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Biogeography of the benthic marine algae of the North Atlantic Ocean – an overview

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ABSTRACT: An overview of the biogeography of the benthic marine algae of the North Atlantic Ocean is presented. General and specific distribution patterns are discussed in the light of current knowledge of extant species, and of known events in the evolution of the North Atlantic Ocean. The close relationships between the Arctic, NW and NE Atlantic floras suggest their possible origin as a single flora in the early Oligocene Arctic Ocean, when it was isolated by the Bering Land Bridge and the Greenland-Scotland Ridge. Migration of the flora into the North Atlantic Ocean could have occurred with the subsidence of the Greenland-Scotland Ridge. The present day distribution patterns are the main clue to unravelling the past, and study of vicariant amphi-Atlantic taxa using a variety of experimental techniques will yield the most valuable information in attempts to interpret major biogeographical events in the North Atlantic Ocean.

INTRODUCTION

One approach to the development of biogeographical theory is through the analysis of the extant flora, thereby allowing conclusions to be drawn as to possible relationships among species or higher taxa, taking into consideration the geological history of the region. At the very least, this approach permits the development of testable hypotheses, and serves as a basis for detailed experimental study of key taxa. For the benthic marine algae, which with the exception of the calcified Rhodophyceae generally lack a reliable fossil record, the extant living species are the only means by which biogeographic questions can be addressed.

During the past fifteen years, the benthic marine algal flora of the North Atlantic Ocean has been subjected to extensive floristic analysis (Hoek, 1975, 1982a, 1982b, 1984; Hoek & Donze, 1967; Lawson, 1978), with the result that the general distribution patterns of the species are reasonably well-known. On the basis of these analyses Hoek (1975) has described the general relationships of the flora on a regional (North Atlantic) basis and, using the genera of the Rhodophyta as an example (Hoek, 1984; Joosten & Hoek, 1986), on a world basis.

Hoek's (1975, 1984) and Joosten & Hoek's (1986) floristic analyses were based largely on available checklists and floras. For the North Atlantic Ocean there has been considerable progress in the cataloguing of the marine algae during the past three decades (cf. South & Tittley, 1986, for a review). Shortcomings in the data base, however, included a lack of detailed distributional information and inconsistency in the taxonomic or nomenclatural treatment of many of the taxa. These inconsistencies inevitably hamper the biogeographer, and it was as a result of this that South & Tittley (1986) undertook the preparation of their checklist and geographical index of the benthic marine algae of the North Atlantic Ocean. They argue that their broad approach provides the necessary basis for taxonomic, floristic, and phytogeographic. investigations.

South & Tittley (1986) have pooled the available information on benthic marine algae of the North Atlantic Ocean, with the objective of standardizing the nomenclature as far as possible, and providing the first region-wide geographic index of the species. Their work now provides a single information source on which to base further studies of N. Atlantic algae. It also provides a more accurate source of information than previously available, on which to develop testable hypotheses regarding vicariant populations of amphi-Atlantic species.

General distribution patterns

South & Tittley (1986) assigned recorded geographical distributions of all benthic marine algae of the northern North Atlantic Ocean according to 32 arbitrary stations. They defined the northern N. Atlantic Ocean as ranging from the Azores to Spitzbergen in the east, and from Virginia to the eastern Canadian Arctic in the west (Fig. 1). A total of 1171 species was included.

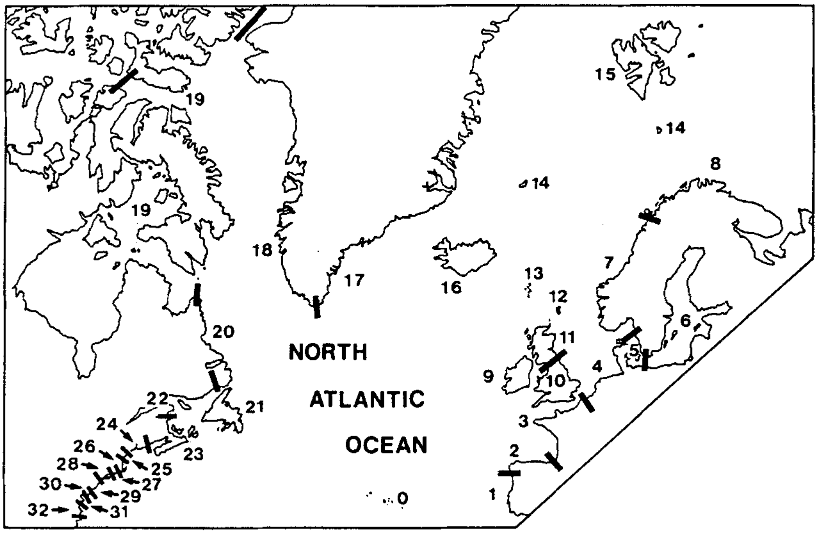

Fig. 1. Stations employed by South & Tittley (1986) in their analysis of benthic marine algal distributions in the North Atlantic Ocean. 0 = Azores; 1 = Southern Spain and Portugal; 2 = Northern Spain; 3 = France (including the Channel Islands); 4 = Southern North Sea; 5 = West Baltic; 6 = East Baltic; 7 = Norway (boreal/subarctic); 8 = Norway (arctic); 9 = Ireland; 10 = England and Wales; 11 = Scotland; 12 = Shetlands; 13 = Faroes; 14 = Jan Mayen and Bjornoya; 15 = Spitzbergen; 16 = Iceland; 17 = East Greenland; 18 = West Greenland, Baffin Bay and Davis Strait; 19 = arctic Eastern Canada; 20 = Labrador; 21 = Island of Newfoundland; 22 = Quebec; 23 = Maritime Provinces of Canada; 24 = Maine; 25 = New Hampshire; 26 = Massachusetts; 27 = Rhode Island; 28 = Connecticut and Long Island; 29 = New Jersey; 30 = Delaware; 31 = Maryland; 32 =

Table 1. Distribution of benthic marine algae of the North Atlantic Ocean (n = 1171). Data derived from South & Tittley (1986)

Group (n)	N.E. N. America n	(%)	Amphi-Atlantic n	(%)	N. Europe n	(%)	Arctic n	(%)
Rhodophyceae (589)	20	(3.5)	138	(23.5)	424	(72.0)	7	(1.5)
Phaeophyceae (324)	13	(4.0)	127	(39.5)	173	(53.5)	11	(3.0)
Chlorophyceae (258)	15	(6.0)	89	(34.5)	149	(58.0)	5	(1.5)
Total flora (1171)	48	(4.0)	354	(30.0)	746	(64.0)	23	(2.0)

Using the classification of Hoek (1975, 1984), the investigated area represents the arctic-cold temperate regions of the North Atlantic Ocean. A breakdown of the general distributions of the Rhodophyceae, Phaeophyceae and Chlorophyceae is provided in Table 1. Distributions can be classified as general, amphi-Atlantic (east and west Atlantic, but with an arctic discontinuity), western Atlantic, eastern Atlantic, and Arctic. Less than a third of the flora has a general or amphi-Atlantic distribution, and a majority of the flora is confined to the eastern (European) Atlantic. Only a very small number of species is confined to the Arctic or the western N. Atlantic cold temperate region.

The proportional differences in general distribution patterns can be determined from Table 1 and Figure 2. The Phaeophyceae dominate the general and amphi-Atlantic groups, while the Rhodophyceae are the most important group in the large European component of the flora.

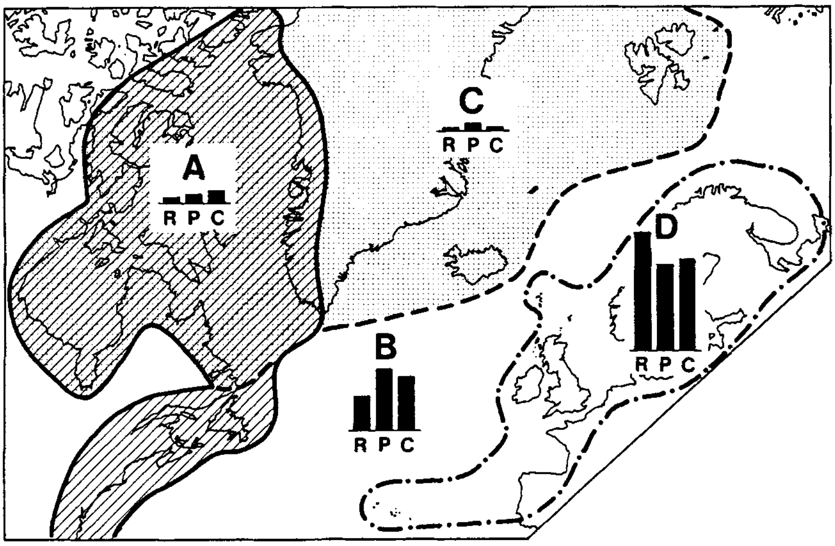

Fig. 2. Proportional differences in general distribution patterns of North Atlantic benthic algae. A = northeastern North America; B = Amphi-Atlantic; C = Arctic; D = European distributions of Rhodophyceae (R), Phaeophyceae (P) and Chlorophyceae (C)

Differences in species richness between the eastern and western N. Atlantic floras in the cold temperate region led Hoek (1975) to conclude that the flora should be subdivided into eastern and western sectors. Subsequent detailed analyses of the Rhodophyceae by Hoek (1984) and Joosten & Hoek (1986), as well as the analysis presented here, confirm these E–W differences. Examination of the Phaeophyceae and Chlorophyceae, however, suggest that these differences are less distinct in these groups, since the amphi-Atlantic elements in both are larger than in the Rhodophyceae. For all groups there is a very low degree of "endemism" in either the Arctic or northeastern N. America. There are certainly few grounds to suggest that the Arctic now possesses a distinctive flora. Wilce (pers. comm.) demonstrated that less than 10 % of the Arctic flora is endemic, and that most of the Arctic species are circumpolar in distribution. More than 90 % of the Arctic species have amphi-North Atlantic affinities. Wilce (pers. comm.) suggested that the phytogeographic, geologic and hydrographic evidence strongly indicate a warm water origin for most Arctic species. They occur in the Arctic through adaptations to ice scouring, and marked seasonal fluctuations in salinity, light and temperature.

The southern limit of the Arctic-cold temperate floristic region (or the northern limit of the warm temperate region) is well defined and has been subjected to numerous analyses (see Searles, 1984). The significance of this boundary was apparent when South & Tittley accumulated records for their index (South & Tittley, 1986), initially including records from North Carolina and hence south of Cape Hatteras. While there is some spill-over between the cold-temperate and warm temperate floras, the warm temperate species predominate south of Cape Hatteras and, if included in the general analysis of the northern N. Atlantic flora, introduce a large number of species and genera otherwise absent from the cold temperate region. There is also a much greater element of western Atlantic endemism in the warm temperate compared with the cold temperate floras (Searles, 1984), and a greater contrast between the warm temperate floras of both sides of the Atlantic than is evident from the cold temperate floras.

Present-day general patterns of algal distribution in the N. Atlantic follow temperature trends, these emphasized by the generally N–S orientation of the coastlines (Fig. 3; cf. also Hoek, 1975, 1984; Yarish et al., 1986; Joosten & Hoek, 1986). The influence of the Gulf Stream and the consequent contraction versus expansion of temperature zones in the western compared with the eastern North Atlantic is well known. Algal distributions show marked differences in latitudinal range as a result of the Gulf stream deflection. Wilce (pers. comm.) discussed the influence of the Gulf Stream on North Atlantic algal distributions. He attributed the low level of endemism in the northeastern North American flora to the fact that the Gulf Stream acts as a one-way donor of species from west to east. There appear, however, to be much stronger reasons for the lack of endemism in the cold-temperate northeastern North American flora, as discussed below. Long-range migration cannot be ruled out, however, and the possibilities of this should be examined experimentally. The importance of substrate must be recognised, as not all distribution patterns strictly follow temperature regimes. Winter or summer lethal temperatures may provide important clues to many of the distribution patterns observed, although differences in responses by different life history or developmental stages must be taken into acount, and for some amphi-Atlantic species there are differences in temperature responses between eastern and western populations of the same species.

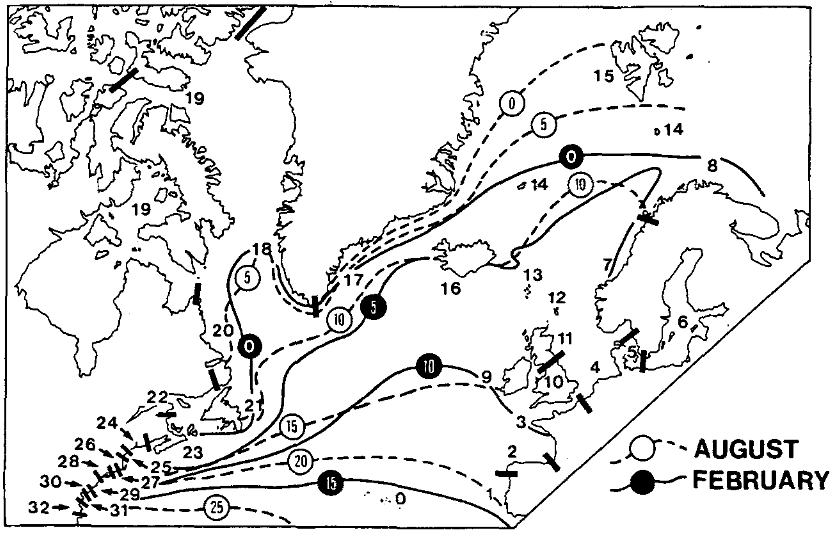

Fig. 3. Distribution of August and February isotherms in the North Atlantic Ocean, in relation to stations given in Fig. 1

Hoek (1982a, 1982b), Cambridge et al. (1984) and Yarish et al. (1986) have examined the hypothesis that biogeographic boundaries can be defined by experimentally examining the relationship between the distributional extremes of a species and the extremes of temperatures within which the species can complete its life history. Two kinds of boundaries have been defined: growth/reproduction boundaries (where a species is not exposed every year to a sufficiently high or low temperature for growth and reproduction in the favourable season), and lethal boundaries (where a species is exposed once in several years to a lethal temperature) (Yarish et al., 1986). Cambridge et al. (1984) confirmed the role of temperature responses for growth and survival of six species of *Cladophora:* with one exception, distribution patterns matched experimentally determined lethal temperature limits. Yarish et al. (1986) showed that for members of the warm-temperate Mediterranean Atlantic group, northern and southern boundaries appeared to be determined by winter and summer lethal temperatures, respectively. For two amphi-Atlantic temperate species, *Callithamnion tetragonum* (With.) S. F. Gray and *Lomentaria orcadensis* (Harvey) F. Collins ex W. Tayl., there appeared to be ecotypic differentiation with regard to temperature tolerance for populations from the same and from either side of the Atlantic.

Specific distribution patterns

Present-day benthic algal distribution patterns in the northern North Atlantic Ocean provide many clues to biogeographers. As described earlier, distributions fall into a number of categories: general; amphi-Atlantic; northeastern North America; Europe; Arctic. Lüning (1985) presented a number of North Atlantic distribution patterns, and a number are referred to briefly here. Vicariant populations of amphi-Atlantic taxa are the

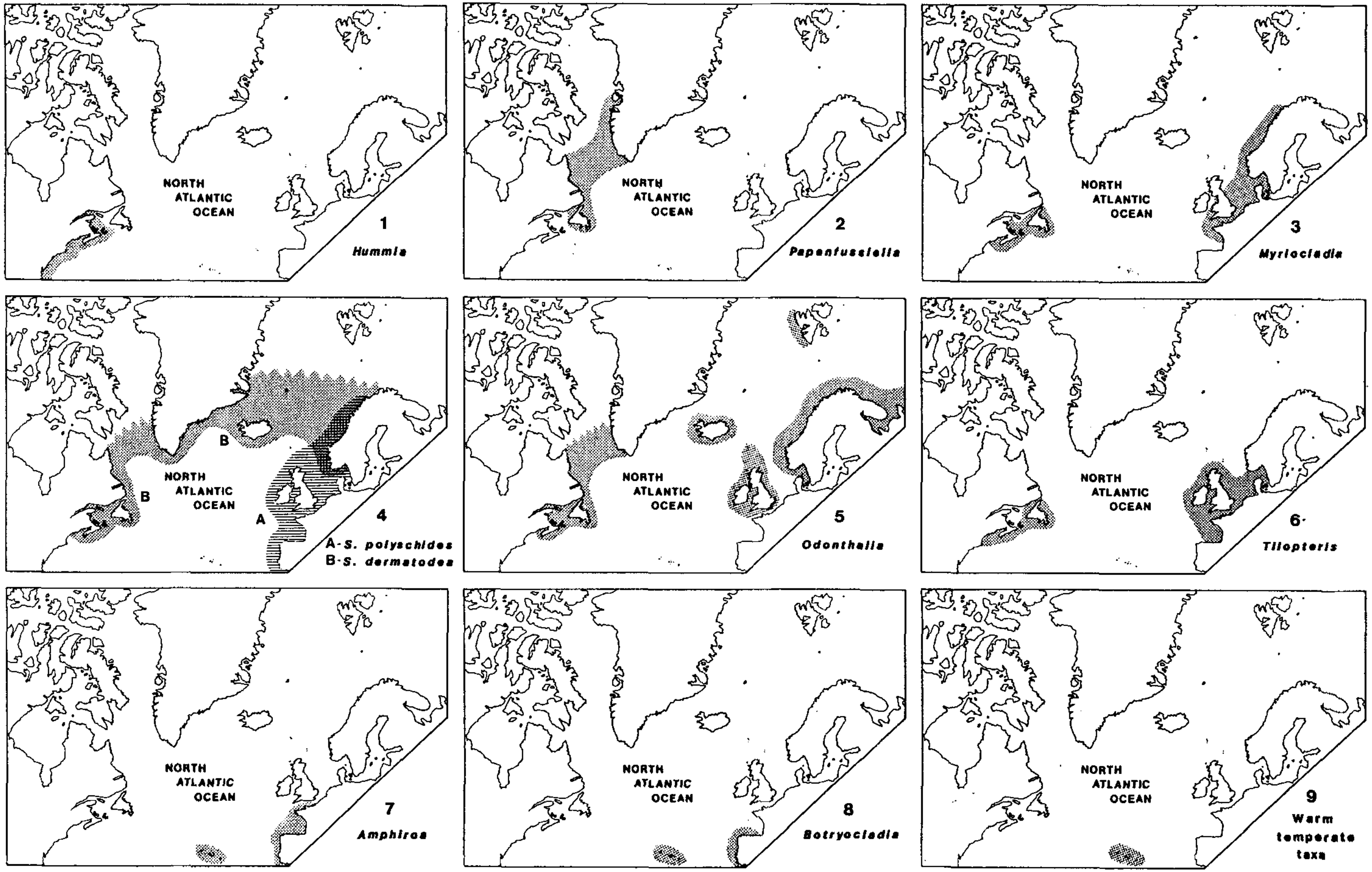

Fig. 4. Specific distribution patterns of North Atlantic benthic marine algae. 4–1 North-eastern North America, e.g. *Hummia onusta* (Phaeophyceae); 4–2 North-eastern North America/Arctic, e.g. *Papenfussiella callitricha* (Phaeophyceae); 4–3 Amphi-Atlantic, e.g. *Myriocladia lovenii* (Phaeophyceae); 4–4 A/B Amphi-Atlantic-European, e.g. *Saccorhiza dermatodea* and *S. polyschides* (Phaeophyceae); 4–5 Arctic/Amphi-Atlantic, e.g. *Odonthalia dentata* (Rhodophyceae); 4–6 Amphi-Atlantic, cold temperate endemics, e.g. *Tilopteris mertensii* (Phaeophyceae); 4–7 to 4–9 Southern European/Warm Temperate elements, e.g. *Amphiroa* spp. (Rhodophyceae) and *Botryocladia* sp. (Rhodophyceae)

most useful potential experimental examples for the biogeographer, since they may provide indications of the rate of evolutionary change.

North-eastern N. America (Fig. 4–1): e.g. *Hummia onusta* (Harvey) Fiore. Approximately 4 % of the northern North Atlantic flora falls into this group (Table 1). Of species listed in South & Tittley (1986), a number can be derived from the endemic warm-temperate group: i.e. they represent spill-over from more southern elements, able to survive in more northerly sites where temperatures are elevated sufficiently during the summer to allow reproduction and growth, and where winter temperatures are not lethal, or where winter can be spent as an ecologically more tolerant alternate phase in the life history. *H. onusta* occurs from N. Carolina northwards to the Maritime Provinces of Canada (including the Gulf of St. Lawrence). It is probably a spill-over species from the warm temperate flora further south, surviving in more northerly sites in sheltered habitats where summer temperatures are elevated compared with the open coast.

Northeastern N. America: Arctic (Fig. 4–2): e.g. *Papenfussiella callitricha* (Rosenv.) Kylin. Members of this group are cold-adapted northern species, perhaps coming the closest to being "arctic endemics", since their occurrence in more southerly locations is generally confined to localities where cold water masses persist, at least below a thermocline. In addition to *Papenfussiella,* other members of this group include *Laminaria solidungula* J. Agardh and *Omphalophyllum ulvaceum* Rosenv. (Phaeophyceae). *Papenfussiella callitricha* occurs as far south as Newfoundland, where it is confined to low-temperature environments (Hooper & South, 1977b; South & Hooper, 1980); its northern limits are not known, but could conceivably include the Canadian eastern Arctic.

The genus *Papenfussiella* is disjunctly distributed between the N. Atlantic and the southern hemisphere; this separation is suggestive of a very early divergence, with the cold adaptation of the northern species enabling it to survive for long periods in the far northern regions.

Amphi-Atlantic (Fig. 4–3): e.g. *Myriocladia lovenii* J. Agardh. As described above, the amphi-Atlantic group, which includes some 30 % of the total flora (Table 1), is the most interesting from the biogeographical standpoint. Lüning (1985) has given a number of examples, and a number (Cambridge et al., 1984; Yarish et al., 1986) have been the subject of experimental investigations. Not all amphi-Atlantic distributions are necessarily a reflection of true patterns; however, *Fucus serratus* L. is well known as an introduction to the western North Atlantic, and other species may have been transported from Europe by man during the past 500 years of exploration. *M. lovenii* is rare in eastern N. America (Hooper & South, 1977a; South & Hooper, 1980) and much more widely distributed in Europe. Little is known of its ecology or temperature tolerance, but it is possible that N. American populations represent relatively recent introductions. The amphi-Atlantic distribution of this species might thus be artificial.

Amphi-Atlantic (Fig. 4–4 A/B): European e.g. *Saccorhiza dermatodea* (Bach. Pyl.) J. Agardh and *S. polyschides* (Lightf.) Batters. The genus *Saccorhiza* provides an interesting example of different distribution patterns within the same genus. Species of *Saccorhiza* exhibit a number of primitive traits compared with other members of the Laminariales, suggesting an early separation (Henry & South, 1987). Their relationship with *Phyllariopsis* (Phyllariaceae), a primitive Mediterranean genus, suggests a Tethyan origin. *S. dermatodea* is cold-adapted and has an arctic-cold temperate distribution, while *S. polyschides* has a strictly European distribution in the cold-temperate, and does not penetrate the Arctic. If *S. polyschides* or species of *Phyllariopsis* were ever distributed in the western N. Atlantic, they were very likely exterminated during the ice ages.

Arctic/Amphi-Atlantic (Fig. 4–5): e.g. *Odonthalia dentata* (L.) Lyngbye. A number of northern North Atlantic species have a wide distribution in the more northerly regions, and exhibit a pan Atlantic-Pacific distribution pattern. These are likely examples of exchange between Pacific and Atlantic floras during periods of depression of the Bering land bridge. Taxonomic and nomenclatural problems have sometimes obscured these relationships (e.g. *Callophyllis cristata* (Agardh) Kuetz.; cf. Hooper & South, 1974). *Odonthalia dentata* is an example of an arctic/cold temperate species with a wide distribution, this extending into the N. Pacific (Lindstrom, 1987). Local distribution in the more southerly parts of the range is restricted to sites not subjected to excessive summer warming.

Amphi-Atlantic, cold temperate endemics (Fig. 4–6): e.g. *Tilopteris mertensii* (Turner in Sm.) Kuetz. *Tilopteris,* together with *Haplospora* and *"Phaeosiphonia"* spec. inedit. (Hooper, pers. comm.) belongs to the order Tilopteridales, the only order of brown algae endemic to the North Atlantic Ocean. *Haplospora* and *"Phaeosiphonia"* are cold-adapted species, the latter with a very restricted geographical distribution in Newfoundland, and with a very low temperature optimum (Henry & Hooper, pers. comm.), whereas *Tilopteris* has a more southern distribution. All exhibit a reduced sexual reproduction, of an advanced oogamous type, and trichothallic growth. There appear to be no really close relatives of this group in the N. Atlantic flora: the cold adaptation suggests that they were able to survive adverse conditions during the Pleistocene; with their lack of apparent close relatives, it could be suggested that they represent an ancient relict group stemming from an early time in the evolution of the N. Atlantic (Arctic) flora.

Southern European/warm temperate elements (Fig. 4–7, 4–9): e.g. *Amphiroa* spp., *Botryocladia* sp. A number of southern European taxa represent a spill-over from the more southern warm temperate flora, or from the Mediterranean flora. Surprisingly few species may fit into the latter category, although *Phyllariopsis purpurata* (cf. Henry & South, 1987) is one example. The larger number have more southern distributions, such as species of *Amphiroa* and *Botryocladia.* Lethal winter temperatures are likely to be the limiting factor preventing their extension northwards.

CONCLUSIONS

Hoek (1984) has suggested that the N. Pacific and N. Atlantic temperate benthic algal floras developed independently since the Oligocene (ca. 40.1 million years [my] BP) deterioration of the climate, and to have partially mixed their cool water genera only after the Pliocene inundation of the Bering Land Bridge (2.1 my BP) (Joosten & Hoek, 1986). The Bering Land Bridge reemerged during the Pleistocene as a result of the lowering of the sea level, with the result that the Pacific became separated again from the Arctic Ocean. The Arctic Ocean remained open to the N. Atlantic, however, with the result that the N. Atlantic experienced much more severe climatic deterioration during the ice ages. This possibly caused more extinctions in the N. Atlantic than in the N. Pacific (Hoek, 1975; Joosten & Hoek, 1986).

Hoek's (1984) analysis showed that the most narrowly related floras on a world basis are those of the NW Atlantic, the NE Atlantic and the Arctic. He suggested that the group may have originated as a single flora in the early Oligocene Arctic Ocean, which was highly isolated by the Bering Land Bridge and the Scotland-Greenland Land Bridge (McKenna, 1983). The flora could have migrated into the N. Atlantic Ocean following the subsidence of the Scotland-Greenland Land Bridge, and could have been distributed along a more or less continuous coastline or series of "stepping stones" until at least the Miocene (10.1 my BP; McKenna, 1983) or even the Pliocene (3.1 my BP; Thiede & Eldholm, 1983). During the glaciations the flora was displaced southward, with much greater displacement in the NW Atlantic than in the NE. Post-glacial recolonisation has subsequently taken place, with the result that the NW and NE Atlantic floras are considered as vicariant portions of a once (Miocene and Pliocene) continuous flora. Their relatively recent separation and isolation (i.e. Pliocene, ca 2.1 my BP) could explain their high degree of resemblance (Hoek, 1984).

A close study of amphi-Atlantic and pan Pacific/Atlantic taxa should be a priority for future research. The importance of combining these studies with an intimate knowledge of paleo-oceanographic and geologic events cannot be overstressed, since it will only be through such detailed comparative work that elements of the evolutionary picture will be revealed. The use of a variety of approaches, such as cladistics (Lindstrom, 1987; Garbary, 1987) and isoenzyme analysis of key taxa will be especially useful. Biogeographers of the North Atlantic Ocean will eagerly wait for the results of the current Arctic deep sea drilling program, since our understanding of the complicated events in the north is still too fragmentary to fully explain the detailed timing and nature of Pacific-Arctic-Atlantic connections in the recent and distant past. Important questions regarding the recent history of the N. Atlantic flora can be addressed by examining vicariant groups with NW and NE Atlantic distributions (Amphi-Atlantic species). Assuming that these vicariant populations were once part of the same population, questions relating to the time of separation and the rate of evolution can be addressed by experimental studies examining physiological responses, reproductive compatibility and genetic isolation.

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LITERATURE CITED

Cambridge, M., Breeman, A. M., Oosterwijk, R. van & Hoek, C. van den, 1984: Temperature responses of some North Atlantic *Cladophora* species (Chlorophyceae) in relation to their geographic distribution. – Helgoländer Meeresunters. *38,* 349–363.

Garbary, D. G. 1987. A critique of traditional approaches to seaweed distribution in light of the development of vicariance biogeography. – Helgoländer Meeresunters. *41,* 235–244.

Henry, E. C. & South, G. R., 1987. *Phyllariopsis* gen nov. and a reappraisal of the Phyllariaceae Tilden 1935 (Phaeophyceae, Laminariales). – Phycologia, *26,* 9–16.

Hoek, C. van den, 1975. Phytogeographic provinces along the coasts of the northern Atlantic Ocean. – Phycologia *14,* 317–330.

Hoek, C. van den, 1982a. The distribution of benthic marine algae in relation to the temperature regulation of their life histories. – Biol. J. Linn. Soc. *18,* 81–144.

Hoek, C. van den, 1982b. Phytogeographic distribution groups of benthic marine algae in the North Atlantic Ocean. – Helgoländer Meeresunters. *35,* 153–214.

Hoek, C. van den, 1984. World-wide latitudinal and longitudinal seaweed distribution patterns and their possible causes as illustrated by the distribution of Rhodophytan genera. – Helgoländer Meeresunters. *38,* 227–257.

Hoek, C. van den & Donze, M., 1967. Algal phytogeography of the European Atlantic coast. – Blumea *15,* 63–89.

Hooper, R. G. & South, G. R., 1974. A taxonomic reappraisal of *Callophyllis* and *Euthora* (Rhodophyta). – Br. phycol. J. *9,* 423–428.

Hooper, R. G. & South, G. R., 1977a. Distribution and ecology of *Papenfussiella callitricha* (Rosenv.) Kylin (Phaeophyceae, Chordariaceae). – Phycologia *16,* 153–157.

Hooper, R. G. & South, G. R., 1977b. Additions to the benthic marine flora of Newfoundland III, with observations on species new to eastern Canada and North America. – Naturaliste Can. *104,* 383–394.

Joosten, A. M. T. & Hoek, C. van den, 1986. World-wide relationships between red seaweed floras: a multivariate approach. – Botanica mar. *29,* 195–214.

Lawson, G. W., 1978. The distribution of seaweed floras in the tropical and subtropical Atlantic Ocean: a quantitative approach. – Bot. J. Linn. Soc. *75,* 99–118.

Lindstrom, S. C., 1987. Possible sister groups and pylogenetic relationships among selected North Pacific and North Atlantic red algae. – Helgoländer Meeresunters. *41,* 245–260.

Lüning, K., 1985. Meeresbotanik. Thieme, Stuttgart, 375 pp.

McKenna, M. C., 1983. Cenozoic paleogeography of North Atlantic land bridges. In: Structure and development of the Greenland Scotland Ridge. Ed. by M. H. P. Bott, S. Saxov, M. Talwani & J. Thiede. Plenum Press, New York, 351–399.

Searles, R. B., 1984. Seaweed biogeography of the mid-Atlantic coast of the United States. – Helgoländer Meeresunters. *38,* 259–271.

South, G. R. & Hooper, R. G., 1980. Catalogue and atlas of the benthic marine algae of the Island of Newfoundland – Occ. Pap. Biol. Mem. Univ. Nfld *3,* 1–136.

South, G. R. & Tittley, I., 1986. A checklist and distributional index of the benthic marine algae of the North Atlantic Ocean. Huntsman Marine Laboratory, St. Andrews, 76 pp.

Thiede, J. & Eldholm, O., 1983. Speculations about the paleodepth of the Greenland-Scotland Ridge during the late Mesozoic and Cenozoic. In: Structure and development of the Greenland-Scotland Ridge. Ed. by M. P. H. Bott, S. Saxov, M. Talwani & J. Thiede. Plenum Press, New York, 444–456.

Yarish, C., Breeman, A. M. & Hoek, C. van den, 1986. Survival strategies and temperature responses of seaweeds belonging to different biogeographic distribution groups. – Botanica mar. *29,* 215–230.