ALGAL PHYTOGEOGRAPHY OF THE EUROPEAN ATLANTIC COASTS

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SUMMARY

It is concluded on the basis of data gathered from the literature and of our personal observations, that the algal phytogeographic provinces as assumed by several authors do not exist.

The algal floras of NW. Spain and Brittany are richest in species. From these two regions down to the south but far more so up to the north the algal flora gradually changes mainly by species dropping out and being only partially replaced by others.

One very obvious floristic discontinuity is not correlated with a discontinuity in the temperature-range of the surface-water, namely the one along the west coasts of the British Isles. The floristic discontinuity Arctic Europe-Spitsbergen is correlated with a temperature discontinuity.

Floristically and as regards temperature-range of the surface-water, the Côte Basque finds its logical place in between NW. Spain and Morocco.

1. INTRODUCTION

In the few publications on the algal phytogeography of the European Atlantic coasts the authors have, in general, based their viewpoints on the assumption that the flora of these coasts can be divided into several phytogeographic provinces, each characterized by its own flora (2, 13, 14, 17, 19, 23, 25, 35, 44, 53). Although the concept of the algal phytogeographic province was not defined in these investigations one may reasonably assume that an algal phytogeographic province was regarded as a part of the coast characterized by a more or less homogeneous flora and separated from other such parts by comparatively small stretches of coast with a rapidly changing flora, i.e. by floristic discontinuities. In our opinion the concept of the algal phytogeographic province is only useful when it conforms to this definition.

The following questions arise, when studying the above publications:

1.1. Do floristic discontinuities actually occur?

1.2. If so, do they correspond to physico-geographic discontinuities?

1.3. Do the parts of the coast lying in between two floristic discontinuities (when these actually can be found) conform to the above definition of the algal phytogeographic province, i.e. are these parts of the coast floristically more or less homogeneous?

1.4. If so, do these phytogeographic provinces then coincide with the phytogeographic provinces of the above-mentioned authors?

2. METHODS

Eleven algologically well-investigated regions (fig. 1) (1, 2, 3, 5, 7, 8, 15, 16, 17, 21, 22, 24, 27, 28, 31, 32, 33, 34, 35, 36, 39, 41, 42, 44, 46, 47, 53, 54, 56, 57) were compared by listing for each region all more or less critically identifiable species (tables 1, 2). The degree of shading roughly indicates the degree of abundance with which each

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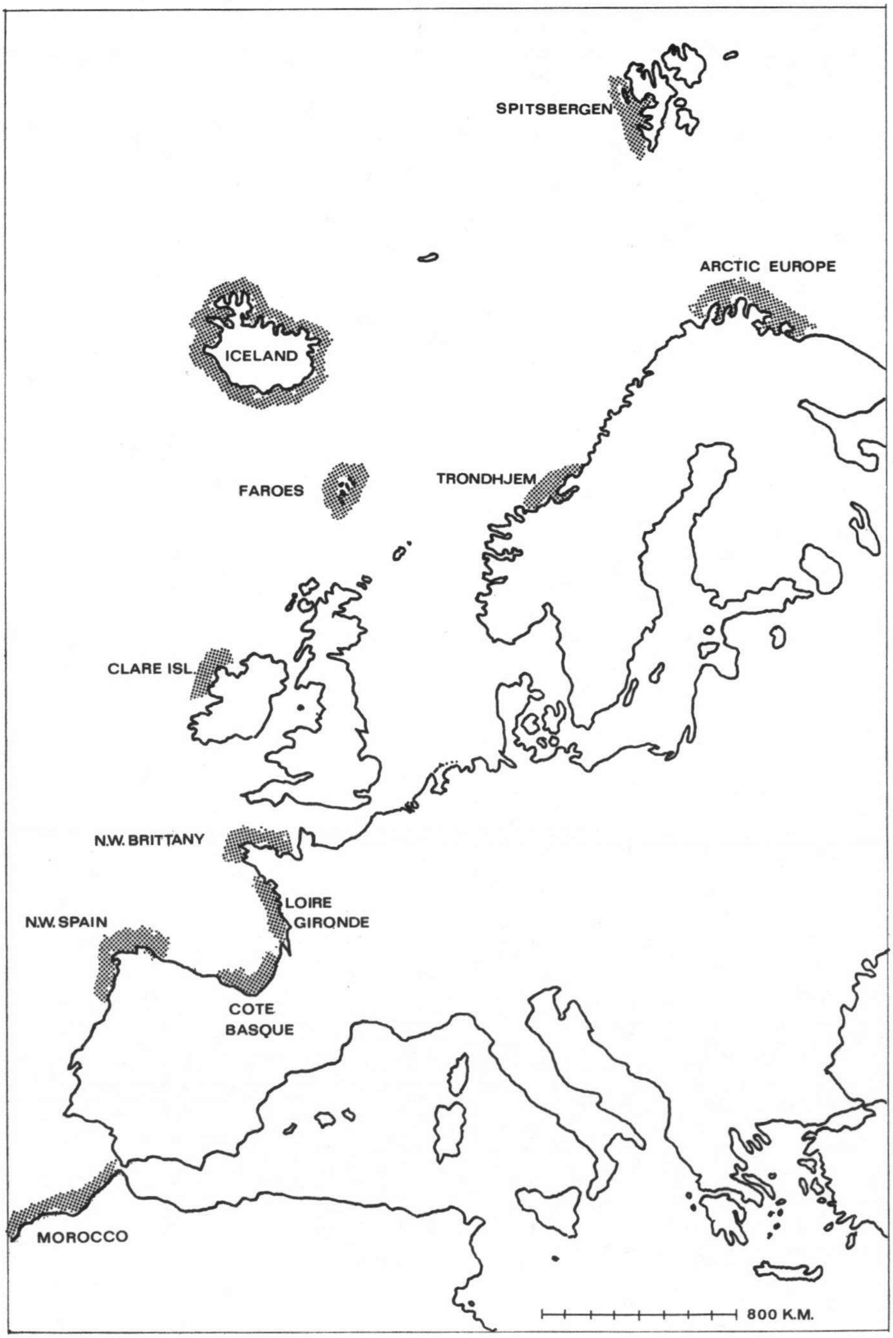

Fig. 1. Map of the European Atlantic coasts showing the regions (shaded) of which the vegetations are enumerated in table 1 and table 2.

species occurs in the region considered (cf. explanation to table 1). Sublittoral and eulittoral species have been listed separately.

Only those species are considered littoral that are not or hardly ever known to occur in the sublittoral.

The North Sea did not seem suitable for a comparison because of its particular geographic configuration (relative enclosure, communication with the Baltic, long stretches of sandy shore).

The data shown in tables 1 and 2 are graphically represented in five different ways (figs. 2—6, sections 2.1—2.4). Apart from fig. 6 the data from the Loire-Gironde region (39) are omitted in the graphs, since too many species probably have been overlooked by the investigator of this area.

For our purpose, all information we are interested in while comparing two floras (A with a species, B with b species, A and B having c species in common) is included in the three numbers a, b, and c. To arrive at a further simplification, these may be combined in several ways, as done by Starmach (51) for example in a coefficient of similarity $P = \frac{c}{a + b - c} 100$. Such simplifications can be of use in more complex situations where distributional patterns and correlated environmental gradients cannot be easily recognized. In fact, a number of the methods employed by numerical taxonomists (49, 50) can directly be applied to phytogeography.

2.1. Each flora is represented by the numbers of species it has in common with each of the other algal floras. In fig. 2 all species are represented, in fig. 3 only the eulittoral species, and in fig. 4 only dominant and common species.

2.2. In fig. 5 the *floristic increase* (b—c) and *decrease* (a—c) from south to north are given. Each is expressed as the percentage of the mean number of species of the two regions between which the floristic change is calculated.

Those parts of the Atlantic European coast are considered *floristically homogeneous* where the floristic changes (i.e. floristic increase and decrease) between the successive investigated regions are relatively small. In other words, when this part of the Atlantic coast shows a *slow floristic change* from the south to the north. The most ideal condition would be where the floristic change within a floristically homogeneous region would be zero, but this is, of course, never realized.

Those parts of the Atlantic European coast are considered *floristically discontinuous* where the floristic changes between the successive investigated regions are suddenly much greater than in adjacent floristically homogeneous parts of the coast. In other words, when this part of the coast shows a much more *rapid floristic change* from south to north than in the adjacent floristically homogeneous parts.

2.3. In fig. 6 table 1 is given in a vertically compressed form; each line corresponds with a bar in the table.

2.4. Previous authors (2, 13, 14, 35, 44, 53) determined the 'phytogeographic nature' of the algal floras they investigated in the following way:

2.4.1. Definition of a number of groups of algae with about the same geographical distribution. These groups were arbitrarily and a priori defined, not a posteriori in accordance with observed floristic discontinuities. Sometimes, in the definition of such distribution-groups, speculative interpretative notions play an important rôle in order to conveniently enlarge or restrict the actual ranges of distribution of certain species. The Mediterranean, for instance, is thought to contain many atlantic-tropical species which have entered through the Straits of Gibraltar (14). Actually, such species are atlantic-tropical-mediterranean.

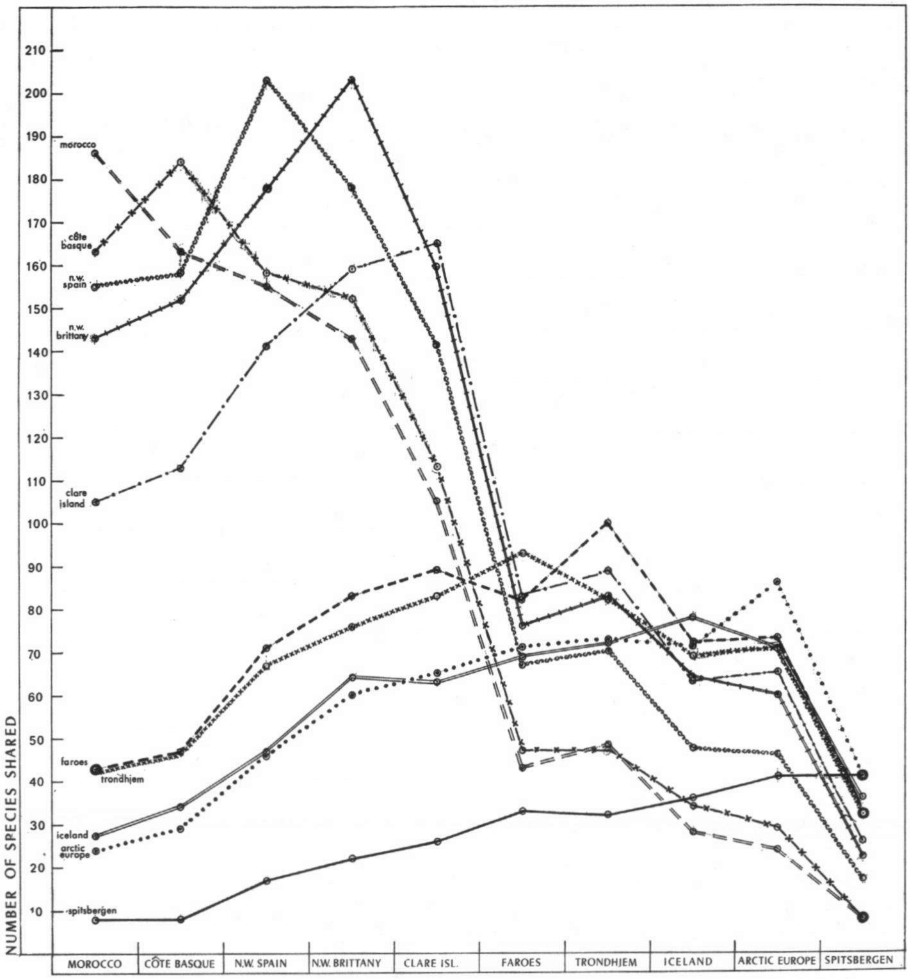

Fig. 2. Graph showing the numbers (c) of species each flora has in common with each of the other algal floras.

These distribution-groups are given in table 3 (cf. also figs. 9, 10). They are borrowed from Jónsson (35), Børgeson (2), and Feldmann (13, 14).
2.4.2. Calculation of the percentages by which the species of each distribution-group participate in the flora investigated.
2.4.3. Assigning to the flora the epithet of the arbitrary distribution-group showing the highest percentage.

In order to be able to compare our results with those of the above-mentioned authors we analysed the data from the literature in the same way, without, however, actually assigning epithets to floras (table 4). In fig. 7 the numbers of species belonging to each

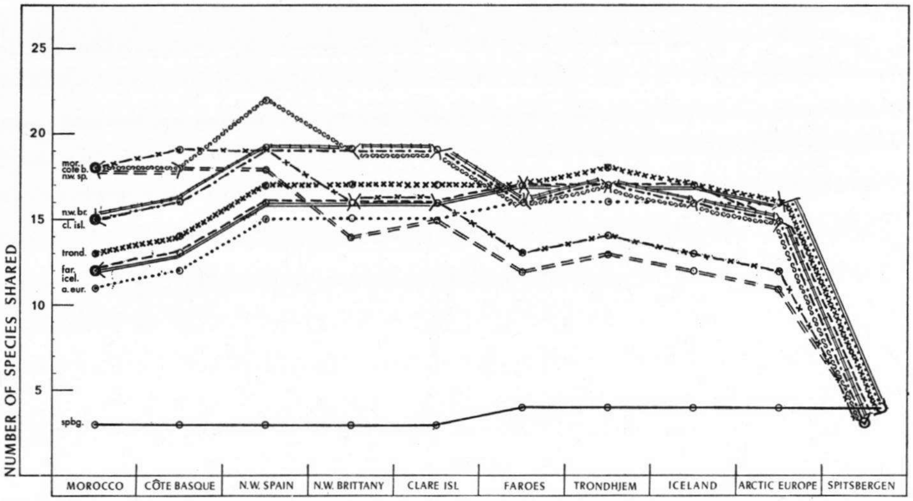

Fig. 3. Graph of the numbers c for eulittoral species.

distribution-group in the areas considered are given, in fig. 8 the same numbers are given as percentages of the total number of species occurring in each area.

The yearly temperature-ranges of the surface-water of the regions considered were compiled from the literature (see fig. 9).

3. RESULTS

3.1. As appears from figures 2 and 4, and more obviously from figure 5, two floristic discontinuities can be distinguished along the Atlantic European coasts, namely the first one from NW. Brittany, via Clare Island, to the Faroes, and the second one from Arctic Europe to Spitsbergen. Both discontinuities predominantly reflect the disappearance of large numbers of species (fig. 2, 4, 5) which are replaced by very few others. Thus 93 % of the species in the flora of the Faroes occur also in NW. Brittany, whereas only 37 % of the species of the latter region occur also in the Faroes. The flora of Spitsbergen consists entirely of species which occur also in NW. Arctic Europe, whereas the flora of the latter area contains only 48 % of species which also occur in Spitsbergen.

Of these two discontinuities only the one between Arctic Europe and Spitsbergen is also shown by the eulittoral species (fig. 3). This very obvious decrease in the number of eulittoral species probably results from the fact that the eulittoral zone is a very unsuitable habitat for algae in Spitsbergen, where it is subject to the heavy scouring action of ice. Evidently the changes in the composition of the eulittoral flora over long distances are much less pronounced than those of the sublittoral flora, a phenomenon which might be connected with a larger ecological amplitude of the littoral species. Scagel (48) records the same phenomenon for a number of littoral species occurring along the Pacific coast of NW. America [1]).

It appears from figures 2, 4, and 9, that floristically and as regards temperature-range of the surface-water the Côte Basque finds its logical place in between Morocco and NW. Spain.

[1]) Part of Scagel's littoral species are probably to be considered sublittoral (Scagel, fig. 11, p. 48).

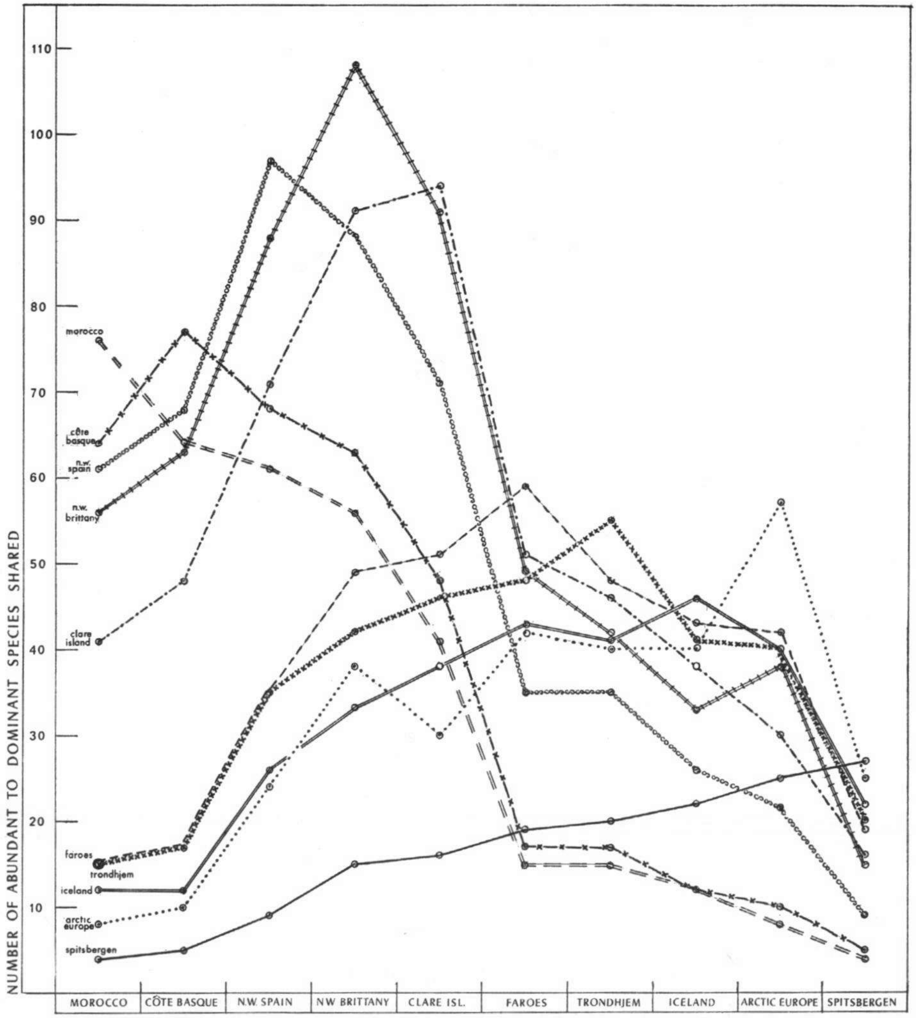

Fig. 4. Graph of the numbers c for abundant and dominant species of each flora (explanation cf. table 1).

3.2. The NW. Brittany — Faroes floristic discontinuity does not correspond to a temperature discontinuity. The Arctic-Europe — Spitsbergen floristic discontinuity does correspond to a temperature discontinuity (compare figs. 2, 4, and 5 with fig. 9).

3.3. The region lying in between the two above-mentioned floristic discontinuities (3.1), i.e. roughly from the Faroes up to Arctic Europe, shows a reasonably homogeneous floristic composition as compared with adjacent floristically discontinuous parts of the coast (cf. fig. 2, 4, and 5). This region, therefore, conforms to our definition of an algal phytogeographic province. It is not known whether the coasts south of the floristic discontinuity NW. Brittany — Faroes have a reasonably homogeneous flora and could therefore be considered as belonging to another algal phytogeographic province, since

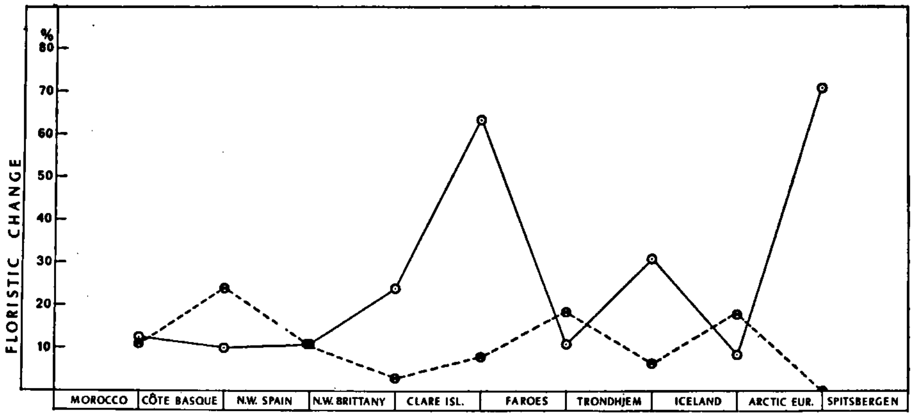

Fig. 5. Floristic change from region to region. Explanation see text (2.2).
Dotted line: floristic increase from S. to N. Drawn line: floristic decrease from S. to N.

no floristic discontinuity that could serve as a southern borderland of such a province is suggested by the data of the present investigation. If future investigations would reveal a gradual change in floristic composition from Morocco southwards, the coasts south of the floristic discontinuity Brittany — Faroes could not be regarded as constituting a phytogeographic province.

More investigations are equally required to decide whether Spitsbergen and other Arctic regions form a floristically homogeneous region or not.

3.4. Thus one phytogeographic province may be delimited along the NW. European coasts. However, this province does not coincide with any of the 'provinces' of the previous authors. It roughly coincides with the Atlantic part of Nienburg's *West Europäisch-Baltisches Florengebiet* which, however, also includes the much diverging (through gradual impoverishment) flora of the North Sea and the Baltic. If it would later appear possible to distinguish a second phytogeographic province covering the coasts from Brittany southwards to a still unknown borderland on the African Atlantic coast, this province would no more than the first one coincide with any of the 'provinces' distinguished by the above-mentioned authors (in fact they assume the existence of many more provinces; cf. table 3).

3.5. Optimum conditions for the development of algal floras seem to exist on the coasts of NW. Spain and Brittany (figs. 2, 4, 5) the floras of which two regions have the largest numbers of species. This effect is enhanced when only dominant and common species are taken into account. (In this way the effect of the more frequent and more intensive investigations in NW. Brittany, producing more rarities, is diminished) (fig. 4).

3.6. Both southwards and northwards from Brittany and NW. Spain the floras become poorer in species, more species dropping out than others coming in. This decrease in number of species is particularly obvious towards the north.

3.7. In the areas investigated no correlation between the yearly temperature-amplitude and the richness of the flora is suggested. If such were the case one would expect that in an area with a relatively narrow yearly temperature-amplitude the flora would be relatively rich as a consequence of 'southern' species being able to survive the 'not-too-low' winter temperatures and 'northern' species the 'not-too-high' summer temperatures. No such effect is suggested by the data here gathered: for example the floras of Morocco,

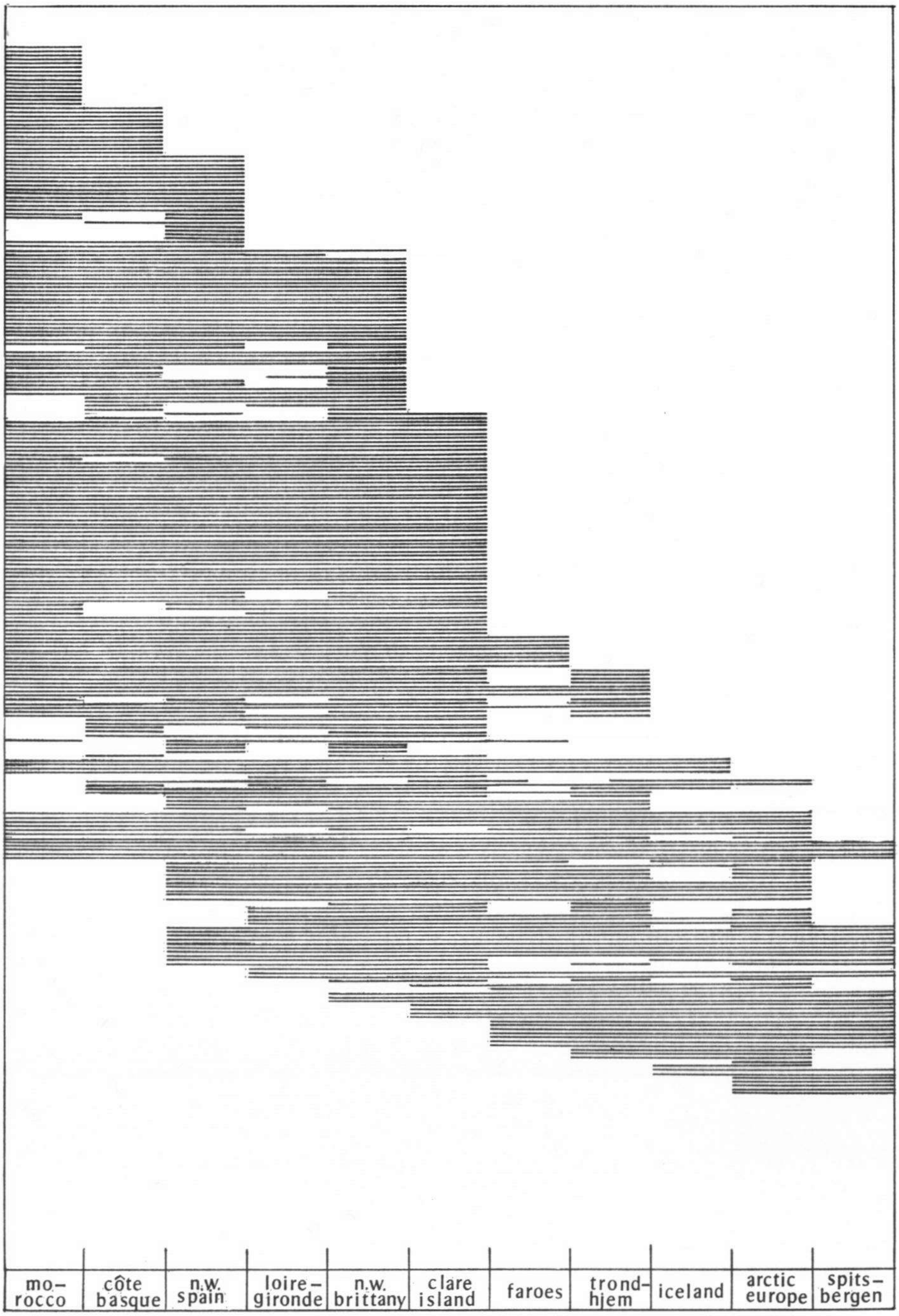

Fig. 6. Graph showing table 1 in a vertically compressed form. Each line represents the distribution of one species.

NW. Spain, and of the Faroes are not relatively rich as compared with adjacent floras. It should be borne in mind that the overall temperature-ranges here presented are much narrower than the extremes which may in fact be found in the different habitats of any one locality (e.g. rocks-pools, shallows, eulittoral zone). These extremes are not included in the ranges shown in fig. 8.

4. DISCUSSION

Apparently it is not convenient to define algal phytogeographic provinces as done by several authors. This is not surprising when one realizes that the existence of such provinces was evidently taken for granted, but never demonstrated.

The only clearly distinguishable algal phytogeographic province is the one delimited to the south by the NW. Brittany — Faroes discontinuity and to the north by the Arctic-Europe — Spitsbergen discontinuity. The floristic changes between the successive areas investigated of this province are small as compared with the changes within the floristic discontinuities (see fig. 5). This province is mainly characterized by the absence of many species occurring in NW. Brittany and farther south. It is interesting to record a discontinuity comparable to the first one mentioned in the distribution of the species of *Cladophora* along the European Atlantic coasts. Only three species out of 19 are known to occur from the Faroes up to the north, 16 dropping out in the same region of discontinuous floristic change (27). Spitsbergen differs from this province only by the absence of many species.

Only very few species are confined to this province (cf. table 1), namely: *Turnerella pennyi*, *Coilodesme bulligera*, *Sphaerotrichia divaricata*, and *Ralfsia deusta*.

One may wonder, however, whether these species would not turn up if the shores of Spitsbergen were more thoroughly searched for them. Anyhow, the data are insufficient to consider these four species characteristic of the province.

Whether it makes sense to designate one part of the European Atlantic coasts as an algal phytogeographic province, whereas in adjacent parts of these coasts no such provinces can be distinguished, is open to doubt.

There could be some reason to consider the Côte Basque a minor algal phytogeographic province. Towards the north it is rather abruptly delimited by the long sandy beaches of Les Landes, towards the west, however, its flora seems to merge gradually into the flora of NW. Spain. No region of discontinuous change that could serve as a western borderland is known to exist. On the contrary, the resemblance between the Côte Basque and the adjacent investigated regions is distinctly more significant than the difference, so that the floristic change from NW. Spain to the Côte Basque is too small to consider the latter a separate phytogeographic province (cf. fig. 5). Floristically and as regards the temperature-range of the surface water, however, the Côte Basque finds its logical place between Morocco and NW. Spain. Several authors (8, 17, 18, 19, 42, 46) have noticed this already and they considered the Côte Basque to be floristically very different from Brittany and NW. Spain. Actually the large majority of species occurring along the coasts of Morocco and the Côte Basque also belong to the flora of NW. Brittany (77 % and 83 %, respectively). This temperature-correlated, only slightly more meridional composition of the flora of the Côte Basque as compared with that of NW. Spain depends on a summer upwelling of cold water against the Spanish northwest coast (37). The narrow temperature-range of the Moroccan coastal water is also the result of upwelling cold water (37). Similar slightly discontinuous changes of the flora correlated with the presence of upwelling cold water have been recorded from Baja California (9, 10, 11) and from South-West Africa (30, 52) where these

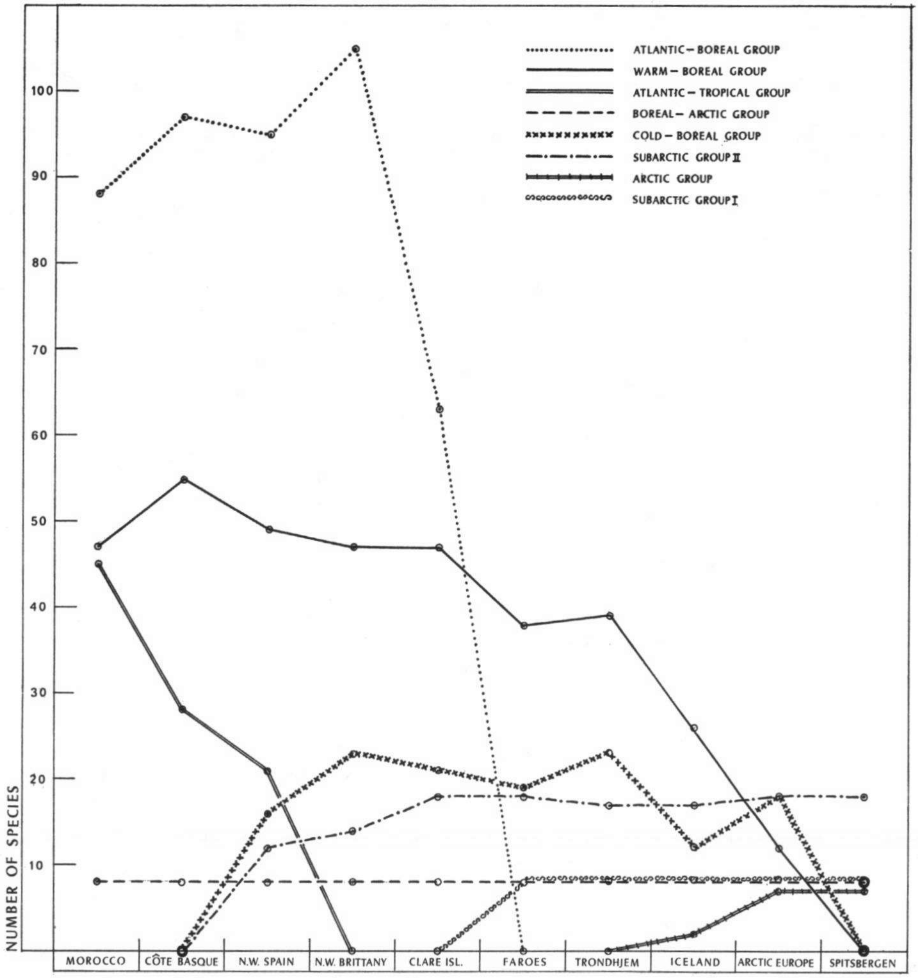

Fig. 7. Graph showing the numbers of species belonging to each arbitrary distribution-group in the areas considered (cf. table 4).

phenomena seem to be more pronounced than along the Spanish northwest coast.

Lami (38, cf. also 17, 19) suggested that the more northern composition of the algal flora of NW. Spain as compared to that of the Côte Basque could be the result of the greater cloud-cover per year in the former region. He thought northern species to be favoured by reduced light-intensities. No data, however, could be brought forward to support these intuitive assumptions. The overwhelming majority of species of both floras are sublittoral. In the sublittoral zone habitats with very diverging light-intensities are always available in such large areas as here considered. The same holds true for the eulittoral zone where, for instance during dry and sunny weather, catastrophic mortalities can ravage the vegatation which later can be reconstituted by recolonization from the sublittoral zone and from shady refuges in the eulittoral zone.

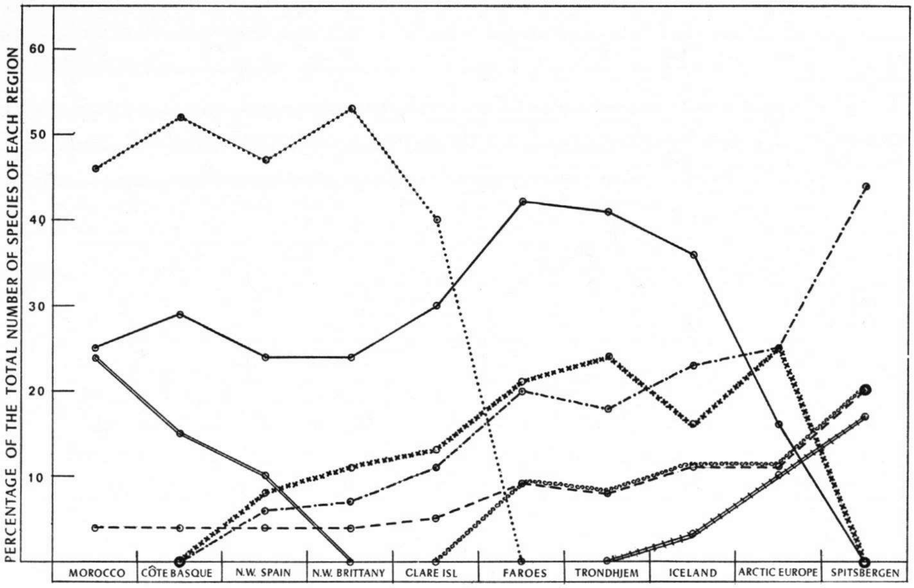

Fig. 8. Graph showing the numbers of species belonging to each arbitrary distribution-group in the areas considered and given as the percentages of the total number of species of each area. For the explanation of the symbols used, cf. fig. 7.

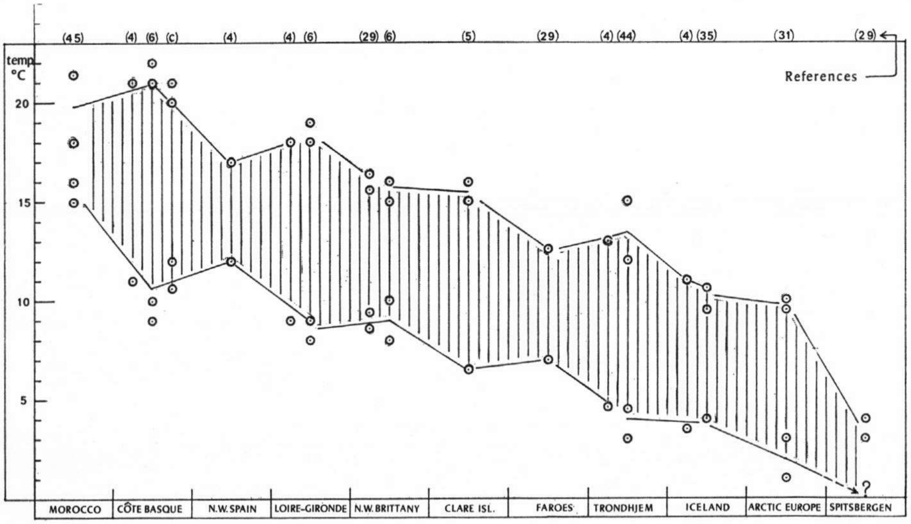

Fig. 9. Graph showing the temperature-ranges of the surface-water in the regions considered.

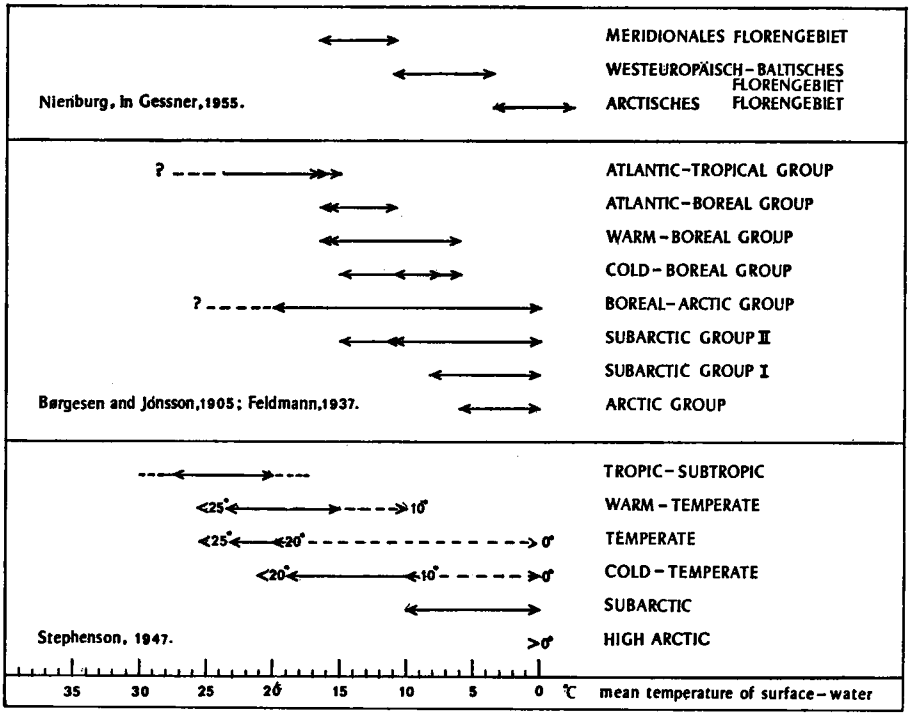

Fig. 10. Arbitrary distribution-groups in relation to the temperatures of the surface-water, according to different authors.

In a review of the literature on marine biogeography of the Pacific coast of North-America Hedgpeth (26) draws attention to the lack of agreement as to the limits of provinces in the temperate regions, a fact which according to him suggests that the resemblances between the areas investigated are perhaps more significant than the differences. According to Hedgpeth the limits of these biogeographic provinces have actually been determined by the 'subjective appraisals of the specialists'.

Scagel (48) describes the gradual transition from the northern to the southern algal flora along the Pacific NW. coast of America in correlation with the gradual change of the marine isotherms. Anomalous, disjunct distributions are correlated with thermal and salinity conditions.

Lewis (40), in a discussion of the distribution of certain marine organisms along the British coasts, points out that there is considerable diversity of range and overlapping of northern and southern species and that there are, consequently, no marked population-bounderies.

We have already mentioned (cf. 2.4) that the usual algal distribution-groups were arbitrarily defined (the groups enumerated in table 3). Moreover, assigning to an investigated flora the epithet of the distribution-group showing the highest percentage of species may lead to curious or contradictory conclusions. Svendsen (53), for example, comes to the conclusion that the flora of Spitsbergen is subarctic as most of its species are subarctic (fig. 7, 8). In fact, as a consequence of the above type of calculations, no flora could be called arctic, however arctic the region geographically might be. When one compares the composition of the algal flora of the Faroes as given in fig. 7 and fig. 8, in both cases one comes to the conclusion that the most important distribution-group is the warmboreal one, followed by the cold-boreal group, and one might characterize this flora as boreal (or rather warm-boreal). However, in fig. 7 it can be seen that in NW. Brittany more cold-and warm-boreal species occur than in the Faroes, a rather significant ıact obscured in fig. 8.

The best result to be expected from this method is that, for instance, the flora of an arctic region as Spitsbergen or northern Siberia (so physico-geographically arctic) can be characterized as arctic, or the flora of a Mediterranean coast as Mediterranean, or of Atlantic southern Europe as Atlantic-South-European (or as Lusitano-African, to use a more sophisticated equivalent). Indeed, the adherents of this method, in defining their distribution-groups, based themselves on such rather reasonable assumptions. In calculating the phytogeographic nature of a flora along these lines one is actually involved in circular reasoning.

Possibly these distribution-groups could have some value as short notions for the geographic distribution of algal species. There are, however, two disadvantages: in the first place the definitions of these groups depend entirely on the subjective appraisals of the various authors, so that there are almost as many systems as authors (cf. fig. 10 in which three such systems are compared; cf. also 26), and in the second place superfluous terminology tends to give more weight to the rather simple information one is trying to communicate.

It is equally unpractical to use the objectively found phytogeographic province in NW. Europe for this purpose, as well because this province is characterized rather by the absence of certain species than by their presence as because the existence of other such provinces is uncertain.

It is our opinion that simple, self-explanatory, descriptive terms are preferable. Such terms are provided by atlases. They can be more or less detailed. A few examples are given in table 5. They help to keep facts and fiction apart.

Acknowledgements. We would like to thank Ir. L. Otto (Royal Netherlands' Meteorological Institute, De Bilt) for help with detection of temperature-data of surface-waters, Prof. Dr. C. G. G. J. van Steenis for critically reading through the manuscript, and Mrs. Y. M. Butler for correcting the English text.

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TABLE 1. Composition of the algal floras here compared. Sublittoral species. The degrees of shading roughly indicate the degree of abundance, according to the following arbitrary scale:

- Very common, often dominant or codominant.
- Very common, but not dominant.
- Common.
- Rare.

	1. Morocco	2. Côte Basque	3. NW Spain	4. Loire-Gironde	5. NW Brittany	6. Clare Island	7. Faroes	8. Trondhjem	9. Iceland	10. Arctic Europe	11. Spitsbergen
Centroceras clavulatum	Very common, often dominant										
Gelidium melanoideum	Very common, often dominant										
Gelidium spinulosum	Very common, often dominant										
Lithophyllum dentatum	Very common, but not dominant										
Valonia utricularis	Very common, but not dominant										
Pseudolithophyllum expansum	Common										
Chaetomorpha pachynema	Common										
Herposiphonia secunda	Common										
Ulva fasciata	Common										
Neoderma tingitanum	Common										
Cystoseira fimbriata	Common										
Rytiphlaea tinctoria	Common										
Platysiphonia miniata	Rare										
Cladophoropsis membranacea	Rare										
Zonaria tournefortii	Rare										
Aglaozonia melanoidea-phase of Cutleria adspersa	Common	Very common, often dominant									
Ctenosiphonia hypnoides	Very common, often dominant	Common									
Liagora viscida	Common	Common									
Colpomenia sinuosa	Common	Rare									
Cryptonemia seminervis	Common	Rare									
Sargassum vulgare	Common	Rare									
Peyssonellia coriacea	Common	Common									
Botryocladia chiajeana	Rare	Rare									
Schimmelmannia schoesboei	Rare	Rare									
Thuretella schoesboei	Rare	Rare									
Chrysymenia ventricosa	Rare	Rare									
Streblocladia collabens	Rare	Rare									
Hypnaea musciformis	Very common, but not dominant	Very common, but not dominant	Rare								

(TABLE 1, continued)	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Gelidium attenuatum	■	■	■								
Leptosiphonia schoesboei	▒	▒	▒								
Phyllaria reniformis	▒	⁛	⁛								
Gymnothamnion elegans	⁛	▒	▒								
Herposiphonia tenella	▒	■	⁛								
Jania longifurca	▒	▒	▒								
Pleonosporium flexuosum	▒	▒	▒								
Ceramium callipterum	⁛	⁛	⁛								
Spathoglossum solierii	⁛	⁛	⁛								
Griffithsia schoesboei	⁛	⁛	⁛								
Gracilaria cervicornis	⁛		⁛								
Cystoseira concatenata	⁛	▒	■								
Laminaria ochroleuca	■		■								
Phyllaria purpurascens	■		⁛								
Grateloupia dichotoma		⁛	⁛	⁛	⁛						
Sauvageaugloia chordariaeformis		⁛	⁛	▒	▒						
Arthrocladia villosa		⁛		⁛	⁛						
Carpomitra costata		⁛			⁛						
Halymenia latifolia			⁛		⁛						
Desmarestia dudresnayi		⁛			⁛	⁛					
Dictyopteris membranacea	■	■	■	■	■	⁛					
Rhodymenia pseudopalmata	■	■	■	▒	▒	▒					
Codium tomentosum	■	■	■	■	▒	▒					
Halopteris scoparia	■	■	■	■	■	⁛					
Cystoseira tamariscifolia	■	■	■	■	▒	▒					
Mesophyllum lichenoides	■	■	■	■	▒	▒					
Acrosorium uncinatum	■	■	■	■	■	■					
Calliblepharis ciliata	■	■	■	■	■	■					
Ceramium ciliatum	■	■	■	▒	■	▒					
Bifurcaria bifurcata	■		■	■	■	▒					
Cystoseira baccata	▒	▒	▒	▒	▒	▒					
Codium adhaerens	▒	▒	▒	??	▒	▒					

(TABLE 1, continued)

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Melobesia membranacea	▓	▓	▓	▓	▓	▓					
Champia parvula	▓	▓	▓	▓	▓	▒					
Jania rubens	▓	▓	▓	▓	▓	▓					
Cladostephus verticillatus	▓	▓	▓	▓	▓	▓					
Chondria dasyphylla	▓	▓	▓	▓	▓	▓					
Dictyota dichotoma	▓	▓	▓	▓	▓	▓					
Gelidium latifolium	▓	▓	▓	▓	▓	▓					
Halurus equisetifolius	▓	▓	▓	▓	▓	▓					
Hypoglossum woodwardii	▓	▓	▓	▓	▓	▓					
Laurencia obtusa	▓	▓	▓	▓	▓	▓					
Ceramium echionotum	▓	▓	▓	▓	▓	░					
Gracilaria verrucosa	▓	▓	▓	▓	▓	▓					
Polysiphonia fruticulosa	▓	▓	▓	▓	▓	▓					
Bornetia secundiflora	▒	▒	▒	▒	▒	▒					
Pterocladia capillacea	▒	▒	▒	▒	▒	▒					
Schizymenia dubyi	▒	▒	▒	▒	▒	▒					
Scinaia furcellata	▒	▒	▒	▒	▒	▒					
Sphaerococcus coronopifolius	▒	▒	▒	▒	▒	▒					
Sphondylothamnium multifidum	▒	▒	▒	▒	▒	▒					
Apoglossum ruscifolium	▒	▒	▒	▒	▒	▒					
Callithamnion tetragonum	▒	▒	▒	▒	▒	▒					
Cladophora laetevirens	?	▓	▓	?	▓	▓					
Corynospora pedicellata	▒	▒	▒	▒	▒	▒					
Cladophora prolifera	▒	▒	▒		░	░					
Radicilingua thysanorhizans		░	░								
Dasya rigidula			░								
Ulva rhacodes			░								
Halymenia bermudensis			░								
Halymenia ulvoidea			░								
Gigartina elegans			░								
Solieria chordalis	░		░	▒	░						
Padina pavonia	▒	▒	▒	▒							

(TABLE 1, continued)

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Gelidium sesquipedale											
Pterosiphonia complanata											
Falkenbergia rufolanosa				??							
Gigartina teedii/ acicularis											
Chondria coerulescens											
Enteromorpha ramulosa											
Gastroclonium ovatum											
Callithamnion tetricum											
Colpomenia peregrina											
Stenogramme interrupta											
Grateloupia filicina											
Halopitys incurvus											
Asparagopsis armata				??							
Codium vermilara				??							
Erythroglossum sandrianum				??							
Gigartina pistillata											
Gracilaria foliifera											
Meredithia microphylla											
Microcladia glandulosa				??							
Spyridia filamentosa				??							
Petroglossum nicaeense				??							
Dilophus spiralis											
Ophidocladus simpliciuscula											
Lophosiphonia reptabunda	??			??							
Ceramium gracillimum											
Gymnogongrus patens											
Pleonosporium borreri											
Pterosiphonia pennata											
Corynospora furcellata											
Zanardinia prototypus											
Cystoseira foeniculacea											
Crouania attenuata											

(TABLE 1, continued)	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Cladophora coelothrix											
Cystoseira myriophylloides											
Cladophora hutchinsiae											
Cladophora pellucida											
Halopteris filicina											
Ceramium flabelligerum											
Cystoseira granulata											
Ptilothamnion pluma											
Gymnogongrus norvegicus											
Antithamnion plumula var. crispum											
Halarachnion ligulatum											
Gymnogongrus griffithsiae											
Taonia atomaria											
Cladophora albida	??			??							
Dasya hutchinsiae											
Compsothamnion thuyioides											
Callymenia reniformis											
Chondria tenuissima											
Brongniartella byssoides											
Griffithsia corallinoides											
Lithophyllum incrustans											
Sphacelaria fusca				??							
Cryptopleura ramosa											
Phyllophora crispa							?				
Callithamnion granulatum				??							
Dermatolithon pustulatum											
Desmarestia ligulata											
Griffithsia flosculosa		?	?								
Gelidium pulchellum/pusillum											
Laurencia pinnatifida											
Saccorhiza polyschides											
Chylocladia verticillata											

(TABLE 1, continued)

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Nitophyllum punctatum											
Callophyllis laciniata											
Lomentaria articulata											
Giffordia granulosa											
Petrocelis cruenta		?		?			?				
Bryopsis plumosa											
Cladostephus spongiosus											
Spermothamnion repens											
Rhodophyllis divaricata											
Callithamnion tetragonum											
Cutleria multifida											
Sauvageaugloia griffithsiana											
Codium fragile											
Rhodochorton floridulum											
Asperococcus turneri (=bullosus)											
Liebmannia leveillei											
Polyneura gmelini											
Polyneura hilliae											
Cylindrocarpus berkeleyi											
Giffordia hincksiae											
Lomentaria clavellosa											
Pterosiphonia parasitica											
Plocamium vulgare											
Sporochnus pedunculatus											
Bonnemaisonia asparagoides											
Polysiphonia elongata											
Striaria attenuata											
Himanthalia elongata											
Ceramium shuttleworthianum				??							
Petalonia zosterifolia											
Eudesme virescens											
Corallina officinalis											

(TABLE 1, continued)	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Polysiphonia macrocarpa/urceolata				??							
Petalonia fascia											
Leathesia difformis											
Monostroma obscurum/fuscum											
Cladophora rupestris											
Sphacelaria cirrosa											
Rhizoclonium riparium											
Chaetomorpha linum											
Ectocarpus arctus											
Ceramium rubrum											
Scytosiphon lomentarius	?										
Lithothamnion polymorphum											
Ahnfeltia plicata											
Laminaria hyperborea											
Polysiphonia brodiaei											
Polyides rotundus											
Halidrys siliquosa											
Chondrus crispus											
Dumontia incrassata											
Polysiphonia nigrescens											
Delesseria sanguinea											
Fucus serratus											
Plumaria elegans											
Spermatochnus paradoxus											
Stilophora rhizodes											
Spongomorpha aeruginosa											
Furcellaria fastigiata											
Cystoclonium purpureum											
Membranoptera alata											
Asperococcus fistulosus											
Rhodymenia palmata											
Laminaria saccharina											

(TABLE 1, continued)

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Pilayella littoralis			■	■	■	■	■	■	■	■	■
Chorda filum			▒	▒	▒	▒	▒	▒	▒	▒	▒
Phycodrys rubens			⁚	⁚	▒	▒	■	■	▒	■	■
Desmarestia aculeata			⁚	⁚	▒	▒	■	▒	▒	▒	■
Spongomorpha 'arcta'			▒	?	▒	▒	▒	▒	▒	▒	?
Dilsea carnosa			▒	▒	▒	▒			⁚	▒	⁚
Mesogloia vermiculata				▒	▒	▒		⁚		▒	??
Laminaria digitata				■	■	■	■	■	■	■	■
Desmarestia viridis				⁚	▒	▒	■	■	▒	▒	▒
Tilopteris mertensii					⁚	⁚		⁚		⁚	
Callithamnion arbuscula						▒	▒	▒	▒	⁚	
Rhodochorton penicilliforme							▒	▒	▒	▒	
Alaria esculenta					▒	■	■	■	■	■	■
Dictyosiphon foeniculaceus					▒	▒	▒	▒	▒	▒	▒
Rhodomela confervoides					▒	▒	▒	▒	▒	▒	■
Chordaria flagelliformis						▒	■	▒	▒	■	■
Ptilota plumosa						▒	■	▒	▒	▒	▒
Phyllophora brodiaei						⁚	▒	▒	▒	▒	■
Chorda tomentosa						⁚	▒	▒	▒	▒	▒
Porphyra miniata							▒	▒	▒	▒	▒
Ptilota pectinata							▒	▒	▒	▒	▒
Chaetopteris plumosa							⁚	▒	▒	■	■
Odonthalia dentata							■	■	▒	▒	▒
Euthora cristata							▒	▒	▒	▒	▒
Halosaccion ramentaceum							▒	▒	■	■	■
Rhodophyllis dichotoma							▒	▒	▒	▒	▒
Turnerella pennyi								▒	▒	▒	
Coilodesme bulligera								⁚	▒	▒	
Sphaerotrichia divaricata										⁚	
Ralfsia deusta									▒	▒	
Phyllaria dermatodea									■	■	■
Laminaria nigripes									▒	▒	⁚
Laminaria solidungula										▒	▒
Sphacelaria arctica										▒	▒
Pantoneura baerii										▒	▒
Dilsea integra										▒	▒
Delamarea attenuata										▒	▒

TABLE 2. Composition of the algal floras here compared. Eulittoral species. See explanation to table 1.

	1. Morocco	2. Côte Basque	3. NW Spain	4. Loire-Gironde	5. NW Brittany	6. Clare Island	7. Faroes	8. Trondhjem	9. Iceland	10. Arctic Europe	11. Spitsbergen
Gelidiella pannosa	■	■	▒								
Caulacanthus ustulatus	■	■	■								
Lithophyllum tortuosum	■	■	■	▒							
Catenella repens	▒	▒	■	■	■	■					
Rivularia bullata	■	■	■	■	■	■					
Nemalion multifidum	▒	▒	▒	▒	▒	▒		⁚			
Callithamnion polyspermum	■	■	■	■	■	■	■	■	■		
Bangia fuscopurpurea	▒	▒	▒	▒	■	■	■	▒	▒	▒	
Lithothamnion Lenormandii	▒	■	■	■	■	■	■	■	▒	▒	
Rhodochorton purpureum	▒	■	■	■	■	■	■	■	■	■	
Rivularia atra	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	
Ralfsia verrucosa	▒	■	■	■	■	■	■	■	▒	▒	
Gigartina stellata	■	⁚	■	■	■	■	■	■	■	▒	
Fucus spiralis	■	⁚	■	■	■	■	■	■	■	⁚	
Fucus vesiculosus	⁚	⁚	■	■	■	■	■	■	■	■	
Blidingia minima	■	■	■	■	■	■	■	■	■	■	▒
Enteromorpha compressa	■	■	■	■	■	■	■	■	■	▒	▒
Hildenbrandia prototypus	⁚	▒	■	■	■	■	■	■	■	■	▒
Spongonema tomentosum		▒	▒	▒	▒	▒	▒	▒	▒	▒	
Ascophyllum nodosum			■	■	■	■	■	■	■	■	
Polysiphonia lanosa			▒	▒	▒	▒	▒	▒	▒	▒	
Pelvetia canaliculata			■	■	■	■	■	■	■	■	
Fucus distichus							■	■	■	■	■

TABLE 3. Distribution groups,
A-E according to Børgesen and Jonsson,
F-G according to Feldmann.

Distribution group	Geographic range
A. Arctic group	Arctic Ocean → N.Norway/S.Iceland
B. Subarctic group	
I	Arctic Ocean → Faroes
II	Arctic Ocean → W.Ireland/Brittany/NW. Spain
C. Boreal-arctic group	Arctic Ocean → Morocco
D. Cold-boreal group	N.Norway/S.Iceland/Faroes → Ireland/ Brittany/NW. Spain
E. Warm-boreal group	N.Norway/S.Iceland → Morocco
F. Atlantic-boreal group	Ireland/W.England/Brittany → Morocco
G. Atlantic-tropical group	SW. France/NW. Spain/Morocco → equator

TABLE 4. Cf. figs. 7 and 8.

Group	Morocco	Côte Basque	NW. Spain	NW. Brittany	Clare Island	Faroes	Trondhjem	Iceland	Arctic Europe	Spitsbergen
Atlantic-tropical	45	28	21	0	0	0	0	0	0	0
%	24%	15%	10%							
Atlantic-boreal	88	97	95	105	63	0	0	0	0	0
%	46%	52%	47%	53%	40%					
Warm - boreal	47	55	49	47	47	38	39	26	12	0
%	25%	29%	29%	24%	30%	42%	41%	26%	16%	
Cold - boreal	0	0	16	23	21	19	23	12	18	0
%			8%	11%	13%	21%	24%	16%	25%	
Boreal - arctic	8	8	8	8	8	8	8	8	8	8
%	4%	4%	4%	4%	5%	9%	8%	11%	11%	20%
Subarctic II	0	0	12	14	18	18	17	17	18	18
%			6%	7%	11%	20%	18%	23%	25%	44%
Subarctic I	0	0	0	0	0	8	8	8	8	8
%						9%	8%	11%	11%	20%
Arctic	0	0	0	0	0	0	0	2	7	7
%								3%	10%	17%

TABLE 5.

Species	Distribution-group, according to the definitions of 1) Jónsson/Børgesen/Feldmann 2) Nienburg 3) Stephenson	proposed (but by no means the only possible) denominations.
Dilsea integra	1) Arctic 2) Arctisch 3) Subarctic	Arctic (Arctic-Europe, Spitsbergen, Greenland).
Coilodesme bulligera	1) Subarctic 2) Westeuropäisch-baltisch-arctisch 3) Subarctic	N. European-Arctic (Trondhjem → Arctic Europe → Spitsbergen)
Laminaria saccharina	1) Subarctic 2) Meridional-westeuropäisch-baltisch-arctisch 3) Cold-temperate	SW. European-Arctic (NW. Spain → Spitsbergen)
Spermatochnus paradoxus	1) Cold-boreal 2) Meridional-westeuropäisch-baltisch 3) Cold-temperate	Mediterranean and W. European (Mediterranean and Brittany → Trondhjem).
Chondrus crispus	1) Cold-boreal 2) Meridional-westeuropäisch-baltisch 3) Cold-temperate	SW. - N. European (NW. Spain → Arctic Europe)
Ceramium rubrum	1) Boreal-arctic 2) Meridional-westeuropäisch-baltisch-arctisch 3) Temperate	Mediterranean and NW. African-Arctic-European (Mediterranean and NW. Africa → Spitsbergen)
Plocamium vulgare	1) Warm-boreal 2) Meridional-westeuropäisch-baltisch 3) Temperate	Mediterranean and NW. African- W. European (Mediterranean and NW. Africa → Iceland)