

Phytogeographic distribution groups of benthic marine algae in the North Atlantic Ocean. A review of experimental evidence from life history studies

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ABSTRACT: Experimentally determined lethal temperatures and temperatures limiting growth or reproduction in the life histories of 15 benthic algal species were used to infer possible phytogeographic boundaries in the North Atlantic Ocean. These appeared to correspond closely with phytogeographic boundaries based on distribution data. Many boundaries appeared to be of a composite nature. For instance, the southern boundary of *Nemalion helminthoides* is interpreted as a "southern reproduction boundary" on the N. Atlantic E. shore and a "southern lethal boundary" on the N. Atlantic W. shore. The northern boundary on both sides of the ocean is a "northern reproduction boundary". *N. helminthoides* is a typical representative of the "amphiatlantic temperate distribution group", to which seven other of the fifteen investigated species belong (*Chondrus crispus*, *Desmarestia aculeata*, *D. viridis*, *Monostroma grevillei*, *Acrosiphonia "arcta"* with a comparable composite southern boundary; *Rhodochorton purpureum* with a "southern lethal boundary"). *Polysiphonia ferulacea* and *Dictyota dichotoma* are treated as representatives of the "amphiatlantic tropical-to-warm-temperate distribution group", and *P. denudata* as representative of the "amphiatlantic tropical-to-temperate group". *P. harveyi* belongs to the N.E. American temperate group and is bounded by a "northern reproduction boundary" and a "southern reproduction boundary". This is one of the very few species endemic to N.E. America. This poor endemism is ascribed to the vast adverse sediment shores and their additional acting as barriers to glacial north-south displacements of the flora; it is not related to the wide annual temperature fluctuations (> 20 °C) typical for N.E. America. The temperate algal flora of Japan, however, which is extremely rich in endemic species is subject to equally wide annual temperature fluctuations. *Bonnemaisonia hamifera* is such a Japanese endemic, which has been accidentally introduced into the North Atlantic Ocean where its life history seems to be disrupted: it is maintained mainly by vegetative propagation of the heteromorphic tetrasporophyte. The species of the "warm temperate Mediterranean-Atlantic group" are probably too stenothermous for life on N.E. American shores; they need annual temperature fluctuations < 20 °C. *Acrosymphyton purpuriferum* seems to belong to this group, but arguments are presented to unite this species with *A. caribaeum* and to range it under the "amphiatlantic tropical-to-warm-temperate group". *Clathromorphum circumscriptum* belongs to the "Arctic distribution group" and has a "southern reproduction boundary" across the ocean along the 3 °C February isotherm. This species is able to survive temperatures of about 20 °C. Five amphiequatorial temperate species discussed in this paper and four in another related paper have similar maximum winter temperatures of 14–17 °C (mean monthly values) allowing reproduction. Their amphiequatorial distribution can be explained by assuming similar low temperatures in the euphotic zone along E. Pacific and E. Atlantic equatorial coasts i.e. in narrow inshore belts of intensified upwelling during the presumably intensified glacial circulation of the ocean gyres.

INTRODUCTION

A recently finished revision (van den Hoek, 1981) and an earlier published one (van den Hoek, 1963) of the genus *Cladophora* (Chlorophyceae) have offered an opportunity to unravel the hitherto confused distribution patterns of 42 species of this genus in the North Atlantic Ocean (van den Hoek, 1979). These 42 species could be assigned to eight phylogeographic distribution groups which apparently had a general applicability to the marine algal flora of the North Atlantic Ocean (van den Hoek, 1982), and hypotheses were formulated about the nature of the phylogeographic boundaries of these distribution groups.

In principle, it is possible to test hypotheses about the nature of phylogeographic boundaries of individual benthic algal species by means of experimental studies on the environmental regulation of their life histories. A number of recent studies on the environmental regulation of life histories were, in general, not devised to answer questions on phylogeographic problems. Consequently the information contained in them is mostly too incomplete to solve such problems. Nonetheless, they contain a wealth of relevant information. Part of this information has been discussed elsewhere (van den Hoek, 1981), and part of it will be reviewed in the present paper.

BASIC GEOGRAPHIC DISTRIBUTION GROUPS IN THE NORTH ATLANTIC OCEAN

The above mentioned eight distribution groups will be described below, together with two additional ones.

(1) The amphiatlantic tropical-to-warm temperate group with a northeastern extension (Fig. 1). Species of this group are entirely or

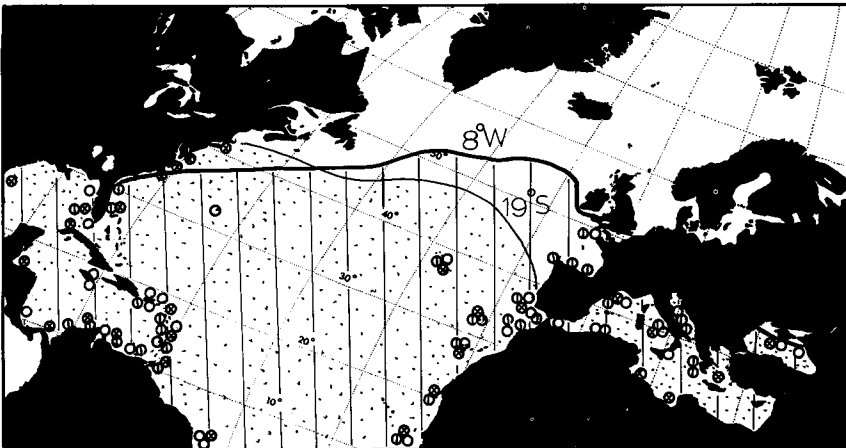


Fig. 1. The distribution of *Cladophora prolifera* (⊖), *Cl. coelothrix* (⊙) and *Hypnea musciformis* (⊗) in the North Atlantic Ocean. 1. (hatched): the amphiatlantic tropical-to-warm temperate group with a northeastern extension (*Cl. coelothrix* type). 2. (stippled): the amphiatlantic tropical-to-warm temperate group with a northwestern extension (*Hypnea musciformis* type). 8 °W = 8 °C winter (February) isotherm. 19 °S = 19 °C summer (August) isotherm

nearly restricted to the tropics in America and extend more or less far into the temperate zone in Europe. *Cladophora coelothrix* and *Cl. prolifera* are examples. Their northern boundary is near the 8°C February isotherm. This suggests that both species are limited to the north by lethal winter temperatures of the surface water. At least 50 species (on a total of c. 580 considered in a phytogeographic study of the N. Atlantic Ocean, see van den Hoek, 1979) seem to belong to this distribution group on the basis of distribution data. Experimental evidence supports the hypothesis that the northern boundary of one species of this group, *Gracilaria foliifera*, does indeed follow the 8°C February isotherm, which can be considered as a "lethal boundary" (McLachlan & Edelman, 1977; van den Hoek, 1982). In another species of this group, *Centroceras clavulatum*, the northern boundary was set by a combination of a summer isotherm in Europe (determined by the lowest temperature allowing growth) and a winter isotherm in America (determined by the lethal winter temperature) (van den Hoek, 1982).

(2) The amphiatlantic tropical-to-warm temperate group with a northwestern extension (Fig. 1). The sole example, *Hypnea musciformis*, has a clearly more northern distribution in North America than in Europe. This is probably caused by the fact that *H. musciformis* needs a high minimum summer temperature for its growth, but can at the same time survive very low winter temperatures (down to c. -1°C).

(3) The amphiatlantic tropical-to-temperate group (Fig. 2). The northern limit of the example, *Cladophora vagabunda*, follows approximately the 12°C summer isotherm, which suggests that this limit is determined by the minimum summer temperature allowing sufficient growth and reproduction. On the basis of distribution data, at least fifteen species (on a total of c. 580 considered in a phytogeographic study of the N. Atlantic Ocean; see van den Hoek, 1979) can probably be attributed to this group, with northern boundaries along the 15°C to 12°C summer isotherms. *Sphacelaria rigidula* Kütz. (= *S. furcigera* Kütz.) has the same distribution as *Cl. vagabunda*. Its northern boundary, the 12°C summer isotherm, is determined by the lowest summer

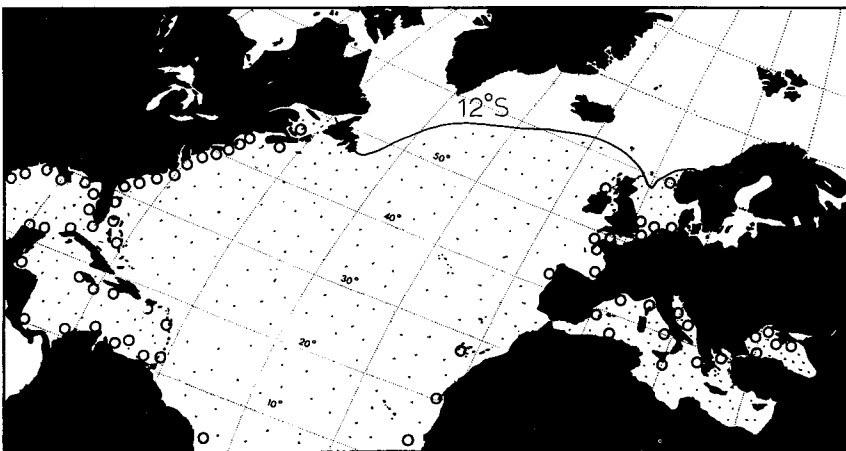


Fig. 2. The distribution of *Cladophora vagabunda* (○ and stippled area) in the North Atlantic Ocean: the amphiatlantic tropical-to-temperate group (*Cladophora vagabunda* type)

temperature allowing formation of propagules (van den Hoek, 1982). This boundary is valid on a world wide scale.

(4, 5) The amphiatlantic temperate group; with a southern boundary near a summer isotherm (4) and near a winter isotherm (5) (Fig. 3). Both *Cladophora rupestris* and *Cl. albida* have northern boundaries approaching August isotherms (the 5°C and 12°C isotherms, respectively). This suggests that they are limited to the north by minimum summer temperatures allowing sufficient growth and/or reproduction. The southern boundary, however, of *Cl. rupestris* is near the 20°C summer isotherm, and of *Cl. albida* near the 14°C winter isotherm. This suggests that *Cl. rupestris* is limited to the south by a lethal summer temperature; and *Cl. albida* by a winter temperature which is sufficiently low to permit growth and/or reproduction. At its southern boundary in Texas *Cl. albida* is a winter species, at its northern boundary a summer species. At least 40 species (on a total of c. 580 considered in a phytogeographic study of the N. Atlantic Ocean, see van den Hoek, 1979) can be attributed to group 4 on the basis of distribution data (van den Hoek, 1979, 1982). Their southern boundaries seem to follow the 17°C–23°C summer isotherms. The northern boundary of *Callithamnion hookeri* follows the 10°C summer isotherm, and this corresponds with a minimum temperature of c. 10°C allowing sufficient growth. The southern boundary at the 25°C summer isotherm corresponds with a lethal temperature of c. 27°C (Edwards, 1979; van den Hoek, 1982). In a comparable way, *Dumontia contorta* (= *D. incrassata*) and *Laminaria saccharina* have southern boundaries along the 19°C summer isotherm corresponding with somewhat higher lethal temperatures (van den Hoek, 1982; Rietema & Klein, 1981; Rietema, in prep.; Lüning, 1980). The southern boundary of *L. digitata*, however, follows approximately the 10°C winter isotherm in Europe, which corresponds with the highest winter temperature allowing sufficient maturation of the female gametophyte. In America the southern boundary is at the 19°C summer isotherm and this corresponds with a lethal temperature of c. 21°C (van den

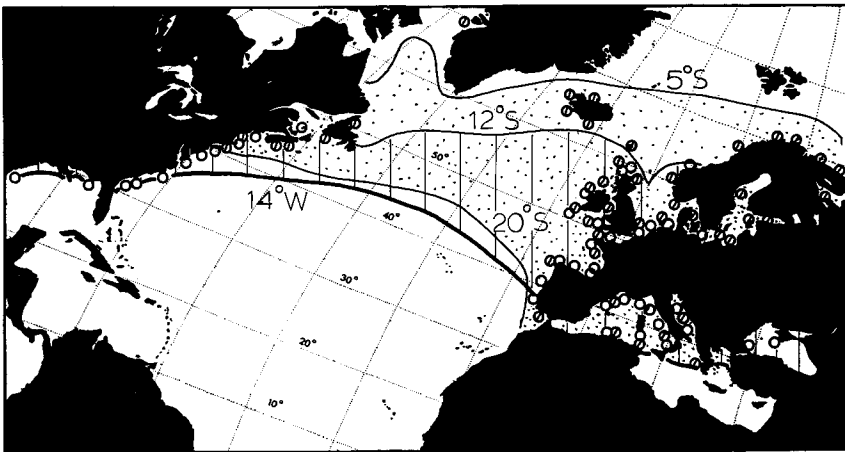


Fig. 3. The distribution of *Cl. rupestris* (⊙, stippled area: the amphiatlantic temperate group with a southern boundary near a summer isotherm). The distribution of *Cl. albida* (○, hatched area: the amphiatlantic temperate group with a southern boundary near a winter isotherm)

Hoek, 1982; Lüning, 1980). A comparatively small number of at least twelve benthic algal species (out of c. 580 in the N. Atlantic Ocean considered in a phytogeographic study) can be assigned to the distribution group 5.

Scytosiphon lomentaria and *Petalonia fascia* are both limited to the south by the 17°C winter isotherm. This corresponds with the highest temperature of c. 20°C which allows, in winter, the initiation of erect thalli from crustose thalli in southern ecotypes (Lüning, 1981a, 1981b; van den Hoek, 1982).

(6) The tropical Western Atlantic group (Fig. 4). *Cladophora catenata* is an example. So far, no experimental data are available to explain the temperature responses of the species in this group, which embraces at least 250 species of the 450 inhabiting the tropical Western Atlantic region (and of the c. 580 species in the N. Atlantic Ocean considered in a phytogeographic study, cf. van den Hoek, 1979) which were considered in the context of phytogeographic comparisons (van den Hoek, 1975).

(7) The American tropical-to-temperate group (Fig. 4). Only five species can be presently assigned to this group with some certainty. *Gracilaria tikvahiae* is limited to the North (in shallow embayments of the southern Gulf of St. Lawrence) by summer temperatures above 20°C allowing sufficient growth, and it is at the same time capable of surviving -2°C below winter ice cover (Edelstein et al., 1976; Bird et al., 1977a, b, 1978; McLachlan and Edelstein, 1977; Edelstein, 1977; von den Hoek, 1982). Three of the four other species (e.g., *Grinnellia americana*) prefer similar shallow embayments, where they profit by high summer temperatures of up to 30°C, but can survive freezing (van den Hoek, 1982).

(8) The N. E. American temperate group (Fig. 4). Very few species, for instance *Chondria baileyana* are endemic to the N.E. American shores between 30°N and 45°N. Just like most species of the previous group, *C. baileyana* inhabits inshore water and embayments with wide annual temperature fluctuations. This scarcity of

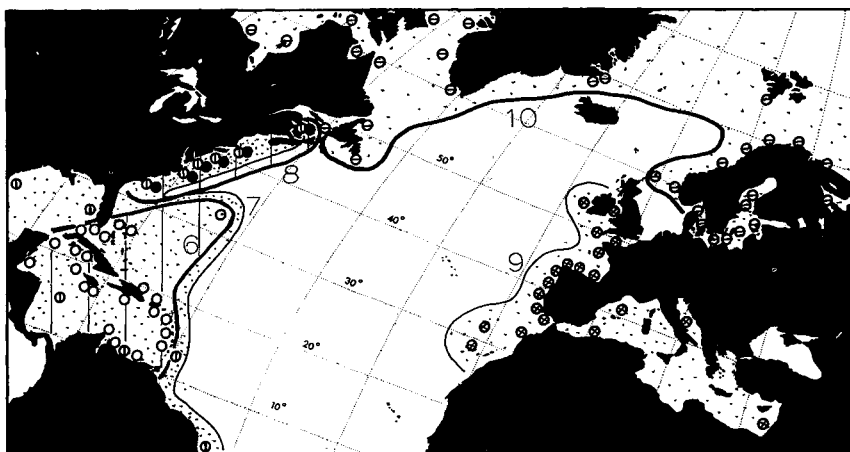


Fig. 4. The distribution of *Cl. catenata* (○, 6: the tropical Western Atlantic group); *Gracilaria tikvahiae* (⊙, 7: the American tropical-to-temperate group); *Chondria baileyana* (● 8: the American temperate group); *Cladophora pellucida* (⊗, 9: the warm temperate Mediterranean-Atlantic group); *Sphacelaria arctica* (⊖, 10: the Arctic group)

endemic species in the American temperate distribution group contrasts sharply with the large number of endemic species in the algal flora of the Japanese coasts which occupy a comparable latitudinal belt between 30°N and 45°N with equally wide annual temperature fluctuations. Here 125 out of 170 "indicator species" (Funahashi, 1974) are endemic. The Japanese flora comprises in total c. 750 Chloro-, Rhodo-, and Phaeophyceae. Experimental evidence indicates that *Campylaeophora hypneoides* J. Ag. (Notoya, 1979) is limited to the north by the 15°C summer isotherm, which indicates the minimum temperature necessary for sufficient growth; and to the south by the 27°C summer isotherm, which corresponds approximately with a lethal temperature of 30°C. As this species is able to survive in its northern range -2°C, it can bridge a temperature range of -2°C to 30°C. *Sargassum muticum*, a Japanese species which has been accidentally introduced in N.W. America and N.W. Europe, has a comparable wide temperature range. It is likely that the poverty of the endemic flora along N.E. American coasts between 30°N and 45°N can be attributed to the adverse nature of the sediment coasts to the growth of benthic macroalgae. Moreover, these adverse coasts have probably acted as barriers to north-south and south-north displacements of the benthic algal flora during glaciations and have thus caused its impoverishment and prevented successful speciation.

(9) The warm temperate Mediterranean-Atlantic group (Fig. 4). *Cladophora pellucida* is one of the numerous examples. At least 180 species of the 430 species inhabiting European Atlantic shores and considered in a phytogeographic comparison embracing c. 580 species in the N. Atlantic Ocean, can be attributed to this distribution group (van den Hoek, 1975, 1979). In one species, *Saccorhiza polyschides* (see Norton, 1977, for the regulation of its life history), the southern boundary in N.W. Africa is situated at about the 15°C February isotherm. This corresponds with the maximum winter temperature of 17°C allowing maturation of female gametophytes (at still higher temperatures they only grow vegetatively). The winter temperature lethal to female gametophytes and young sporophytes is 3°C. The summer temperature lethal to sporophytes of *S. polyschides* is 25°C. The corresponding lethal boundaries are the 4°C winter isotherm in the north and the 23°C summer isotherm in the south, embracing 19°C of mean monthly temperatures of the surface water. This maximum temperature span makes *S. polyschides* unfit for inhabiting temperate American coasts where all species must be capable of bridging temperature spans of more than 20°C (mean monthly temperature). This is a very obvious cause of the absence of species endemic to European coasts from N.E. American coasts (van den Hoek, 1982). *S. polyschides* bridges, along African and European shores, an enormous latitudinal span of 25°N to 65°N. Nonetheless it is incapable of inhabiting the N.E. American coasts as a result of its temperature responses. Endemic species with still narrower latitudinal spans in Europe are probably even less fit for life on American shores than *Saccorhiza polyschides*.

(10) The Arctic group (Fig. 4). *Sphacelaria arctica* is an example which follows the general trend of Arctic species to penetrate more or less far into the cool temperate zone. About at least 20 species (on a total of 580 considered in a phytogeographic study of the N. Atlantic Ocean, see van den Hoek, 1979) can be assigned to the Arctic group on the basis of distribution data (van den Hoek, 1979). The southern boundary of *Saccorhiza dermatodea* is near the 4°C February isotherm in Europe, and the 15°C August isotherm in America. The 4°C February isotherm corresponds with the

highest winter temperature (5°C) allowing sufficient maturation of the female gametophyte. The 15°C summer isotherm in America corresponds with a lethal temperature of 17°C for the sporophyte (Norton, 1977; van den Hoek, 1982). *Sphacelaria arctica* has also a southern boundary set, in Europe, by the maximum temperature in winter allowing reproduction (the 4°C winter isotherm); and, in America, by a lethal summer temperature (the 16°C August isotherm). These boundaries allow *S. arctica* to inhabit the Baltic Sea with winter temperatures lower than 4° and summer temperatures lower than 16°C in the greatest part. Apparently *S. arctica* can tolerate salinities as low as 5‰ (van den Hoek, 1982).

NEW EVIDENCE FROM LIFE HISTORY STUDIES IN SUPPORT OF THE BASIC GEOGRAPHIC DISTRIBUTION GROUPS

When one tries to extract phytogeographically relevant information from studies on life histories, one should realize that the species may be confronted with at least the following boundaries corresponding with various types of limiting temperature conditions which should all be checked when perusing the results of the above studies. In essence, the significance of these boundaries has been previously stressed by Hutchins (1947):

(1) The "northern lethal boundary" corresponds with the lowest winter temperature which a species can survive for a period of c. ½–1 month. (2) The "northern growth boundary" corresponds with the lowest summer temperature which, in a period of several months, allows sufficient growth. (3) The "northern reproduction boundary" corresponds with the lowest summer temperature which in a period of several months allows sufficient reproduction. Often "sufficient growth" ends with reproductive maturation but in many cases the formation of reproductive structures is governed by other temperatures than those governing growth. (4) The "southern lethal boundary" corresponds with the highest summer temperature which a species can survive during a period of ½–1 month. (5) The "southern growth boundary" corresponds with the highest winter temperature which, in a period of several months, allows sufficient growth. (6) The "southern reproduction boundary" corresponds with the highest winter temperature which, in a period of several months, allows sufficient reproduction.

For species with an alternation of generations the six boundaries described above should be determined in principle for both generations. However, in species with an isomorphic alternation both generations have mostly, but not always, similar temperature responses. Photoperiodic responses may modify the temperature responses and should consequently always be taken into account.

It is, moreover, necessary to make an estimate of the difference between the experimental temperature limits and the corresponding mean monthly temperatures of the sea surface in order to be able to "translate" an experimental temperature limit to a boundary approaching a surface isotherm. These estimates can be made in the following way.

A "southern lethal summer temperature" is considered to correspond with the maximum August temperature of the uppermost surface water, which is taken, in its turn, to correspond approximately with a three centigrades lower mean August tempera-

ture (cf. Earle, 1969). It should be realized, however, that this difference can be greater in protected lagoons.

A "southern growth and/or reproduction winter temperature" corresponds with the mean maximum February temperature (for the correct temperature has to be provided each year); which is taken, in its turn, to correspond with a two centigrades lower mean February temperature for temperatures above 10 °C, and with a one centigrade lower mean February temperature below 10 °C.

A "northern lethal winter temperature" is considered to correspond with the minimum February temperature of the surface layer. This corresponds with a one centigrade higher mean February temperature (two centigrades for temperatures above 10 °C).

A "northern growth and/or reproduction temperature" is considered to correspond with a mean minimum August temperature of surface water, and this with a two centigrades higher mean August temperature.

The present study presents evidence for the validity of the following phytogeographic distribution groups: the amphiatlantic tropical-to-warm temperate group with a northeastern extension (group 1, Fig. 1); the amphiatlantic tropical-to-temperate group (group 3, Fig. 2); the amphiatlantic temperate group of the *Cladophora rupestris* type (group 4, Fig. 3) and a type with features of the *Cl. rupestris* as well as the *Cl. albida* type (Fig. 3) (groups 4 and 5); the N.E. American temperate group (group 8, Fig. 4); the Japanese equivalent of the American temperate group (group 8); and the Arctic group (group 10, Fig. 4).

Table 1 lists the species and corresponding distribution groups for which the evidence is reviewed in the present paper.

Distribution data from the following publications were used for the construction of the distribution maps: Abbott & Hollenberg (1976); Adey (1973); Adey et al. (1976); Ardré (1970, 1971); Baardseth (1941); Boudouresque & Perret (1977); Brauner (1975); Breeman (1979); Chamberlain (1965); Chapman (1969); Chiang (1972, 1973); Chihara & Yoshizaki (1970); Christensen & Thomsen (1974); Dawes (1974); Dawson (1946); Day (1969); De May et al. (1977); De Sève et al. (1979); Diannelidis et al. (1977); Dixon & Irvine (1977); Edelstein (1964); Edelstein et al. (1969, 1970); Edelstein & McLachlan (1966, 1968); Edwards (1970a, 1979); Earle (1969); Feldmann (1942, 1954); Feldmann-Mazoyer (1940); Funahashi (1966, 1967, 1974); Funk (1955); Furnari et al. (1977); Furnari & Scammacca (1973); Giaccone (1969, 1978); Giaccone & Longo (1976); Hamel (1930); Hamel (1931–39); Haritonidis & Tsekos (1974); Den Hartog (1959); Hawkes et al. (1978); Hirose & Kajimura (1973); van den Hoek & Donze (1967); Humm (1979); Jaasund (1965); John et al. (1977); Jonsson (1912); Juett et al. (1976); Kapraun (1977); Knaggs (1967); Konno (1973); Kornmann & Sahling (1977); Kühnemann (1972); Lawson (1966); Lawson et al. (1975); Lawson & John (1977); Lee (1980); Lee & Kim (1977); Lee & Lee (1976); Lindauer et al. (1961); Lipkin (1972); Levring (1960, 1974); Makienko (1975); Mathieson (1979); Moura Baptista (1977); Munda (1977, 1978, 1980); Nakaniwa (1975); Newton (1931); Nizamuddin et al. (1979); Ogawa & Machida (1976); Oliveira Filho (1977); Orris & Taylor (1973); Pankow (1971); Papenfuß (1964); Pedersen (1976); Perez-Cirera (1975); Pielou (unpublished list of distribution records along American coasts); Price et al. (1978); Rhodes (1970); Rueness (1977); Santelices (1980); Scagel (1957); Sčapova & Vozžinskaja (1960); Schmidt (1931); Schneider (1976); Schneider et al. (1979); Searles &

Table 1. Species and corresponding distribution groups for which evidence on the nature of phytogeographic limits is reviewed

Group No.	Name of distribution group	Representative species treated	Taxonomic categories
(A) Amphiatlantic			
(1)	Amphiatlantic tropical-to-warm-temperate with a northeastern extension	<i>Dictyota dichotoma</i> (Huds.) Lamour. <i>Polysiphonia ferulacea</i> Suhr	Phaeophyceae, Dictyotales Rhodophyceae, Ceramiales
(2)	Amphiatlantic tropical-to-warm-temperate with a northwestern extension	<i>Polysiphonia denudata</i> (Dillw.) Grev. ex Harv. in Hook.	Rhodophyceae, Ceramiales
(3)	Amphiatlantic tropical-to-temperate	<i>Rhodochorton purpureum</i> (Lightf.) Rosenv. <i>Nemalion helminthoides</i> (Vell. in With.) Batt. <i>Chondrus crispus</i> Stackh. <i>Desmarestia aculeata</i> (L.) Lamour. <i>Desmarestia viridis</i> (O. F. Müll.) Lamour. <i>Monostroma grevillei</i> (Thur.) Wittt. <i>Acrosiphonia "arcta"</i> (Dillw.) J. Ag. <i>Punctaria latifolia</i> Grev.	Rhodophyceae, Nemaliales Rhodophyceae, Nemaliales Rhodophyceae, Gigartinales Phaeophyceae, Desmarestiales Phaeophyceae, Desmarestiales Chlorophyceae, Ulotrichales Chlorophyceae, Acrosiphoniales Phaeophyceae, Dictyosiphonales
(4)	Amphiatlantic temperate: with a southern boundary near a summer isotherm		
(5)	Amphiatlantic temperate: with a southern boundary near a winter isotherm		
(B) America			
(6)	Tropical Western Atlantic		
(7)	American tropical-to-temperate		
(8)	N.E. American temperate	<i>Polysiphonia harveyi</i> Bailey	Rhodophyceae, Ceramiales
(8')	Japanese temperate	<i>Bonnemaisonia hamifera</i> Hariot	Rhodophyceae, Bonnemaisoniales
(C) Europe/North Africa			
(9)	Warm temperate Mediterranean-Atlantic	<i>Acrosymphyton purpuriferum</i> (J. Ag.) Sjöst.	Rhodophyceae, Cryptonemiales
(D) Amphiatlantic, polar			
(10)	Arctic	<i>Clathromorphum circumscriptum</i> (Strömfeldt) Foslie	Rhodophyceae, Cryptonemiales

Schneider (1978); Sears (1971); Setchell & Gardner (1919–20, 1925); South (1976); South & Hooper (1980); Stephenson & Stephenson (1972); Tanaka & Itono (1972); Taylor (1945, 1957, 1960); Tokida (1954); Tsekos & Haritonidis (1977); Tsuda & Wray (1977); Velasquez et al. (1975); Velasquez & Lewmanomont (1975); Vozžinskaja (1964, 1965); Wilce (1959); Womersley (1965, 1967); Womersley & Bailey (1970); Zaneveld (1972, 1976); Zimmermann & Livingston (1976); Zinova (1953, 1955, 1967).

The amphiatlantic tropical-to-warm temperate group with a northeastern extension

Dictyota dichotoma

Life history

Dictyota dichotoma has an isomorphic alternation between a tetrasporophyte generation and a dioecious gametophyte generation with oogamy. *Dictyota dichotoma* grows rapidly, and several generations may follow each other in the course of one year. Sporophytes and gametophytes are present at the same time and not connected in a seasonal sequence. The production of eggs is claimed to have a lunar periodicity (Müller, 1962; Vielhaben, 1963). The influence of temperature on reproduction has not been investigated.

Near its northern boundary in N.E. America (in N. Carolina) *D. dichotoma* disappears from January through March. It appears to survive the winter in the form of small decumbent germlings which resume growth by the formation of erect blades after transfer to higher temperatures (Richardson, 1979). These germlings remain "dormant" under "winter conditions" (12 °C) in culture, and resume growth (by formation of blades) after transfer to 24 °C in culture.

At Beaufort (N. Carolina) inshore populations of *D. dichotoma* must be able to survive intermittently winter temperatures as low as 3 °C (Brauner, 1975). In Virginia this lowest temperature may even be 2 °C (Humm, 1979). This suggests a lethal winter temperature near 2 °C. In short term experiments (12 h exposures) *Dictyota dichotoma* from Roscoff (Brittany, W. France) survived 3 °C, but not –2 °C (Biebl, 1959). However, in the same type of experiments conducted with material from Puerto Rico, *D. dichotoma* survived 5 °C, but not 3 °C (Biebl, 1962). This indicates that *D. dichotoma* embraces a number of temperature ecotypes. There are comparable differences in the highest temperatures tolerated: plants from Roscoff survived 27 °C, but not 30 °C; and plants from Puerto Rico survived 32 °C, but not 35 °C.

At 12 °C *Dictyota* germlings did not grow (Richardson, 1979). Apparently the minimum temperature allowing growth must be higher than 12 °C.

Geographic distribution in the North Atlantic Ocean

The northern boundary of *D. dichotoma* in N.E. America approximates the 2 °C February isotherm, which limit can be explained as a "northern lethal boundary", approximately corresponding with a minimum February temperature of 1 °C.

The northern boundary in Europe approximates the 13 °C summer isotherm, which limit can be explained as a "northern growth and reproduction boundary". This would

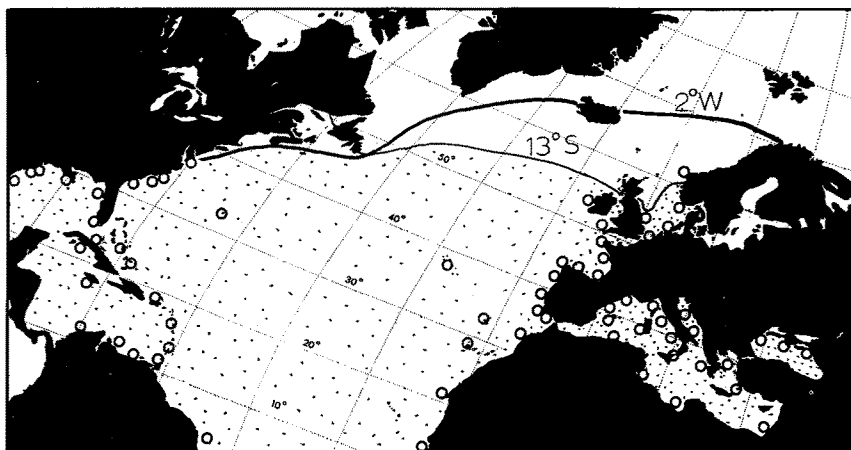


Fig. 5. Distribution of *Dictyota dichotoma* in the North Atlantic Ocean (○). 2°W = 2 °C winter (February) isotherm. 13°S = 13 °C summer (August) isotherm

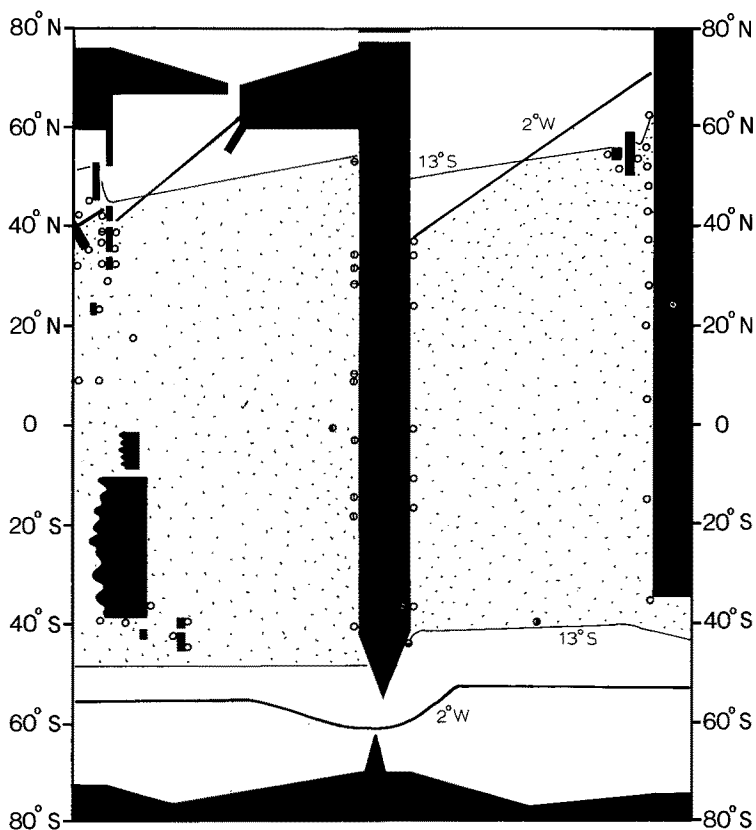


Fig. 6. Distribution of *Dictyota dichotoma* in the Pacific Ocean (left part in diagram) and Atlantic Ocean (right part in diagram) (○). In addition, the distributions are given of several entities which are difficult to differentiate from the form range of *D. dichotoma*. *Dictyota flabellata* (Coll.) S. & G. (□); *D. binghamiae* J. Ag. (⊖); *D. major* Taylor (●); *D. cervicornis* Kütz. and *D. divaricata* Lamour. (⊙); *D. liturata* J. Ag. (⊕). The southern and northern boundaries are, at the same time, boundaries of the genus *Dictyota*

correspond with a minimum temperature of 12 °C (the mean minimum August temperature) allowing growth and reproduction. According to the above experiments this temperature should be higher than 12 °C (Fig. 5).

Geographic distribution in the Pacific and Atlantic Oceans

In Fig. 6, records of several other *Dictyota* species have been indicated. These species are difficult to differentiate from the form range of *Dictyota dichotoma*. Apparently, investigators of W. American material tended to attribute their material to species described for N.W. America.

The distribution of this complex of entities (in the majority of cases identified as *D. dichotoma*), can be explained by the same boundaries as those of *D. dichotoma* in the N. Atlantic Ocean.

On the east sides of both oceans "northern growth and reproduction boundaries" (~ the 13 °C summer isotherm) limit *D. dichotoma* to the north, and on the west sides "northern lethal boundaries" (~ the 2 °C winter isotherm) limit *D. dichotoma* to the north. However, near Japan the northernmost records correspond with a lower temperature (-1 °C).

In the southern hemisphere the southern boundary follows entirely a "southern growth and reproduction boundary" (~ the 13 °C summer isotherm). The "southern lethal boundary" (the 2 °C winter isotherm) is far more to the south than the actual southern boundary.

Dictyota dichotoma has the same type of distribution in the Atlantic and Pacific Oceans as *Centroceras clavulatum* (van den Hoek, 1982).

Polysiphonia ferulacea

Life history

P. ferulacea has an isomorphic alternation between gametophytic and tetrasporophytic phases (*Polysiphonia* type).

Isolates from Wrightsville Beach, North Carolina, grew well at 15, 20 and 25 °C and poorly or not at all at 10 °C and 30 °C. Tetrasporangia were formed at 15, 20, 25 and 30 °C; mature gonimocarps at 20 and 25 °C (Kapaun, 1978a). In nature (at Wrightsville Beach), gonimocarps were found at temperatures from 18°-28 °C (Kapaun, 1980).

Geographic distribution in the North Atlantic Ocean

The northern boundary of *Polysiphonia ferulacea* in N.E. America approximates the 10 °C February isotherm (Fig. 7). This can be explained as a "northern lethal boundary", corresponding with a lethal temperature of 8 °C. Poor growth occurred at 10 °C in the above experiments; lower temperatures were not tested. In short term experiments (12 h exposure) *P. ferulacea* from Puerto Rico survived 3 °C but not 1 °C; short term experiments are apparently less relevant in the present context than long term experiments (Biebl, 1962).

The northern boundary in Europe approximates the 20 °C summer isotherm. This can be explained as a "northern reproduction boundary", corresponding with a minimum temperature of 18 °C allowing formation of mature gonimocarps. This distribu-

tion pattern of *Polysiphonia ferulacea* in the North Atlantic Ocean is very similar to that of *Centroceras clavulatum* (van den Hoek, 1982).

No records of *P. ferulacea* are known from the Mediterranean and N.W. Africa, although the species could be expected there. One possible reason is the partly confused taxonomy of *Polysiphonia* which is in need of revision for large areas.

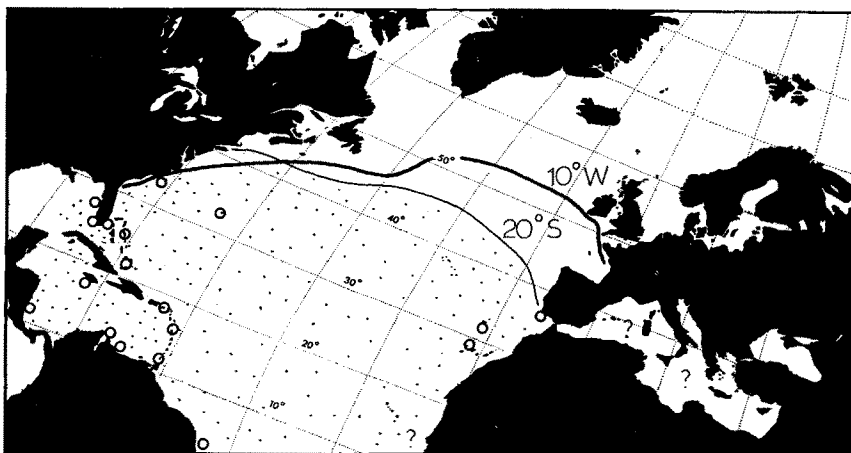


Fig. 7. Distribution of *Polysiphonia ferulacea* in the North Atlantic Ocean

The absence along the northern coast of the Gulf of Mexico can be explained by winter temperatures being intermittently as low as 4 °C in inshore water.

The amphiatlantic tropical-to-temperate group

Polysiphonia denudata

Life history

P. denudata has an isomorphic alternation between gametophytic and tetrasporophytic phases (*Polysiphonia* type).

Isolates from Wrightsville Beach, North Carolina, grew well at 15, 20 and 25 °C, and slowly at 10 °C and 30 °C. Tetrasporangia were formed at 15, 20, 25 and 30 °C; antheridia were formed at 10–30 °C, carpogonia at 15–30 °C (Kapraun, 1978). Mature gonimocarps were obtained in cultures at 20–23 °C. In nature, at Wrightsville Beach, gonimocarps occurred at temperatures from 11–28 °C.

Isolates from Port Aransas, Texas, had slightly different temperature responses (Edwards, 1970b). The isolates grew well at 19, 23, 26.5, and 30 °C, poorly at 14.5 °C, and not at all at 10.5 °C. Mature gonimocarps were formed at 23 °C and 26.5 °C; tetrasporangia at 19, 23, 26.5, and 30 °C. These isolates are better adapted to the higher maximum temperatures at Port Aransas than at Wrightsville Beach. Apparently *P. denudata* comprises various temperature ecotypes.

Geographic distribution in the North Atlantic Ocean

The northern boundary of *P. denudata* approximates the 16 °C August isotherm on both sides of the Ocean (Fig. 8). This limit can be explained as a "northern reproduction boundary", corresponding with a minimum temperature of 15 °C necessary for the production of one of the reproductive stages, in this case probably the production of tetraspores by the tetrasporophyte. This on the assumption that the northern populations have the same temperature requirements as the Wrightsville Beach isolates.

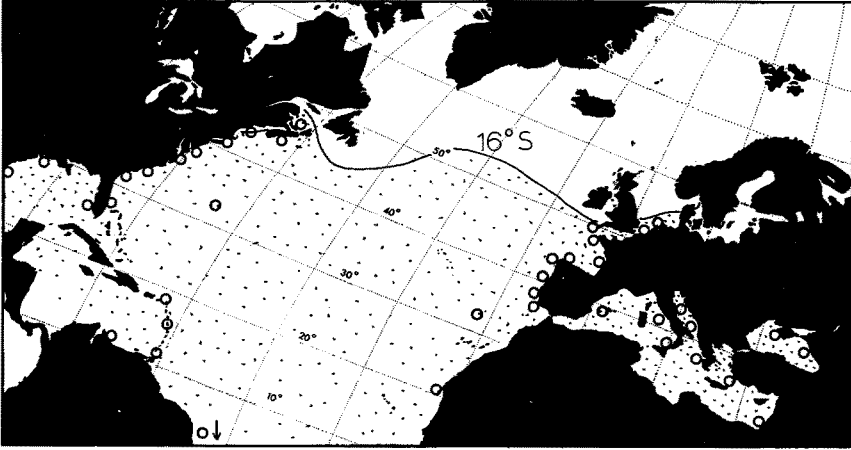


Fig. 8. Distribution of *Polysiphonia denudata* in the North Atlantic Ocean

At its northern point of occurrence in N.E. America *P. denudata* must be capable of surviving ice cover and temperatures as low as $-2\text{ }^{\circ}\text{C}$ in winter. In the protected and shallow embayments where *P. denudata* occurs summer temperatures may rise above $20\text{ }^{\circ}\text{C}$ and thus cause optimal growth and reproduction.

Apparently the temperature requirements of *P. denudata* correspond to the wide annual temperature fluctuations (more than $20\text{ }^{\circ}\text{C}$ on one point) along the N.E. American coasts.

Polysiphonia denudata is quite characteristic for the "tropical-to-temperate distribution group" in being restricted, at its northern boundary, to shallow protected embayments. Other examples are *Cladophora vagabunda*, *Cl. liniformis*, *Chondria dasyphylla*, *C. tenuissima*, *Spyridia filamentosa*.

The species of the American tropical-to-temperate distribution group (group 7, Fig. 4) bridge a comparably wide temperature span and are also mostly restricted to shallow protected embayments. Examples are *Gracilaria tikvahiae*, *Grinnellia americana*, *Solieria tenera*, *Lomentaria baileyana* (van den Hoek, 1982).

The amphiatlantic temperate group with a southern boundary near a winter isotherm

The species of the *Cladophora rupestris* type are characterized by having summer isotherms, corresponding with lethal summer temperatures, as southern boundaries

(Fig. 3). *Rhodochorton purpureum* is an example which will be discussed more fully below. *Ulvaria obscura* probably also belongs to this distribution group.

A close examination of the distribution and the temperature requirements of a number of species in this distribution group has revealed that the majority of species have a composite southern boundary. Along E. Atlantic shores these boundaries follow winter isotherms (corresponding with maximum winter temperatures allowing reproduction) and along American shores summer isotherms (corresponding with lethal summer temperatures). *Nemalion helminthoides*, *Chondrus crispus*, *Desmarestia viridis*, *D. aculeata*, *Monostroma grevillei* and probably also *Acrosiphonia arcta* are examples with such composite southern boundaries in the North Atlantic Ocean.

Rhodochorton purpureum

Life history

Rhodochorton purpureum is a small filamentous rhodophyte which forms dense velvety turfs on shaded rocks in the eulittoral and in the sublittoral zones. In the peculiar life history of this species the carpogonia on dwarf female gametophytes are fertilized by spermatia produced by dwarf male gametophytes. The fertilized carpogonia develop into small gonimoblasts which develop directly into tetrasporophytes which in the end overgrow completely the dwarf female gametophyte to which they grow attached. The gametophytes are mostly dioecious, but there are also monoecious strains (West, 1969, 1970; Stegenga, 1978; Ohta & Kurogi, 1979).

The formation of tetrasporangia is influenced by photoperiod as only under short daylength conditions are tetrasporangia formed. A light break during the long dark period has no effect, so that the response cannot be considered a true photoperiodic response (in the sense of Vince-Prue, 1975). As in *Scytosiphon lomentaria* (Lüning, 1981a) there are different latitudinal daylength-temperature ecotypes (West, 1972; Stegenga, 1978; Hoeksema & Breeman, in prep.). In N.W. America, two northern strains had tetrasporangia formed in culture at daylengths of 12 hours or less and temperatures of 5° and 10 °C (not at 15° and 20 °C) (Fig. 9a, b).

One southern strain in N.W. America (Fig. 9c) had its tetrasporangia formed at daylengths of 10 hours or less, and at temperatures of 10° and 15 °C (not at 5° and 20 °C).

One strain from Chile (Fig. 9d) had its tetrasporangia formed at 5, 10, and 15 °C, and not at 20 °C. Only at 15 °C, did daylengths of 10 hours or less clearly promote formation of tetrasporangia (not at 5 °C and 10 °C). Apparently the response to daylength restricting tetrasporulation to the winter months, only operates under the prevalent temperature conditions along the Chilean coasts.

Two strains from the Netherlands (Fig. 9e, f) formed tetrasporangia at daylengths of less than 12 hours, and at temperatures of 4, 8, 12 and 16 °C (not at 18 °C). These strains have been isolated from water with mean annual temperature fluctuation of c. 3°–19 °C. The maturation of the gametophytes appeared not to be influenced by photoperiod.

The average monthly temperatures at the points where the five strains were collected, probably never had values blocking tetrasporogenesis so that, there, photoperiod is the primary factor restricting tetrasporogenesis to the winter half year. However, all strains can be expected to become intermittently subjected to extreme summer temperatures that are several centigrades higher than the mean monthly August temper-

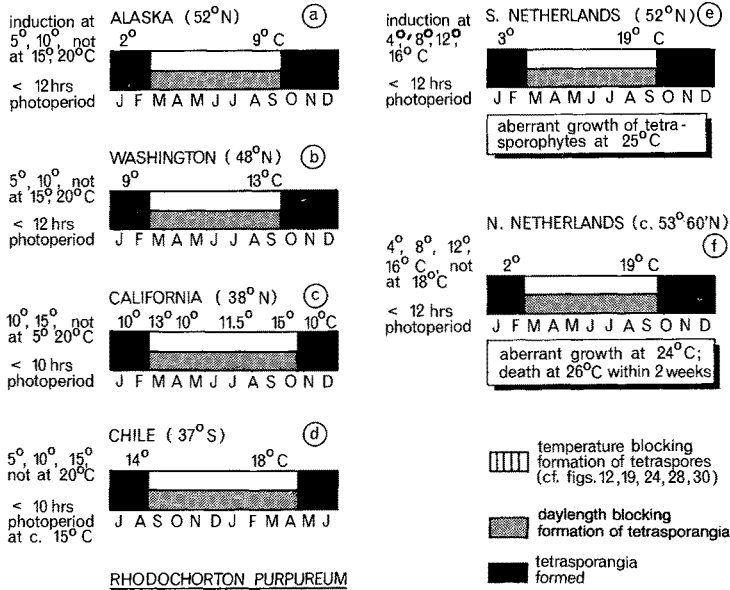


Fig. 9. *Rhodochorton purpureum*. Conditions (temperature, daylength) influencing tetrasporogenesis in the course of the year. (a, b, c) Three N.W. American strains and (d) a S.W. American strain (based on West, 1972); (e) material from the S. Netherlands (based on Stegenga, 1978); (f) material from the N. Netherlands (Hoeksema & Breeman, 1982, in prep.)

ature, and in that case tetrasporogenesis can be expected to be blocked by too high temperatures in autumn. Vegetative growth appeared to be clearly slower under short day than under long day conditions. No vegetative growth was observed in W. American strains at 20 °C (West, 1969), whereas a Dutch strain grew well at temperatures from 8° through 20 °C, but hardly above 20 °C. At 24 °C and 25 °C the Dutch strains showed abnormal growth; and at 26 °C one strain was repeatedly observed to die within two weeks (Hoeksema & Breeman, 1982, in prep.).

Phylogeographic boundaries in the North Atlantic Ocean

The "southern reproduction boundary" of *Rhodochorton purpureum* must be situated near a point where, during a period of 1 to 2 months in each winter, temperature drops below c. 17 °C in order to allow tetrasporogenesis. This on the assumption that the southernmost strains in Europe have the same temperature requirements as the investigated Dutch strains. This would correspond with a mean maximum February temperature of 17 °C of the upper layer of inshore water, and roughly with a mean February temperature of 15 °C. The 15 °C winter isotherm, however, is more to the south than the actual southern boundary in the North Atlantic.

The "southern lethal boundary" of *R. purpureum* must be situated near a point where, during a period of c. 2 weeks temperature of inshore surface water exceeds 24 °C during an excessively warm summer. This would correspond with a maximum August temperature of 24 °C and a mean August temperature of 21 °C. The actual southern

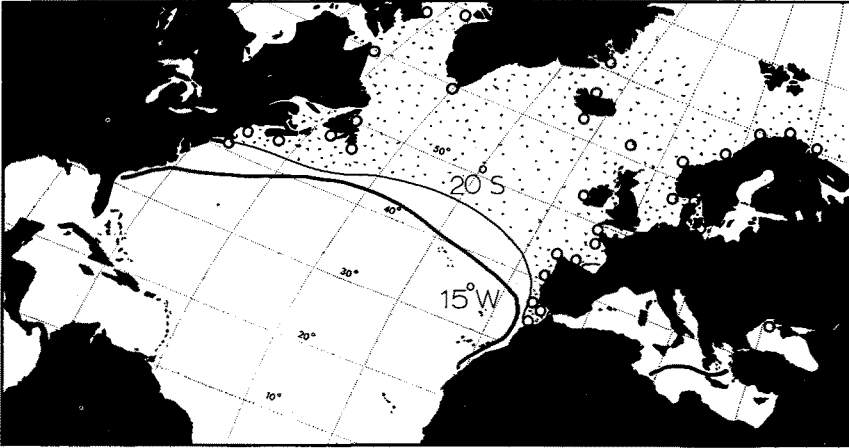


Fig. 10. Distribution of *Rhodochorton purpureum* in the North Atlantic Ocean. 20 °S = 20 °C summer isotherm; 15 °W = 15 °C winter isotherm. Records from the Mediterranean are uncertain

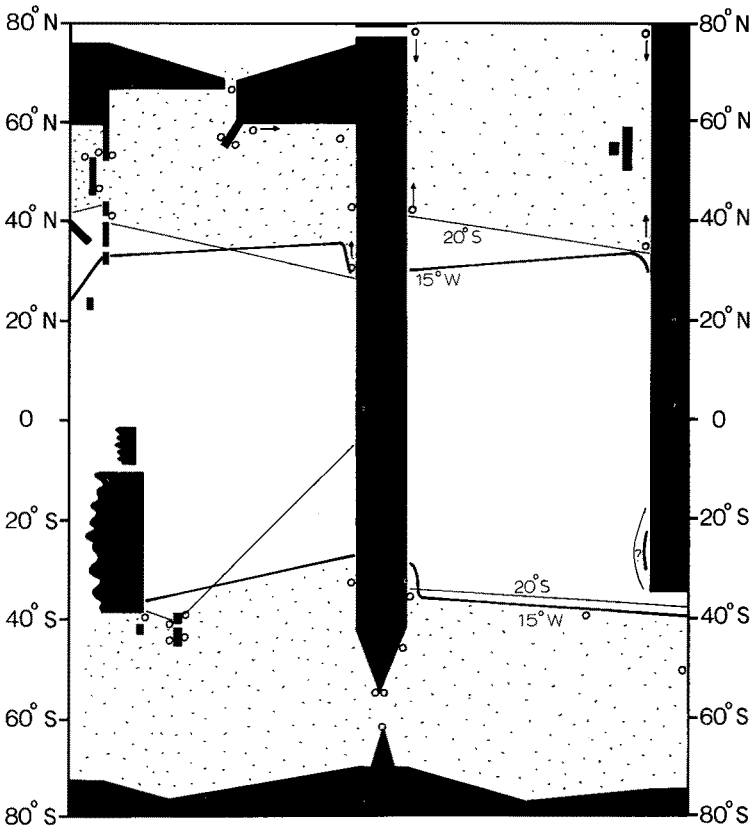


Fig. 11. Distribution of *Rhodochorton purpureum* in the Pacific Ocean (left part of diagram) and Atlantic Ocean (right part of diagram)

boundary is near the 20 °C August isotherm (Fig. 10). The rare records of *R. purpureum* from the Mediterranean should be checked to exclude confusion with other species.

The intertidal shade populations are exposed at low tide, to still higher temperatures than 25 °C at the southern geographic boundary.

In the north, *R. purpureum* extends into the Arctic Region, where it must cope with extremely low temperatures during the Arctic winter. For instance, at Spitsbergen the mean monthly temperature of the seawater is -1.1 °C in February and 1.3 °C in August; and the mean monthly air temperature is -16.1 °C (with a minimum of -42 °C) in January and 5.6 °C (with a maximum of 13 °C) in July (Biebl, 1962). In summer, the species must be able to grow and reproduce at water temperatures between 0 and 5 °C, and this at comparatively long, short photoperiods. Only if *R. purpureum* has daylength-temperature ecotypes adapted to Arctic daylength and temperature conditions, such as *Scytosiphon lomentaria* has, is it imaginable that this species can flourish in Arctic regions. The influence of Arctic conditions on *R. purpureum*'s life history has not yet been experimentally investigated.

Distribution in the Pacific and Atlantic Oceans

The available distribution data (Fig. 11) suggest that *R. purpureum* in the North and South Atlantic Ocean and the North Pacific Ocean is limited towards the equator by 20 °C summer isotherms (August isotherm in the northern hemisphere; February isotherm in the southern hemisphere). However, in the South Pacific Ocean the species seems to be bounded towards the equator by the 15 °C winter isotherm along the American coast, and by the 20 °C summer isotherm along the New Zealand and Australian coasts. The species occurs in Antarctica, although it is possibly restricted to parts projecting from the mainland. This global distribution pattern suggests that *R. purpureum* has the same genotypic range of temperature and daylength adaptation in the northern and the southern hemispheres.

Nemalion helminthoides

Life history

The slippery, worm-like gametophytes of *Nemalion* appear in summer on wave-exposed rocks in most of its distribution area. The life history comprises, in addition, a strongly heteromorphic tetrasporophyte which is composed of irregularly branched filaments. The multiaxial gametophyte arises from a similar filamentous stage. The species apparently hibernates in the form of these filamentous stages (Fries, 1967, 1969; Martin, 1967; Umezaki, 1967*), which can be termed tetrasporophytic and gametophytic microthalli (van den Hoek et al., 1972). Both tetrasporophytic and gametophytic microthalli appear to reproduce vegetatively by monospores under a wide range of conditions.

In two recent studies (Chen et al., 1978; Masuda & Umezaki, 1977) the temperature and daylength conditions influencing the life history have been studied; the results of both studies are in agreement, and their results will be summarized here.

Tetrasporogenesis is induced by short day conditions (photoperiods \leq 12 hrs) and

* *N. vermiculare* Suringar is here considered to belong to the form range of *N. helminthoides*.

relatively high temperatures ($\geq 10^\circ\text{C}$; $\leq 18^\circ\text{C}$); tetrasporangia are formed in 1 to 2 weeks. Tetrasporangia are not formed under 5 and 22°C short day conditions.

Macrothalli are initiated from gametophytic microthalli only under long day conditions (photoperiods > 12 hrs) and at temperatures between about 12 and 22°C . Macrothalli need about 4 months to mature and to form carpospores.

In axenic cultures, microthalli show positive, though slow growth at 12°C , and maximum growth at 20°C . Temperatures between 26 and 27°C are lethal (Fries, 1966).

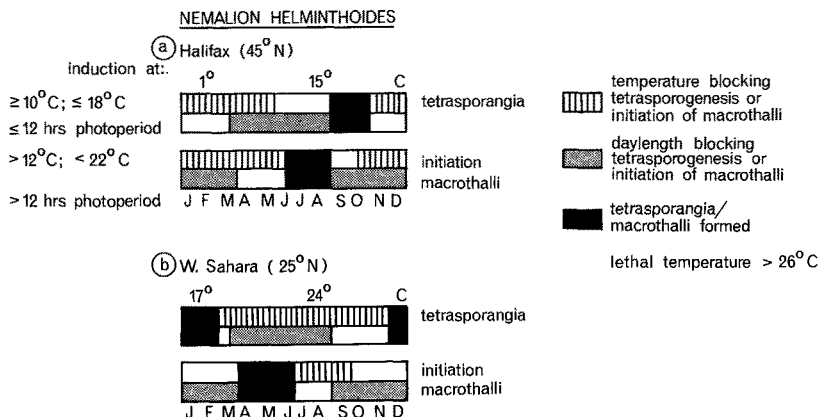


Fig. 12. *Nemalion helminthoides*. Model of the seasonal reproductive cycle in Halifax, Nova Scotia (near northern boundary) and in the W. Sahara (southern boundary), by applying culture results to the conditions in both regions

When one applies the above culture data to the seasonal conditions at Halifax, Nova Scotia (45°N), a model of the seasonal sequence of the phases is obtained as pictured in Fig. 12a. The occurrence of tetrasporangia in nature is unknown, but the gametophytes appear indeed in midsummer, to disappear gradually in autumn (South & Hooper, 1980). Where spring temperatures are higher the gametophyte appears earlier.

At the southernmost point of its geographic area, in the western Sahara (25°N) the gametophyte can be expected to appear in spring (Fig. 12b).

Geographic boundaries in the North Atlantic Ocean

The "southern growth and reproduction boundary" of the gametophyte can be expected near a point where, in the period April through August (when daylengths are 12 hours or longer) temperature drops below 22°C for about 2–3 months. This would approximately correspond with a June temperature of 21°C ; and this with an August temperature of c. 23°C . As the species can survive in the form of microthalli, these conditions can be average conditions. Thus, the "southern growth and reproduction boundary" of the gametophyte can be expected near the 23°C summer isotherm. In general, "southern growth and reproduction boundaries" approximate winter isotherms, because they represent the highest possible temperature allowing growth and reproduction of northern species. In *N. helminthoides*, however, the "southern growth and reproduction boundary" of the gametophyte is determined by a summer temperature, as short photoperiods (≤ 12 hrs) block growth in winter and restrict it to the summer.

The "southern lethal boundary" can be expected near a point where the temperature rises above 27 °C. This would approximately correspond with a maximum August temperature of surface water of 27 °C, and this with a mean August temperature of about 24 °C. Thus, the "southern lethal boundary" can be expected near the 24 °C summer isotherm, and to coincide approximately with the "southern growth and reproduction boundary" of the gametophyte. Particularly in the Mediterranean, the actual southern boundary is near the 25 °C summer isotherm (Fig. 13).

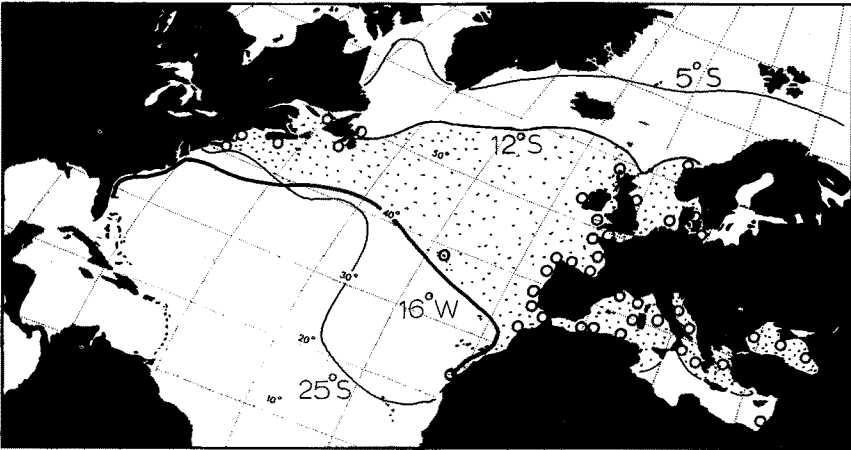


Fig. 13. *Nematolium helminthoides*. Distribution in the North Atlantic Ocean

The "southern reproduction boundary" for the formation of tetraspores by the tetrasporophyte and consequently of the formation of gametophytes, can be expected near a point where, in the period September through half March, temperature is 18 °C or lower for about 2 weeks in each year. This would correspond with a mean February temperature of c. 16 °C. This corresponds indeed with the southern boundary.

The "northern reproduction boundary" for the formation of tetraspores and consequently of gametophytes can be expected near a point where, in the period September through half March, temperature is each year above 10 °C for about two weeks. This corresponds approximately with a mean September temperature and August temperature of 11 °C.

The "northern growth and reproduction boundary" of the gametophyte can be expected near a point where in the period April through August (with photoperiods > 12 hours) temperature is above 12 °C for at least two months in an average summer (for the species can survive cold summers as self-reproducing microthallus). This would approximately correspond with a mean August temperature of 12 °C. The actual northern boundary follows indeed closely the 12 °C summer isotherm.

The "northern lethal boundary" of *N. helminthoides* has not been experimentally tested, but microthalli grow slowly at 5 °C, and must be able to survive frost during low tide at its northern boundary. This would position the "northern lethal boundary" north of the 0 °C winter isotherm. Possibly therefore the 5 °C summer isotherm is the "northern

growth boundary" of the microthalli. The capacity of the microthalli for independent vegetative reproduction by monospores makes it likely that *Nemalion* occurs to the north of the 12 °C summer isotherm in the form of hitherto unrecognized microthalli, much in the way as the tetrasporophytes of *Bonnemaisonia hamifera* has a much more northern extension than the gametophyte.

Geographic distribution in the Atlantic and Pacific Oceans

In the northern hemisphere *Nemalion helminthoides* is bounded on both sides of the Pacific and Atlantic Oceans by approximately the 12 °C summer isotherm in the north and the 25 °C summer isotherm and the 16 °C winter isotherm in the south (Fig. 14).

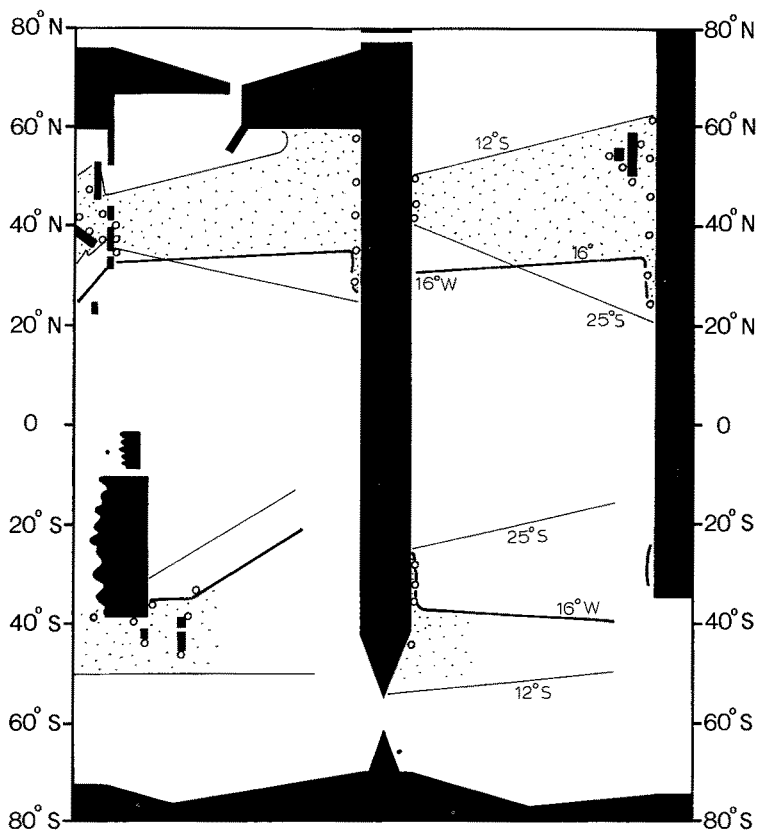


Fig. 14. *Nemalion helminthoides*. Distribution in the Pacific Ocean (left part of diagram) and Atlantic Ocean (right part of diagram)

In the southern hemisphere the species occurs on the western sides of both oceans and here their distribution accords with that in the northern hemisphere. I did not find records for the eastern Pacific and Atlantic coasts, nor for subantarctic islands, in the southern hemisphere. This is especially unexpected for the Chilean coasts, as these are directly connected, via Fuegia, with the coast of Argentina. In a personal communication, Dr. B. Santelices has confirmed the absence of records for Chilean coasts.

The point should be stressed that only one type of environmental regulation, valid for Japanese and Nova Scotia material, can explain the distribution of *N. helminthoides*. Other widely distributed, amphiequatorial species, such as *Scytosiphon lomentaria* and *Rhodochorton purpureum*, have different latitudinal temperature-daylength ecotypes.

Chondrus crispus

Life history

Chondrus crispus has an alternation between isomorphic tetrasporophytes and gametophytes. Both phases consist of basal crusts from which fan-like erect fronds arise. The basal crusts do not have independent means of reproduction.

In cultures, carpospores and tetraspores germinated at temperatures from 5 °C–20 °C, but not higher than 20 °C (Chen & McLachlan, 1972).

Growth was slow at 5 °C and 25 °C, and maximal at 15 °C and 20 °C (Bird et al., 1978; Simpson & Shacklock, 1979). At 30 °C plants died within ten days (Simpson & Shacklock, 1979).

Cultures grown from spores at 15 °C and a 16 hours photoperiod needed about 8–10 months to attain a length of 5–8 cm and to become mature. Gametophytes matured only under long day conditions (16 h photoperiod, not 12 h) and 15 °C. Tetrasporogenesis took place under long day and short day conditions, and temperatures of 15 °C, 13 °C, and 5 °C, but seemed to be promoted by transfer to short day conditions (10 and 8 h photoperiods). Mature plants continued the formation of reproductive cells for several months. After that, male plants and tetrasporophytes resumed growth; gametophytes were reduced to the basal crust which could give off new erect fronds. Basal crusts are in general important for the maintenance of populations in nature (Chen & McLachlan, 1972).

In accordance with these culture results, gametophytes and sporophytes can be found throughout the year in subtidal populations on the coast of New Hampshire. Mid-littoral populations show a summer interruption in the production of reproductive cells, probably as a result of adverse intertidal conditions (later maturation as a result of ice scouring, desiccation, higher temperatures). Adverse high temperatures were also found in the above culture results (no reproduction at 20 °C). Tetraspore production is also reduced in summer in subtidal populations, and is maximal in autumn. These field observations suggest that tetrasporogenesis is promoted by, but not restricted to, short daily photoperiods. In short: the reproduction of *Chondrus crispus* does not present a distinct seasonality (Tveter-Gallagher et al., 1980).

Geographic boundaries in the North Atlantic Ocean

The culture results indicate that the erect fronds must have a minimum length of about 5 cm before they can mature. This suggests that temperatures must have, during a period of several months, a value allowing sufficient vegetative growth.

The "southern growth boundary" can consequently be expected near a point where temperature drops in winter below 25 °C for several months. Even then thalli should probably grow for several seasons to reach maturity. This would approximately correspond with a mean temperature of 22–23 °C in February (incidental warmer winters could

be survived as crusts). The 22–23 °C winter isotherm in the Atlantic is far more to the south than the actual southern phytogeographic boundary (Fig. 15).

Another possible southern boundary might be set by the inability of spores to germinate at temperatures above 20 °C. This suggests a "southern germination boundary" roughly on the 20 °C winter isotherm, as occasional higher winter temperatures could be survived as basal crusts. Again, the 20 °C winter isotherm is far more to the south than the actual southern boundary.

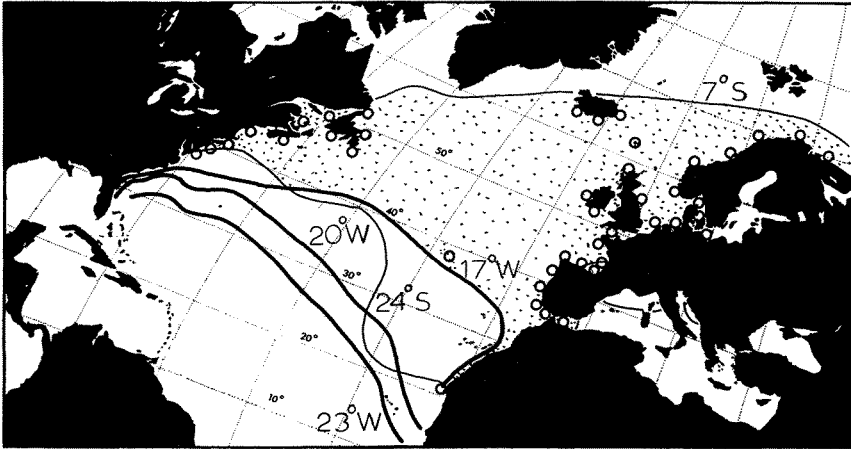


Fig. 15. Distribution of *Chondrus crispus* in the North Atlantic Ocean

A southern reproduction boundary can be expected at a point where temperature drops, in winter, below about 17 °C for several months (as reproductive cells are formed at 15 °C, and not at 20 °C). This would correspond with a 17 °C mean February temperature, as occasional warmer winters can be survived. This explains indeed the occurrence of *C. crispus* in Mauritania (W. Africa) where especially winter upwelling provides cool surface water of 16 °C. It also explains the absence of *C. crispus* in the Canaries and Madeira (where winter temperatures are about 18 °C) and its presence on the Azores.

The "southern lethal boundary" can be expected where during one week, temperature of the surface water exceeds c. 27 °C in an excessively warm summer. This corresponds approximately with a mean August temperature of 24 °C. This would suggest a "southern lethal boundary" near the 24 °C summer isotherm, which is near the actual southern limit of *Chondrus crispus* in America on the coast of Delaware (Zaneveld, 1972) and in Africa on the coast of Mauritania (Lawson & John, 1977). However, the species is not recorded for the coasts between southern Portugal and Mauritania. In southern Portugal the species is rare and the plants remain small. Here the mean August temperature of the surface water is 20 °C, and the maximum temperature 23 °C. Comparable conditions exist on the Côte Basque (S.W. France) where the species is rare and intermittently present. Winter temperatures are here certainly low enough for reproduction. In southern Portugal low littoral and upper sublittoral populations run a much greater risk of being exposed to high air temperatures than in northern Portugal. In S. Portugal the number of days per month with a temperature of 25 °C or more is 26 or

less per month (with maxima in July and August); in N. Portugal (where *Chondrus* abounds) only 6 days or less (Ardré, 1971).

One would expect *C. crispus* in the N. Mediterranean within the 24 °C summer isotherm. Probably life is too hazardous here on the limits of its existence and without the possibility of being reestablished from more northern populations.

The "northern growth and reproduction boundary" can be expected near a point where temperatures rise in summer several months above 5 °C. Even then the thalli should probably have perennial growth before becoming mature. Excessively cold summers are probably survived as basal crusts. This would approximately correspond with a mean August temperature of 7 °C. The actual northern boundary is indeed near to the 7 °C summer isotherm. In Iceland, the species is restricted to the southern and southwestern coasts (Jónsson, 1912; Munda, 1977, 1978, 1980).

No experimental data are available to infer the "northern lethal boundary", but *Chondrus crispus* must be able to survive, in the Gulf of St. Lawrence, temperatures below 0 °C. Basal crusts in the intertidal zone can probably survive exposures to severe frost.

Geographic boundaries in the North Atlantic and North Pacific Oceans

Chondrus crispus is also known to occur along the northwestern coasts of the Pacific Ocean, where it also seems to be bounded by the 7 °C summer isotherm to the north and the 24 °C summer isotherm to the south (Fig. 16). It is missing along the northeastern coasts of the Pacific Ocean which it seems to be potentially capable of inhabiting. This distribution pattern resembles very much that of *Dumontia contorta* and *Cladophora rupestris* (van den Hoek, 1979, 1982).

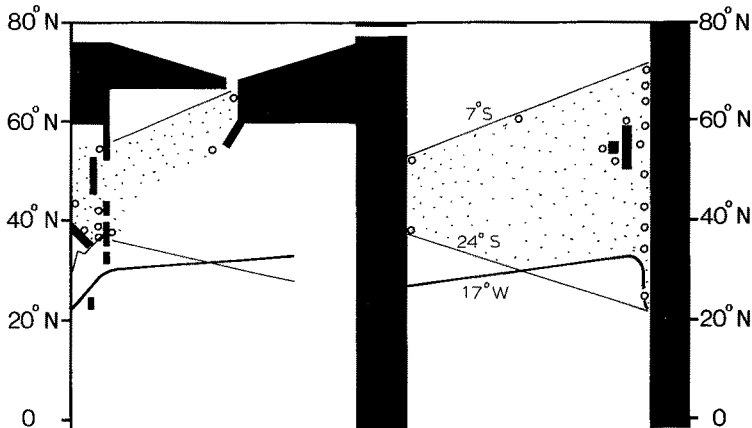


Fig. 16. Distribution of *Chondrus crispus* in the North Atlantic and North Pacific Oceans. The distribution data from the Bering Sea and Unalaska (Aleutian Islands) (Dawson, 1946) need confirmation

An explanation for this distribution pattern is that *Chondrus crispus* has succeeded in spreading from the Atlantic Ocean, through the Canadian Arctic and the Bering Straits into the Pacific Ocean during a warmer pleistocene interglacial period than the present one. This would have required summer temperatures of 7 °C in Canadian Arctic

Waters. At present summer surface temperatures range from 2.2 °C in the western part to 6.4 °C in Baffin Bay (Lee, 1973), while at some points summer temperature may be as high as 9 °C (Lee, 1980).

The southward currents (East Kamchatka Current, Oyashio Current) along the Asian shores have possibly promoted *C. crispus*' further dispersal to Japan; the northward current along the Alaskan shores having prevented its dispersal along American shores.

The genus *Chondrus* is represented in Japan by seven highly variable species. Possibly *C. crispus*, upon its arrival in Japan, has given rise to intense speciation. Alternatively, *Chondrus crispus* may have originated in Japan and dispersed through the Bering Straits and the Canadian Arctic to the Atlantic Ocean. The direction of the currents in the North Pacific Ocean does not support this hypothesis; whereas the general southeasterly direction of the currents through the Canadian Arctic Archipelago does support this hypothesis.

However, it seems unlikely that a benthic algal species could not disperse along an uninterrupted coastline within its temperature boundaries, even against the prevalent direction of the currents. Another explanation is that true *Chondrus crispus* does not occur along Japanese and adjacent coasts; this is the case according to J. McLachlan (pers. comm.).

Desmarestia aculeata

Life history

Desmarestiales resemble Laminariales in having a markedly heteromorphic life history, in which macroscopic sporophytes alternate with microscopic dioecious gametophytes with oogamy.

The perennial sporophytes become fertile in autumn, and show active growth in the early summer. The gametophytes produce gametes which give rise to new sporophytes which appear in spring (Chapman & Burrows, 1970, 1971; Kornmann, 1962c).

Female gametophytes of *D. aculeata* became fertile at 5 °C and 10 °C, but not at 15 °C and 20 °C; those of *D. viridis* at 5 °C, less than 10 % at 10 °C, and not at 15 °C and 20 °C (Lüning, 1981a). Photoperiod did not influence fertility of the gametophytes. The factors influencing sporulation of the sporophyte were not investigated. Sporophytes of *D. aculeata* grew at temperatures from 0 °C through 20 °C, but not at 25 °C. The optimum temperature for growth was 10 °C (Fortes & Lüning, 1980).

Geographic distribution in the North Atlantic Ocean

The southern limits of *D. aculeata* and *D. viridis* along European shores can be explained as "southern reproduction boundaries" along the 12 °C and 10 °C winter isotherms, respectively. These correspond with maximum winter temperatures of 14 °C in *D. aculeata*, and 12 °C in *D. viridis*, allowing fertility of the female gametophytes at the southern boundaries. This is supported by the above cited experimental data (Lüning, 1981a). The southern boundaries in America are likely to be "southern lethal boundaries" and to follow consequently summer isotherms (Fig. 17).

The southern boundaries of both *D. aculeata* and *D. viridis* in N.E. America are near the 20 °C summer isotherm, which would correspond with a lethal temperature of approximately 23 °C. This accords with the observation that growth of *D. aculeata*

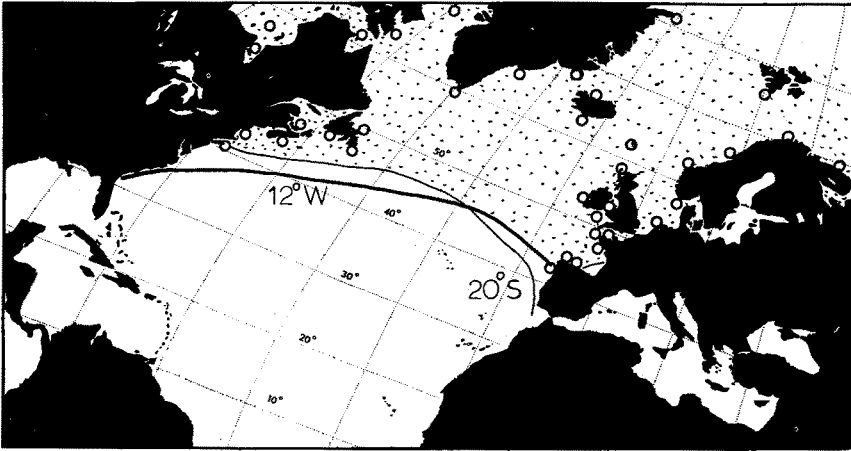


Fig. 17. Distribution of *Desmarestia aculeata* in the North Atlantic Ocean

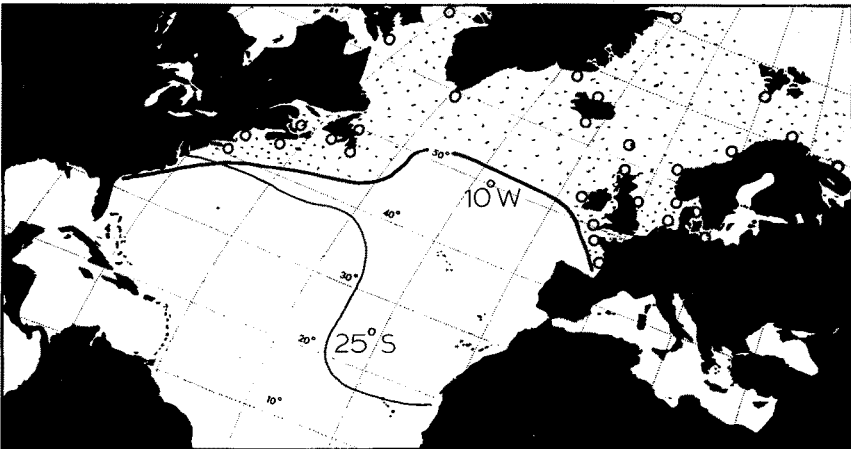


Fig. 18. Distribution of *Desmarestia viridis* in the North Atlantic Ocean

sporophytes ceases at a temperature between 20 °C and 25 °C. For *D. viridis* similar observations on growth of the sporophyte are not available.

However, the southern limit of *D. aculeata* in Japan (in Sachalien and Hokkaido) is near the 17 °C summer isotherm, and this suggests somewhat different temperature requirements of the Japanese population of *D. aculeata*. The winter temperature here is c. 0 °C, far below the maximum winter temperature allowing fertility of female gametophytes in Europe. In N.W. America the southernmost point of distribution of *D. aculeata* corresponds approximately with the 10 °C February isotherm, and this does not differ much from the European southern limit. The mean August temperatures are here c. 14 °C.

The southern limit of *D. viridis* in Japan (on the E. and W. coasts of Honshu) is situated near the 10 °C winter isotherm and, at the same time, near the 25 °C summer

isotherm. In N.W. America the southern limit is near the 11 °C winter isotherm (summer temperatures here are on an average 15 °C) (Fig. 18). Possibly the southern limit of *D. viridis* in N.E. America also approaches the 25 °C August isotherm, but the lack of suitable substrata between its actual southernmost station (New Jersey) and the potential southernmost point (in Delaware), is possibly responsible for its absence in this southernmost portion of its potential range in N.E. America. Another possibility is that Japanese and N.E. American populations have somewhat different upper lethal temperatures.

Distribution in the southern hemisphere

Whereas *Desmarestia viridis* has been recorded from the temperate belt of the southern hemisphere, *D. aculeata* has not been recorded there. The records of *D. viridis* suggest that it is restricted to the North by the 8 °C winter isotherm, which includes the subantarctic islands and southernmost South America, but excludes Australia, New Zealand and South Africa. Papenfuß (1964) thinks that these records need confirmation. The Antarctic species *D. willii* Reinsch has formerly been confused with *D. viridis*.

Monostroma grevillei

Life history

Monostroma grevillei has a heteromorphic life history, in which blade-like dioecious gametophytes alternate with unicellular "Codiolum-like" sporophytes (Kornmann, 1962a; Jónsson, 1968; for a review, see Tatewaki, 1972). The blade-like gametophyte is a spring annual. The species survives the rest of the year in the form of the unicellular sporophyte which in this respect resembles hypnozygotes of numerous freshwater Chlorophyceae.

The sporophyte becomes fertile (produces quadriflagellate meiospores) under short day conditions (8/16 h light/dark) and at 5 °C, 10 °C, and 15 °C for 10 % of the plants; but not at 1 °C and 20 °C. The sporophytes remain sterile under long day conditions (16/8 h light/dark) and at all temperatures tested. A light break given in the long dark period reverses the photoperiodic response, this indicating a "true photoperiodic response" (Lüning, 1981a, b).

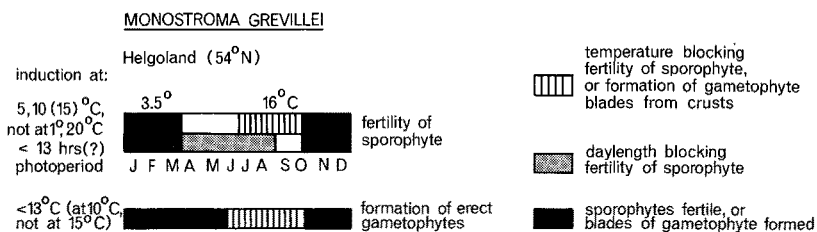


Fig. 19. Model of the seasonal sequence of events in the life history of *Monostroma grevillei* on Helgoland (based on Lüning, 1981a, b). The model is approximative, as the critical daylength has not been established, and the number of temperature values tested is too limited. A critical daylength has been assumed of 13 h (the critical daylength of *Scytosiphon lomentaria* on Helgoland, see Lüning, 1981a, b)

The development of the blade-like fronds of the gametophyte from a basal crustose phase takes place at 5 °C and 10 °C, but not at 15 °C and 20 °C (Lüning, 1981a).

The presumed sequence of events in the life history of *M. grevillei* on Helgoland is given in the model of Fig. 19.

Distribution in the North Atlantic Ocean

The southern limits of *Monostroma grevillei* along European (and N.W. American) shores, can be explained as a "southern reproduction boundary" along the 12 °C February isotherm (Fig. 20). This is supported by Lüning's experimental data indicating a maximum temperature of 15 °C allowing fertility of the sporophyte (this corresponds with a mean maximum temperature of inshore water of about 15 °C and a mean February temperature of 13 °C).

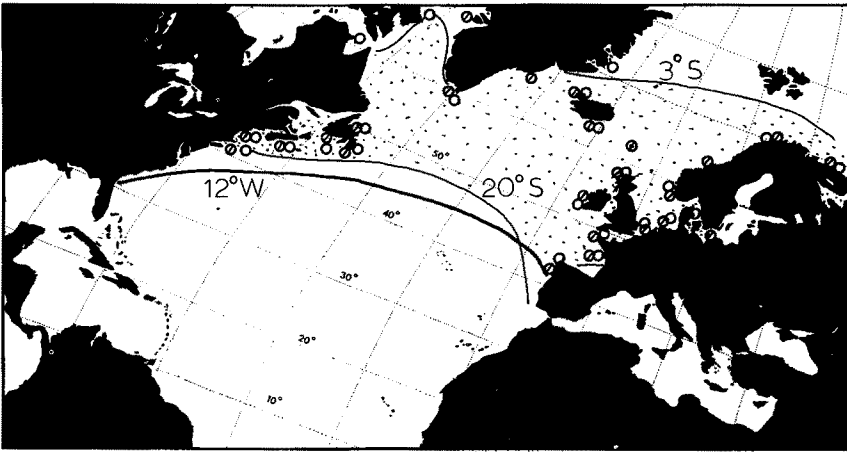


Fig. 20. Distribution of *Monostroma grevillei* (⊕) and *Acrosiphonia arcta* (○) in the North Atlantic Ocean

The southern limits in N.E. America (and in Japan) are likely to be "southern lethal boundaries" approximately along the 20 °C summer isotherm, which would correspond with a lethal temperature of about 23 °C. This should be the lethal temperature of the sporophyte, which is the "over-summering" phase. Lethal temperatures have not been experimentally tested so far.

The northern limit of *M. grevillei* in the North Atlantic Ocean can be explained as a "northern reproduction boundary" along the 3 °C August isotherm. This is supported by Lüning's (1981b) observation that sporophytes need a minimum temperature somewhere between 1 °C and 5 °C to become fertile. This minimum temperature should be realized in the period with sufficiently short daylengths, in early autumn (cf. Fig. 15).

Distribution in the southern hemisphere

M. grevillei has been recorded from the southern hemisphere (Fuegia and Kerguelen Islands) (Papenfuß, 1964). However, the taxonomic status of these records is uncertain, and the *Monostroma*-like Chlorophyceae in the southern hemisphere are in need of revision.

Acrosiphonia "arcta"

Life history

Acrosiphonia arcta has a heteromorphic life history comparable to that of *M. grevillei*, in which monoecious isogamous gametophytes alternate with unicellular "Codiolum"-like sporophytes. The gametophytes are tufts of branched uniseriate filaments composed of multinucleate cells (Jónsson, 1962, as *A. spinescens*). The taxonomy of this genus is presently confused and needs revision for a large area (cf. Kornmann, 1962b; Kornmann & Sahling, 1977). It is likely, however, that records of *A. arcta* and *A. spinescens* (or *Spongomorpha arcta* and *S. spinescens*) in the N. Atlantic refer to the same species. It is not clear whether the population of *A. arcta* on Helgoland, which lacks a "Codiolum phase" but is morphologically similar to *A. arcta* populations with a sporophytic phase, deserves the status of a separate species (Kornmann, 1962b; Kornmann & Sahling, 1977).

Geographic distribution

The southern distribution of *A. arcta* in the North Atlantic is identical to that of *Monostroma grevillei* (Fig. 20). This suggests the same causes of this distribution pattern as in *M. grevillei*, particularly so because both species have similar life histories. Experimental evidence in support of this hypothesis is not available.

A. arcta is also recorded from the N.W. Pacific Ocean where it is bounded to the south approximately by the 20 °C summer isotherm (as in the N.W. Atlantic Ocean). *S. arcta* is also recorded from the N.E. Pacific Ocean (as *Spongomorpha arcta* and *S. spinescens*, cf. Scagel, 1966), where it can hardly be differentiated from *Spongomorpha coalita* (Rupr.) Coll. This latter species has its southern boundary at about the 12 °C winter isotherm.

Acrosiphonia arcta has also been recorded from the southern hemisphere (as *Spongomorpha arcta* and *S. spinescens*), where it occurs south of the 12 °C winter isotherm. However, the taxonomic status on the species level of these southern records is uncertain (Papenfuß, 1964).

The amphiatlantic temperate group with a southern boundary near a winter isotherm

The species of the *Cladophora albida* type are characterized by having winter isotherms as their southern boundaries: these correspond with "southern growth and/or reproduction boundaries" (Fig. 3).

Punctaria latifolia seems to be, on the basis of its distribution, another example of this distribution group. Two other examples, *Scytosiphon lomentaria* and *Petalonia fascia*, have been treated elsewhere (van den Hoek, 1982).

Punctaria latifolia

Life history

The life history of *Punctaria latifolia* comprises a prostrate filamentous phase with apical growth (the microthallus phase) from which erect lanceolate blades arise with

intercalary growth (the macrothallus phase). Both microthallus phase and macrothallus phase reproduce only by plurilocular zoidangia in one strain from the Netherlands (Rietema & van den Hoek, 1981). All plurizoids grow into new microthalli; macrothalli can only be formed as shoots from microthalli.

In other strains plurilocular as well as unilocular zoidangia are formed whose zoids also directly grow into new microthalli. There are no clear indications of a sexual cycle (Danggaard, 1963, 1966; Clayton & Ducker, 1970).

The initiation of macrothalli in the above strain from the Netherlands was markedly influenced by temperature (Rietema & van den Hoek, 1981: as *Desmotrichum undulatum*). Higher temperatures (20°, 25°, 30 °C) favoured the rapid development of ephemeral, predominantly uniseriate macrothalli which disintegrated soon (within 1–2 weeks) by intensive sporulation. 16 °C was the highest temperature allowing the formation of lanceolate macrothalli which, however, reached their maximum size within 2–4 weeks, when intensive sporulation put an end to vegetative growth. At still lower temperatures (4°, 8°, 12°C) the final size of the macrothalli was much larger, despite slower growth. This was caused by a much later onset of zoidogenesis at lower temperatures (at 12 °C after 3–4 weeks, at 8 °C after 4–8 weeks, and at 4 °C after 8–13 weeks). Under short day conditions the onset of zoidogenesis was advanced, particularly so at lower temperatures. Therefore the largest blades were formed at lower temperatures and long day conditions, that is, in late spring.

At 30 °C growth was abnormal and characterized by disintegration by precocious and abundant zoidogenesis of microthalli and abortive macrothalli. At 35 °C microthalli died.

In culture, widely varying macrothalli were obtained embracing the characters of *Desmotrichum balticum* Kütz., *D. scopulorum* Reinke, *D. undulatum* (J. Ag.) Reinke, and *Punctaria latifolia* Grev. (Rietema & van den Hoek, 1981).

Punctaria crouanii (Thur.) Born. and *P. crispata* (Kütz.) Batt. probably also belong to the range of *P. latifolia*.

Geographic distribution in the North Atlantic Ocean

The southern limit along the N.E. Atlantic shores at the 14 °C winter isotherm (Fig. 21) can be explained as a "southern growth boundary", corresponding with the highest winter temperature (16 °C) allowing the formation of macrothalli from microthalli. This is in accordance with the above experimental results.

The southern limit along the N.W. Atlantic shores (at Beaufort, N. Carolina) near the 27 °C summer isotherm can be explained as a "southern lethal boundary", corresponding with a lethal temperature of c. 30 °C. This accords with the above experimental results, which indicated abnormal growth at 30 °C and a lethal temperature limit between 30 °C and 35 °C. This explanation of the southern limit of *P. latifolia* differs from that given in Rietema & van den Hoek (1981), where the 15 °C winter isotherm ("the southern growth boundary") is considered to limit *P. latifolia* to the south both in Europe and N.E. America. However, in that case the southernmost point of *P. latifolia* could be expected much more to the south in N.E. America than the actual, southernmost limit at Beaufort, N. Carolina.

Apparently, the southern limit of *P. latifolia* does not differ from most other southern limits so far investigated in the North Atlantic Ocean. It is also of a composite nature, and

consists along the E. Atlantic coast of a "southern growth boundary" (a winter isotherm), and along the W. Atlantic coast of a "southern lethal boundary" (a summer isotherm).

Apparently there is no fundamental difference between the *Cl. rupestris*-type and *Cl. albida*-type of the amphiatlantic distribution group. Clearly distribution data alone may lead to incorrect conclusions as to the causes of distribution patterns.

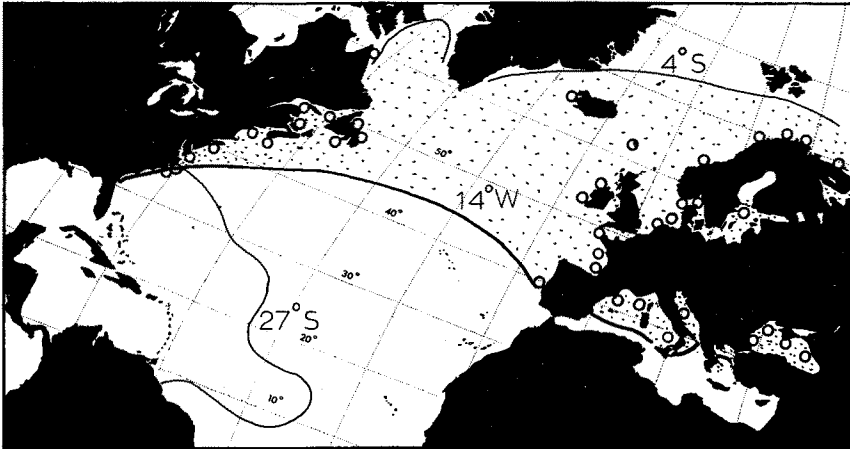


Fig. 21. Distribution of *Punctaria latifolia* in the N. Atlantic Ocean

So far only *Scytosiphon lomentaria* and *Petalonia fascia* seem to have southern boundaries along winter isotherms (of 17 °C) at both sides of the ocean and corresponding with the maximum winter temperatures allowing initiation of macrothalli. However, even in these two species a lethal temperature of c. 33 °C probably prevents their establishment in most of the N. Gulf of Mexico.

The northern limit of *P. latifolia* (near the 4 °C winter isotherm) can probably be explained as a "northern reproduction boundary". At 4 °C in culture slow growth of macrothalli and fertility occurred; lower temperatures were not investigated.

Distribution in the Atlantic and Pacific Oceans

The distribution pattern of *P. latifolia* in the North Pacific Ocean accords with that in the N. Atlantic Ocean with regard to the limiting isotherms (Fig. 22). The comparatively few records from the southern hemisphere are contained between the 14 °C winter isotherm to the north and the 4 °C summer isotherm to the south.

The N.E. American temperate group

The few species in this distribution group are endemic to N.E. American coasts, where they are adapted to the wide annual temperature fluctuations. *Chondria baileyana* is one possible example, but this species is difficult to differentiate from *C. tenuissima*. Another possible example is *Polysiphonia harveyi*. However, the genus *Polysiphonia* is in need of a taxonomic revision for large areas.

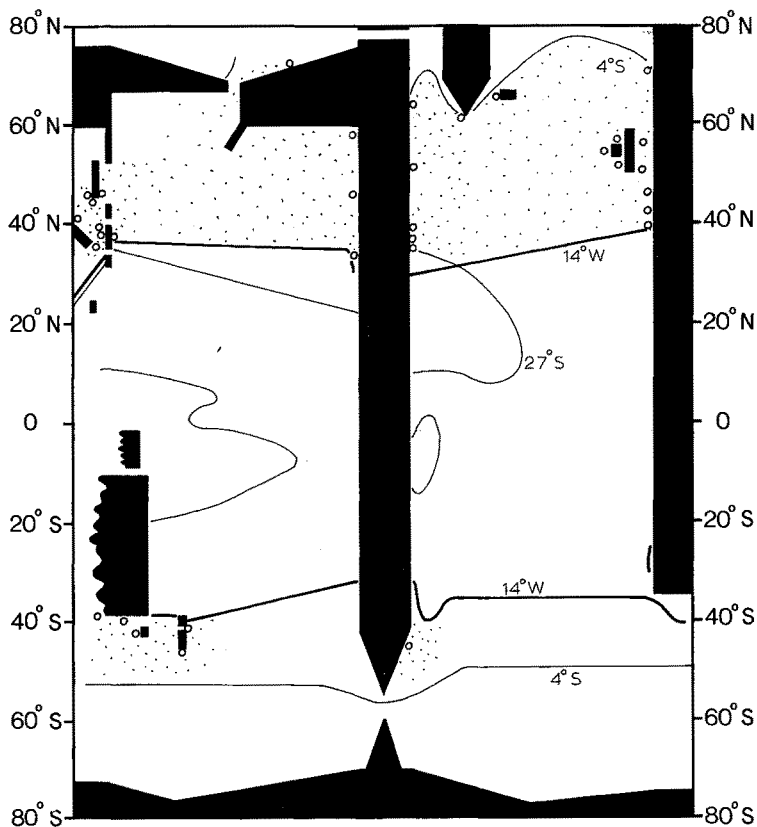


Fig. 22. Distribution of *Punctaria latifolia* in the Atlantic and Pacific Oceans

Polysiphonia harveyi

Life history

Polysiphonia harveyi has an isomorphic alternation between gametophytic and tetrasporophytic phases (*Polysiphonia*-type).

Isolates from Wrightsville Beach, North Carolina, grew well at 10, 15, 20, and 25 °C, and poorly at 30 °C. Antheridia and carpogonia were formed at 10–25 °C, mature gonimocarps at 20 °C; in nature gonimocarps were found at 11–23 °C (the formation of tetrasporangia was not investigated) (Kapraun, 1980).

Geographic distribution along N.E. American shores

The northern boundary of *P. harveyi* is near the 12 °C August isotherm (Fig. 23). This limit can be explained as a "northern reproduction boundary", corresponding with a minimum summer temperature of 11 °C necessary for the formation of mature gonimocarps.

The southern boundary of *P. harveyi* is near the 19 °C winter isotherm. This can be explained as a "southern reproduction boundary", approximately corresponding with a

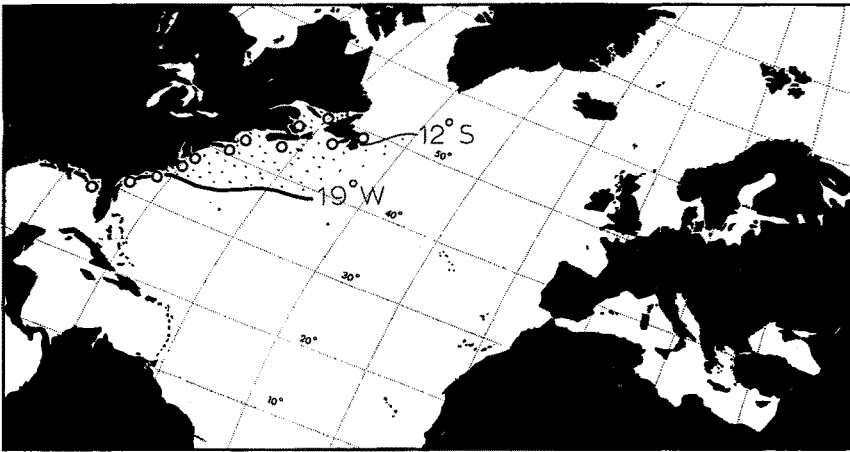


Fig. 23. Distribution of *Polisiphonia harveyi* in the North Atlantic Ocean

maximum summer temperature of 21 °C allowing formation of mature gonimocarps (in nature, the highest temperature at which mature gonimocarps were found, was 23 °C).

At the northern boundary, *P. harveyi* is a summer annual in protected, shallow embayments; at the southern boundary it is a winter annual. At the northern boundary it must be able to survive winter temperatures as low as -2 °C; at the southern boundary summer temperatures as high as 33 °C. *P. harveyi* is apparently well adapted to the wide temperature fluctuations characteristic for N.E. American temperate coasts.

Bonnemaisonia hamifera

Bonnemaisonia hamifera is an invader from the Japanese temperate distribution group. This distribution group contains the numerous species endemic to Japanese and adjacent coasts (approximately between 30 °N and 45 °N). This group is equivalent to the N.E. American temperate group which contains only very few endemic species.

Life history

Bonnemaisonia hamifera has a heteromorphic alternation between a perennial filamentous tetrasporophyte (microthallus-phase) and an annual dioecious erect gametophyte (macrothallus-phase) of a complex architecture. The tetrasporophyte is also known as the Trailliella-phase (Fig. 24).

In cultures from Helgoland, tetrasporangia were formed by the tetrasporophyte after exposure for about one month to a photoperiod of 11 hours or less per day and a temperature between 12° and 19 °C (Lüning, 1981a, b; see also Chihara, 1961; Chen et al., 1969). A light break during the long dark period blocked tetrasporogenesis thus indicating a true photoperiodic response. The combination of relatively high temperatures and short daylengths inducing tetrasporogenesis is realized for only a short period (October) on Helgoland, and for a longer period (November/December) at Tsuyazaki, Japan (Lüning, 1981a, b; see Fig. 24).

Gametophytes develop from the tetraspores in autumn and grow into maturity in the course of spring. The influence of photoperiod and temperature on the growth and

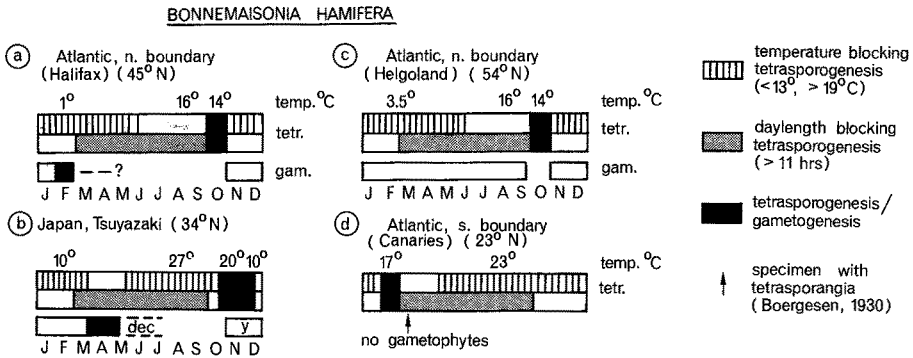


Fig. 24. *Bonnemaisonia hamifera*. Conditions (temperature, daylength) influencing tetrasporogenesis of tetrasporophytes. Models in which experimental results obtained in cultures of material from Helgoland are applied to field conditions at Halifax (a) (cf. Edelstein et al., 1969a, b); Tsuyazaki, Japan (b) (cf. Chihara, 1961); Helgoland, Europe (c); and Canaries (d). Tetr. = tetrasporophytes; Gam. = gametophytes; dec. = decay; y = young gametophytes

maturation of the gametophyte has not been experimentally investigated. However, growth of the gametophytes was clearly inhibited at temperatures higher than 20 °C (Koch, 1950), and they died after one week of exposure to 25 °C (they survived 23 °C; Lüning, 1981b). In short term experiments (12 h exposure) gametophytes survived 17 °C, but not 27 °C (Biebl, 1959). Tetrasporophytes died after one week at 28 °C (they survived 25 °C; Lüning, 1981b) and at -2.9 °C within two hours when ice was formed, but not when ice was not formed (Koch, 1950). This indicates that the *Trailliella*-phase can survive subtidal winter temperatures as low as -2 °C. This is also valid for the gametophyte (Koch, 1950). In short term experiments (12 h exposure) gametophytes survived -2 °C, but not -8 °C (with ice formation) (Biebl, 1959).

Phytogeographic boundaries in the North Atlantic Ocean

The "southern reproduction boundary" of the tetrasporophyte of *Bonnemaisonia hamifera* can be expected near an E-W line where, during a period of about one month, temperature drops below 19 °C in an average winter in order to allow tetrasporogenesis and consequently the initiation of gametophytes. This would approximately correspond with a monthly mean February temperature of 19 °C in the sublittoral. The "southern reproduction boundary" of the tetrasporophyte can therefore be expected near the 19 °C winter isotherm.

The "southern growth boundary" of the tetrasporophyte has not been experimentally tested, but the "southern lethal boundary" can be expected at a point where temperature never exceeds 28 °C for one week, which corresponds with a maximum August temperature of about 28 °C and with a mean August temperature of c. 25 °C. Thus the "southern lethal boundary" of the *Trailliella*-phase can be expected to approximate the 25 °C summer isotherm, which is not far from the actual southern boundary (Fig. 25).

The "southern growth and reproduction boundary" of the gametophyte has not been experimentally tested, but the seasonal development of the gametophyte at Shimoda, Japan, suggests that temperature should drop below c. 15 °C for about four months in winter to allow sufficient growth and reproduction; this approximately corresponds with

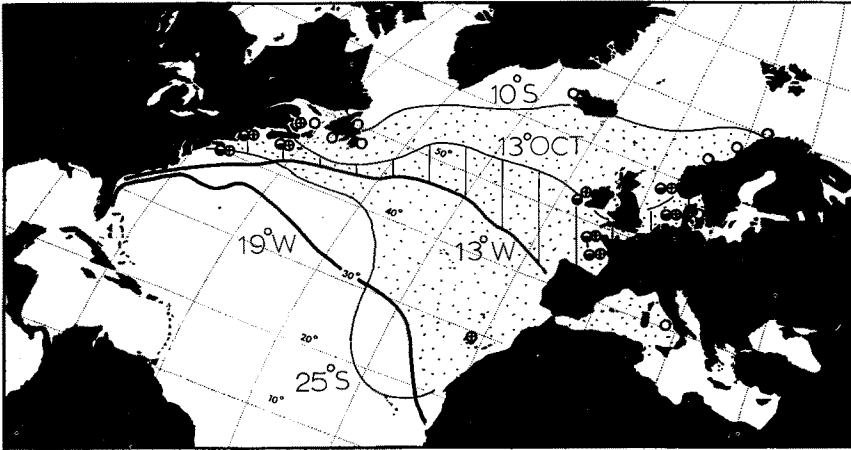


Fig. 25. Distribution of *Bonnemaisonia hamifera* in the North Atlantic Ocean. Hatched: distribution area of the gametophyte (⊕). Stippled: distribution area of the tetrasporophyte with (⊕) and without (⊙) tetraspores. 19°W = 19°C winter isotherm. 25°S = 25°C summer isotherm. 13°Oct.:13°C October isotherm. 10°S = 10°C summer isotherm

the 13°C winter isotherm (Chihara, 1961, 1962). At 15°C, normal gametophytes are obtained in culture (Chen et al., 1969). At 20°C growth of gametophytes is inhibited (Koch, 1950).

The "southern lethal boundary" of the gametophyte can be expected at a point where temperature exceeds 23°C for several weeks in summer; actually this is not relevant as the gametophyte is a spring annual which has terminated its life-span before summer.

The "northern reproductive boundary" of the tetrasporophyte can be expected near a point where, for about one month, temperature is above 12°C in the period with the short daylengths (≤ 11 hrs) inducing tetrasporogenesis. This month is apparently October (Fig. 24c) and it means that the northern reproductive boundary of the tetrasporophyte approximates the 13°C October isotherm, which corresponds with about the 15°C summer isotherm in Europe and about the 16°C summer isotherm in N. E. America. This northern reproductive boundary of the tetrasporophyte is at the same time the northern boundary of initiation of the gametophytes (which can only start from tetraspores). The actual northern boundary of the gametophyte approximates indeed the 13°C October isotherm (Fig. 25).

The "northern growth boundary" of the tetrasporophyte was not investigated, but distribution data suggest that temperatures in summer must be above 8°C for 1–2 months to allow sufficient growth of the Trailliella-phase, which has its northern boundary near the 10°C summer isotherm. Trailliella can maintain itself and disperse by means of vegetative multiplication by fragmentation.

The "northern lethal boundary" of the tetrasporophyte can be expected at -2°C . Its occurrence in waters around Labrador indicates that it can indeed survive temperatures of -2°C . Mature gametophytic plants were present in February on the Atlantic coast of Nova Scotia in water with a temperature of 2°C (Chen et al., 1969); this indicates that the

gametophyte must be able to grow and reproduce at considerably lower temperatures than the tetrasporophyte.

The various above-treated boundaries have been integrated in Fig. 25 which shows that *B. hamifera* gametophytes occupy only a narrow latitudinal belt both in N. E. America and along European shores. This belt is limited to the North by the "northern reproductive boundary" of the tetrasporophyte, which is near the 13 °C October isotherm; and to the south by the "southern growth and reproduction boundary" of the gametophyte (the 13 °C winter isotherm) in Europe, and the "southern lethal boundary" of the tetrasporophyte in America (the 25 °C summer isotherm).

Fig. 25 also shows that the tetrasporophyte – the *Trailliella*-phase – has a much wider latitudinal span than the gametophyte, and is limited to the north by the "northern growth boundary" (c. 10 °C summer isotherm) and to the south by the "southern lethal boundary" (the 25 °C summer isotherm). Apparently the vegetative reproduction by the tetrasporophyte is much more important than the sexual cycle.

At its northern boundary, the gametophyte can be expected to be present some years, and to be absent in other years, as Octobers colder than 13 °C will block tetrasporogenesis. This is actually the case, in Europe (Helgoland) as well as in N.E. America (Halifax) (Lüning, 1981b; Chen et al., 1969). Comparable year-to-year fluctuations can be expected along the southern distribution boundary. The close proximity of these instable boundaries along European coasts is probably the reason that gametophytes are comparatively rare, and that female gametophytes often fail to become fertilized (Hamel, 1930) probably because male and female gametophytes are too scattered.

Distribution in Japan

Bonnemaisonia hamifera is thought to have been accidentally introduced into the North Atlantic Ocean from Japan at the end of the previous century (McLachlan et al., 1969; Lüning, 1981b). The vehicle for this introduction is unknown. The species has probably also been introduced to Pacific American coasts.

The distribution of *Bonnemaisonia hamifera* in Japan is given in Fig. 26. Apparently the southern distribution boundaries of the tetrasporophyte and gametophyte phase are more or less congruent. The 27 °C summer isotherm is the "southern lethal boundary" of the tetrasporophyte. The 13 °C winter isotherm is the "southern growth and reproduction boundary" of the gametophyte.

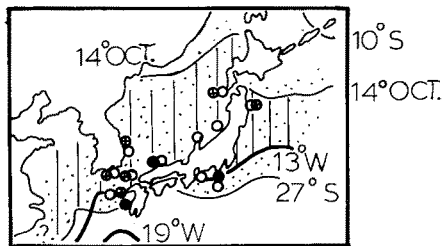


Fig. 26. Distribution of *Bonnemaisonia hamifera* in Japan. Stippled: distribution area of the tetrasporophyte (⊕). Hatched: distribution area of the gametophyte (○). 10 °S = 10 °C summer isotherm. 14 °Oct. = 14 °C October isotherm. 13 °W = 13 °C winter isotherm. 27 °S = 27 °C summer isotherm. 19 °W = 19 °C winter isotherm

The 19 °C winter isotherm is the "southern reproductive boundary" of the tetrasporophyte; this does not function as a real boundary, as it is situated to the south of the "southern lethal boundary".

To the north the 14 °C October isotherm corresponds with the "northern reproductive boundary" of the tetrasporophyte in Japan. Purely vegetative tetrasporophytes can be expected up to the 10 °C summer isotherm in the Kurillian Isles (45 °N). No distribution data are available to corroborate this. To the south, gametophytes and tetrasporophytes can be expected to occur along Chinese coast (to about 25 °N); distribution data for the Chinese coasts could not be obtained.

The much better congruence of the distributional boundaries of *B. hamifera* in Japan than in Europe, supports the opinion that this species is a native of Japan where it is adapted to the prevailing temperature conditions. Temperature conditions along European coasts have enabled the tetrasporophyte to disperse, in the course of the past decades, through a much wider latitudinal span than it inhabits in Japan, whereas completion of the sexual cycle is more difficult than in Japan because conditions inducing tetrasporogenesis – mainly the sharp autumnal temperature drop coinciding with short daylengths – are less easily realized. The vigorous vegetative multiplication of the tetrasporophyte is a necessary prerequisite for its successful dispersal in Europe.

It is interesting that many other species which are considered to be characteristic for the Japan Sea shores of Japan, such as *Coccophora langsdorfii*, *Grateloupia divaricata*, and *Sargassum confusum* have comparable distribution patterns along the coasts of Japan (Chihara & Yoshizaki, 1970; cf. Funahashi, 1974).

Distribution along Pacific North American shores

Bonnemaisonia hamifera is in Pacific North America (Fig. 27) an infrequent species which is restricted to a narrow latitudinal belt between Point Conception (34°30') and Punta San Quintín (c. 30 °N). In this belt, temperatures in the short day period (October through February) may have values inducing the formation of tetrasporangia, namely 13°–19 °C, with annual fluctuations (mean monthly values) of c. 12–15 °C at 34°30', and

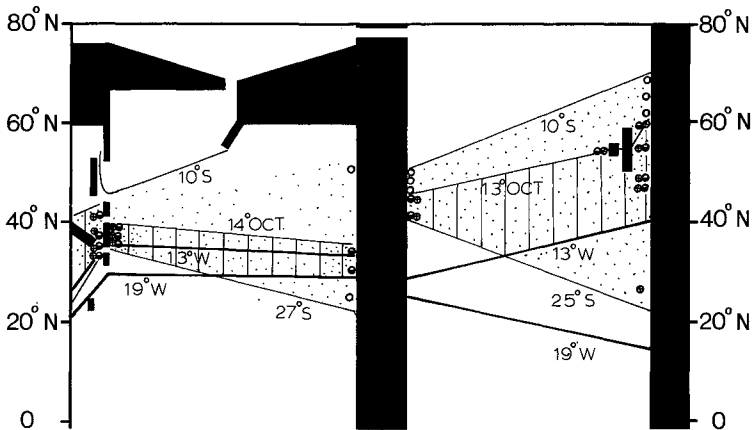


Fig. 27. Distribution of *Bonnemaisonia hamifera* in the North Pacific and North Atlantic Oceans. (For explanation of symbols, see text to Fig. 25)

17–20° at 30°. This southern boundary of the gametophyte apparently has the character of “the southern reproductive boundary” of the tetrasporophyte, as gametophytes can only grow from tetraspores. It approximates the 19 °C winter isotherm. The northern boundary of the gametophyte corresponds in the same way with the “northern reproductive boundary” of the tetrasporophyte (14 °C October isotherm). North of Point Conception the temperatures are too low throughout the year for tetrasporogenesis (less than 7–12 °C, cf. West, 1972). The annual fluctuations may be quite irregular due to changes in upwelling and circulation. In other words: there is not a distinct autumnal drop in temperature which times, together with short photoperiod, the onset of tetrasporogenesis, such as it does in Japan. Temperatures can be expected to be occasionally too high or too low for tetrasporogenesis, thus causing an irregular presence of the gametophytes in the winter half year. Moreover, temperatures should remain below 15 °C in the winter half year in order to allow growth and maturation of the gametophyte.

The tetrasporophyte has a much wider latitudinal distribution, although it has not been found throughout its potential range (especially towards the north).

Apparently *B. hamifera* is as poorly adapted to temperature conditions in N.W. America as it is in Europe.

The warm temperate Mediterranean-Atlantic distribution group

This distribution group contains the species endemic to European temperate shores (Fig. 4; see “Introduction”). The distribution of *Acrosymphyton purpuriferum* suggests that this species belongs to this distribution group (Fig. 29). The following discussion, however, will present arguments to attribute *A. purpuriferum* rather to distribution group 1, the amphiatlantic tropical-to-temperate distribution group with a northeastern extension (Fig. 1).

Acrosymphyton purpuriferum

Life history

A. purpuriferum has a heteromorphic alternation between a perennial crustose tetrasporophyte (microthallus) and an annual erect monoecious gametophyte (Cortel-Breeman & van den Hoek, 1970). In cultures from Banyuls (S. France) tetrasporangia were formed after exposure, for at least one week, to a photoperiod of 13 hrs or less and a

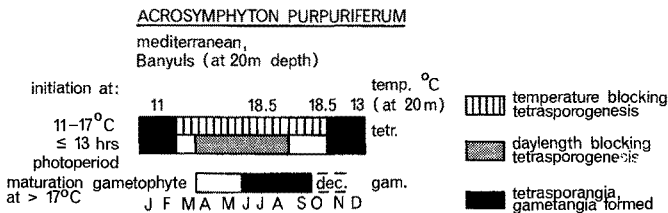


Fig. 28. *Acrosymphyton purpuriferum*. Conditions (temperature, daylength) influencing tetrasporogenesis and gametogenesis. Model in which experimental results obtained from cultures of material from Banyuls are applied to field conditions at Banyuls (at 20 m depth). Based on Breeman (1979). Tetr. = tetrasporophyte; Gam. = gametophyte; dec. = decay

temperature between 11°–17 °C. The combined influence of temperature and short photoperiods restricts the formation of tetrasporangia to the period November through February at a depth of 20 m at Banyuls (Fig. 28). Young gametophytes appear in spring, and mature in the course of spring and summer. They matured at temperatures above 17 °C (and up to 27 °C) without a photoperiodic influence (Breeman, 1979, with further references). Vegetative growth of the gametophytes took place over the entire temperature range experimentally tested (12 °C–28 °C). The perennial tetrasporophytes are probably capable of vegetative multiplication by means of vegetative fragments. Vegetative growth of tetrasporophytes took place over the entire temperature range experimentally tested (8 °C–20 °C). Lethal temperatures were not investigated.

The unique type of photoperiodic response in *Acrosymphyton* is presently further being investigated (Cortel-Breeman & ten Hoopen, 1978; ten Hoopen & Breeman, in prep.).

Phytogeographic boundaries

The "southern reproduction boundary" of the microthallus-phase of *Acrosymphyton purpuriferum* can be expected near a point where, during a period of at least two weeks, temperature drops below 17 °C in most winters in order to allow tetrasporogenesis and consequently the initiation of gametophytes: this on the assumption that Atlantic populations have the same temperature and daylength requirements as strains from Banyuls. This would approximately correspond with a monthly mean temperature of 17 °C at the depth (15–30 m) where *Acrosymphyton* grows. If, in some years, temperature does not drop below 17 °C it can survive as the perennial crust with its own vegetative multiplication. This boundary can therefore be expected to approximate the 17 °C winter isotherm, which it does (Fig. 29) according to available distribution data.

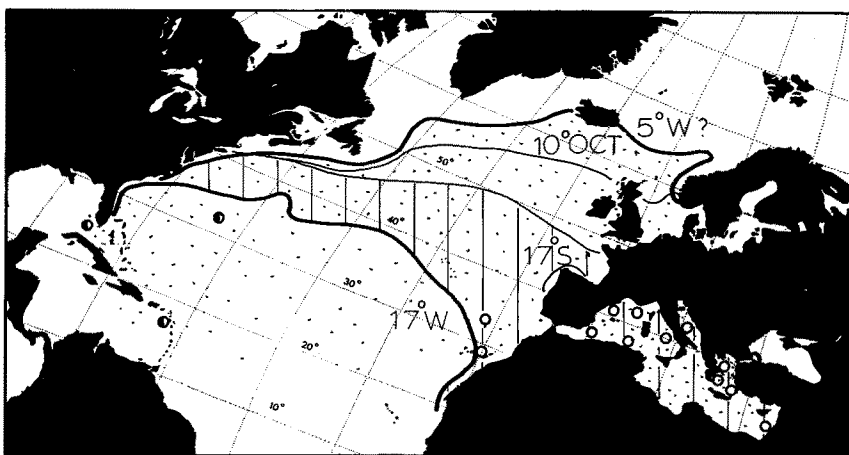


Fig. 29. Distribution of *Acrosymphyton purpuriferum* (○) and *A. caribaeum* (●) in the North Atlantic Ocean. Hatched area: potential distribution area of fertile *A. purpuriferum* gametophytes. Stippled area: potential distribution area of tetrasporophytes. 5 °W = 5 °C winter isotherm; 10 °Oct. = 10 °C October isotherm; 17 °S = 17 °C summer isotherm; 17 °W = 17 °C winter isotherm. Distribution data from Breeman (1979)

Theoretically, the "southern growth boundary" of the microthallus-phase can be expected farther to the south as vegetative growth is possible at up to at least 20 °C.

The "northern reproduction boundary" of the microthallus-phase can be expected near a point where, during at least two weeks in the period September through March (when photoperiods are ≤ 13 hrs/day), temperature remains above 10 °C thus allowing tetrasporogenesis. This point would approximate the 10 °C October isotherm which roughly corresponds with the 13 °C summer isotherm in Europe and about the 16 °C summer isotherm in America. Again, purely vegetative growth and multiplication of microthalli is possible at still lower summer temperatures (down to at least 8 °C).

The "southern growth and reproduction boundary" of the gametophytic phase cannot be inferred from culture results, as the whole temperature range permitting growth and reproduction was not investigated. However, if the highest temperature (28 °C) permitting vegetative growth and maturation of the gametophyte were near the limit, this would position the "southern growth and reproduction boundary" of the macrothallus-phase near a 30 °C winter temperature. This suggests that the gametophyte of *A. purpuriferum* might flourish throughout the tropical belt, particularly so in deeper water (15–30 m) along oceanic coasts. Apparently it is restricted to warm temperate waters by the blocking of tetrasporogenesis at temperatures above 17 °C.

The "northern growth and reproduction boundary" of the gametophyte can be expected near a point where, during a period of at least one month, temperature arises above 17° in summer, that is near the 17 °C summer isotherm. If, in some summers, temperature remains too low, the species can survive as microthallus.

The lethal boundaries of both phases have not been experimentally tested. Especially the lethal boundaries of the perennial tetrasporophyte are important as absolute distribution boundaries. The "northern lethal boundary" of the microthallus must be near a winter temperature below 8 °C, the lowest temperature allowing growth and vegetative multiplication. Assuming that this boundary is near the 5 °C winter isotherm, this would allow occurrence of the microthallus along the coasts of the British Isles and on offshore reefs of the Carolinas, and not in N.E. America and on inshore coasts of the Carolinas. Crustose rhodophytes resembling the tetrasporophyte of *Acrosymphyton* and known as *Hymenoclonium serpens* are indeed known from the British Isles (Cortel-Breeman, 1975) but have probably partly been confused with *Hymenoclonium*-like tetrasporophytes of *Bonnemaisonia asparagoides*.

The highest experimental temperature to which the tetrasporophyte has been subjected is 20 °C, at which good growth is possible (but not tetrasporogenesis). If the tetrasporophyte could grow at the same high temperatures as the gametophyte (28 °C), it could be expected to grow in the tropical belt where it could maintain itself by vegetative multiplication.

In the hatched area of Fig. 29 *A. purpuriferum* is able to complete its life history; this area is clasped between the 17 °C winter isotherm (the southern boundary of tetrasporogenesis and consequently the initiation of gametophytes) and the 17 °C summer isotherm (the northern boundary for maturation of the gametophyte). The available distribution data are compatible with this area. However, *A. purpuriferum* is a comparatively rare species which has possibly been overlooked in other parts of its geographic range.

Tetrasporophytes can theoretically be expected far to the north of the 17 °C summer

isotherm (Fig. 29, stippled area). The occurrence of *Hymenoclonium serpens* in Brittany and the British Isles is compatible with this expectation (but confusion with tetrasporophytes of other rhodophytes is possible).

Tetrasporophytes can also be expected to the south of the 17 °C winter isotherm (Fig. 24, stippled area).

Actually, to the south of the 17 °C winter isotherm the Caribbean species *Acrosymphyton caribaeum* occurs (Taylor, 1952, 1960) (Fig. 29). This species differs from *A. purpuriferum* only in minor details of the carpogonial and auxiliary cellbranches, which details seem to be covered by the ranges of these characters in *A. purpuriferum*. This suggests that *A. caribaeum* and *A. purpuriferum* are conspecific. Tetrasporogenesis in the Caribbean populations can be expected to be initiated at higher temperatures than in the Banyuls populations. This would be by no means unusual, as comparable temperature ecotypes are now known for various other algal species (*Scytosiphon lomentaria*, *Dumontia contorta*, *Rhodochorton purpureum*).

If this is correct, *A. purpuriferum* belongs to the amphiatlantic tropical-to-temperate distribution group with a northeastern extension (*Cl. coelothrix* type).

The Arctic distribution group

Clathromorphum circumscriptum

The crustose coralline *C. circumscriptum* treated as an example comprises isomorphic tetrasporophyte and gametophyte generations in its life history; but reproduction takes place mostly by means of asexual bispores which are formed in bisporangial conceptacula.

The influence of combinations of temperature, light intensity, and daylength on the formation of bisporangia has been experimentally investigated by Adey (1973). Although it is difficult to disentangle in his experiments the influence of the three different factors, his results suggest that photoperiods of more than 12 hrs/day and temperatures higher than 5 °C block bisporogenesis (the formation of abortive conceptacula is less strictly blocked). Perhaps relatively high daily light doses, rather than photoperiod, block bisporogenesis. When these experimental data are applied to field conditions (a few m deep water) in Eastern Maine, bisporogenesis seems to be restricted there to the period December–March (Fig. 30), which roughly agrees with field data.

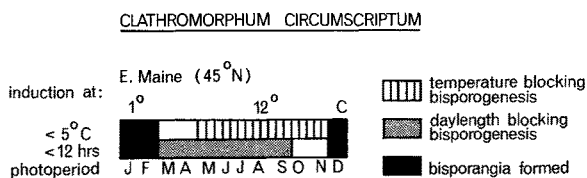


Fig. 30. *Clathromorphum circumscriptum*. Model of the seasonal reproductive cycle in E. Maine, by applying culture results to conditions in E. Maine (Adey, 1970, 1973)

Other experiments (Adey, 1970) indicate that *C. circumscriptum* shows good growth at temperatures between 0 °C and 17 °C (700 lx, 14 h light/day), but at 20 °C growth stops.

A positive photosynthetic effort is possible between 0° and 20 °C. The compensation point varies from c. 30 lx at 0 °C to 500 lx at 20 °C. Apparently in cold Arctic water a positive photosynthetic effort is possible at very low light intensities; this accords with the deep occurrence of this species in the Arctic (this is shown by many other benthic algae in the Arctic).

Phytogeographic boundaries in the North Atlantic

The "southern reproduction boundary" of *Clathromorphum circumscriptum* can be expected near a point where, during about 1–2 months in most winters, temperature drops below 5 °C. This corresponds approximately with a mean February temperature of 4 °C. The actual southern boundary is situated near the 3 °C winter isotherm (Fig. 31).

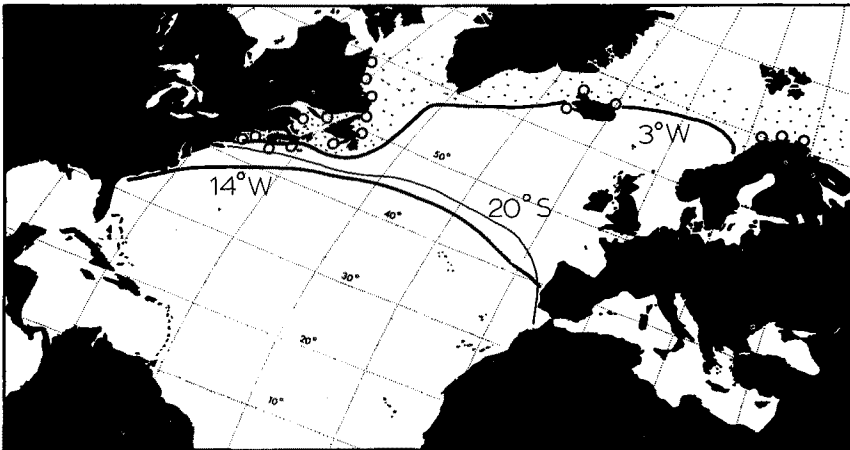


Fig. 31. *Clathromorphum circumscriptum*. Distribution in the North Atlantic Ocean (based on Adey, 1973)

The "southern growth boundary" can be expected near a point where, during a period of 1–2 months in each winter, temperature drops below 17 °C. This would correspond with a mean maximum February temperature of c. 16 °C, and a mean February temperature of around 14 °C. Apparently the species remains far to the north of this boundary.

The "southern lethal boundary" has not been experimentally tested, but it can be expected at a temperature somewhat above 20 °C. This would correspond with about the 20 °C summer isotherm, which is near the southernmost point of occurrence in N.E. America of this species.

Phytogeographic boundary in the North Atlantic and North Pacific

Also in the North Pacific the southern boundary is the "southern reproductive boundary" which closely follows the 3 °C winter isotherm (see also Adey et al., 1976). In N.E. America, but still more so in Japan, the "southern reproduction boundary" and the "southern lethal boundary" almost coincide. In Japan, the "southern lethal boundary" is,

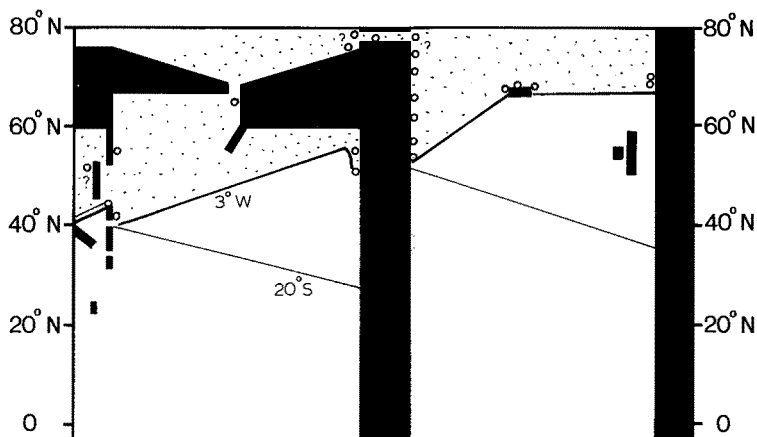


Fig. 32. *Clathromorphum circumscriptum*. Distribution in the North Atlantic and the North Pacific Oceans. Based on Adey, 1973, and on Adey et al. 1976; Hawkes et al., 1978; Lee, 1980 (O?: probably included in *C. compactum*); Vozžinskaja, 1964 (O?: probably included in *Phymatolithon compactum*)

in the Japan Sea, even situated somewhat to the north of the "southern reproduction boundary" and probably functions there as the real phytogeographic boundary (Fig. 32).

DISCUSSION

Distribution groups

The present paper reviews experimental evidence in support of seven out of ten geographic distribution groups of benthic marine algae previously distinguished in the North Atlantic Ocean on the basis of distribution data only. This evidence is also in agreement with experimental data reviewed in another recent paper (van den Hoek, 1982).

Three distribution groups consist of stenothermous species with a difference of 18–22 °C between minimum and maximum lethal temperatures (expressed as highest and lowest mean monthly values), and of 5–12 °C between minimum and maximum temperatures (mean monthly values) allowing growth and/or reproduction. These groups are the "tropical Western Atlantic group" (group 6) (for which no experimental evidence is available); the "warm temperate Mediterranean-Atlantic group" (group 9); and the "Arctic group" (group 10). These three groups consist of species endemic to the corresponding regions. Especially the first two groups are extremely rich in species, as are corresponding distribution groups from the Pacific Ocean, namely the "tropical Western Pacific group", and the "warm-temperate Californian group".

The numerous species contained in group 9 (the warm-temperate Mediterranean-Atlantic group) and the "warm-temperate Californian group" inhabit the eastern coasts of the Atlantic and North Pacific Oceans which are characterized by small annual temperature fluctuations (with a difference of 2–6 °C to 6–10 °C between mean February

and August temperatures, and up to 16 °C difference between extreme values). These species are probably unfit for life on the western coasts of both oceans where annual temperature fluctuations occur of c. 20 °C or more.

The large numbers of species endemic to the temperate coasts of the southern hemisphere probably have the same temperature requirements as group 9, as these coasts are also characterized by small annual temperature fluctuations (c. 5 °C between highest and lowest mean monthly values, and 10 °C between extreme values).

It is likely that the species endemic to Antarctica have temperature responses comparable to those of the stenothermous Arctic species.

The remaining seven distribution groups (1, 2, 3, 4, 5, 7, 8) consist of comparatively eurythermous species with the capacity to bridge a difference of more than 20 °C between the minimum and maximum lethal temperatures (expressed as mean monthly values; the extreme difference is up to 35 °C). Although these eurythermous species are potentially capable of having wide geographic ranges those of distribution group 8, the "North East American temperate group" and the corresponding "Japanese temperate group" are restricted to N.E. American coasts and Japanese (and adjacent) coasts, respectively. Only very few species are known to belong to this group in N.E. America. *Polysiphonia harveyi* (this work) is an example, whereas Japanese coasts are probably inhabited by hundreds of endemic species belonging to this distribution group. It is likely that the adverse nature of the vast sediment coasts in E. America between 30 °N and 45 °N is responsible for this striking difference. These coasts are also likely to have acted as barriers to latitudinal displacements of the benthic macroalgal flora during the glaciations, thus causing their impoverishment (van den Hoek, 1975, 1982).

Despite their capacity to bridge wide temperature spans and their potential capacity to inhabit many other temperate coasts, the numerous endemic Japanese species are restricted to Japanese and adjacent coasts. This points to a lack of capacity for long distance dispersal in these algae. Several Japanese endemics which have been accidentally introduced elsewhere appear to have spread indeed over wide latitudinal spans. Examples are *Sargassum muticum* (van den Hoek, 1982) and *Bonnemaisonia hamifera* (this work). The temperature-daylength regulation of this latter species is apparently adapted to conditions in Japan; elsewhere (in N.W. America, N.E. America and Europe) the life history makes the impression of having been disrupted; and the species, to maintain itself predominantly in the form of the tetrasporophyte, uses the capacity of this phase for vegetative multiplication.

Sargassum muticum, on the other hand, has a normal reproduction on the coasts of N.W. America and Europe, where it has been introduced (see van den Hoek, 1982, for further references).

The species of distribution groups 1, 2, 3, 4, 5 and 7 can bridge wide temperature spans (more than 20 °C difference between highest and lowest mean monthly values) and have wide geographic distributions. Many of them have amphiatlantic, amphipacific and part of them even amphiequatorial distributions. An interesting question is whether these species are originally endemic to the N.W. Pacific or N.W. Atlantic, and have succeeded to disperse to other coasts subsequently. One would consequently expect these species to have effective means of long distance dispersal, and this in contrast to species of distribution group 8.

Phytogeographic boundaries

The ten distribution groups discussed in this paper were primarily distinguished on the basis of distribution data (Figs 1–4). For each amphiatlantic species it seemed possible to approximate the northern boundary with either a summer isotherm (corresponding with a "northern growth and reproduction boundary") or with a winter isotherm (corresponding with a "northern lethal boundary"). In a similar way, it seemed possible to approximate the southern boundary with either a winter isotherm (corresponding with a "southern growth and reproduction boundary") or a summer isotherm (corresponding with a "southern lethal boundary").

Actually, a large proportion of investigated boundaries, particularly of southern boundaries appeared to be of a composite nature (Table 2), and corresponded with temperatures limiting reproduction (sometimes growth) along N.E. Atlantic shores and with lethal temperatures along N.W. Atlantic shores.

Most northern boundaries, however, are growth and/or reproduction boundaries on both sides of the N. Atlantic Ocean.

The large majority of investigated boundaries on the N.E. Atlantic shores are growth and reproduction boundaries, and only comparatively few are lethal boundaries. This is apparently related to the small annual temperature fluctuations along the N.E. Atlantic coasts. However, distribution group 9 (the warm-temperate Mediterranean-Atlantic group) contains possibly many species with a "northern lethal boundary" of 0° to 5 °C, restricting it to Europe (as in *Saccorhiza polyschides*, cf. van den Hoek, 1982). This remains to be investigated.

Apparently, distribution data alone may give useful suggestions about the nature of phytogeographic boundaries, but they may quite easily lead to incorrect conclusions. Experimental checks are necessary, as boundaries are often of a composite nature.

Consequently, the available evidence does not support the distinction between an amphiatlantic temperate group "with a southern boundary near a summer isotherm" (group 4) and an amphiatlantic temperate group "with a southern boundary near a winter isotherm" (group 5).

The phytogeographic boundaries of a species are determined by the temperature responses of the boundary populations. Ideally, therefore, these temperature responses should be checked for boundary populations and several populations in the intervening part of the geographic range. For none of the species considered in the present discussion are such complete sets of data available. For comparatively few species (*Dumontia contorta*, *Scytosiphon lomentaria*, *Rhodochorton purpureum*) were temperature-daylength responses investigated of populations from various points of these species' geographic areas. These three species appeared to have various temperature-daylength ecotypes. The southern boundaries could be explained by the temperature responses of investigated populations which were nearest to these boundaries. Possibly the lethal temperatures are less subject to ecotypic variation than temperatures limiting growth or reproduction. For instance, *Dumontia contorta* populations from the Isle of Man, the Grevelingen (S.W. Netherlands) and Roscoff differed in temperatures allowing initiation of macrothalli from microthalli, but not in the lethal temperature (26 °C) of the microthalli (Rietema, 1982, in prep.; van den Hoek, 1982). However, the upper lethal temperature of full-grown *Laminaria saccharina* sporophytes was c. 17 °C for sporophy-

tes from the Isle of Man, and more than 17 °C for sporophytes from Helgoland (Lüning, 1975). Tropical *Dictyota dichotoma* from Puerto Rico seems to have a higher lethal temperature than a temperate population from Roscoff, Brittany (Biebl, 1959, 1962; this work).

For most species given in Table 1, however, the temperature responses of material from only one station are known. Nonetheless it was possible to use these to explain these species' geographic distribution, and this suggests that possible ecotypes do not differ much in their temperature responses. However, a population of *Sphacelaria rigidula* was investigated not far from the northern boundary of this species' vast tropical-to-temperate area, and this population may consequently have temperature responses typical for a boundary population. The same is true for the investigated populations of *Gracilaria foliifera*, *Polysiphonia ferulacea*, and *Centroceras clavulatum* (van den Hoek, 1982; this study).

Most species with wide distributions in the North Atlantic and the North Pacific Oceans, and some also in the southern hemisphere, are bounded throughout their geographic ranges by approximately the same temperature boundaries. Examples are *Dictyota dichotoma* (Fig. 6); *Rhodochorton purpureum* (Fig. 11); *Nemalion helminthoides* (Fig. 14); *Punctaria latifolia* (Fig. 22); *Clathromorphum circumscriptum* (Fig. 27); and *Centroceras clavulatum*, *Sphacelaria rigidula*, *Laminaria saccharina*, *Scytosiphon lomentaria*, *Petalonia fascia*, *Macrocystis pyrifera* (van den Hoek, 1982). This suggests that these species have the same genotypic range of temperature and daylength adaptation throughout their vast, and in some cases even disjunct, geographic areas. Notable exceptions are *Dumontia contorta* (van den Hoek, 1982, Fig. 16) and *Chondrus crispus* (Fig. 16) which occur in both the North Pacific and the North Atlantic Oceans, but are restricted to the N.W. Pacific coasts. One possible explanation is that these N.W. Pacific populations are bounded by much lower temperatures, limiting reproduction, than the N. Atlantic populations. Another explanation is that the records of these species from the N.W. Pacific are based upon misidentifications. This is apparently the case for *Chondrus crispus*, according to J. McLachlan (pers. comm.).

Taxonomic problems

One needs for the delineation of geographic areas, of course, taxonomically reliable records. Species belonging to critical groups which are in need of taxonomic revision are apparently less suitable for the present type of discussions. For instance, *Callithamnion byssoides* Arnott & Harv. in Hook. seems to belong to the amphiatlantic tropical-to-temperate distribution group on the basis of distribution data, and to be bounded to the North by the 15 °C summer isotherm (which can be explained as a "northern growth and reproduction boundary") (Edwards, 1971; Kapraun, 1978b). However, the gonimoblast depicted by Edwards (1969) is uncharacteristic of *C. byssoides* (Rueness & Rueness, 1980) so that it is likely that American and European samples identified as *C. byssoides* belong to more than one species. Comparable uncertainties exist with regard to *Polysiphonia*, *Ceramium*, *Enteromorpha*, *Ulva*, etc. The examples belonging to *Polysiphonia* and treated in the present paper are thought to be sufficiently characteristic to preclude much confusion.

The taxonomy of the genus *Laminaria* (cf. Table. 2) is presently in a state of flux. In

Table 2. Nature of the northern and southern geographic boundaries of marine benthic algae in the North Atlantic Ocean. *Borrowed from van den Hoek (1982); other species treated in this work. **Estimates entirely based on distribution data (culture data lacking)

Northern boundaries	Distribution group No.	W. side N. Atlantic		E. side N. Atlantic	
		lethal boundary (winter isotherm)	reproduction/growth boundary (summer isotherm)	lethal boundary (winter isotherm)	reproduction/growth boundary (summer isotherm)
<i>Dictyota dichotoma</i>	1	2°C			13°C**
<i>Gracilaria foliifera</i> *	1	8°C		8°C	
<i>Polysiphonia ferulacea</i>	1	10°C			20°C
<i>Centroceras clavulatum</i>	1	12°C			20°C
<i>Hypnea musciformis</i>	2		19°C**		19°C**
<i>Sphacelaria rigidula (furcigera)</i> *	3		12°C		12°C
<i>Polysiphonia denudata</i>	3		16°C		16°C
<i>Callithamnion hookeri</i>	4		10°C		10°C
<i>Nemalion helminthoides</i>	4		12°C		12°C
<i>Dumontia contorta</i> *	4		5°C		5°C**
<i>Chondrus crispus</i>	4		7°C		7°C
<i>Monostroma grevillei</i>	4		3°C		3°C
<i>Punctaria latifolia</i>	5		4°C**		4°C**
<i>Scytosiphon lomentaria</i>	5		0°C**		0°C**
<i>Petalonia fascia</i>	5		0°C**		0°C**
<i>Gracilaria tikvahiae</i> *	7		15°C		
<i>Polysiphonia harveyi</i>	8		12°C		
<i>Saccorhiza polyschides</i> *	9			4°C	
<i>Laminaria hyperborea</i> *	9			2°C**	or 5°C**
<i>Acrosymphyton purpuriferum</i>	9				17°C
Southern boundaries	Distribution group No.	W. side N. Atlantic		E. side N. Atlantic	
		lethal boundary (summer isotherm)	reproduction/growth boundary (winter isotherm)	lethal boundary (summer isotherm)	reproduction/growth boundary (winter isotherm)
<i>Rhodochorton purpureum</i>	4	20°C		20°C	
<i>Callithamnion hookeri</i>	4	24°C		24°C	
<i>Nemalion helminthoides</i>	4	25°C			16°C
<i>Dumontia contorta</i> *	4	21°C			12°C
<i>Chondrus crispus</i>	4	24°C			17°C
<i>Laminaria saccharina</i> *	4 → 10	19°C		19°C	
<i>L. digitata</i> *	4 → 10	19°C			10°C
<i>Desmarestia aculeata</i>	4 → 10	20°C**			12°C
<i>D. viridis</i>	4 → 10	25°C**			10°C
<i>Monostroma grevillei</i>	4	20°C**			12°C
<i>Punctaria latifolia</i>	5	27°C			14°C
<i>Scytosiphon lomentaria</i> *	5		17°C		17°C
<i>Petalonia fascia</i> *	5		17°C**		17°C**
<i>Polysiphonia harveyi</i>	8		19°C		
<i>Saccorhiza polyschides</i> *	9				15°C
<i>Laminaria hyperborea</i> *	9			19°C	
<i>Acrosymphyton purpuriferum</i>	9				17°C
<i>Clathromorphum circumscriptum</i>	10		3°C		3°C
<i>Saccorhiza dermatodea</i> *	10	15°C			4°C
<i>Sphacelaria arctica</i> *	10	16°C**			4°C

the North Atlantic, *L. hyperborea* and *L. ochroleuca* are quite distinct. In the S. Atlantic Ocean (S. Africa, Tristan da Cunha) this latter species is difficult to differentiate from *L. pallida* and the digitate species *L. brasiliensis* Joly & Oliveira Filho (1967) from deep water (70–95 m) near Rio de Janeiro, Brazil. *L. digitata* and *L. saccharina* are presently conceived as polymorphic species in the N. Atlantic, and their relation to N. Pacific entities needs revision (for a review, see Kain, 1979). *L. saccharina* from the N. Pacific seems to be somewhat different from N. Atlantic *L. saccharina* (Kain, 1979). Its relation to the simple *L. abyssalis* Joly & Oliveira Filho (1967) from deep water in Brazil needs clarification.

Species and genera with amphiequatorial distributions

Particularly the eurythermous temperate distribution groups contain species with a world wide amphiequatorial distribution. Examples are *Rhodochorton purpureum* (Fig. 11), *Nemalion helminthoides* (Fig. 14), and *Ulvaria obscura* (Fig. 33) in the amphi-

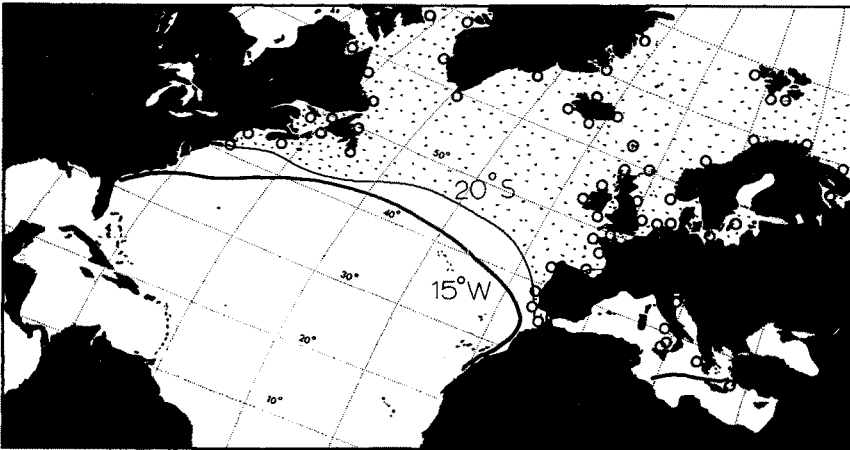


Fig. 33. *Ulvaria obscura*. Distribution in the North Atlantic Ocean. The bounding isotherms are entirely inferred from distribution data and are consequently provisional. The 20 °C summer isotherm (20 °S) is thought to be the southern lethal boundary. *U. obscura* consequently belongs to the amphiatlantic distribution group of the *Cl. rupestris* type (group 4). The 15 °C winter isotherm (15 °W) represents the southern reproduction boundary, which does not function as actual boundary

atlantic temperate distribution group of the *Cl. rupestris* type (group 4) (Table 3). The bounding isotherms of *U. obscura* are entirely based on distribution data and should consequently be considered as provisional. *Scytosiphon lomentaria*, *Petalonia fascia* and *Punctaria latifolia* (Fig. 22) are examples in the amphiatlantic temperate distribution group of the *Cl. albida* type (group 5). *Macrocystis pyrifera*, *Laminaria ochroleuca/pallida*, and *Desmarestia ligulata* (Figs 34, 35) are comparatively stenothermous and function as examples in the warm-temperate distribution groups (group 9). In the N. Atlantic Ocean, *D. ligulata*'s temperature requirements probably make this species unfit for life on the W. Atlantic shores; in the N. Pacific, however, these temperature requirements allow *D. ligulata* to inhabit just a narrow latitudinal zone along Japanese

and adjacent shores. As the bounding isotherms of *D. ligulata* are entirely based on distribution data, they should be considered as provisional.

These amphiequatorial distributions can be explained by assuming exchange of the species concerned between the hemispheres during glacial temperature drops. The tropical east coasts of the Atlantic Ocean and Pacific Ocean are the most likely points of such an exchange, as the tropical belts are here and were during the glaciations much narrower than along the west coasts of these oceans. Moreover, the present near-equator coasts on the east sides of both oceans are characterized by upwelling. This upwelling causes in equatorial W. Africa local temperature drops to about 20 °C in August, while maximum temperatures in March may be 28 °C (mean monthly temperatures) (Lawson, 1966; John et al., 1977; Corcoran & Mahnken, 1969).

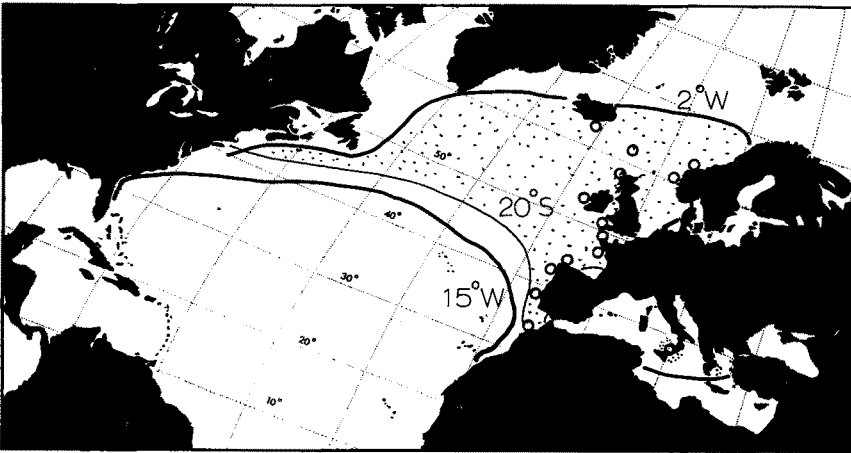


Fig. 34. *Desmarestia ligulata*. Distribution in the North Atlantic Ocean. The bounding isotherms are entirely inferred from distribution data and are consequently provisional. The 2 °C winter isotherm (2 °W) is the northern lethal boundary, the 20 °C summer isotherm (20 °S) the southern lethal boundary. The 15 °C winter isotherm (15 °W) represents the southern reproduction boundary, which does not function as an actual boundary. *D. ligulata* apparently belongs to the "warm temperate Mediterranean-Atlantic distribution group" and is unable to grow in N.E. America, where it is not able to bridge the wide annual temperature fluctuations

As we know the equatorwards temperature requirements of these amphiequatorial species, we can estimate the glacial temperature drop necessary to create a passage for temperate species across the equator. This passage was probably a narrow inshore zone of intense upwelling related to the intensified circulation of the ocean gyres during the glaciations (McIntyre et al., 1976). Table 3 summarizes the temperature requirements of the above mentioned amphiequatorial species at their present equatorwards boundaries, the present corresponding equatorial temperatures of the surface water in the Pacific and Atlantic Oceans, and the estimated glacial temperature drops necessary for creating the passage at the surface. In the East Pacific Ocean the minimum equatorial surface temperature should have dropped c. 10–13 °C and in the East Atlantic Ocean c. 8–11 °C, to allow reproduction of the species (or formation of macrothalli from microthalli in *Scytosiphon lomentaria*, *Petalonia fascia* and *Punctaria latifolia*). The maximum equato-

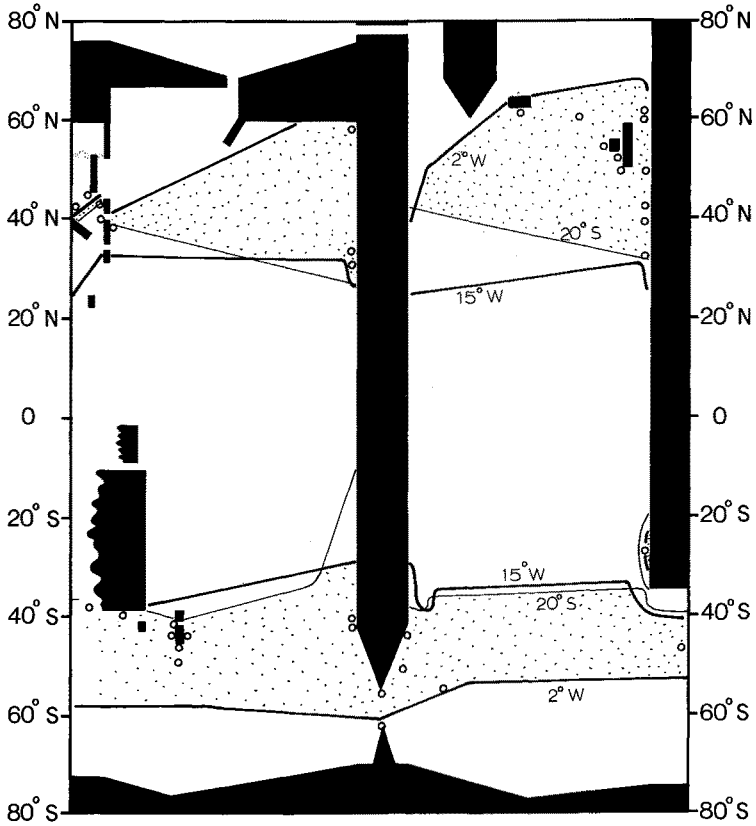


Fig. 35. *Desmarestia ligulata*. Distribution in the Atlantic and Pacific Oceans. In the N. Pacific Ocean, temperature requirements of *D. ligulata* allow this species to occupy just a very narrow latitudinal belt along Japanese and adjacent shores

rial temperatures should have dropped c. 0 to 10 °C (depending on species) to allow survival (all temperatures as mean monthly values).

Such glacial temperature drops of c. 10 °C of the surface water along eastern equatorial coasts of the Atlantic and Pacific Oceans, and the much earlier pliocene closing of the isthmus of Panama, could also explain the widely disjunct distribution of many strictly tropical species, such as *Cladophora catenata* (= *C. fuliginosa*), *Neomeris dumetosa*, *Valonia aegagropila*, *Dictyosphaeria cavernosa*, *Caulerpa mexicana*, *Udotea flabellum* and *Halimeda simulans*. These species are restricted to the western sides of the tropical Atlantic and Pacific Oceans possibly as a result of extinction by low glacial temperatures (down to 15 °C, mean monthly value) along the eastern coasts of the tropical Atlantic and Pacific Oceans (van den Hoek, 1982).

However, these hypothetical paleotemperatures are considerably lower than those in a recent reconstruction of paleotemperatures of the oceans during the last glaciation (18,000 y b.p.; McIntyre et al., 1976; Frakes, 1979). In this reconstruction, low glacial temperatures are assumed to have extended much farther towards the equator than at present along the eastern coasts of the Pacific and Atlantic Oceans, and this in conjunc-

Table 3. Species and genera with amphiequatorial distribution. Temperature drops required near equator to allow reproduction and survival. *Data borrowed from van den Hoek (1982). **Entirely based on distribution data. †These species are also mentioned for the southern hemisphere, but are here possibly confused with other species. For comparison, a few species are listed with comparable temperature requirements, but without amphiequatorial distribution

Species	Pacific Ocean					Atlantic Ocean										
	Maximum winter temperature allowing reproduction (corresponding winter isotherm)	Actual winter temperature near equator	Temperature drop required near equator	Lethal summer temperature (corresponding summer isotherm)	Actual summer temperature near equator	Temperature drop required near equator	Maximum winter temperature allowing reproduction (corresponding winter isotherm)	Actual winter temperature near equator	Temperature drop required near equator	Lethal summer temperature (corresponding summer isotherm)	Actual summer temperature near equator	Temperature drop required near equator				
Species with amphiequatorial distribution:																
<i>Macrocystis pyrifera</i> *	16	27	11	18	28	10	17	25	8	c. 30	28	0				
<i>Scytosiphon lomentaria</i> *	17	27	10	c. 30	28	0	17	25	8	c. 30	28	0				
<i>Petalonia fascia</i> *	17	27	10	c. 30	28	0	16	25	9	23	28	5				
<i>Laminaria ochroleuca</i> *	15	27	12	20	28	8	15	25	10	20	28	8				
<i>Rhodochorton purpureum</i>	16	27	11	25	28	3	16	25	9	25	28	3				
<i>Nemalion helminthoides</i>	14	27	13	27	28	1	14	25	11	27	28	1				
<i>Punctaria latifolia</i>	15	27	12	26	28	8	15	25	10	20	28	8				
<i>Desmarestia lignata</i> **	15	27	12	20	28	8	15	25	10	20	28	8				
<i>Ulvaria obscura</i> **	15	27	12	20	28	8	15	25	10	20	28	8				
N. hemisphere species belonging to genera amphiequatorial distribution:																
<i>Desmarestia aculeata</i> †	12	27	25	20	28	8	12	25	13	20	28	8				
<i>D. viridis</i> †	10	27	17	25?	28	3	10	25	15	25	28	3				
<i>Monostroma grevillei</i> †	12	27	15	20	28	8	12	25	13	20	28	8				
<i>Acrosiphonia arcta</i> ** †	12	27	15	20	28	8	12	25	13	20	28	8				
<i>Laminaria digitata</i>	15	27	12	19	28	9	10	25	15	19	28	9				
<i>L. saccharina</i>	15	27	12	19	28	9	15	25	10	19	28	9				
<i>L. hyperborea</i>	15	27	12	19	28	9	15	25	10	19	28	9				
Species without amphiequatorial distribution but with temperature responses resembling those of species with amphiequatorial distribution:																
<i>Dumontia contorta</i>						Temperature requirements in W. Pacific uncertain					12	15	13	21	28	7
<i>Chondrus crispus</i>											17	25	8	24	28	4
<i>Saccorhiza polyschides</i>											15	25	10	22	28	6

tion with increased upwelling and advection of cool water, but the temperatures of the equatorial surface waters are assumed to have had values comparable to the present ones. These paleotemperatures were inferred mainly from assemblages of microfossils (foraminifera, coccoliths, radiolaria) entombed in 247 sediment cores taken from the world's seabed.

In a recent review (Sarnthein et al., 1981) the glacial paleotemperatures of the equatorial surface waters along the African W. coast (18,000 b.p.) are assumed to have differed from present temperatures only by 1–2 °C in February but by 2–8 °C in August. A lowering of 2 °C in February and of 8 °C in August (as compared with present temperature conditions) would have allowed passage of the shallow water species *Scytosiphon lomentaria*, *Petalonia fascia*, *Punctaria latifolia* and (nearly) of *Nemalion helminthoides*; but not of *Macrocystis pyrifera*, *Laminaria ochroleuca*, *Rhodochorton purpureum*, *Desmarestia ligulata* and *Ulvaria obscura* (cf. Table 2).

The passage, across the equator, of these latter five shade tolerant species can be explained by assuming that they used the still lower temperatures of deep euphotic layers in highly transparent waters in the glacial equatorial regions. Temperatures in the lower reaches of deep euphotic layers may be considerably lower than these of the surface water. For instance, along Brazilian coasts (21–23 °S) *Laminaria abyssalis* (related to *L. saccharina*) and *L. braziliensis* (related to *L. ochroleuca/pallida*) are restricted to deep water (70–95 m) where temperature fluctuates between 16–20 °C; the surface temperatures vary here between 20 and 25 °C (mean monthly values) (Joly & Oliveira Filho, 1967; Kain, 1979; Oliveira Filho, 1976).

At present, the waters along the equatorial African W. coast are highly turbid; the lower limit of the benthic algae at Ghana has been recorded at 30 m (John et al., 1977). If the euphotic zone were c. 100 m deep instead, the prevailing temperature conditions at that depth (15–17 °C, cf. Postel, 1966) would allow reproduction and survival of most species listed in Table 2. Possibly, 18,000 years before present, the equatorial waters along W. Africa were more transparent than they are now, as the arid belt had shifted to the south and the freshwater discharge of the rivers, such as the Niger was low (Sarnthein et al., 1981). Moreover, the c. 100 m lower glacial sea level probably brought submerged offshore seamounds within the reach of this deep euphotic layer, which could thus function as stepping stones for the passage of temperate benthic algae across the equator.

From the point of view of low transparency, the E. Pacific shores seem to offer a better pathway than E. Atlantic shores as there are no great rivers and uninterrupted flat sediment shores. Actually our knowledge of the deep water floras of E. Atlantic and E. Pacific equatorial shores (continental shores as well as island shores) is very limited; these floras should be explored for possible temperate elements. In this respect the occurrence, in the deep water flora of the Galapagos Islands, of endemic species of the temperate algal genera *Eisenia* (*E. galapagensis*) and *Desmarestia* (*D. tropica*) is relevant (Taylor, 1945). The genus *Eisenia* (Phaeophyceae, Laminariales) is distributed along N.W. and N.E. Pacific shores and its nearest known point of occurrence is southern Baja California (where the narrowly related *Eisenia arborea* occurs in upwelling areas). The genus *Desmarestia* is widely distributed in the temperate zones of both hemispheres.

Here the enigmatic records of *Desmarestia aculeata* and *D. ligulata* dredged from

deep water (50–70 m) off Puerto Rico should be mentioned (Diaz-Piferrer, 1969). According to the data in the present paper, *D. aculeata* and *D. ligulata* need 12 °C or less and 15 °C or less, respectively, for their reproduction, and both 20 °C or less for survival (as mean monthly temperatures; Table 3). It is hardly likely that such low temperatures occur near Puerto Rico at 50–70 m depth. It is, however, equally unlikely that these specimens have drifted to Puerto Rico (18 °N) from their nearest point of occurrence (40 °N in N.E. America for *D. aculeata*, and 35 °N in N.W. Africa for *D. ligulata*).

The combination of 2–8 °C lowered glacial surface temperatures and an increase in thickness of the euphotic layer cannot explain the absence of stenothermous tropical algal species along the East Atlantic shores by extinction, as these species can apparently reproduce and survive in surface waters which are 2–8 °C cooler than they are at present along equatorial African coasts. Possibly intermittent short catastrophic cold spells lowering the surface temperature to 10–15 °C in the course of the numerous glaciations and which cannot be traced in the microfossil record were responsible for a gradual extinction of stenothermous tropical species.

An alternative explanation for the amphiequatorial distribution of the above temperate species (Table 3) is that these species once had warm water ecotypes capable of crossing the equator using only slightly lower temperatures than the present temperatures. This is unlikely in view of the world wide similar temperature requirements of these species at their present boundaries. Moreover, this could not explain the disjunct distribution of strictly tropical species.

Table 3 also lists seven species belonging to genera with an amphiequatorial distribution. Four of these species (*Desmarestia aculeata*, *D. viridis*, *Monostroma grevillei*, *Acrosiphonia arcta*) have also been recorded from cool temperate waters in the southern hemisphere, but they have probably been confused with other species in these genera (Papenfuß, 1964). For passage of the equator, these four species would have required a temperature drop of c. 15 °C in order to allow reproduction (c. 10 °C in the lowest part of a deep euphotic layer and c. 5 °C more than the species with amphiequatorial distribution). The temperature drop required to allow survival of maximum temperatures would have been 3–8 °C near the surface, and up to 3 °C in the lowest part of a deep euphotic layer which is within the range of the nine amphiequatorial species. This suggests that ancestor species in *Desmarestia*, *Monostroma* and *Acrosiphonia* having about the same temperature requirements as the present nine amphiequatorial species, were exchanged between both hemispheres during early temperature drops, and that the isolated populations in the temperate zones of both hemispheres developed lower limiting temperatures allowing reproduction, but not or hardly lower lethal temperatures.

The temperature requirements of *Laminaria saccharina* and *L. hyperborea* are within the ranges of the nine amphiequatorial species, and consequently exchange could be expected. Actually, the occurrence of *Laminaria* species in the South Atlantic Ocean is in favour of this hypothesis. The taxonomic relationship between the digitate species *L. pallida* (S. Africa, Tristan da Cunha), *L. schinzii* (S. Africa) and *L. braziliensis* (a Brazilian deep water species) on the one hand, and the N. Atlantic *L. hyperborea* and *L. ochroleuca* on the other hand needs further investigation, as does the relationship between *L. saccharina* and the simple Brazilian deep water species *L. abyssalis* (Kain, 1979; Joly & Oliveira Filho, 1967). These species probably represent isolated relictual

populations of glacial immigrants from the North Atlantic which use local cool water conditions (upwelling in S. Africa; cool [16–20 °C, cf. Oliveira Filho, 1976] deep water in Brazil [21–23 °S] comparable to the cool deep water harbouring *L. ochroleuca* in the Mediterranean).

The numerous climatic pulsations accompanying the gradually steepening temperature gradient between equator and poles in the course of the tertiary and the pleistocene (Frakes, 1979) are probably an important agent of repeated exchange of cool water species across the equator during cooler periods and the subsequent isolation of populations during warmer periods. Comparatively recent exchanges are probably reflected by amphiequatorial species, and comparatively old exchanges by amphiequatorial genera. The closure of the isthmus of Panama in pliocene and the subsequent glaciations causing the contraction of the tropical belt probably resulted in the widely disjunct distribution of apparently very old tropical species which are now restricted to the western sides of the tropical Pacific and Atlantic Oceans, and which were extinguished along the eastern sides of these oceans.

These climatic pulsations necessitated the repeated latitudinal displacements of the benthic algal floras, causing, on the one hand, the extinction of species lacking escape routes along uninterrupted rocky coast lines or series of stepping stones (islands, rocky outcrops on sediment coasts), and thus creating at the same time new room for renewed speciation. Also the glacial sea-level changes causing alternating closure and opening of sea straits (such as the Bering Straits) may have contributed to isolation and subsequent extinction or speciation. Lateral seas such as the Mediterranean, the Gulf of Mexico and the Gulf of California, may have contributed to speciation by the repeated isolation of populations during climatic changes.

It is an attractive hypothesis that Japanese and adjacent shores are the main centre of speciation of eurythermous temperate species with wide distributions, which succeeded in dispersing to N.E. Pacific shores, and towards the Atlantic Ocean through the Canadian Arctic, during relatively warm interglacial periods; and finally towards the southern hemisphere across the equator during glacial temperature drops.

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