

## The phytogeography of *Cladophora* (Chlorophyceae) in the northern Atlantic Ocean, in comparison to that of other benthic algal species

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**ABSTRACT:** About 43 *Cladophora* species inhabit the coasts of the northern Atlantic Ocean. These can be subdivided into seven distribution groups: (a) the tropical western Atlantic group (16 species); (b) the warm temperate Mediterranean-Atlantic group (9 species); (c) the warm temperate North American group (1 species); (d) the Arctic group (1 species); (e) the amphiatlantic tropical to warm temperate group (7 species); (f) the amphiatlantic tropical to temperate group (4 species), and (g) the amphiatlantic temperate group (5 species). These groups agree with general phytogeographic patterns. Thus, the high numbers of species restricted to the tropical western Atlantic region and the warm temperate Mediterranean-Atlantic region are in agreement with the richness and high degree of endemism of these regions. The fact that all species occurring in northeast America also occur in Europe agrees with the high floristic similarity of the boreal areas in America and Europe. The sediment coasts of the Carolinas are an efficient barrier to the south-north dispersal of benthic algae. The temperature bound phytogeographic limits are set in most cases by the species ability to survive adverse temperatures; for "northern" species to survive a high summer temperature in the south, and for "southern" species to survive a low winter temperature in the north. The limits in the Arctic region are all set by the species ability for sufficient growth and reproduction in summer. Conversely, only few northern species have a southern limit which is set by a winter temperature that is not too high for sufficient growth and reproduction. Most species of this group are winter-annuals at their southern limit, and summer-annuals at their northern limit. A comparatively small number of species with a tropical-to-warm temperate distribution have a northern limit at temperate latitudes which is set by a sufficiently high summer temperature for growth and reproduction. A high proportion of this group are lagoonal or quiet water species, which profit by higher summer temperatures in sheltered waters. *C. vagabunda* is an example. *C. rupestris* and *C. sericea* have an amphiboreal distribution and also occur in the southern temperate belt. They probably used a Pleistocene temperature drop to disperse, through the Atlantic along the African coast, from one hemisphere to the other. In the Pacific temperatures were not sufficiently low for this dispersal; and hence these two species reached the Pacific probably by way of the Bering Strait.

### INTRODUCTION

The completion of my work on a taxonomic revision of the northeastern American and Caribbean marine species of *Cladophora* (van den Hoek, in prepara-

tion) offered the opportunity to unravel the hitherto confused distribution patterns within this taxonomically difficult genus for the northern Atlantic Ocean. For this purpose I used distribution data compiled in my "Revision of the European species of *Cladophora*" (van den Hoek, 1963). I was interested in seeing whether or not the distribution patterns of the individual species would be in accordance with general phytogeographic patterns, and whether or not these patterns could be explained by the temperature regime, by the existence of phytogeographic barriers, and by historical factors.

In an earlier paper (van den Hoek, 1975) I gave a possible subdivision into phytogeographic provinces of the northern Atlantic Ocean. The main conclusions of this paper will be summarized below. This paper also cites most literature from which distribution data of species belonging to genera other than *Cladophora* were borrowed.

#### THE PHYTOGEOGRAPHIC SUBDIVISION OF THE NORTHERN ATLANTIC OCEAN

On the basis of mutual similarity in species composition (as expressed by Jacard's similarity index) five regions could be demarcated along the coast of the northern Atlantic Ocean, two of which were subdivided into provinces. The regions and provinces are pictured in Figure 1. When comparing Figure 1 with Figure 2, a correlation between the temperature regime and the pattern of phytogeographic regions is evident. This correlation is diagrammatically pictured in Figure 3. There are apparently striking differences in the latitudinal ranges of comparable climatic regions on both sides of the ocean. The much vaster extension of the temperate regions along the eastern Atlantic coast as compared with that along the western Atlantic coast, is caused by the system of currents. The Norwegian current, the northeast extension of the Gulf Stream, brings relatively warm water as far north as northern Norway and Murmansk. The major portion, however, of the Gulf Stream stays within the subtropical gyre, and opposite the Iberian Peninsula it turns towards the south as the Canarian current. An offshore component (caused by the Coriolis effect) of this southbound current, causes the upwelling of colder water along the Iberian and North African coast, thus extending the warm temperate region far to the south.

The rich flora of the tropical western Atlantic region (Figs 1, 3: B) and of the warm temperate Mediterranean-Atlantic region (Figs 1, 3: C, D, E) probably evolved to about their present composition towards the beginning of the Pleistocene, some two million years ago, after the late Tertiary (Pliocene) formation of the Isthmus of Panama and the filling of the Mediterranean after a period of drying up.

The Pleistocene ice-ages are probably responsible for a considerable impoverishment of the flora in the cold temperate Atlantic-boreal region (Figs 1, 3: F, G) and of the Arctic region (Figs 1, 3: H, J). The Pleistocene temperature fluctuations forced the flora of these regions to vast latitudinal shifts which caused the extinction of many species. This effect was possibly enhanced by latitudinal barriers, namely the

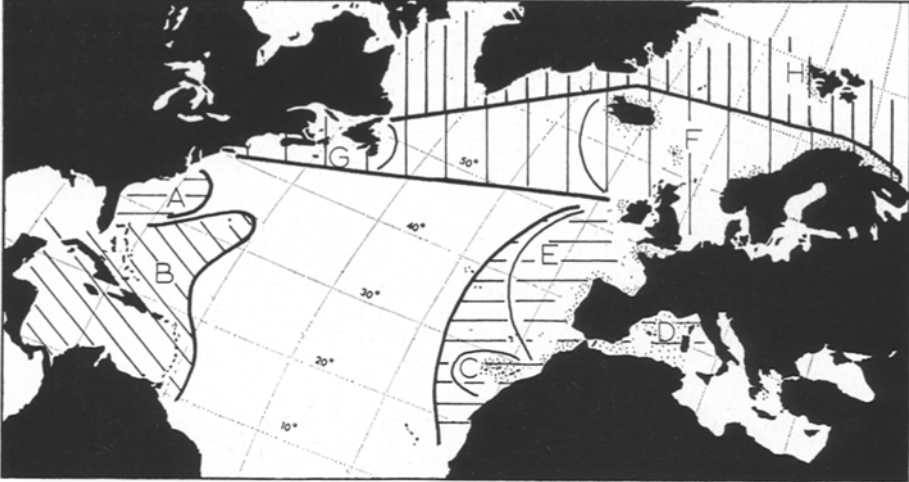


Fig. 1: Phytogeographic regions and provinces along the Northern Atlantic coasts. A, warm temperate Carolina region; B, tropical Western Atlantic region; C, D, and E, Canaries province, Mediterranean province and Lusitania province of warm temperate Mediterranean-Atlantic region, respectively; F, G, Eastern province and Western province of cold temperate Atlantic-Boreal region, respectively; H, J, Arctic region. (After van den Hoek, 1975)

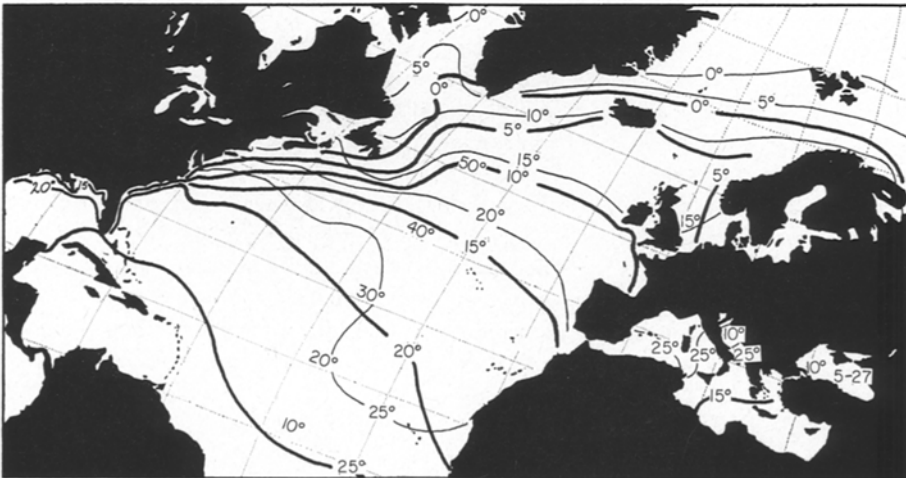


Fig. 2: Surface temperatures in August and February of the Northern Atlantic. — surface temperatures in August; - - - surface temperatures in February. (After van den Hoek, 1975)

lowland sediment shores of the Carolinas along the American coasts, and the North Sea and British Isles along the European coasts.

There is much evidence that the Pacific Ocean underwent much smaller temperature drops during Pleistocene, and that consequently the cold temperate boreal

flora along its coast is twice to thrice as rich in species as the Atlantic cold temperate boreal flora (cf. Briggs, 1974; van den Hoek, 1975).

It is likely that the poverty of the warm temperate Carolina region is caused by its sediment coasts that are inhospitable to most benthic algae, and to the very unstable temperature regime of the inshore waters. Only scattered deep sublittoral offshore reefs which are bathed, in winter, by warm tropical water (Fig. 2) bear a relatively rich benthic algal flora composed of predominantly tropical western Atlantic species (van den Hoek, 1975; Schneider, 1976).

#### THE PHYTOGEOGRAPHY OF *CLADOPHORA* IN THE NORTH ATLANTIC, IN COMPARISON TO THAT OF OTHER BENTHIC ALGAL SPECIES

In comparing the distribution patterns of individual species one should realize that these may, but need not coincide with phytogeographic regions or provinces. The boundaries between these regions are more or less steep floristic discontinuities, that is regions where many species drop out and new species appear, and which need not but may coincide with barriers to dispersal such as the Atlantic Ocean and the continents. Thus in north to south direction along the Atlantic coasts the boundaries between the regions are narrow, floristically discontinuous areas.

Once I had delimited these phytogeographic regions and provinces, I could use these to describe, and possibly to explain, the distribution patterns of the individual species.

43 *Cladophora* species inhabit the coasts of the Northern Atlantic. I distinguished seven distribution-groups: (1) the tropical Western Atlantic group; (2) the warm temperate Mediterranean-Atlantic group; (3) the warm temperate North American group; (4) the Arctic group; (5) the amphiatlantic tropical-to-warm temperate group; (6) the amphiatlantic tropical-to-temperate group; (7) the amphiatlantic temperate group.

(1) The tropical Western Atlantic group (Fig. 4: nrs 1-3, 5, 6, 11). This is the largest group: 15 species that are endemic to the tropical Western Atlantic Region (Fig. 1: B), and probably largely limited to the Caribbean. However, the rocky coasts of tropical Brazil need to be more thoroughly searched for them.

The very high proportion of endemic *Cladophora* species accords with the richness, the great endemism (ca. 55 % of the species) and hence the high degree of individuality of this phytogeographic region (van den Hoek, 1975).

The following nine endemic species have a rather general distribution over the Caribbean:

*C. brasiliensis* Martens, *C. catenata* (L.) Kütz. (= *C. fuliginosa* Kütz), *C. crispula* Vickers, *C. montagneana* Kütz (= *C. delicatula* Montagne), *C. howei* Collins, *C. jongiorum* van den Hoek (1969), *C. uncinata* Boergesen, and two new, as yet undescribed species.

For a definite conclusion about the possible endemic nature of these nine species we need, however, to know the *Cladophora* species occurring along the West African tropical coasts better.

Two species have a local distribution and are each restricted to one island, namely *C. intertexta* Collins (Jamaica) and *C. longicellulata* van den Hoek (1969) (Bermuda). *C. longicellulata*, which grows in shady localities around the low water line, is a very distinct species belonging to the section *Longiarticulatae* (van den Hoek, 1963). It has always been identified as *C. catenifera* Kütz., a synonym of *C. pellucida* (Huds.) Kütz., which is another distinctly different species of the same section (van den Hoek, 1969).

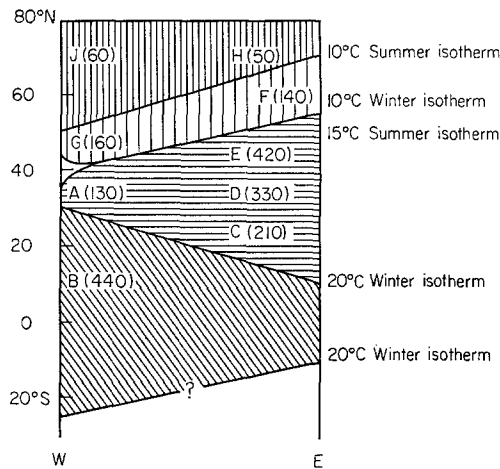


Fig. 3: Diagram of the Northern Atlantic Ocean, demonstrating the striking differences in latitudinal extension of the same climatic regions on both sides of the Atlantic Ocean, and the approximate isotherms that coincide with boundaries of regions. A–G: regions and provinces depicted in Figure 1. Between brackets: numbers of the benthic algal species considered in van den Hoek (1975)

Only single collections are available of four new, as yet undescribed species, so that one can only speculate that these are also local endemics.

(2) The warm temperate Mediterranean – Atlantic group (Fig. 4, nrs 7–10, 12). It consists of 7 species that are endemic to the warm temperate Mediterranean – Atlantic region (Fig. 1: C, D, E): *C. hutchinsiae* (Dillw.) Kütz., *C. lehmanniana* (Lindenb.) Kütz., *C. retroflexa* (Bonnem. ex Crouan) van den Hoek, *C. battersii* van den Hoek, *C. echinus* (Bias.) Kütz., *C. parriaudii* van den Hoek, and *C. nigrescens* Zanard. ex Frauenfeld. *C. pellucida* (Huds.) Kütz.\* also occurs in the warm temperate South Africa Region, and *C. feredayi* Harv. in warm temperate Tasmania.

\* On the basis of cultural evidence, *C. pseudopellucida* van den Hoek (1963) must be merged in *C. pellucida*.

*C. echinus* [a close relative of the freshwater *C. aegagropila* (L.) Rabenh.] and *C. nigrescens* are restricted to the Mediterranean.

The rather high proportion of endemic species of this group is in accordance with the generally high degree of endemism of the benthic algal flora (about 40%) in the Mediterranean – Atlantic region. However, both the general endemism and the endemism within the genus *Cladophora* are lower than those in the tropical western Atlantic Region.

*C. battersii* and *C. retroflexa* are highly specialized species, belonging to the sections *Rupestres* and *Longiarticulatae*, respectively. Both species have stiff, curved filaments with which they grow entangled in other algae or hooked around *Zostera rhizomes*. They lack rhizoids. The species are restricted to a few sheltered bays and sea-inlets. They seem to reproduce only by fragmentation. *C. retroflexa* in its morphology closely approaches *C. prolifera*, from which species it differs by the lack of rhizoids, the absence of zoids, and the hooked apices. Both species are dark brown when dried.

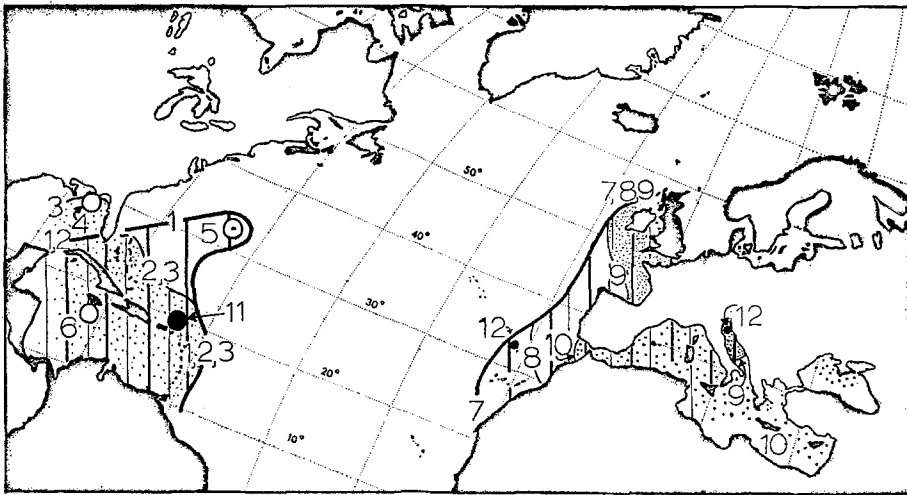


Fig. 4: Distribution of *Cladophora* species of the tropical Western Atlantic group (nrs. 1–3, 5, 6, 11), the warm temperate North American group (4), and of the warm temperate Mediterranean-Atlantic group (nrs. 7–10, 12). 1. *C. howei*, *C. uncinata*, *C. catenata*; 2. *C. crispula*, *C. brasiliana*; 3. *C. jongiorum*; 4. *C. blomquistii*; 5. *C. longicellulata*; 6. *C. intertexta*; 7. *C. pellucida*; 8. *C. hutchinsiae*, *C. lehmanniana*; 9. *C. retroflexa*, *C. battersii*; 10. *C. echinus*, *C. nigrescens*; 11. *C. att. ad aegagropila*; 12. *C. feredayi*

(3) The warm temperate North American group (Fig. 4, nr. 4). This group contains only one species, *Cladophora blomquistii*, an inedited species of Aziz and Humm. It is restricted to a few lagoons in the north-eastern corner of the Gulf of Mexico, along the coast of Florida. It is interesting that this species is a New World counterpart of *C. retroflexa*: it is a free-living lagoonal form that is closely allied to *C. prolifera*. It differs, however, markedly from *C. prolifera*

as well as *C. retroflexa*. As in *C. retroflexa*, the rhizoids are poorly developed and it seems to lack reproduction by zooids.

The warm temperate Carolina region of which the northern part of the Gulf of Mexico is probably a westward extension (Briggs, 1974; van den Hoek, 1975) is poor in benthic algal species (cf. Fig. 3), because its sediment coasts and its vast bar built estuarine areas are inhospitable to most benthic algae. It is interesting that the sole endemic *Cladophora* species – *C. blomquistii* – of this region is a specialized lagoonal form. All other *Cladophora* species in this region are tropical-to-temperate species with wide distributions (Figs 5, 6, 7). In general, the warm temperate Carolina region has a low degree of endemism (ca. 5 %) (cf. Earle, 1969; van den Hoek, 1975; Schneider, 1976). The majority of these recently discovered endemic species occur on offshore reefs which are bathed, during winter, by warm tropical water of the Gulf Stream. These reefs are predominantly inhabited by species which also occur in the tropical western Atlantic region (Fig. 1) (Schneider, 1976).

(4) The Arctic group (Fig. 5, nr. 6). Only one species seems to be entirely restricted to the Arctic Region, namely *Cladophora pachyderma* (Kjellm.) Brand, a species that seems to occur only north of the 5 °C summer isotherm (but the number of collections is too limited, cf. van den Hoek, 1963). It is interesting that a closely allied species, *C. incompta* Hooker et Harvey, is from Tierra del Fuego (about on the 8 °C summer isotherm). Both species belong to the section Affines (cf. van den Hoek, 1963). *C. incompta* is much thicker than *C. pachyderma* (diameter of branches 70–120 µm versus 20–40 µm), but apart from this the morphologies of both species are alike. The section Affines, as to its marine species, is probably Arctic-Antarctic (*C. basiramosa* Schmidle, which also belongs to this section, is a freshwater species known from Europe). The Arctic region has a low degree of endemism: about 5 % (van den Hoek, 1975).

(5) The amphiatlantic tropical-to-warm temperate group (Fig. 5, nrs 1–5). The remaining 15 species have all more or less wide distributions and are all amphiatlantic. Seven of these form the amphiatlantic tropical-to-warm temperate group, namely: *C. liebetruthii* Grun., *C. ordinata* (Boergesen) nov. comb.\*, *C. coelothrix* Kütz., *C. socialis* Kütz., *C. prolifera* (Roth) Kütz., *C. laetevirens* (Dillw.) Kütz., and *C. vadorum* (Aresch.) Kütz. Six of the seven species (*C. vadorum*, *C. laetevirens*, *C. prolifera*, *C. socialis*, *C. coelothrix*, *C. ordinata*) are likely to have a tropical-to-warm temperate cosmopolitan distribution.

Four of these seven species are lagoonal species, three species – *C. socialis*, *C. coelothrix*, and probably *C. liebetruthii* – occur on open coasts but may also develop massively in lagoonal habitats. *C. socialis* and *C. liebetruthii* are quite common species in the deeper parts of the coral reef of Curaçao, where they occur down to a depth of 65 m. They are probably shade species capable of growing well in

\* I consider *Willeella ordinata* Boergesen a species of the genus *Cladophora*, for which I propose the new combination *Cladophora ordinata* (Boerg.) nov. comb. (cf. van den Hoek & de Rios, 1972).

murky lagoonal water as well as in the dusk of the deep coral reef (van den Hoek *et al.*, 1978). One species – *C. vadorum* – grows exclusively in lagoonal habitats where it may form extensive floating masses.

Algal species with wide phylogeographic distributions are often species capable of developing massively in sheltered or lagoonal habitats, which, at higher latitudes, may warm up considerably during summer. By comparing the northern boundaries

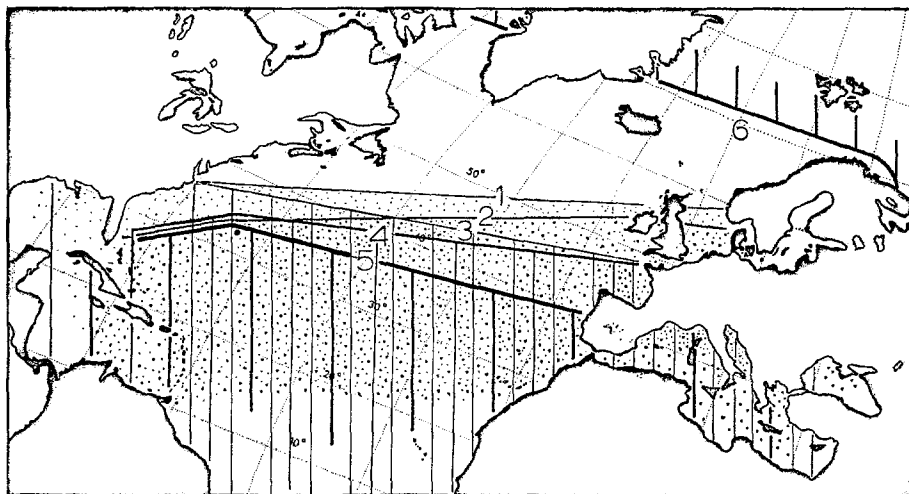


Fig. 5: Distribution of *Cladophora* species of the amphiatlantic tropical-to-warm-temperate group (nrs 1–5) and of the Arctic group (nr. 6). 1. *C. vadorum*; 2. *C. laetevirens*; 3. *C. prolifera*; 4. *C. coelothrix*, *C. socialis*; 5. *C. liebetruhii*; 6. *C. pachyderma*

of these species with the summer- and winter-isotherms (cf. Fig. 5 with Fig. 2) we can obtain suggestions about the factors that set these boundaries. This is possible because the annual temperature fluctuation along the western Atlantic coast is much more pronounced (up to more than 20 °C) than on the eastern Atlantic coast (often c. 6 °C).

The most distinct correlation is that between the 10 °C, or rather the 9 °C, winter isotherm and the northern limit of *C. prolifera*. This is understandable, because this species at its northernmost limit is restricted to shady, low – littoral pools or to the sublittoral of open, rocky, coasts. In the Carolinas it grows, at ca. 34 °N latitude, on offshore and nearshore, sublittoral, rocky reefs that are bathed by water not colder than 10 °C (Williams, 1951; Schneider, 1976). It is likely, therefore, that this northern limit of *C. prolifera* is set by its capacity to survive winter temperatures not lower than 8–10 °C. The summer temperature on the Brittany coast of about 17 °C is high enough for sufficient growth and reproduction. On the Carolina coast the temperature rises to a tropical value of 25 °C in summer. At more southern latitudes, for instance in the Mediterranean, *C. prolifera* also occurs in sheltered sunny bights. It probably avoids such sheltered bights at its northernmost limit, because these cool down too much during winter (and not be-



cause they warm up too much during summer). The Carolina lagoonal waters at 35 °N cool down to about 5 °C in winter, which is too low for this species.

This inshore lagoonal water along the Carolina coast cools down during winter to temperatures much lower than the off-shore surface water (5 °C versus 10 °C nearshore and 20 °C offshore at 34 °N (Fig. 2; cf. Schneider, 1976)). In summer the temperatures in these lagoonal waters may rise as high as 33 °C (25 °C in offshore water) (cf. van den Hoek, 1975). This is probably the reason why the tropical-to-warm temperate species *C. socialis* and *C. coelothrix* have their northern limit on the American coast in Florida, south of that point where in winter surface temperatures of the lagoons may drop down to temperatures not lower than 8 °C. On the European coasts their northern limit lies roughly at the same point as that of *C. prolifera*, where winter surface temperatures do not drop below 8–10 °C. So, on both Atlantic coasts the northernmost limit seems to be set by both species' inability to survive a surface winter temperature lower than about 8 °C. The species are not limited in their distribution by summer temperatures too low for growth and reproduction: for in that case both species could be expected to occur as far north as New Brunswick (c. 45 °N), where the summer surface temperatures reach about the same values as those in Brittany and southern England, where the species have their northern European limit.

It is interesting that the difference in habitat of *C. prolifera* enables this species to have, along the American coast, a much more northern limit than *C. coelothrix* and *C. socialis*: the temperatures bathing the nearshore and offshore reefs where it occurs are much higher (10 °C and 20 °C, respectively) in winter than those of the inshore lagoons (ca. 5 °C) at 34 °N where *C. socialis* and *C. coelothrix* could be expected, provided the winter temperatures were not too low. However, both latter species are not strictly lagoonal but also occur on open coasts. *C. socialis* is known to have a wide depth range in coral reefs of Curaçao, where it has been observed down to 65 m (van den Hoek *et al.*, 1975, 1978). Possibly these taxonomically difficult species have been overlooked so far on the offshore reefs of the Carolinas.

The distribution of *C. laetevirens* along the coasts of the British Isles and the North Sea suggests that its northernmost limit is set here by the 15 °C summer-isotherm, i.e. by a minimum temperature for sufficient growth and reproduction. Apparently it can survive the minimum winter temperatures of about 3 to 5 °C in the southern part of the North Sea. If these low temperatures are also this species' minimum temperatures then, again, this would push its northern limit considerably back to the south along the American coast.

It is likely that its winter temperature minimum is situated somewhere along the Carolina coasts (at about 35 °N), but that it is not to be found there because suitable rocky substrates are rare and therefore the northernmost limit is situated in Southern Florida.

The same is true for *C. liebetruhii*, whose northern limit is roughly set by the 11 °C winter-isotherm in the Mediterranean. In the shallow coastal water along the American coast this point is situated near 30 °N.

In the Atlantic Ocean, *C. ordinata* is only known from two localities, one on the coast of Venezuela (van den Hoek & de Rios, 1972) and one on the coast of

Ghana (Lawson & Price, 1969). It is also known from South Africa, India, and Japan, and this latter occurrence suggests that it is tropical-to-warm temperate (van den Hoek & de Rios, 1972).

The last species of this group, *C. vadorum*, reaches the northernmost limits within this distribution group: along the American coasts at 35 °N, and along the European coasts at 60 °N. *C. vadorum* is an exclusively estuarine and lagoonal species, which forms extensive floating masses in quiet water. Therefore the nature of the Carolina coast, where lagoons abound, is not adverse to this species. Its northern limit roughly coincides with the 5 °C winter-isotherm. Probably it can stand still lower temperatures, as the shallow waters where this species abounds tend to closely follow the air temperature.

Summarizing, two factors cooperate to push back towards the tropics the northern limits of four of these seven tropical-to-warm temperate species along the American coast: firstly the far southward shift of low winter temperatures, particularly in shallow inshore, lagoonal waters, secondly the inhospitable nature of the sediment substrates along the American warm temperate coasts.

The same distribution pattern – extension into warm temperate water along the European coast, and restriction to the tropics along the American coast – is shown by a considerable number of other amphiatlantic benthic algal species, namely at least 27 species which do not present taxonomic difficulties. These 27 species have their northernmost limit along the American coast at about 25 °N, of which 18 species have their northernmost limit in Europe between 40–45 °N, and 9 species between 45–55 °N.

The following species have their northern limit in Europe between 40–45 °N: *Amphiroa rigida* Lamour., *Coelothrix irregularis* (Harv.) Børg., *Centroceras clavulatum* (C. Ag.) Mont., *Chrysymenia ventricosa* (Lamour.) J. Ag., *Digenia simplex* (Wulf.) C. Ag., *Dipterosiphonia ringens* (Schousb.) Falk., *Gracilaria armata* (C. Ag.) J. Ag., *Gracilaria cervicornis* (Turn.) J. Ag., *Griffithsia schousboei* Mont., *Gymnothamnion elegans* (Schousb.) J. Ag., *Halimeda tuna* (Ell. & Sol.) Lamour., *Halodictyon mirabile* Zanard., *Herposiphonia secunda* (C. Ag.) Ambr., *Hydroclathrus clathratus* (Bory) Howe, *Platoma cyclocolpa* (Mont.) Schm., *Sargassum vulgare* C. Ag., *Valonia macrophysa* Kütz., *Wrangelia penicillata* C. Ag.

The following species have their northern limit in Europe between 45–55 °N: *Catenella repens* (Lightf.) Batt., *Ceramium codii* (Rich.) Feldm. – Maz., *Crouania attenuata* (Bonnem.) J. Ag., *Gracilaria compressa* (C. Ag.) Grev., *Grateloupia dichotoma* J. Ag., *Helminthocladia calvadosii* (Lamour.) Setch., *Laurencia obtusa* (Huds.) Lamour., *Padina pavonia* (L.) Lamour., *Pterocladia capillacea* (Gmel.) Born. & Thur.

One species – *Nitophyllum punctatum* (Stackh.) Grev. – even has its northern European limit at 60 °N.

An attractive explanation for this restriction of so many species to tropical waters in America and their far extension into temperate waters in Europe is the effectiveness of the warm temperate Carolina region as a phytogeographic barrier against the northward dispersal of potentially warm temperate species.

Distribution data suggest that two of the seven *Cladophora* species of this group

succeeded in passing this barrier and reaching a far more northern point along the American coast than the other five species, but for two different reasons: *C. prolifera* because it succeeded in using the scattered sublittoral reefs that are bathed, during winter, by sufficiently warm and, as to temperature, stable water; *C. vadorum* because it is a lagoonal species that is particularly well adapted to the prevailing lagoonal habitat of this region of bar-built estuaries, and which thus could reach its northernmost temperature limit, in this case a roughly 2–5 °C winter temperature.

At least 20 well identifiable benthic algae have the same distribution pattern as *C. prolifera*, and these apparently succeeded, after the last glaciation, in penetrating into this adverse region by settling on the subtidal reefs on the shelf. Of these 19 the following species have their northern limit on European coasts between 40 °N and 45 °N: *Anadyomene stellata* (Wulf.) C. Ag., *Caulerpa prolifera* (Forssk.) Lamour., *Halymenia floresia* (Clem.) C. Ag., *Heterosiphonia wurdemannii* (Bail.) Falk., *Valonia utricularis* C. Ag., *Zonaria tournefortii* (Lamour.) Mont., and the next ones between 45 °N and 55 °N: *Ceramium gracillimum* (Kütz.) Griff. et Harv., *Comptoshamnion thyooides* (Sm.) Schm., *Dasya ocellata* (Grat.) Harv., *Dictyopteris membranacea* (Stackh.) Batt., *Dictyota dichotoma* (Huds.) Lamour., *Sporochnus pedunculatus* (Huds.) C. Ag.

Species belonging to this distribution group that also grow in the intertidal belt of a rocky pier at Cape Lookout, such as *Bachelotia antillarum* (Grun.) Gerloff, *Codium decorticatum* (Woods.) Howe, *Dictyota dichotoma* (Huds.) Lamour., *Gigartina acicularis* (Wulf.) Lamour., *Herposiphonia tenella* (C. Ag.) Ambr., *Hypnea musciformis* (Wulf.) Lamour., *Jania rubens* (L.) Lamour., *Sphacelaria furcigera* Kütz., *Sphacelaria tribuloides* Menegh. are probably capable after a severe winter of recolonizing the lower intertidal belt from the sublittoral reefs.

No other benthic algal species are known with a distribution pattern comparable to that of *C. vadorum*. The obvious reason is that taxonomically difficult genera as *Enteromorpha* and *Ulva*, which contain such estuarine-lagoonal species, have not been considered in this study.

(6) The amphiatlantic tropical-to-temperate group (Fig. 6). The four species which constitute this group are estuarine-lagoonal: *C. liniiformis* Kütz. and *C. globulina* Kütz. are completely estuarine-lagoonal, whereas *C. vagabunda* (L.) van den Hoek and *C. dalmatica* Kütz. also occur on open coasts.

The northern limit of *C. liniiformis* coincides roughly with the 10 °C summer isotherm, the estuarine form of *C. vagabunda* with the 13 °C summer isotherm, and *C. dalmatica* and the open coast form of *C. vagabunda* with the 15 °C summer isotherm. The number of collections of *C. globulina*, a species which has undoubtedly often been confused with *Rhizoclonium riparium*, is too limited for generalizations. *C. globulina* also grows in fresh water; it is the only *Cladophora* species known to occur both in freshwater and the sea.

Contrary to the previous group, the northernmost limits of the present species are not set by minimum winter temperatures, but by minimum summer temperatures, that is by sufficiently high temperatures for growth and reproduction in the vegetation period. Apparently all four species are capable of surviving severe

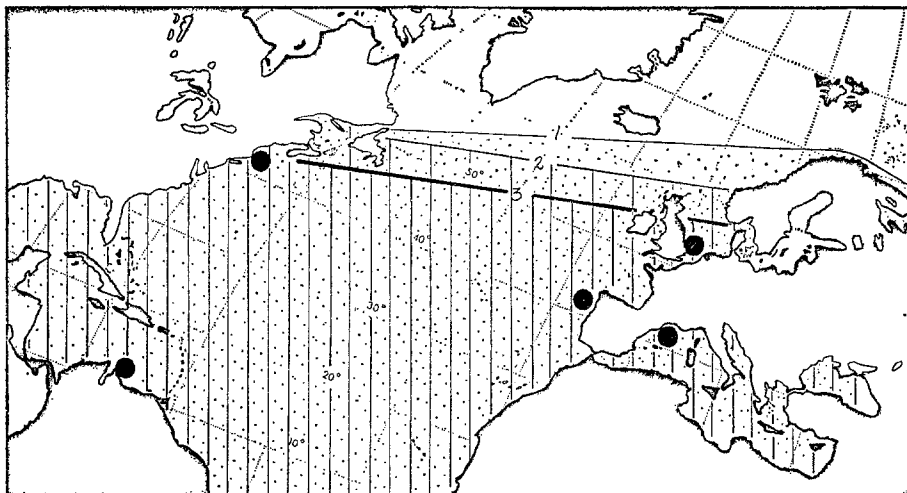


Fig. 6: Distribution of *Cladophora* species of the amphiatlantic tropical-to-temperate group (nrs 1–3). 1. *C. liniformis*; 2. *C. vagabunda*, estuarine form; 3. *C. vagabunda*, open coast form and *C. dalmatica*; 4. (dots) *C. globulina*

winter conditions, because on the American coasts they reach the 0 °C winter isotherm, and two of them even live to the north of it, where considerable ice formation occurs along the northern coast of Nova Scotia, in the Gulf of St. Lawrence, and along the coast of Newfoundland (cf. Stephenson & Stephenson, 1972, p. 81–94). This is also the reason why the estuarine form of *C. vagabunda* has a more northern limit than the open coast form: the summer temperatures of embayments and lagoons where this form occurs may reach considerably higher summer temperatures (up to c. 25 °C) than the open ocean water and it can survive the lower winter temperatures.

*C. dalmatica*, *C. vagabunda*, and *C. liniformis* share their distribution pattern with at least 16 other well identifiable benthic algal species, of which a striking proportion – 7 species – are estuarine or quiet-water species that can profit by higher summer temperatures than those of the open sea. A large proportion of these species (14) have a northern limit that roughly coincides with the 15 °C summer isotherm of the open sea, namely *Antithamnion cruciatum* (C. Ag.) Näg., *Champia parvula* (C. Ag.) Harv., *Chondria dasyphylla* (Woodw.) C. Ag., *Derbesia tenuissima* J. Ag., *Gymnogongrus griffithsiae* (Turn.) Martius, *Scinaia furcellata* (Turn.) Biv., and the marine-estuarine/lagoonal species *Bryopsis hypnoides* Lamour., *Chondria tenuissima* (Good. & Woodw.) C. Ag., *Dasya baillouviana* (Gmel.) Mont., *Eudesme zosteræ* (J. Ag.) Kyl., *Gracilaria foliifera* (Forssk.) Børg., *Gracilaria verrucosa* (Huds.) Papenf., *Monostroma oxyspermum* (Kütz.) Doty, *Spyridia filamentosa* (Wulf.) Harv. The intertidal estuarine species *Bostrychia scorpioides* (Gmel.) Mont. also belongs to this group.

The northern limit of *Gelidium crinale* (Turn.) Lamour. roughly coincides with the 13 °C summer isotherm.

All these species must be capable of surviving, along the American coasts, much lower winter temperatures (c. 0 °C, or lower in lagoons) than on the European coasts (c. 5–8 °C). The intertidal species *Bostrychia scorpioides* and *Gelidium crinale* are also subject to still lower air temperatures on the American coasts.

(7) The amphiatlantic temperate group (Fig. 7, nrs 1–4). This group contains *C. rupestris* (L.) Kütz., *C. sericea* (Huds.) Kütz., *C. albida* (Huds.) Kütz., *C. ruchingeri* (Ag.) Kütz., and *C. pygmaea* Rke. The species are widely distributed over the warm temperate and cold temperate regions in the Atlantic Ocean. *C. rupestris* even extends into the Arctic Region (cf. Fig. 7 with Fig. 1).

The southern limit of *C. sericea* is roughly situated on the 12 °C winter isotherm. This limit is apparently set by the maximum winter temperature at which sufficient vegetative growth and reproduction are still possible. The northern limit of *C. sericea* roughly lies on the 10 °C summer isotherm and this is the limit for sufficient growth and reproduction in the summer. Apparently, for *C. sericea* the northern and southern limits are set by their minimum requirements for growth and reproduction and not by their ability to survive the adverse season. Thus, along the American coast, it must be able to survive, at a latitude of about 33 °N, temperatures as high as 30 °C and at a latitude of about 50 °N temperatures as low as –1 °C.

*C. albida* and *C. ruchingeri* have the same type of distribution pattern, with the only difference that their limits are situated more to the south. Thus, the southern limit roughly coincides with the 14 °C winter isotherm, and the northern limit with the 14 °C summer isotherm.

Contrary to this, the southern limit of *C. rupestris* is set by this species ability to survive temperatures not higher than about 23 °C, for its southern limit roughly coincides with the 23 °C summer isotherm. Apparently *C. rupestris* it not capable of surviving the extremely high summer temperatures along the American warm temperate coast. The northern limit is probably situated on the 2–3 °C summer-isotherm, thus it is restricted by a minimum temperature necessary for growth and reproduction during the polar summer. All benthic algal limits in the far North appear to be of this nature; all species in this region must be equally resistant to the extremely severe conditions of the polar winter.

There are comparatively few other benthic algal species that are limited to both the south and the north by the minimum requirements, as to temperature, for growth and reproduction. The following species have about the same distribution as *C. albida* and *C. ruchingeri* (between the 13–15 °C winter isotherm in the south and the 10–13 °C summer isotherm in the north): *Arthrocladia villosa* (Huds.) Duby, *Bangia fuscopurpurea* (Dillw.) Lyngb., *Gigartina stellata* (Stackh.) Batt., *Lomentaria orcadensis* (Harv.) Coll., *Porphyra umbilicalis* (L.) J. Ag., *Punctaria latifolia* Grev.

*Porphyra leucosticta* Thur. also belongs to this subgroup, but it has its limits at the 17 °C winter isotherm and the 15 °C summer isotherm, respectively. Except *Lomentaria orcadensis* and *Gigartina stellata* these species are known to be winter-to spring annuals at their southern limits, and summer annuals at their northern limits; this is also true for *Cladophora albida* and *C. ruchingeri*.

The following two species have about the same distribution as *C. sericea*

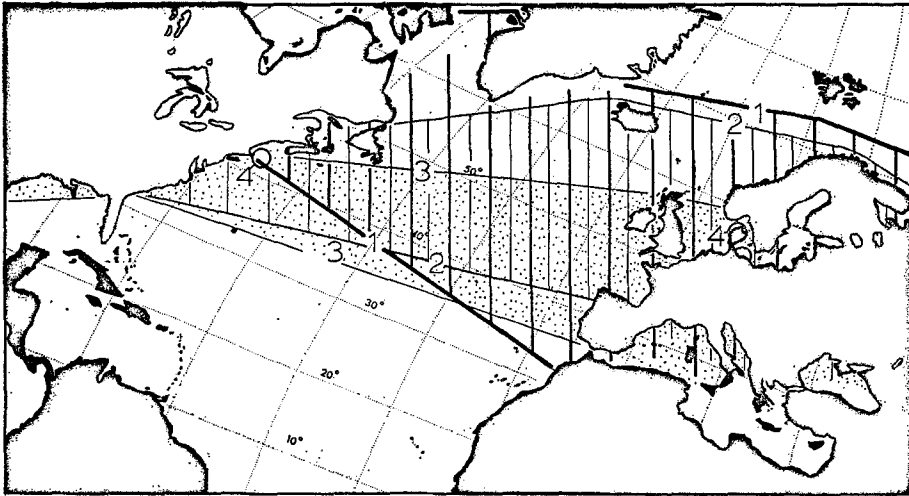


Fig. 7: Distribution of *Cladophora* species of the amphiatlantic temperate group. 1. *C. rupestris*; 2. *C. sericea*; 3. *C. albida*, *C. ruchingeri* (this species not known from Gulf of Mexico); 4. *C. pygmaea*

(between the 10–13 °C winter isotherm in the south and the 10–12 °C summer isotherm in the north): *Polysiphonia nigrescens* (Huds.) Grev. and *Stilophora rhizodes* (Ehr.) J. Ag. These are, just as *C. sericea*, winter to spring species at their southern limit. Based upon data of Williams (1948) and Schneider (1976) *Corallina officinalis* L. should also have this distribution pattern. This is a temperate perennial species whose intertidal populations would be exposed, along the Carolina coasts, to very high tropical temperatures during summer. Possibly these intertidal populations are regularly reestablished from subtidal populations. One would expect these subtidal populations to flourish during winter, but the three records of such populations were collected in summer (Schneider, 1976).

Summarizing, only a limited number of annual species with a vegetation period in the winter half year at their southern boundary and in the summer half year at their northern boundary have the distribution of *C. sericea*, *C. albida* and *C. ruchingeri*. Other species, belonging to taxonomically difficult groups not considered here, probably also have this type of distribution (e.g. in *Enteromorpha*).

The vast majority of the amphiatlantic temperate species have, in principle, the same distribution pattern as *C. rupestris*; both the southern and the northern boundaries coinciding with summer isotherms, which signifies that the southern limit is determined by the highest temperature the species can survive and the northern limit by a minimum temperature necessary for growth and reproduction. Of course, the values of these summer isotherms vary from species to species. Three arbitrary groups can be distinguished:

(a) The southern limit is situated on the 17–23 °C summer isotherms, the northern limit on the 0–3 °C summer isotherms: *Acrosiphonia arcta* (Dillw.) J. Ag., *Ahnfeltia plicata* (Huds.) Fries, *Alaria esculenta* (L.) Grev., *Asperococcus fistulosus*

(Huds.) Hook., *Chorda filum* (L.) Stackh., *Cladophora rupestris* (L.) Kütz., *Desmarestia aculeata* (L.) Lamour., *Desmarestia viridis* (O. F. Müll.) Lamour., *Dictyosiphon foeniculaceus* (Huds.) Grev., *Fucus vesiculosus* L., *Isthmoplea sphaerophora* (Carm. ex Harv. in Hook.) Kjellm., *Laminaria digitata* (Huds.) Lamour., *Laminaria saccharina* (L.) Lamour., *Monostroma grevillei* (Thur.) Wittr., *Monostroma obscurum* (Kütz.) J. Ag., *Phycodrys rubens* (L.) Batt., *Pilayella littoralis* (L.) Kjellm., *Punctaria plantaginea* (Roth) Grev., *Ralfsia verrucosa* (Aresch.) J. Ag., *Rhodochorton purpureum* (Lightf.) Rosenv., *Rhodomela confervoides* (Huds.) Silva, *Rhodymenia palmata* (L.) Grev., *Sphacelaria cirrosa* (Roth) C. Ag., *Spongomorpha aeruginosa* (L.) van den Hoek, *Urospora penicilliformis* (Roth) Aresch.

(b) The southern limit lies on the 17–23 °C summer isotherms, the northern limit on the 10–13 °C summer isotherms: *Ascophyllum nodosum* (L.) Le Jol., *Chondrus crispus* Stackh., *Cystoclonium purpureum* (Huds.) Batt., *Dumontia incrassata* (O. F. Müll.) Lamour., *Fucus spiralis* L., *Furcellaria fastigiata* (L.) Lamour., *Gloiosiphonia capillaris* (Huds.) Carm. ex Berk., *Membranoptera alata* (Huds.) Stackh., *Myriotrichia clavaeformis* Harv., *Nemalion helminthoides* (Vell. in With.) Batt., *Phyllophora membranifolia* (Good. & Woodw.) J. Ag., *Polyides rotundus* (Huds.) Grev., *Polysiphonia lanosa* (L.) Tandy, *Spongonema tomentosum* (Hud.) Kütz.

(c) The southern limit lies on the 23 °C summer isotherm and the northern limit on the 17 °C summer isotherm: *Seirospora seirosperma* (Harv.) Dixon, *Giraudia sphacelarioides* Derb. et Sol. in Castagne.

(d) The southern limit lies on the 14–10 °C summer isotherms, the northern limit on about the 0 °C summer-isotherm: *Antithamnion boreale* (Gobi) Kjellm., *Chordaria flagelliformis* (O. F. Müll.) C. Ag., *Chorda tomentosa* Lyngb., *Cladophora pygmaea* Rke, *Fucus distichus* L., *Phyllophora brodiaei* (Turn.) Endl., *Porphyra miniata* (C. Ag.) C. Ag., *Ptilota plumosa* (Huds.) C. Ag., *Rhodochorton penicilliforme* (Kjellm.) Rosenv., *Stictyosiphon tortilis* (Rupr.) Rke.

(8) The tropical-to-arctic group. This group contains a few species occurring from the Caribbean to the Arctic Sea. No *Cladophora* species belong to it, but a few others do, for instance *Chaetomorpha linum* (O. F. Müll.) Kütz., *Ectocarpus siliculosus* (Dillw.) Lyngb., *Hildenbrandia prototypus* Nardo, *Rhizoclonium riparium* (Roth) Harv.

#### SPECIES OCCURRING IN THE TEMPERATE ATLANTIC AND PACIFIC OCEANS, BOTH ON THE NORTHERN AND THE SOUTHERN HEMISPHERE

It is interesting that at least three *Cladophora* species of the amphiatlantic temperate distribution group also occur in the Northern Pacific, namely *C. rupestris*, *C. albida* and *C. sericea*. Sakai (1964) gives very distinct pictures and descriptions of these species for the coasts of Japan. I do not know, however, whether these species occur along the Northern Pacific coasts of America where the taxonomy of this genus is at present insufficiently known, but it is unlikely that such a

distinctive species as *C. rupestris* could have been overlooked or wrongly identified by the numerous phycologists working along the American Pacific coasts. I expect, however, *C. sericea* (under the name of *C. flexuosa*) and *C. albida* (under the name of *C. bertolonii*) to occur on these coasts. These three species probably belong to the relatively small group of benthic algal species that were exchanged between the North Pacific and the North Atlantic since the late Tertiary and subsequent interglacial openings of the Bering Strait. This group mainly consists of species with wide arctic to temperate distributions – as *C. sericea* and *C. rupestris* have – and which were capable of passing the still low temperatures of the interglacial Arctic (van den Hoek, 1975).

Other species belonging to this group are *Abnfeltia plicata*, *Bangia fuscopurpurea*, *Fucus distichus*, *Hildenbrandia prototypus*, *Nemalion helminthoides*, *Scytosiphon lomentaria*, *Dumontia incrassata*, *Urospora penicilliformis*.

Into which direction did these species pass the Bering Strait? The unmistakable occurrence of *C. rupestris* and *C. sericea* in the cold temperate part of the southern hemisphere could suggest that these species reached the North Atlantic via the North Pacific through the Bering Strait. I investigated *C. rupestris* from New Zealand (the type of *C. colensoi* Harvey) and from subantarctic Gough Island (Chamberlain, 1965); *C. sericea* from the Straits of Magellan (in the herbarium of the U.S. National Museum, Hassler exp. no. 2023) and from Tasmania (the type of *C. stuartii* Harvey). One could imagine that the passage of these species from the southern to the northern Pacific hemisphere occurred along the American coasts during a Pleistocene glaciation, when the marine temperate regions approached each other, or even reached each other, along the American coasts of the Pacific.

As to *C. rupestris* a latitudinal belt with a width of about 35° latitude (between the 23 °C summer-isotherms), would have to be reduced to about 0° latitude, and this would have required a cooling of the surface water of about 7° to 8 °C. This conflicts with Briggs' (1974) opinion that the North Pacific Ocean was only slightly subjected to Pleistocene temperature drops, and this in contrast to the North Atlantic, in which the Pleistocene temperature drops and the concomitant latitudinal shifts of the fauna and flora caused a striking reduction in diversity. According to Briggs, the greater Pleistocene temperature instability of the Atlantic was caused by its smaller size and its open connection with the Arctic Ocean. At present, there is much greater annual temperature stability along the Pacific coast of America as compared with that of the Atlantic coasts of Europe and Africa. For instance: the waters along the larger part of the warm and cold temperate Pacific coasts of America are subject to annual temperature fluctuations of only 2–6 °C, whereas those along the corresponding coasts of Europe are subject to annual temperature fluctuations of 6–10 °C (see Schott's map, Fig. 65, in Dietrich, 1965); along the African Atlantic coast, the 20 °C isotherm shifts from 30 °N in summer down to 15 °N in winter; along the Pacific American coast only from 28 °N to 25 °N. On the southern hemisphere these shifts are narrower, from 20 °S to 8 °S along the African coast, and from 7 °S to 5 °S along the American coast. If it were possible to replace "winter" by "glaciation" and "summer" by "interglacial" the differences between the Eastern coasts of both oceans would become obvious. In that case it



would be much more likely that the exchange of temperate benthic algal species occurred along the Atlantic African coasts during the glaciations. I estimate that, during the glaciations, the temperate benthic algal flora along the eastern coasts of the Atlantic were forced to shift over about 15°–20° latitude (van den Hoek, 1975) as a result of a temperature drop of about 6 °C, and this would have been sufficient to reduce the tropical belt to almost nothing. This point of view is supported by the distribution of *C. pellucida* and *C. rupestris* (as *C. capensis* (Ag.) Kütz., cf. Simons, 1960) temperate species occurring in Europe as well as South Africa. Moreover, *C. rupestris* is not known to occur along the North American Pacific coast, and this suggests that this species reached the Japanese coasts from the North Atlantic through the Bering Strait, and this would also seem to have been the most logical route for *C. albida* and *C. sericea*.

On the other hand, the distribution of *Macrocyctis pyrifer* along both the northern hemisphere and southern hemisphere Pacific American coasts can only be explained by assuming exchange (probably from the south to north) during a Pleistocene temperature drop. As this species is limited, into equatorial direction, by about the 25 °C summer-isotherms, a drop of about 2 °C would have been sufficient (cf. distribution map in Fritsch, 1952). Therefore, the distribution of *Macrocyctis pyrifer* does not seem to invalidate Briggs' point of view.

The above explanation does not seem to be applicable to the bipolar distribution of the section Affines (with *C. pachyderma* and *C. incompta*). Here, higher temperature preferences must be assumed for ancestral forms and the common origin probably has a longer history, which is reflected by the higher hierarchical status (the section-level) shared by the related forms. This is probably also valid for the bipolar genera *Spongomorpha* and *Acrosiphonia*.

On the specific level, true bipolar distributions do not seem to exist (based upon reliable identifications, cf. Papenfuss, 1964), and this agrees with the absence (or taxonomic uncertainty) of bipolar benthic animal species (Dell, 1972). Only species with wide Arctic/Antarctic to warm temperate or Boreal/Antiboreal to warm temperate distributions have been exchanged; for these trans-equatorial dispersals were possible during Pleistocene temperature drops. Such species occurring in the Atlantic are: *Petalonia fascia*, *Rhodochorton purpureum*, *Gracilaria verrucosa*, *Plocamium coccineum*, *Ahnfeltia plicata*, *Ceramium rubrum*, *Bostrychia scorpioides*, *Sphacelaria cirrosa*. This is also true for the few species with a tropical to Arctic distribution (see above). Other records are unreliable (Papenfuss, 1964).

#### CONCLUDING REMARKS

The distribution patterns of the individual *Cladophora* species show a high degree of correlation with the general benthic algal phytogeography of the northern hemisphere Atlantic.

Thus the high proportions of *Cladophora* species restricted to the tropical Western Atlantic Region on the one hand, and to the warm temperate Medi-

terranean-Atlantic Region on the other hand, are in agreement with the high degrees of endemism and hence individuality of these two algologically rich floras.

The fact that all North East American *Cladophora* species also occur in Europe agrees with the high degree of similarity between the American and European cold temperate boreal floras which I therefore united into one phytogeographic region: the cold-temperate Atlantic-Boreal Region.

As I reached my conclusions on the general benthic algal phytogeography of the northern hemisphere Atlantic and those on the taxonomy of *Cladophora* in this region along independent lines, they confirm each other to a high degree. Confused distribution patterns within *Cladophora*, without agreement with general distribution patterns, would indicate wrong taxonomic concepts. Of course, this does not prove the validity of all species distinguished by me.

The vast majority of benthic algal species have limited distributions, because there are obstacles to their world wide dispersal: the longitudinal barriers formed by the continents and the Atlantic and Pacific Oceans; latitudinal barriers as the sediment coasts of the Carolinas; and adverse temperatures. I have tried to demonstrate the effectiveness of the Carolinas barrier by comparing distributions of the same species on both sides of the ocean. A considerable number of species with a wide tropical to temperate distribution along the European coast are entirely (or almost entirely) restricted to the tropics along the American coasts, probably because they did not succeed in penetrating through this barrier.

Recent collections from offshore reefs along the coasts of the Carolinas (Schneider, 1976) have shifted the known distributional limits of a number of tropical species to about 35 °N. However, these results do not invalidate the theory that the warm temperate Carolina region is a distributional barrier.

There are two types of temperature bound phytogeographic limits:

(1.) The limit set by the species ability to survive adverse temperatures in the unfavourable season, that is for "northern" species in the northern hemisphere to survive a high summer temperature in the south and for "southern" species to survive a low winter temperature in the north. This appeared to be the predominant type of temperature bound phytogeographic limit.

(2.) The limit set by the species ability to grow and reproduce sufficiently in the favourable season, that is for "southern" species the ability to grow and reproduce sufficiently during summer at their northern limit, and for "northern" species to grow and reproduce sufficiently during winter at their southern limit.

All northern, Arctic limits appeared to conform to this latter type. High up in the north all species are apparently limited by a temperature sufficiently high to grow and reproduce in summer, and all are equally capable of surviving the severe winter conditions.

Only few southern limits belong to this category, for instance those of *C. sericea*, *C. albida*, and *C. ruchingeri*. In this case the temperatures on both the northern limit (a summer-isotherm) and the southern limit (a winter-isotherm) have approximately the same magnitude (e.g. about 10–12 °C for *C. sericea*). This probably means that the optimum temperatures for growth and reproduction of this species are about 10–12 °C and that higher and lower temperatures markedly

reduce growth and reproduction in nature. Apparently this species is capable of surviving extremely diverging temperatures during the unfavourable season: frost in the northern winter, 35 °C in the southern summer.

Of course a temperature bound limit is, in general, not a sharp line, but rather a transition area where the species becomes more and more restricted to gradually more reduced stations along the coast where conditions are not yet insuperably adverse. E. Y. Dawson (1951, 1952) gives interesting and well documented examples of local differences in the degree of upwelling of cold water along the Pacific coast of Baja California (between 32 °N and 24 °N) and the correlated patchy occurrence of temperate algal floras. Ardré (1970) gives interesting examples for the Atlantic coast of the Iberian Peninsula.

Irradiance or daylength could possibly also cause latitudinal limits for benthic algal species. However, one would expect such limits to parallel the latitudes, which is the case for only a few limits and these can better be explained by temperature conditions. Therefore, daylength effects are undoubtedly important in regulating life histories of many algal species within their geographic ranges, but the limits of these ranges are set by temperature conditions and phytogeographic barriers.

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