biogéographie intercotidale des deux rives de la Manche. Journ. Linn. Soc. Zool. **40**: 181—272.

Fischer-Piette, E., 1955. Répartition, le long des côtes septentrionales de l'Espagne, des principals espèces peuplant les rochers intercotidaux. Ann. Inst. Océan. **31**.

Foslie, M., 1890. Contribution to knowledge of the marine algae of Norway 1. East Finmarken. Tromsø Mus. Aarsh. **13**.

Foslie, M., 1893. Algological Notices. Kgl. Norske Vidensk. Selsk. Skrifter 1891: 263—266.

Foslie, M., 1893. List of the Marine Algae of the Isle of Wight. Kgl. Norske Vidensk. Selsk. Skrifter 1891: 267—282.

Foslie, M., 1894. The Norwegian Forms of Ceramium. Kgl. Norske Vidensk. Selsk. Skrifter 1893: 1—21.

FOSLIE, M., 1894. New or critical Norwegian Algae. Kgl. Norske Vidensk. Selsk. Skrifter 1893: 114—144.

FÖYN, B., 1955. Specific differences between Northern and Southern European populations of the green alga Ulva lactuca L. Pubbl. Staz. Zool. Napoli. **27**: 261—270.

FRITSCH, F. E., 1952. The structure and reproduction of the algae. Univ. Press. Cambridge. 2e ed. 2 parts.

FRITSCH, F. E., 1954. Problems in the classification of the green algae. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 83—89.

FUNK, G., 1927. Die Algenvegetation des Golfs von Neapel nach neueren ökologischen Untersuchungen. Pubbl. Staz. Zool. Napoli. *suppl.* **7**: 1—507.

GARDNER, N. L., 1922. The genus Fucus on the Pacific Coast of North America. 180 p.

GIBB, D. C., 1950. A survey of the commoner Fucoid algae on Scottish shores. Journ. Ecol. **38**: 253—269.

GIBB, D. C., 1957. The free-living forms of Ascophyllum nodosum (L.) LeJol. Journ. Ecol. **45**: 49—84.

GISLÉN, T. 1930. Epibioses of Gullmar Fjord. II. Kristineberg's Zool. Stat. **4**: 1—380.

GOOR, A. C. J. van, 1919. Het zeegras (Zostera marina L.) en zijn beteekenis voor het leven der visschen. Rapp. en Verh. Rijksinst. Visserijonderz. **1**: 415—498.

GOOR, A. C. J. van, 1920. Naamlijst der Wieren, aanwezig in het Herbarium van het Zoölogisch Station Helder, 2e ed.: 1—19.

GOOR, A. C. J. van, 1921. Die Zostera-Assoziation des holländischen Wattenmeeres. Rec. Trav. Bot. Néerl. **18**: 103—123.

GOOR, A. C. J. van, 1922. Algenflora, in: Flora en Fauna der Zuiderzee: 54—91.

GOOR, A. C. J. van, 1923. Die Holländischen Meeresalgen. Verh. Kon. Ak. Wetensch. Amsterdam. sect. 2, **23**: 1—232.

GOOR, A. C. J. van, 1923. Les algues marines de la Hollande. Bull. Soc. Bot. Fr. **70**: 629—636.

GRAN, H. H., 1893. Algevegetationen i Tønsbergfjorden. Vidensk. Selsk. Forh. Kristiania. **2**.

GRENAGER, B., 1957. Algological observations from the polluted area of the Oslofjord. Nytt Mag. f. Bot. **5**: 41—60.

GROEN, P., 1951. De wateren der wereldzee. Amsterdam. 1—375.

GRUB, V. M., 1924. Observations on the Ecology and reproduction of Porphyra umbilicalis (L.) J. Ag. Rev. Alg. **1**: 223—234.

GUILER, E. R., 1949. The intertidal ecology of Tasmania. Pap. Proc. Roy. Soc. Tasmania. **84**: 135—201.

GUILER, E. R., 1953. Intertidal Classification in Tasmania. Journ. Ecol. **41**: 381—384.

GUILER, E. R., 1955. Australian intertidal beltforming species in Tasmania. Journ. Ecol. **43**: 138—148.

HAMEL, A. and G. HAMEL, 1929. Sur l'héterogamie d'une Cladophoracée, Lola (nov. gen.) lubrica Setch. et Gardn. C-R. Ac. Sc. **189**: 1094.

HAMEL, G., 1924. Sur l'apparition d'une algue nouvelle sur les côtes de Bretagne et de Normandie. Rev. Alg. **1**: 50—52.

HAMEL, G., 1924-28. Quelques Cladophora des côtes françaises. Rev. Alg. **1**: 168—174, 293—297, 458—461; **2**: 68—71; **4**: 43—76.

HAMEL, G., 1924-30. Floridées de France I-VI. Rev. Alg. **1**: 278—292, 427—457; **2**: 39—67, 280—309; **3**: 99—158; **5**: 61—109.

HAMEL, G., 1926. Sur les genres Acrochaetium Naeg. et Rhodochorton Naeg. Rev. Alg. **3**: 159—210.

HAMEL, G., 1929. Les Algues de Vigo. Rev. Alg. **4**: 81—95.

HAMEL, G., 1930-31. Chlorophycées des côtes françaises. Rev. Alg. **5**: 1—54, 383—430; **6**: 9—73.

HAMEL, G., 1931-39. Phéophycées de France: 47 p. + 1—432.

HAMEL, G., 1939. Sur la classification des Ectocarpales. Bot. Not. Lund: 65—70.

HAMEL, G., 1940. Les ceintures de chlorophycées de la côte basque française. Rev. gén. Bot. **52**: 433.

HAMEL, G., 1942. Sur les chlorophycées de la côte basque française et leur répartition en ceintures. Blumea. **3**, *suppl.* **2**: 41—51.

HAMEL, G. and J. FELDMANN, 1928. La répartition géographique des Fucacées et des Laminaires sur les côtes occidentales de la peninsula ibérique. C-R. Ac. Sc. **187**: 1162—1163.

HAMEL, G. and J. FELDMANN, 1936. Floridées de France VII. Rev. Alg. **9**: 85—140.

HAMEL, G. and R. LAMI, 1930. Liste préliminaire des algues récoltées dans la région de St. Servan. Bull. Lab. St. Servan. **6**: 1—34.

HAMEL, G. and P. LEMOINE, 1953. Corallinacées de France et d'Afrique du Nord. Arch. Mus. Nat. d'Hist. nat. ser. 7, **1**.

HANSTEEN, B., 1892. Algeregioner og Algeformationer ved den norske Vestkyst. Nyt Mag. Naturv. Kristiania. **32**.

HARDER, R., 1918. Einordnung von Trailliella intricata in der Generationswechsel der Bonnemaisoniaceae. Nachr. Akad. Wiss. Göttingen. Math. Phys. Kl.-Biol.-Physiol. Chem. Abt.: 24—27.

HARDER, R. and W. KOCH, 1949. Life-history of Bonnemaisonia hamifera (Trailiella intricata). Nature. **163**: 106.

HARDING, J. P., 1954. The copepod Thelastris rhodymeniae (Brady) and its nauplius, parasitic in the seaweed Rhodymenia palmata (L.) Grev. Proc. Zool. Soc. London. **124**: 153—161.

HARTOG, C. den, 1953. Immigration, dissemination and ecology of Elminius modestus Darwin in the North Sea, especially along the Dutch coast. Beaufortia. **4**: 9—20.

HARTOG, C. den, 1953. Porphyra leucosticta along the Dutch coast. Act. Bot. Neerl. **2**: 308—315.

HARTOG, C. den, 1954. New Dutch Marine Algae 1. Act. Bot. Neerl. **3**: 412—416.

HARTOG, C. den, 1955. L'association à Monostroma wittrockii et Porphyra leucosticta dans le port de Nice. Rev. Alg. ser. 2, **1**: 167—168.

HARTOG, C. den, 1955. A classification system for the epilithic algal communities of the Netherlands' coast. Acta Bot. Neerl. **4**: 126—135.

HARTOG, C. DEN, 1955. Roodwieren van de kwelders van Terschelling. Lev. Natuur. **58**: 169—173.

HARTOG, C. DEN, 1956. De verspreiding van Bostrychia scorpioides in Nederland. Natura. **53**: 71—73.

HARTOG, C. DEN, 1956. Speculations on the immigration of the barnacle Elminius modestus in France. Beaufortia. **5**: 141—142.

HARTOG, C. DEN, 1956. Algen van Tholen. Zeepaard. **16**: 59—63.

HARTOG, C. DEN, 1958. De vegetatie van het Balgzand en de oeverterreinen van het Balgkanaal. Wetensch. Med. K.N.N.V. **27**: 1—28.

HARTOG, C. DEN, 1958. Epilithische Algengemeenschappen in Nederland. Hand. Hydrobiol. Ver. **10**: 6—8.

HARTOG, C. DEN, 1958. Nieuwe gegevens over de kwelderroodwieren van Terschelling. Lev. Natuur. **61**: 231—235.

HARTOG, C. DEN, 1959. Distribution and Ecology of the slugs Alderia modesta and Limapontia depressa in the Netherlands. Beaufortia. **7**: 15—36.

HARTOG, C. DEN, and J. A. W. LUCAS, 1958. Natuurlijke adventieven van het Nederlandse Strand. Natura. **55**: 118—119.

HARTOG, C. DEN, and A. S. TULP, 1953. Notities betreffende het litoraal van Ameland. Zeepaard. **13**: 59—64.

HARVEY, W. H., 1846—51. Phycologia brittannica. **1-4**.

HATTON, H., 1938. Essais de bionomie explicative sur quelques espèces intercotidales d'algues et d'animaux. Ann. Inst. Océan. **17**: 241—348.

HAUCK, F., 1885. Die Meeresalgen Deutschlands und Österreichs. Rabenhorts Kryptogamenflora. **2** (2e ed.).

HAYRÉN, E., 1910. Über den Saprophytismus einiger Enteromorpha-Formen. Medd. Soc. Fauna. Flor. Fenn. **36**.

HAYRÉN, E., 1914. Über die Landvegetation und Flora der Meeresfelsen von Tvarminne. Acta Soc. Fauna Flora Fenn. **39**.

HEPPER, B. T., 1957. Notes on Mytilus galloprovincialis Lamarck in Britain. Journ. Mar. Biol. Ass. **36**: 33—40.

HESSE, R., 1924. Tiergeographie auf ökologischer Grundlage.

HOCKE HOOGENBOOM, K. J., 1937. Wierenbegroeiing van de IJsselmeerkusten 1932 tot (Juni) 1935. Ned. Kruidk. Arch. **47**: 280—334.

HOEK, C. VAN DEN, 1958. Zeewieren van Voorne, waaronder Symphoricoccus stellaris (Areschoug) Kuckuck, nieuw voor de Nederlandse kust. Zeepaard. **18**: 3—11.

HOEK, C. VAN DEN, 1958. Observations on the algal vegetation of the Northern Pier at Hoek van Holland, made from October 1953 till August 1954. Blumea. **9**: 187—205.

HOEK, C. VAN DEN, 1958. The Algal Microvegetation in and on barnacle shells, collected along the Dutch and French coasts. Blumea. **9**: 206—214.

HOFFMANN, C., 1928. Über eine in der Kieler Föhrde neu aufgetretene Rotalge: Porphyra atropurpurea (Olivi) de Toni. Wiss. Meeresunt. N. F. Abt. Kiel. **21**: 1—9.

HOFFMANN, C., 1933. Die Vegetation der Nord- und Ostsee, in GRIMPE-WAGLER: Tierwelt der Nord- und Ostsee. **1 c**: 1—32.

HOFFMANN, C., 1950. Über das Vorkommen endemischer Algen in der Ostsee. Kieler Meeresforsch. **7**: 24—34.

HOFFMANN, C., 1953. Neufunde von Benthosalgen in der Kieler Bucht. Kieler Meeresforsch. **9**: 228—230.

HOLTHUIS, L. B., 1949. The Isopoda and Tanaïdacea of the Netherlands, including the description of a new species of Limnoria. Zoöl. Meded. **30**: 163—190.

HOLTHUIS, L. B., 1952. Enige interessante, met drijvende voorwerpen op de Nederlandse kust aangespoelde zeepissebedden en zeepokken. Lev. Natuur. **55**: 72—77.

HOLTHUIS, L. B., 1956. Isopoda en Tanaidacea. Fauna van Nederland. **16**: 1—280.

IRVINE, D. E. G., 1956. Notes on British species of the genus Sphacelaria Lyngb. Trans. Proc. Bot. Soc. Edinb. **37**: 24—45.

ISAAC, W. E., 1951. Observations on the ecology of Bifurcaria brassicaeformis. Journ. Ecol. **39**: 94—105.

ISAAC, W. E., 1957. The distribution, ecology and taxonomy of Porphyra on the South African Coast. Proc. Linn. Soc. London. **168**: 61—64.

JAASUND, E., 1951. Marine Algae from northern Norway I. Bot. Not. Lund: 28—142.

JAASUND, E., 1957. Idem II. Bot. Not. Lund. **110**: 205—231.

JOHNSON, D. S. and A. F. SKUTCH, 1928. Littoral Vegetation on a headland of Mt. Desert Island, Maine. Ecology. **9**: 188—215, 307—338.

JOLIS, A. LE, 1864. Liste des algues marines de Cherbourg. Mém. Soc. imp. Sci. Nat. Cherbourg. **10**.

JONSSON, H., 1902—1903. The marine algae of Iceland. Bot. Tidsskr. **24**: 127—201; **25**: 141—195, 337—385.

JONSSON, H., 1904. The marine algae of East Greenland. Medd. Grønland. **30**.

JONSSON, H., 1912. The Marine algal vegetation of Iceland. Bot. Iceland. **1**: 1—186.

JORDE, I., 1933. Untersuchungen über den Lebenszyklus von Urospora Aresch. und Codiolum A. Braun. Nytt Mag. Naturvid. **73**: 1—19.

Katadi, M. and T. Matsui, 1953. Studies on the repopulation of the tidal vegetation I. Bull. Soc. Plant Ecol. **3**: 17—23.

Kitching, J. A., 1937. Studies in sublittoral ecology II. Recolonisation at the upper margin of the sublittoral region; with a note on the denudation of Laminaria-forests by storms. Journ. Ecol. **25**: 482—495.

Kjellman, F. R., 1875—77. Om Spetzbergens marina klorophyllfoerande thallophyter. Bih. Kgl. Svenska vet. akad. Handl. **3**^{7}, **4**^{6}.

Kjellman, F. R., 1877. Über die Algenvegetation des Murmanschen Meeres an der Küste Nowaja Semlja und Waigatsch. Nova Acta Reg. Soc. Upsal. **3**.

Kjellman, F. R., 1878. Über Algenregionen und Algenformationen im östlichen Skagerrak. Bih. Kgl. Svenska vet. akad. Handl. **5**^{6}: 1—35.

Kjellman, F. R., 1883. The Algae of the Arctic Sea. Kgl. Svenska vet. akad. Handl. **20**^{5}.

Kjellman, F. R., 1893. Studier öfver Chlorophycéslägtet Acrosiphonia J. Ag. och dess Skandinaviska arter. Bih. Kgl. Svenska vet. akad. Handl. **18**^{3}: 1—114.

Knebel, G., 1936. Monographie der Algenreihe der Prasiolales, insbesondere von Prasiola crispa. Hedwigia. **75**: 1—120.

Kniep, H., 1925. Über Fucusbastarde. Flora **118**: 331—338.

Kniep, H., 1928. Die Sexualität der niederen Pflanzen: 1—554.

Knight, M. and M. Parke, 1931. Manx Algae, an algal survey of the south end of the Isle of Man. Liverpool Mar. Biol. Comm. Mem. **30**: 1—155.

Knight, M. and M. Parke, 1950. A biological study of Fucus vesiculosus L. and F. serratus L. Journ. Mar. Biol. Ass. **29**: 439—514.

Koch, W., 1950. Entwicklungsgeschichtliche und physiologische Untersuchungen an Laboratoriumkulturen der Rotalge Trailliella intricata Batters (Bonnemaisoniaceae). Archiv f. Mikrobiol. **14**: 635—660.

Kornaś, J., 1957. Roślinność denna Polskiego Baltyku. Stan badań i postulaty ich przyszlego rozwoju. Wiadomości Bot. **1**: 187—201.

Kornaś, J. and A. Medwecka-Kornaś, 1948. Podwodne zespoty roślinne zatoki Gdańskiej. Les associations végétales sous-marines dans le Golfe du Gdańsk (Baltique polonaise) Bull. Ac. Polon. Sc. et Lettres. **1**: 71—88.

Kornaś, J. and A. Medwecka-Kornaś, 1950. Associations végétales sous-marines dans le Golfe de Gdańsk. Vegetatio. **2**: 120—127.

Kornmann, P., 1938. Zur Entwicklungsgeschichte von Derbesia und Halicystis. Planta. **28**: 464—470.

Kornmann, P., 1952. Die Algenvegetation von List auf Sylt. Helg. Wiss. Meeresunt. **4**: 55—61.

Kornmann, P., 1953. Die Formenkreis von Acinetospora crinita (Carm.) nov.comb. Helg. Wiss. Meeresunt. **4**: 205—224.

Kornmann, P., 1954. Giffordia fuscata (Zan.) Kuck. nov. comb., eine Ectocarpacee mit heteromorphen, homophasischen Generationen. Helg. Wiss. Meeresunt. **5**: 41—52.

Kornmann, P., 1956. Zur Morphologie und Entwicklung von Percursaria percursa. Helg. Wiss. Meeresunt. **5**: 261—272.

Kornmann, P., 1956. Über die Entwicklung einer Ectocarpus confervoides-Form. Pubbl. Staz. Zool. Napoli. **28**: 32—43.

Kornmann, P., 1957. Artspezifische Entwicklungsgänge in der Gattung Ectocarpus. Helg. Wiss. Meeresunt. **6**: 84—99.

Korringa, P., 1940. Experiments and observations on swarming, pelagic life and setting of the European flat Oyster, Ostrea edulis L. Thesis: 1—249.

Korringa, P., 1942. Crepidula fornicata's invasion in Europe. Basteria. **7**: 12—23.

Korringa, P., 1951. The shell of Ostrea edulis as a habitat. Arch. Néerl. Zool. **10**: 32—152.

Koster, J. Th., 1936. Algae van Ameland. Ned. Kruidk. Arch. **46**: 354—355.

KOSTER, J. TH., 1937. Bijdrage tot de Algenflora van Terschelling. Ned. Kruidk. Arch. **47**: 264—265.

KOSTER, J. TH., 1939. A review of the taxonomical and ecological studies on Netherlands' Algae. Rec. Trav. Bot. Néerl. **36**: 494—501.

KOSTER, J. TH., 1941. Quelques observations sur les Bryopsis du Golfe de Naples. Blumea. **4**: 225—258.

KOSTER, J. TH., 1952. Rare or otherwise interesting marine Algae from the Netherlands. Act. Bot. Neerl. **1**: 201—215.

KOSTER, J. TH., 1954. Quelques aspects de la végétation d'algues marines de la Zélande (Pays Bas). Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 141—142.

KOSTER, J. TH., 1954. Sur la végétation d'algues marines de la Zélande. Blumea. **7**: 558—569.

KOSTER, J. TH., 1955. The genus Rhizoclonium Kütz. in the Netherlands. Pubbl. Staz. Zool. Napoli. **27**: 335—357.

KUCKUCK, P., 1896. Bemerkungen zur marinen Algenvegetation von Helgoland. II. Wiss. Meeresunt. N. F. Abt. Helgoland. **2**: 396—399.

KÜHL, H., 1954. Über das Auftreten von Elminius modestus Darwin in der Elbmündung. Helg. Wiss. Meeresunt. **5**: 53—56.

KÜHL, H. and H. MANN, 1953. Beiträge zur Hydrochemie der Unterelbe. Veröffentl. Inst. f. Meeresf. in Bremerhaven. **2**: 236—268.

KÜHL, H. and H. MANN, 1954. Über die Hydrochemie der unteren Ems. Veröffentl. Inst. f. Meeresf. in Bremerhaven. **3**: 126—158.

KUNIEDA, H., 1934. On the life-history of Monostroma. Proc. Imp. Acad. **10**: 103—106.

KÜTZING, F. T., 1843. Phycologia generalis.

KÜTZING, F. T., 1845. Phycologia germanica — Deutschlands Algen, 340 p.

KÜTZING, F. T., 1845—69. Tabulae phycologicae. **1-19**.

KYLIN, H., 1907. Studien über die Algenflora der schwedischen Westküste. 288 p.

KYLIN, H., 1910. Zur Kenntnis der Algenflora der norwegischen Westküste. Ark. f. Bot. **10**: 1—37.

KYLIN, H., 1917. Über die Kälteresistenz der Meeresalgen. Ber. Deutsch. Bot. Ges. **35**: 370—384.

KYLIN, H., 1918. Svenska västkustens alregioner. Svensk. Bot. Tidskr. **12**: 65—90.

KYLIN, H., 1935. Über einige kalkbohrende Chlorophyceen. Fysiogr. Sällsk. Lund Förhandl. **5**.

KYLIN, H., 1938. Über die Chlorophyceengattungen Entocladia, Epicladia und Ectochaete. Bot. Not. Lund: 67—76.

KYLIN, H., 1942. Zur Nomenklatur von Pylaiella litoralis und Pylaiella rupincola. Blumea. **3**, *suppl.* **2**: 64—71.

KYLIN, H., 1944. Die Rhodophyceen der schwedischen Westküste. Lunds Univ. Årsskr. **40**^{2}: 1—104.

KYLIN, H., 1946. Über den chemischen Aufbau der Zellwände bei Ulva und Enteromorpha. Kungl. Fysiogr. Sällsk. Lund Förhandl. **16**: 102—105.

KYLIN, H., 1947. Die Phaeophyceen der schwedischen Westküste. Lunds Univ. Årsskr. **43**^{4}: 1—99.

KYLIN, H., 1947. Über die Fortpflanzungsverhältnisse in der Ordnung Ulvales. Kungl. Fys. Sällsk. Lund Förh. **17**: 174—182.

KYLIN, H., 1949. Die Chlorophyceen der schwedischen Westküste. Lunds Univ. Årsskr. **45**^{4}: 1—79.

KYLIN, H., 1956. Die Gattungen der Rhodophyceen. Lund, 15+673 p.

LAKOWITZ, K., 1907. Die Algenflora der Danziger Bucht, Gdańsk.

LAKOWITZ, K., 1929. Die Algenflora der gesamten Ostsee, Gdańsk.

LAMI, R., 1930. Un essai de propagation de Fucus lutarius dans la Rance. Rev. Alg. **5**: 230—231.

LAMI, R., 1931. Le Fucus lutarius Ktz. dans ses stations françaises de la Manche occidentale. Trav. Crypt. vol. jub. L. Mangin: 363—372. Pl. 27—29.

LAMI, R., 1935. Stations nouvelles de quelques algues rares dans la Manche occidentale. Rev. Alg. **7**: 183—184.

LAMI, R., 1940. Sur les épiphytes hivernaux des stipes de Laminaires et sur deux Rhodochorton qui s'y observent dans la région de Dinard. Bull. Lab. Mar. Dinard. **22**: 46—60.

LAMI, R., 1940. Sur les conditions d'éclairement et d'hygrométrie nécessaires à quelques algues cavernicoles de la région malouine. Bull. Lab. Mar. Dinard. **22**: 61—68.

LAMI, R., 1943. Notules d'Algologie marine IX. Sur l'écologie et la répartition dans la Manche de Laminaria ochroleuca De la Pylaie. Bull. Lab. Mar. Dinard. **25**: 75—90. Pl. 1.

LAPICQUE, L., 1931. Sur Laminaria ochroleuca de la Pylaie (= L. lejolisii Sauvageau). Trav. Crypt. vol. jub. L. Mangin: 397—404.

LAWSON, G. W., 1954. Intertidal zonation in West Africa in relation to ocean currents. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 153—155.

LAWSON, G. W., 1956. Rocky Shore Zonation in the Gold Coast. Journ. Ecol. **44**: 153—170.

LAWSON, G. W., 1957. Seasonal variation of intertidal zonation on the coast of Ghana in relation to tidal factors. Journ. Ecol. **45**: 831—860.

LEVRING, T., 1935. Zur Kenntnis der Algenflora von Kullen an der schwedischen Westküste. Lunds Univ. Årsskr. **31**: 1—64.

LEVRING, T., 1937. Zur Kenntnis der Algenflora der norwegischen Westküste. Lunds Univ. Årsskr. **33**^{8}: 1—148.

LEVRING, T., 1940. Studien über die Algenvegetation von Blekinge, Südschweden. Thesis. Lund. 178 p.

LEVRING, T., 1950. Algological excursion to the Swedish west coast. 7th Int. Bot. Congr. Stockholm. 1950. Excursion guides. **A III a**: 1—8.

LEVRING, T., 1955. Some remarks on the structure of the gametes and the reproduction of Ulva lactuca. Bot. Not. Lund. **108**: 40—45.

LEVRING, T., 1956. Contribution to the marine algae of New Zealand I. Rhodophyta: Goniotrichales, Bangiales, Nemalionales and Bonnemaisoniales. Ark. f. Bot. ser. 2, **3**: 407—432.

LEWIS, E. A., 1935. An Investigation of the Seaweeds within a marked zone of the shore at Aberystwyth, during the year 1933—34. Journ. Mar. Biol. Ass. **20**: 615—620.

LEWIS, J. R., 1955. The mode of occurrence of the universal intertidal zones in Great-Britain. Journ. Ecol. **43**: 270—290.

LINDSTEDT, A., 1943. Die Flora der marinen Cyanophyceen der schwedischen Westküste. Thesis, Lund. 121 p. 10 Pl.

LINKE, O., 1939. Die Biota des Jadebusenwattes. Helg. Wiss. Meeresunt. **1**: 201—348.

LORENZ, J. R., 1863. Physikalische Verhältnisse und Vertheilung der Organismen im Quarnerischen Golfe. Vienna, 379 p.

LUCAS, J. A. W., 1950. The algae transported on drifting objects and washed ashore on the Netherlands' coast. Blumea. **6**: 527—543.

LUCAS, J. A. W., 1953. Ceramium diaphanum (Lightf.) Roth, its varieties and forms as found in the Netherlands. Act. Bot. Neerl. **2**: 316—326.

LUCAS, J. A. W., 1954. Het genus Patella in Nederland. Basteria. **18**: 36—40.

LUND, S., 1936. Die Algenvegetation in Stege Nor. Bot. Tidsskr. **42**: 17—39.

LUND, S., 1936. Nogle interessante Rødalgefund fra Københavns Havn. Bot. Tidsskr. **43**: 57—58.

LUND, S., 1940. On the genus Codium Stackh. in Danish waters. Kgl. Danske Vidensk. Selsk. Biol. Medd. **15**^{9}: 1—37.

LUND, S., 1940. On Dictyota dichotoma (Huds.) Lamour og andre nye Arter for Floraen i Nissum Bredning. Bot. Tidsskr. **45**.

LUND, S., 1945. On Colpomenia perigrina Sauv. and its Occurrence in Danish waters. Rep. Danish Biol. Stat. **47**.

LUND, S., 1949. Nye Alger for de Danske Farvande. Bot. Tidsskr. **48**: 231—253.

LUND, S., 1954. The algal zones in East Greenland and their ecological factors. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 132—133.

LUTHER, H., 1954. Über Krustenbewuchs an Steinen fliessender Gewässer, speziell in Südfinnland. Act. Bot. Fenn. **55**: 1—61.

MAGNE, F., 1954. Les chrysophycées marines de la station biologique de Roscoff. Rev. gén. Bot. **61**: 389—415.

MAGNE, F., 1956. Sur la présence de l'Halicystis ovalis (Lyngb.) Areschoug et du Derbesia marina (Lyngb.) Kjellm. dans la Manche. Bull. Soc. Bot. Fr. **103**: 488—490.

MAGNE, F., 1956. La végétation marine du Grand Congloué. in: Résultats scientifiques des Campagnes de la "Calipso". Ann. Inst. Océan. **32**: 163—184.

MAN, J. G. DE, 1892. Über eine neue in Gallen einer Meeresalge lebende Art der Gattung Tylenchus Bast. Festschr. 70. Geburtstag R. Leuckart. Leipzig: 121—125.

MARINE BIOLOGICAL ASSOCIATION, 1957. Plymouth marine fauna, 3e ed.: 1—457.

MARTINSSON, A., 1955. Monostroma grevillei (Thuret) Wittrock, a spring alga on the coast of Öland. Sv. Bot. Tidskr. **49**: 252—258.

MINISTERIE VAN MARINE, afd. Hydrografie, 1951. Stroomatlas voor de Nederlandse kust.

MIRANDA, F., 1932. Remarques sur quelques algues marines des côtes de la Manche. Rev. Alg. **6**: 275—295.

MOLINIER, R., 1954. La cartographie marine en Méditerranée. C-R, Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 56—57.

MOLINIER, R., 1954. L'installation et l' évolution des herbiers de Posidonies en Méditerranée occidentale. C-R, Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 62—64.

MOLINIER, R., 1954. Première contribution à l'étude des peuplements marins superficiels des îles Pithyuses (Baléares). Vie et Milieu. **5**: 226—242.

MOLINIER, R. and R. MOLINIER, 1955. Éléments de Bionomie marine et de Phytosociologie aux îles Sanguinaires (Corse). Rev. gén. Bot. **62**: 675—682.

MOLINIER, R. and J. PICARD, 1951. Biologie des herbiers de Zosteracées des côtes françaises de la Méditerranée. C-R. Ac. Sc. **233**: 1212—1214.

MOLINIER, R. and J. PICARD, 1953. Recherches analytiques sur les peuplements littoraux méditerranéens se developpant sur substrat solide. Rec. Trav. Stat. Mar. d'Endoume **9**: 1—18.

MOLINIER, R. and J. PICARD, 1954. Parallélisme dans la répartition des peuplements terrestres et marins benthiques du Bassin Méditerranéen occidental. Rev. gén. Bot, **61**: 701—739.

MORTON, J. E., A. D. BONEY and E. D. S. CORNER, 1957. The adaptations of Lasaea rubra (Montagu), a small intertidal lamellibranch. Journ. Mar. Biol. Ass. **36**: 383—405.

MULDER, A. F., 1956. De Wester- en de Oosterschelde, tegenstelling tussen riviermond en binnenzee. Zeepaard. **16**: 3—12, 21—26, 39—42.

NAYLOR, G. L., 1930. Note on the distribution of Lichina confinis and L. pygmaea in the Plymouth District. Journ. Mar. Biol. Ass. **16**: 909—918.

NEWELL, G. E., 1958. The behaviour of Littorina littorea (L.) under natural conditions and its relation to position on the shore. Journ. Mar. Biol. Ass. **37**: 229—240.

NEWELL, G. E., 1958. An experimental analysis of the behaviour of Littorina littorea (L.) under natural conditions and in the laboratory. Journ. Mar. Biol. Ass. **37**: 241—266.

Newton, L., 1931. A Handbook of the British Seaweeds, London.

Nienburg, W., 1925. Die Besiedlung des Felsstrandes und der Klippen von Helgoland. Wiss. Meeresunt. Abt. Helgoland. **15**^{4}: 1—15.

Nienburg, W., 1925. Eine eigenartige Lebensgemeinschaft zwischen Fucus und Mytilus. Ber. Deutsch. Bot. Ges. **43**: 292—298.

Nienburg, W., 1927. Zur Ökologie der Flora des Wattenmeeres. Wiss. Meeresunt. Abt. Kiel. **20**.

Nienburg, W., 1930. Die festsitzenden Pflanzen der nord-europäischen Meere. Handb. Seefischerei. **1**: 1—52.

Nienburg, W., 1932. Fucus mytili spec. nov. Ber. Deutsch. Bot. Ges. **50**: 28—41.

Nordhagen, R., 1936. Versuch einer neuen Einteilung der subalpinen Vegetation Norwegens. Bergens Mus. Aarbok. Nat. Vid. Rekke. **7**.

Okamura, K., 1927. On the Nature of Marine algae of Japan and the origine of the Japan Sea. Bot. Magaz. **41**: 558—592.

Oliver, W. R. B., 1923. Marine litoral plant and animal communities in New Zealand. Transact. New Zealand Int. **54**: 496—645.

Ollivier, G., 1929. Étude de la Flore marine de la Côte d'Azur. Ann. Inst. Océan. **7**: 53—173.

Oltmanns, F., 1922—23. Morphologie und Biologie der Algen, 2e ed.

Oord, A. M. van den, and L. B. Holthuis, 1959. De Columbuskrab in Nederland gevonden. Lev. Natuur. **62**: 30—32, f. 1.

Papenfuss, G. F., 1944. Notes on algal nomenclature III. Miscellaneous species of Chlorophyceae, Phaeophyceae and Rhodophyceae. Farlowia. **1**: 337—346.

Papenfuss, G.F., 1946, Proposed names for the phyla of algae. Bull. Torrey Bot. Club. **73**: 217—218.

Papenfuss, G. F., 1947, Generic names of algae proposed for conservation I. Madroño. **9**: 8—17.

Papenfuss, G. F., 1947, Extension of the brown algal order Dictyosiphonales to include the Punctariales. Bull. Torrey Bot. Club. **74**: 398—402.

Papenfuss, G. F., 1950. Generic names of algae proposed for conservation II. Madroño. **10**: 179—184.

Papenfuss, G. F., 1955. Classification of the algae, in: A century of progress in the natural sciences 1853—1953. California Acad. Sc. San Francisco: 115—224.

Papenfuss, G. F., 1957. Progress and outstanding achievements in phycology during the past fifty years. Amer. Journ. Bot. **44**: 74—81.

Parke, M., 1948. Studies on British Laminariaceae I. Growth in Laminaria saccharina (L.) Lamour. Journ. Mar. Biol. Ass. **27**: 651—709.

Parke, M., 1948. Laminaria ochroleuca De la Pylaie, growing on the coast of Britain. Nature. **162**: 295—296.

Parke, M., 1950. Notes on the Plymouth marine flora: Algal records for the Plymouth region. Journ. Mar. Biol. Ass. **29**: 257—261.

Parke, M., 1953. A preliminary checklist of British Marine Algae. Journ. Mar. Biol. Ass. **32**: 497—520.

Parke, M., 1956. Corrections and additions 1953—1955. Phycol. Bull. **4**: 26—31.

Parke, M., 1957. Corrections and additions 1956 II. Phycol Bull. **5**: 36—37.

Parke, M. and H. B. Moore, 1935. The Biology of Balanus balanoides II. Algal Infection of the Shell. Journ. Mar. Biol. Ass. **20**: 49—56.

Petersen, H. E., 1905. Contributions à la connaissance des Phycomycètes marins (Chytridinae Fischer). Overs. Kgl. Danske Vidensk. Selsk. Forh.: 439—488.

Post, E., 1936. Systematische und pflanzengeografische Notizen zur Bostrychia-Caloglossa-Assoziation. Rev. Alg. **9**: 1—84.

Post, E., 1939. Weitere Daten zur Verbreitung des Bostrychietum. III. Arch. Protistenk. **93**: 6—37.

Post, E., 1955. Idem, IV. Arch. Protistenk. **100**: 351—377.

Post, E., 1955. Idem. V. Ber. Deutsch. Bot. Ges. **68**: 205—216.

Postma, H., 1950. The distribution temperature and salinity in the Wadden Sea. Wadden Symposium. Tijdschr. Kon. Ned. Aardr. Gen. **67**: 34—42.

Postma, H., 1954. Hydrography of the Dutch Waddensea. A study of the relations between water movement, the transport of suspended materials and the production of organic matter. Arch. Néerl. Zool. **10**: 405—511.

Postma, H., 1957. Opzet van het hydrographisch onderzoek. Hydrobiologisch Instituut afd. Delta Onderzoek. 11 p.

Postma, H. and J. Verwey, 1950. Resultaten van hydrografisch onderzoek in de Waddenzee. Waddensymposium. Tijdschr. Kon. Ned. Aardr. Gen. **67**: 3—33.

Powell, H. T., 1957. Studies in the genus Fucus L. 1. Fucus distichus L. emend. Powell. Journ. Mar. Biol. Ass. **36**: 407—432.

Powell, H. T., 1957. Studies in the genus Fucus L. 2. Distribution and ecology of forms of Fucus distichus L. emend. Powell in Britain and Ireland. Journ. Mar. Biol. Ass. **36**: 663—693.

Pratje, O., 1931. Einführung in die Geologie der Nord- und Ostsee (Entwicklung, Formen, Küsten und Sedimenten). Tierwelt der Nord- und Ostsee. **I d.**: 1—44.

Printz, H., 1926. Die Algenvegetation des Trondhjemsfjordes. Norske Vidensk.-Akad. Skr. **1**^{6}: 1—274.

Printz, H., 1953. On some rare or recently immigrated marine algae on the Norwegian coast. Nytt Mag. f. Bot. **1**: 135—151.

Priou, M. L. and M. Serpette, 1954. Sur les associations algales des anses vaseuses du sud de la Bretagne. Rev. Alg. ser. 2, **1**: 25—28.

Rayss, T., 1954. Les algues tropicales de la Méditerranée orientale et leur origine probable. Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 148—149.

Redeke, H. C., 1910. Naamlijst der wieren aanwezig in het herbarium van het Zoologisch Station Helder, 1e ed.

Redeke, H. C., 1932. Abriss der regionalen Limnologie der Niederlande. Hydrobiol. Club A'dam. **1**: 1—39.

Reinbold, Th., 1889—91. Die Chlorophyceen (Grüntange) der Kieler Föhrde. Schr. Nat. Wiss. Vereins f. Schleswig-Holstein. **8**^{1}: 109—144.

Reinke, J., 1889. Algenflora der westlichen Ostsee deutschen Anteils. 6e Ber. Komm. Wiss. Unters. Deutsch. Meere in Kiel. Berlin.

Reinke, J., 1889—92. Atlas deutscher Meeresalgen I, II. Berlin.

Remane, A., 1940. Einführung in die zoologische Ökologie der Nord- und Ostsee. Tierwelt der Nord- und Ostsee. **1 a**: 1—238.

Rieth, A., 1956. Zur Kenntnis halophiler Vaucherien I, II. Flora. **143**: 127—160, 281—294.

Rietz, E. G. du, 1921. Zur methodologischen Grundlage der modernen Pflanzensoziologie. Thesis, 272 p.

Rietz, E. G. du, 1925. Die Hauptzüge der Vegetation der Insel Jungfurn. Sv. Bot. Tidskr. **19**: 323—346.

Rietz, E. G. du, 1925. Götlandische Vegetationstudien. Svensk. Vaxt. sociol. Sällsk. Handl. **11**: 1—65.

Rietz, E. G. du, 1930. Classification and Nomenclature of Vegetation. Sv. Bot. Tidskr. **24**: 489—503.

Rietz, E. G. du, 1932. Zur Vegetationsökologie der ostschwedischen Küstenfelsen. Beih. Bot. Centralbl. **49**: 61—112.

Rietz, E. G. du, 1936. Classification and Nomenclature of Vegetation Units 1930—35. Sv. Bot. Tidskr. **30**: 580—589.

Rietz, E. G. du, 1940. Das limnologisch-thalassologisch Vegetationsstufensystem. Verhandl. Int. Ver. Limn. **9**: 102—110.

Rietz, E. G. du, 1947. Wellengrenzen als ökologische Äquivalente des Wasserstandslinien. Zool. Bidr. fr. Uppsala. **25**: 534—550.

Rietz, E. G. du, 1953. Nomenclature of Laminaria digitata (Huds.) Lamour. and Laminaria hyperborea (Gunn.) Foslie. Sv. Bot. Tidskr. **47**: 16—23.

Rosenvinge, L. K., 1893. Groenlands Havalger. Medd. Grønland. **3**: 763—881.

Rosenvinge, L. K., 1894. Les algues marines du Grønland. Ann. Sc. nat. ser. **7**: 53—164.

Rosenvinge, L. K., 1898. Deuxième Mémoire sur les Algues marines du Groenland. Medd. Grønland. **20**.

Rosenvinge, L. K., 1910. On the marine Algae from North-East-Greenland, Medd. Grønland. **43**.

Rosenvinge, L. K., 1909—31. The Marine Algae of Denmark. 1. Rhodophyceae. Kgl. Danske Vidensk. Selsk. Skr. 7 Raekke. I (1909): 1—152; II (1917): 153—284; III (1924): 285—488; IV (1931): 489—630.

Rosenvinge, L. K., 1932. Note sur Monostroma obscurum (Kütz.) J. Agardh. Rev. Alg. **6**: 297—300.

Rosenvinge, L. K., 1935. Distribution of the Rhodophyceae in the Danish waters. Kgl. Danske Vidensk. Selsk. Skr. Raekke. **6^2**: 1—43.

Rosenvinge, L. K., 1935. On some Danish Phaeophyceae. Kgl. Vidensk. Selsk. Skr. Raekke. **6^3**: 1—40.

Rosenvinge, L. K. and S. Lund, 1941—50. The marine algae of Denmark 2. Phaeophyceae. Kgl. Danske Vidensk. Selsk. Biol. Skr. **1^4** (1941): 1—79; **2^6** (1943): 1—59; **4^5** (1947): 1—99; **6^2** (1950): 1—80.

Ross, R., 1958. The type species of Bifurcaria Stackhouse. Journ. Linn. Soc. London. **55**: 753—754.

Santesson, R., 1939. Amphibious Pyrenolichens I. Ark. f. Bot. **29** A^{10}: 1—67.

Sauvageau, C., 1907. Sur deux Fucus vivant sur le sable. Sur un Fucus qui vit sur la vase. C-R. Soc. Biol. Bordeaux. 1907.

Sauvageau, C., 1908. Sur deux Fucus récoltés à Arcachon (Fucus platycarpus et Fucus lutarius). Bull. Stat. Biol. d'Arcachon **11**: 65—216.

Sauvageau, C., 1921. Observations biologiques sur le Polysiphonia fastigiata Grev. Rec. Trav. Bot. Néerl. **18**: 213—235.

Schmidt, O. C., 1928. Die Algenvegetation Helgolands. Vegetationsbilder. **19^5**.

Schmidt, O. C., 1931. Die marine Vegetation der Azoren in ihre Grundzüge dargestellt. Bibliotheca Botanica. **102**: 1—116. Stuttgart.

Schmidt, O. C., 1936. Neue oder bemerkenswerte Meeresalgen aus Helgoland I. Hedwigia. **75**: 150—158.

Schulz, B., 1923. Einführung in die Hydrographie der Nord- und Ostsee. Tierwelt der Nord- und Ostsee. **Id. 2**: 45—88.

Schussnig, B., 1955. Systematik und Phylogenie der Algen. Fortschr. der Botanik **18**: 118—210.

Sernander, R., 1917. De nordeuropeiska hafvens växtregioner. Sv. Bot. Tidskr. **11**: 72—124.

Setchell, W. A., 1893. On the classification and geographical distribution of the Laminariaceae. Trans. Connecticut Ac. **9**: 333—375.

Setchell, W. A., 1917. Geographical distribution of the marine algae. Science. **45**: 197—204.

Setchell, W. A., 1920. Geographical distribution of the marine spermatophytes. Bull. Torrey Bot. Club. **47**: 563—579.

Setchell, W. A., 1926. Phytogeographical notes on Tahiti. II. Marine Vegetation. Univ. Calif. Publ. Bot. **12**: 291—324.

Setchell, W. A., 1935. Geographic elements of the marine flora of the North Pacific Ocean. The Amer. Nat. **69**: 560—577.

Setchell, W. A. and N. L. Gardner, 1919—25. The marine algae of the Pacific coast of North America 1—3. Univ. Calif. Publ. Bot. **8**. I. Myxophyceae (1919) 1—138; II. Chlorophyceae (1920): 139—374; III. Melanophyceae (1925): 377—739.

SILVA, H., 1953. Fifteen new algae. Bull. Torrey Bot. Club. **80**: 342—348.

SILVA, H., 1954. Discussion of a portion of the Ulotrichaceae. Castanea. **19**: 61—75.

SILVA, P. C., 1952. A review of nomenclatural conservation in the algae from the point of view of the type method. Univ. Calif. Publ. Bot. **25**: 241—324.

SILVA, P. C., 1955. The dichotomous species of Codium in Britain. Journ. Mar. Biol. Ass. **34**: 565—577.

SILVA, P. C., 1957. Remarks on algal nomenclature. Taxon. **6**: 141—145.

SILVA, P. C., 1957. Codium in Scandinavian waters. Sv. Bot. Tidskr. **51**: 117—134.

SILVA, P. C., 1957. Notes on Pacific marine algae. Madroño. **14**: 41—51.

SILVA, P. C. and H. B. S. WOMERSLEY, 1956. The genus Codium (Chlorophyta) in Southern Australia. Austr. Journ. Bot. **4**: 261—289.

SINOVA, E. S., 1928. Algae maris japonensis 1. Chlorophyceae. Bull. Pac. Sc. Fish. Res. Stat. **2**^{2}: 1—52.

SINOVA, E. S., 1929. Algae maris japonensis 2. Phaeophyceae. Bull. Pac. Sc. Fish. Res. Stat. **3**^{4}: 1—63.

SINOVA, E. S., 1929. Algues de la Novaja Zemlja. Explor.mers U.R.S.S. **10**: 41—128.

SINOVA, E. S., 1929. Les algues de la Mer Blanche et leur application pratique. Trav. Inst. Recherch. Industr. Comité exécut. Archangel. **6**: 1—48.

SINOVA, E. S., 1934. Nouvelles recherches sur les algues de la Mer Blanches le long de la côte Lietnaïa et leur utilisation. Explor. Mers U.R.S.S. **20**: 65—85.

SINOVA, E. S., 1935. Algues de la baie Novorossysk dans la Mer Noire et leur utilisation. Trav. Stat. Biol. Sébastopol. **4**: 1—136.

SJÖSTEDT, L. G., 1920. Algologiska Studier vid Skånes södra och östra kust. Lunds Univ. Årsskr. **16**: 1—40.

SJÖSTEDT, L. G., 1922. Om Prasiola cornucopiae J. G. Ag. och Prasiola stipitata v. Suhr. samt deras för hållanden inbördes. Bot. Not. Lund: 37—45.

SJÖSTEDT, L. G., 1928. Revision of some dubious Swedish Ceramium types, their classification and ecology. Lunds Univ. Årsskr. **23**: 1—30.

SJÖSTEDT, L. G., 1928. Litoral and supralitoral studies on the Scanian shores. Lunds Univ. Årsskr. **24**: 1—36.

SLOFF, J. G., 1925—'26. Wierglooiingen. Lev. Natuur. **29**: 321—328, 353—360; **30**: 321—327.

SLOOTWEG, A. F. G., 1948. The Netherlands' Marine Cladophora-Species. Blumea. **6**: 274—281.

SMITH, G. M., 1944. Marine Algae of the Montorey Peninsula, California. Stanford Univ.: I—IX + 622 p., 98 Pl.

SOURIE, R., 1954. Principaux types de zonation verticales des algues sur le littoral rocheux de la presqu'île du Cap Vert (zone intercotidale). Rapp. et Comm. 8e Congr. Int. Bot. Paris. *sect.* **17**: 151—153.

SOUTHWARD, A. J., 1951. Distribution of Chthamalus stellatus in the Irish Sea. Nature. **167**: 410.

SOUTHWARD, A. J., 1953. The ecology of some rocky shores in the south of the Isle of Man. Proc. Trans. Liverpool. Biol. Soc. **59**: 1—50.

SOUTHWARD, A. J., 1953. The fauna of some sandy and muddy shores in the south of the Isle of Man. Proc. Trans. Liverpool. Biol. Soc. **59**: 51—71.

SOUTHWARD, A. J., 1953. Fluctuations in the sea and air temperatures at Port Erin during the past fifty years. Ann. Rep. for 1952 (no. 65) of the Mar. Biol. Stat. Port Erin, Isle of Man: 28—31.

SOUTHWARD, A. J., 1956. The population balance between limpets and seaweeds on wave-beaten rocky shores. Rep. Mar. Biol. Stat. Port Erin 1955 (no. 68): 20—29.

SOUTHWARD, A. J., 1958. Note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. Journ. Mar. Biol. Ass. **37**: 49—66.

SOUTHWARD, A. J., 1958. The zonation of plants and animals on rocky sea shores. Biol. Rev. **33**: 137—177.

SOUTHWARD, A. J. and D. J. CRISP, 1952. Changes in the distribution of intertidal barnacles in relation to the environment. Nature. **170**: 416—417.

SOUTHWARD, A. J. and D. J. CRISP, 1954. The distribution of certain intertidal animals around the Irish coast. Proc. Roy. Irish Ac. sect. B. **57**: 1—29.

SOUTHWARD, A. J. and D. J. CRISP, 1954. Recent changes in the distribution of the intertidal barnacles Chthamalus stellatus Poli and Balanus balanoides L. in the British Isles. Journ. Animal Ecol. **23**: 163—177.

SOUTHWARD, A. J. and D. J. CRISP, 1956. Fluctuations in the distribution and abundance of intertidal barnacles. Journ. Mar. Biol. Ass. **35**: 211—229.

SOUTHWARD, A. J. and J. H. ORTON, 1954. The effects of wave-action on the distribution and numbers of the commoner plants and animals living on the Plymouth breakwater. Journ. Mar. Biol. Ass. **33**: 1—19.

SPARROW, F. K., 1943. Aquatic Phycomycetes. Univ. Mich. Studies Scient. **15**. Ann Arbor.

SPOONER, G. M., 1950. Notes on the Plymouth marine flora: Additional records of Laminaria ochroleuca de la Pylaie. Journ. Mar. Biol. Ass. **29**: 251—262.

SPREE, TH., 1870. Additamentum ad floram batavum cryptogamicam. Ned. Kruidk. Arch. **5**: 317—331.

STEEMANN NIELSEN, E., 1951. The marine vegetation of the Isefjord. A study on ecology and production. Medd. f. Komm. f. Danmarks Fiskeri- og Havundersøgelser. serie Plankton. **5**^{4}: 1—114.

STEPHENSON, T. A., 1939. The constitution of the intertidal fauna and flora of South Africa 1. Journ. Linn. Soc. Lond. Zool. **40**: 487—536. Pl. 14—17.

STEPHENSON, T. A., 1942. The causes of the vertical and horizontal distribution of organisms between tide-marks in South Africa. Proc. Linn. Soc. London. **154**: 219—231.

STEPHENSON, T. A., 1944. The constitution of the intertidal fauna and flora of South Africa 2. Ann. Natal Mus. **10**: 261—358, Pl. 12—14.

STEPHENSON, T. A., 1948. The constitution of the intertidal fauna and flora of South Africa 3. Ann. Natal Mus. **11**: 207—324. Pl. 15—16.

STEPHENSON, T. A. and A. STEPHENSON, 1949. The universal features of zonation between tidemarks on rocky coasts. Journ. Ecol. **37**: 289—305.

STEPHENSON, T. A. and A. STEPHENSON, 1950. Life between Tidemarks in North America I. The Florida Keys. Journ. Ecol. **38**: 354—402. Pl. 9—15.

STEPHENSON, T. A. and A. STEPHENSON, 1952. Life between Tide marks in North America. II. Northern Florida and the Carolinas. Journ. Ecol. **40**: 1—49. Pl. 1—6.

STEPHENSON, T. A. and A. STEPHENSON, 1954. Life between Tide marks in North America III. Nova Scotia and Prince Edward Island. Journ. Ecol. **42**: 14—70.

STEPHENSON, T. A., A. STEPHENSON, G. TANDY and M. SPENDER, 1931. The structure and ecology of Low Isles and other reefs. Sci. Rep. Gr. Barrier Reef. Exped. **3**^{2}: 17—112.

STOCK, J. H., 1950. Littorina neritoides petraea (Montagu 1803) op drie plaatsen in Nederland autochthoon aangetroffen. Basteria. **14**: 11—14.

STOCK, J. H., 1952. Revision of the European representatives of the genus Callipallene Flynn, 1929. Beaufortia. **1**^{13}: 1—14.

STOCK, J. H., 1954. Nieuwe en zeldzame amphipoda van drijvende voorwerpen. Zeepaard. **14**: 25—27.

STOCK, J. H., 1955. Een allochthone zeespin nieuw voor ons land. Zeepaard. **15**: 36—37.

STOCK, J. H. and A. E. M. H. BLOKLANDER, 1952. Notes on adventive Amphipoda on the Dutch coast. Beaufortia. **1**^{10}: 1—9.

STOMPS, TH. J., 1911. Études topographiques sur la variabilité des Fucus vesiculosus L., platycarpus Thur. et ceranoides L. Rec. de l'Inst. Bot. Léo Errera. **8**: 325—377. Pl. 1—31.

Sundene, O., 1953. The algal vegetation of Oslofjord. Skrifter Norske Vidensk.-Ak. Oslo. **2**: 1—244.

Suneson, S. 1939. On Ectocarpus fasciculatus growing on the finspines of fishes. Bot. Not. Lund: 53—56.

Suneson, S., 1939. Zur Algenflora der schwedischen Westküste. Bot. Not. Lund: 57—64.

Suneson, S., 1947. Notes on the life-history of Monostroma. Sv. Bot. Tidskr. **41**: 235—246.

Suringar, W. F. R., 1857. Observationes Phycologicae in floram Batavum. Thesis, Leiden.

Suringar, W. F. R., 1870. Algae in H. de Vries: Flora van Nederland, in Algemene Statistiek van Nederland. **1**^{8}: 39—50.

Svedelius, N., 1901. Studier öfver Östersjöns havsalgflora. Thesis, Uppsala. 140 p.

Svedelius, N., 1906. Über die Algenvegetation eines ceylonischen Korallenriffes mit besonderer Rücksicht auf ihre Periodizität. Bot. Stud. till. F. R. Kjellman: 182—220.

Svedelius, N., 1924. On the discontinuous geographical distribution of some tropical and subtropical marine algae. Ark. f. Bot. **19**^{3}: 1—70.

Svedelius, N., 1933. On the development of Asparagopsis armata Harv. and Bonnemaisonia asparagoides (Woodw.) Ag. A contribution to the cytology of the haplobiontic Rhodophyceae. Nova Acta Reg. Soc. Sc. Upsal. ser. 4, **9**: 1—61.

Swennen, C., 1957. Vorstschade langs onze kust. Zeepaard. **17**: 74—78.

Taylor, W. R., 1928. The marine algae of Florida, with special reference to the Dry Tortugas. Carnegie Inst. Washington Publ. **379**: 1—219.

Taylor, W. R., 1931. A synopsis of the marine algae of Brazil. Rev. Alg. **5**: 279—313.

Taylor, W. R., 1936. Notes on algae from the tropical Atlantic Ocean III. Pap. Michigan Ac. of Sc., Arts and Lett. **21**: 199—207.

Taylor, W. R., 1937. Notes on North Atlantic Marice Algae I. Pap. Michigan Ac. of Sc., Arts. & Lett. **22**: 225—234.

Taylor, W. R., 1940. Marine algae from Long Island. Torreya **40**: 185—195.

Taylor, W. R., 1941. Notes on the marine algae of Texas. Pap. Michigan Ac. of Sc., Arts and Lett. **26**: 69—79.

Taylor, W. R., 1950. Plants of Bikini and other Northern Marshall Islands. Univ. Michigan Press, Ann Arbor. 227 p.

Taylor, W. R., 1951. Survey of the marine algae of Bermuda. Yearb. Amer. Phil. Soc. 1951: 167—171.

Taylor, W. R., 1954. Distribution of marine algae in the Gulf of Mexico. Pap. Michigan Ac. of Sc., Arts and Lett. **39**: 85—109.

Taylor, W. R., 1955. Notes on algae from the tropical Atlantic Ocean IV. Pap. Michigan Ac. of Sc., Arts and Lett. **40**: 67—76.

Taylor, W. R., 1957. Marine algae of the North eastern Coast of North America. 2e ed. Ann Arbor. 509 p. 60 Pl.

Tesch, P., 1942. De Noordzee van historisch-geologisch standpunt. Meded. Rijksgeol. Dienst A **9**.

Thuret, G., 1854. Note sur la synonymie des Ulva lactuca et latissima L. suivie de quelques remarques sur la tribu des Ulvacées. Mém. Soc. Sc. nat. Cherbourg. **2**: 17—32.

Thuret, G., and E. Bornet, 1878. Études phycologiques. Analyses d'algues marines. Paris. 105 p.

Tulp, A., 1955. Aantekeningen betreffende het litoraal van Ezumazijl. Zeepaard. **15**: 2—4.

VEEN, J. VAN, 1950. Eb- en vloedschaarsystemen in de Nederlandse getijwateren. Waddensymposium. Tijdschr. Kon. Ned. Aardr. Gen. **67**: 43—65.

VELDKAMP, H., 1950. The genus Polysiphonia in the Netherlands. Blumea. **6**: 517—526.

VERWEY, J., 1952. On the ecology and the distribution of cockle and mussel in the Dutch Waddensea, their rôle in the sedimentation and the source of their food supply. Ach. Néerl. Zool. **10**: 171—239.

WAERN, M., 1940. Cladophora pygmaea und Leptonema lucifugum an der schwedischen Westküste. Acta Phytogeogr. Suec. **13**: 1—6.

WAERN, M., 1945. Remarks on some Swedish Sphacelariaceae. Sv. Bot. Tidskr. **39**: 396—418.

WAERN, M., 1950. Algological Excursions to the Middle part of the Swedish East coast. Stockholm. 7th Int. Bot. Congr. Excursion guides, 38 p.

WAERN, M., 1952. Rocky shore Algae in the Öregrund Archipelago. Act. Phytogeogr. Suec. **30**: 1—298.

WALTER, H., 1923. Zur Biologie des Bangia fusco-purpurea Lyngb. Flora. **116**: 316—322.

WEBER-VAN BOSSE, A. A., 1886. Bijdrage tot de Algenflora van Nederland. Ned. Kruidk. Arch. ser. 2, **4**: 363—368.

WEBER-VAN BOSSE, A. A., 1891. Tweede Bijdrage tot de Algenflora van Nederland. Ned. Kruidk. Arch. ser. 2, **5**: 67—70.

WEDDELL, H. A., 1875. Excursion lichénologique dans l'Ile d'Yeu, sur la côte de la Vendée. Mém. Soc. Sc. Nat. Cherbourg. **19**: 251—316.

WEMELSFELDER, P. J., 1954. Tienjarig Overzicht 1941—1950 der Waterhoogten, langs Zeeuwse stromen, Noordzee, Waddenzee, Lauwerszee, Eemsmond, Hoofdrivieren en IJsselmeer. Algem. Dienst der Rijkswaterstaat, The Hague.

WESTHOFF, V., 1947. The vegetation of dunes and salt marshes on the Dutch islands of Terschelling, Vlieland and Texel. 131 p.

WESTHOFF, V., 1950. Het associatiebegrip in geografisch verband. Ned. Kruidk. Arch. **57**: 98—100.

WESTHOFF, V., 1951. An analysis of some concepts and terms in vegetation study or phytocenology. Synthese **8**: 194—206.

WESTHOFF, V. and W. G. BEEFTINK, 1950. De vegetatie van duinen, slikken en schorren op de Kaloot en in het Noord Sloe. Lev. Natuur. **53**: 124-133, 225-233.

WILDEMAN, E. DE, 1896. Flore des algues de Belgique. Brussels.

WOHLENBERG, E., 1937. Die Wattenmeer-Lebensgemeinschaften im Königshafen von Sylt. Helg. Wiss. Meeresunt. **1**: 1—92.

WOITUSIAK, R. J., A. KORNAŚ, J. KORNAŚ and H. FRANCKIEWICZ, 1950. Badania nad faunas i floras dennas zatoki Gdańskiej dokonane przy użyciu helmu nurkowego Cz. III. (Investigations on the Bottom Fauna and Flora in the Gulf of Gdańsk made by using a diving helmet III). Materialy do Fizjografii kraju. **26**: 1—20.

WOITUSIAK, R. J., W. KALKOWSKI, A. MEDWECKA-KORNAŚ and J. KORNAŚ, 1953. Investigations of the bottom fauna and flora in the Gulf of Gdańsk made by using a diving helmet V. Bull. Ac. Polon. Sc. Lettres. 1951: 117—143.

WOMERSLEY, H. B. S., 1947—50. The marine algae of Kangaroo Island 1—3. Trans. Roy Soc. S. Austral. **71** (1947): 228—252, Pl. 9—13: **72** (1947): 143—166, Pl. 10—15; **73** (1950): 137—197.

WOMERSLEY, H. B. S. and S. J. EDMONDS, 1952. Marine coastal zonation in Southern Australia in relation to general schemes of classification. Journ. Ecol. **40**: 84—90.

IJZERMAN, R., 1937. Transporteerend zeewier. Lev. Natuur. **42**: 149—150.

ZANEVELD, J. S., 1937. The littoral zonation of some Fucaceae in relation to desiccation. Journ. Ecol. **25**: 431—468.

ZONNEVELD, I. S., 1952. De Biesbosch, een zoetwatergetijdendelta. Natuur en Landschap. **6**: 170—182, 204—221.