

## The possible significance of long-range dispersal for the biogeography of seaweeds

C. van den Hoek

*Department of Marine Biology, Biological Centre, University of Groningen; P.O.Box 14, NL-9750 AA Haren (Gn), The Netherlands*

**ABSTRACT:** Indirect evidence of the existence of long-distance dispersal of seaweeds is provided by the fact that mid-oceanic islands of volcanic origin are inhabited by well-developed seaweed floras which could reach these islands only overseas from continental donor areas. For instance, the flora of Tristan da Cunha (S. Atlantic Ocean) was established by long-distance dispersal in less than 1 million years (the approximate age of the island); the seaweed flora of the Faeroes (N. Atlantic Ocean) could be constituted in less than 10,000 years (the end of the Pleistocene ice cover of these islands). There is no evidence for either supporting or discounting the possible role of planktonic stages of seaweeds (spores, propagules, zygotes) in the long-distance dispersal of seaweeds. There is, however, some evidence of long-distance dispersal as floating plants, or as plants attached to floating objects (including floating algae). There are a few examples of "artificial" long-range dispersal by man (possibly on ship hulls, oysters, in ballast water). Long-range dispersal of seaweeds does exist, but it is an exception rather than the rule. If it were the rule, the world's seaweed floras would show similar latitudinal gradients in species composition in the oceans and on both hemispheres. This is, however, not the case.

### INTRODUCTION

So far, long-range dispersal has never been an object of serious research in seaweed biogeography. Of course, long-range dispersal has been the object of frequent and elaborate speculation. The lack of serious investigations on this topic reflects the methodological problems which one encounters when one tries to tackle questions regarding long-range dispersal in seaweeds. The greatest problem is probably the formulation of hypotheses that can be tested.

### EVIDENCE OF LONG-RANGE DISPERSAL: SEAWEED FLORAS OF VOLCANIC ISLANDS

Does long-range dispersal of seaweeds exist? The answer must be: yes. Even though the evidence is indirect it is none the less compelling. The existence of seaweed floras on isolated, mid-oceanic volcanic islands is convincing evidence that long-range dispersal of seaweeds does take place. These islands were never connected with continental land masses. They rose from the bottom of the ocean, and the seaweeds growing there must have come overseas.

In Table 1, I have summarized some data on four islands or island groups on or near

Table 1. Summary of various properties, relevant to the topic of long-range dispersal of seaweeds, of mid Atlantic volcanic islands and archipelagos. Based on (1) Kühnemann (1972); (2) Seagrief (1984); (3) Ardré (1970, 1971); (4) Ruess (1977); (5) Papenfuss (1964); (6) Brown & Jarman (1978); (7) Donze (1968); (8) Printz (1926)

Criteria	Gough Island	Tristan da Cunha	Azores	Faeroes
Age (appr. in 10 <sup>5</sup> years)	1	1	5-3	10 (Fragmentation Ice-land-Faeroe ridge)
Latitude (appr.)	40° S	37° S	38° N	62° N
Longitude (appr.)	9° W	13° W	28° W	7° W
Size	13 × 6 km	14 × 14 km	9 islands, 3 × 2 km to 65 × 13 km	18 islands, 3 × 1 km to 50 × 10 km
Recent temperature range (winter & summer-isotherms)	10-13.5°C	13-17.5°C	15-23°C	7-13°C
Pleistocene temperature range	10-13°C	13-16.5°C	12-20°C	0-2°C
Approximate number of species	35	125	140	220
Most related flora in:	Cold temperate SE America	S. Africa	SW Europe, NW Africa	NW Europe
Approximate number of spp. in most related flora	350 (1)	550 (2)	450 (3)	450
Number of spp. in portion of related flora	175 on Falkland Islands (5)	150 on Cape Peninsula and vicinity (6)	200 in Ria de Arosa area (7)	in whole Norway (4)
Distance to most related flora	4000 km	2500 km	1600 km	260 in Trondhjems-Fjord (8)
Current (direction of dispersal)	With current; West Winddrift	Against current; West Winddrift	Against current; N. Atlantic Drift	300 km (Shetlands) 600 km (Norway)
Time required to travel (13 km d <sup>-1</sup> )	ca 300 days	??	??	Against current; N. Atlantic Drift
Influence of Pleistocene	Probably none	Probably none	Probably none	??
Some conspicuous species	<i>Macrocystis pyrifera</i> <i>Laminaria pallida</i> <i>Durvillea antarctica</i> <i>Iridaea laminarioides</i> <i>Rhodoglossum revolutum</i>	<i>Macrocystis pyrifera</i> <i>Laminaria pallida</i> <i>Gigartina striata</i> <i>Gymnogongrus gregarius</i> <i>Halopteris funicularis</i>	<i>Fucus spiralis</i> <i>Laurencia pinnatifida</i> <i>Gelidium spinulosum</i> <i>Laurencia obtusa</i> <i>Caulacanthus ustulatus</i> <i>Cystoseira abies-marina</i>	<i>Fucus spiralis</i> <i>F. vesiculosus</i> <i>F. distichus</i> Not <i>F. serratus</i> <i>Ascophyllum nodosum</i> <i>Palmaria palmata</i> <i>Mastocarpus stellatus</i> <i>Laminaria</i> spp. <i>Alaria esculenta</i>

the Mid Atlantic Ridge, all of volcanic origin (Fig. 1). Gough Island, Tristan da Cunha and the Azores arose as islands from the Mid Atlantic Ridge. The two former islands are approx. one million years old; the latter 5 to 3 million years old (Chamberlain et al., 1985; Schmincke, 1982). The Faeroes are a leftover fragment of the once continuous Greenland-Iceland-Scotland Ridge (in Eocene, some 40 million years ago). The Faeroes became islands in the Miocene, some 10 million years ago (Nielsen, 1983; McKenna, 1983; Thiede & Eldholm, 1983).

Gough Island and Tristan da Cunha are situated 370 km from one another. Despite this proximity there are quite distinct differences between their floras (Chamberlain, 1965; Chamberlain et al., 1985; Baardseth, 1941). The flora of Gough Island has the characteristics typical of the cold temperate climate of the southern hemisphere; the Tristan da Cunha flora shows the mark of a more warm temperate zone. This is probably correlated with the fact that the temperatures of the surface water at Gough Island are lower. Gough Island lies just south of the Subtropical Convergence, and Tristan da Cunha just north of it.

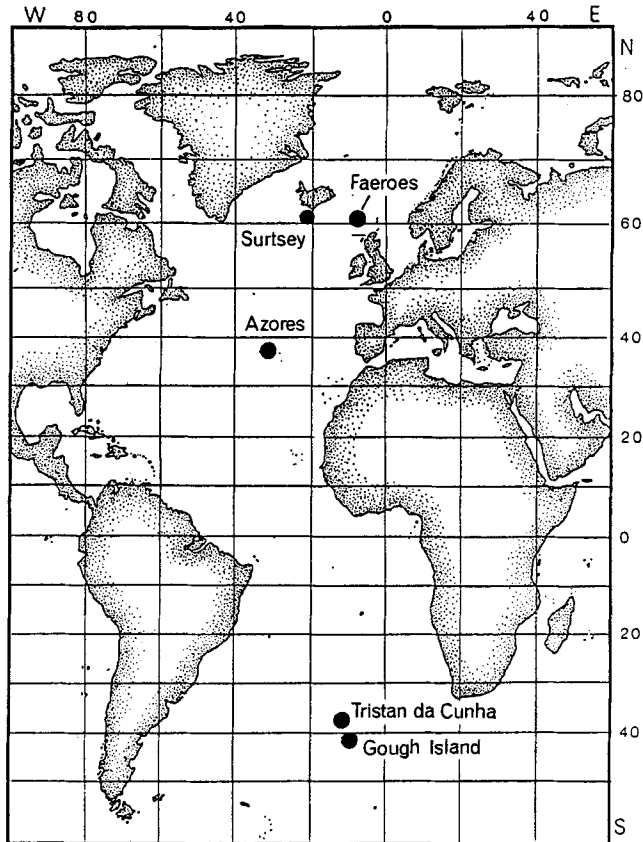


Fig. 1. Volcanic islands and archipelagos in the Atlantic Ocean, whose seaweed floras have been formed by long-range dispersal (Gough Island, Tristan da Cunha, Azores, Faeroes) and short-range dispersal (Surtsey)

The Gough Island flora is most closely related with the cold temperate Southeast American flora. It is imaginable that species from SE Argentine and the Falklands travelled over 4000 km in the West Wind Drift to reach Gough Island (Chamberlain et al., 1985). At a mean current velocity of  $13 \text{ km d}^{-1}$  this would take them about 300 days ( $\sim 1$  year). They would stay in their own temperature zone. On the other hand, the flora of Tristan da Cunha is most closely related to the S. African flora (Baardseth, 1941; Hommersand, 1986). Species from S. Africa would have to reach Tristan da Cunha against the direction of the currents, or at least the prevalent direction. The floras of the Azores and the Faeroes would also have to be settled by algae travelling against the prevalent direction of the currents (see below).

I have considered the question whether the Pleistocene ice ages could have had some influence. For instance: did the temperatures drop to such an extent that the floras became partly or entirely extinct? Recent reconstructions of the sea surface temperatures during the last glaciation (McIntyre et al., 1976) do not suggest distinctly lower temperatures for either Gough Island or Tristan da Cunha. This suggests that their present floras have developed in the course of about 1 million years. The low number of species in both floras could reflect the fact that only a small proportion of the donor floras has succeeded in "hitting" the islands and in establishing themselves.

However, one should also consider the species-area problem. A larger area (here: a longer coast) can harbour more species than a smaller area, a well-known relation in biogeography (for an overview, see Brown & Gibson, 1983). Therefore, I have added to Table 1 the species numbers of portions of the presumptive donor-floras; these portions are better comparable to the island floras with regard to the area available. However, this procedure is of course rather arbitrary. Nonetheless, it prevents the assumption that a small island would in the end harbour the entire flora of the donor area.

Table 1 suggests, therefore, that Tristan da Cunha is perhaps nicely underway to having a "saturated" flora, whereas Gough Island still has room for many more species. However, Gough Island has clearly been undersampled; new records will undoubtedly become available in the forthcoming studies of Hay et al. (see Chamberlain et al., 1985).

The Azores (Table 1) differ from the previous two islands in their greater age ( $3$  to  $5.10^6$  y), and in the much larger area available for algal settlement. Nonetheless, the number recorded so far (Schmidt, 1931) is not much higher than that recorded for tiny Tristan da Cunha. The flora of the Azores is most closely related with the SW European-NW African flora. Their algal species had to travel against the prevalent direction of the currents (N. Atlantic Drift).

The Pleistocene ice ages probably hardly influenced the seaweed flora of the Azores. The Azores were then not very far to the south of the polar front, but their temperatures were probably only 2 to 3 °C lower than they are now (McIntyre & Kipp, 1976; Sarnthein et al., 1982). The Pleistocene annual temperature range at the Azores was similar to the present temperature range on the coasts of W. Iberia where most of the warm temperate species of the Azores also occur. The large majority, if not all, of the species now living on the Azores could probably have survived the lowered Pleistocene temperatures.

The total number of species on the Faeroes is around 200 according to Børgesen (1908), and 220 according to Irvine (1982). The Faeroes as an island group are much older than any of the other examples. However, in the present context this old age is probably hardly relevant at all, as the Faeroes were covered by thick ice sheets during the

Pleistocene glaciations. If portions of rocky coasts were still available for algal growth, only Arctic-to-cold-temperate species could survive, i.e. species now occurring on the coast of Spitsbergen (van den Hoek & Dönze, 1967). This would mean that ca 40 species of the 220 now living on the Faeroes would have survived during the glaciations. The large majority, then, of the seaweed flora, or perhaps the whole seaweed flora of the Faeroes, must have been reestablished after the last glaciation (10 000 years ago). If one considers NW Europe (Scotland, Norway) as the donor-area, dispersal must have taken place against the prevalent direction of the currents. At the beginning of our century there was a rather heated debate between Børgesen, on the one hand, and Porsild and Simmons, on the other hand, about the reestablishment of the Faeroes' seaweed flora after the last glaciation (see Børgesen, 1908). Porsild and Simmons postulated a post-Pleistocene American-European landbridge over the Faeroes, whereas Børgesen argued that such a landbridge existed much longer ago in the Tertiary, before the Pleistocene. Børgesen demonstrated that the actual directions of the surface currents were very variable and often opposite to the prevalent direction of the currents. One should, in this context, also consider the role of the huge eddies along the main stream of the currents (Pickard & Emery, 1982).

The distances to be bridged by the prospective algal inhabitants of the Faeroes were comparatively small: 300 km from the Shetlands, 600 km from Norway. Comparison with the seaweed flora of the Trondhjemsfjord suggests that the flora of the Faeroes is more or less "saturated". However, Børgesen suggests that *Fucus serratus* is lacking there because it did not succeed in reaching the Faeroes. The reason would be this species' lack of floating vesicles.

In summary, we can conclude that oceanic islands receive their floras by long-range dispersal. It seems as if a very distant island like Tristan da Cunha can collect a fairly "complete" flora in a period of less than ca 1 million years; "complete" meaning here that the number of species found is what one would expect for the island in relation to its size.

There is quite attractive evidence that the Faeroes could collect a fairly complete flora by long-range dispersal in a timespan of less than 10 000 years. The Faeroes, however, are comparatively close to their donor areas. Similarly, there is evidence that long-range dispersal can take place against the prevalent direction of the currents.

A recent example of a volcanic island invaded by a seaweed flora is the Island of Surtsey (Fig. 1). The seaweed vegetation on this isle was followed by Jónsson (1970) during the period 1964–1970, that is from its emergence in 1964. In 5 years, a seaweed flora consisting of 25 species had developed. Among these were *Laminaria hyperborea*, *Phycodrys rubens* and *Desmarestia ligulata*. Early colonizers were species of *Urospora*, *Ulothrix* and *Enteromorpha*; *Alaria esculenta* also appeared as early as 1 year after emergence of the isle. *Petalonia fascia* and *Scytosiphon lomentaria* were also early colonizers. Although drift *Ascophyllum nodosum* was the first seaweed found on the island, this species did not establish itself there during the whole period of observation (Jónsson, 1966, 1970).

However, Surtsey is only 5 km from the nearest rocks and 30 km from the mainland of Iceland. Here we cannot speak, therefore, of "long-distance dispersal".

Jónsson also mentions which Icelandic species were still lacking; *Fucus* species, *Mastocarpus stellatus*, *Plumaria elegans*, *Palmaria palmata*, *Corallina officinalis*, *Laminaria digitata* and others.

If oceanic islands can be populated by seaweeds arriving by long-distance dispersal, it is likely that long-distance dispersal could also cause exchange of species between widely distant continental coasts, such as the E. and W. coast of the Atlantic Ocean, and could maintain gene flow between amphioceanic populations of species occurring on both sides of the ocean. For instance, one wonders whether the similarity between the cold temperate floras of NE America and NW Europe reflects the exchange of species by recent or subrecent long-range dispersal. Or are these floras disjunct portions of a once continuous flora, for instance continuous along a Pliocene northern island chain representing the subsiding Greenland-Scotland ridge (van den Hoek, 1984; Joosten & van den Hoek, 1986)?

Another example is quite suggestive. About 45 % of the Canarian flora consists of tropical-to-warm temperate species shared with the Caribbean. This similarity in species composition suggests exchange between the Canaries and the Caribbean by long-range dispersal. Another possible explanation would be that these species had a once continuous distribution area which broke into two vicariant portions. This continuous distribution could have been situated in the early Tertiary (van den Hoek, 1975, 1984; Joosten & van den Hoek, 1986).

#### LONG-RANGE DISPERSAL BY PLANKTONIC STAGES OF BENTHIC ANIMALS: EVIDENCE IS AVAILABLE

It seems obvious to consider unicellular spores and zygotes of benthic algae as planktonic stages suited to long-range dispersal. These spores, so it seems, can be compared to the pelagic dispersal stages of marine benthic invertebrates. The dispersal of a number of planktonic invertebrate larvae has been investigated in the tropical-to-warm temperate zone of the Atlantic Ocean (see Scheltema, 1971, for a review). These studies confirm the suggestion from distribution data that algal species might regularly be exchanged, by long-range dispersal, between the eastern and western Atlantic coasts in tropical-to-warm temperate waters. Especially in these warm oceans, benthic animals tend to have planktonic larvae whose larval development is of a long enough duration to permit long-range dispersal. In cold water species, this development is mostly too short to permit the crossing of an ocean (Thorson, 1946).

The advantage of the planktonic stages of invertebrates is that they can be morphologically recognized. Larvae capable of long-range dispersal have been collected throughout the tropical and warm temperate Atlantic Ocean. They belong to diverging groups: gastropods, bivalves, polychaetes, sipunculids, zoantharians, crustaceans, echinoderms. They have morphological adaptations to their pelagic life. Scheltema terms them "teleplanic larvae". To cross, as a larva, the Atlantic from the Cape Verde Islands to the Caribbean would take 150 days (3700 km; velocity  $0.9 \text{ km h}^{-1}$ ; in the North Equatorial Current). To cross the ocean through the South Equatorial Current would take ca 90 to 150 days (4600 km; velocity  $1.3$  to  $2.2 \text{ km h}^{-1}$ ). To cross the ocean in the Equatorial Undercurrent (Eastward current beneath the South Equatorial Current at 50 to 100 m depth) would take ca 40 to 110 days (at  $1.8$  to  $5.4 \text{ km h}^{-1}$ ). The distance of 4000 km between Cape Hatteras and the Azores could be crossed in ca 130 days (19 weeks) at a velocity of  $1.3 \text{ km h}^{-1}$ .

The "teleplanic" larvae are adapted to long-distance dispersal by their long larval

development and their capacity to delay their final settlement (sometimes for more than one year). According to Scheltema there is no doubt that there is a reciprocal exchange of larvae between the eastern and western Atlantic, and consequently gene flow between the two disjunct populations. However, he was apparently searching for evidence in support of the concept of long-range dispersal in benthic invertebrates. The majority of the invertebrate species in the Caribbean does not occur in the E. Atlantic (see also Vermey, 1978, for a discussion of this topic). Can we be as positive about the role of planktic stages of benthic algae? Are they adapted to long life (months) in the phytoplankton?

#### LONG-RANGE DISPERSAL BY PLANKTONIC STAGES OF BENTHIC ALGAE: NO EVIDENCE IS AVAILABLE

There is some evidence with regard to dispersal over short distances. Anderson & North (1966) determined the establishment of juvenile *Macrocystis pyrifera* plants around one transplanted adult specimen. The maximum distance was only 4 m. A similar result was found by Dayton (1973) for *Postelsia palmaeformis*. Anderson & North ascribe this to a combination of a dilution effect, and of a decreasing chance that male and female gametophytes are sufficiently close to one another for fertilization. They also investigated the establishment of juveniles from a dense stand. At a distance of 40 m, juveniles still had an appreciable density (on average  $9 \text{ m}^{-2}$ ). The boundary of their occurrence was not determined.

Imagine that chance dispersal carries one spore of *Macrocystis* to a distant shore. For the development of a new sporophyte, at least one other spore of the opposite sex would be required and this does not favour the idea that long-range dispersal of this species has been brought about by spores. Rather, floating adult plants seem a much more effective agent for long-distance dispersal.

On the other hand, Kain (1964) found that, in culture, most zoospores of *Laminaria hyperborea* lost motility in a day but remained suspended for many days. Some spores were able to survive for at least 40 d at  $17^\circ\text{C}$  and 60 d at  $5^\circ\text{C}$ .

Microscopic female gametophytes bearing few-celled sporophytes would seem to be more suited to long-range dispersal. Moss et al. (1981) speculate that this is the dispersal stage which establishes *Laminaria* populations on the oil platforms in the North Sea.

Small size (5 to  $20 \mu\text{m}$ ) is much more important for a planktonic mode of life than motility. Therefore, the observation that some swimmers of *Enteromorpha intestinalis* can remain motile for about 8 days is not so relevant for the problem of long-range dispersal (Jones & Babb, 1968).

I know three studies in which the pelagic realm was actually sampled for spores of benthic algae. Hruby & Norton (1979) took 500 ml surface water samples from three areas in the Firth of Clyde. These were filtered through 45-mm glass fibre filters and the disseminules retained on the filters were cultured afterwards. The sporelings were identified. *Blidingia*, *Enteromorpha*, *Ulothrix* and small filamentous browns were highly predominant (21 species were recognized in total). This accords with their observation that the same species were predominant colonizers of glass slides exposed for 1 week on the shore.

In a similar approach (cultures of filtered sea-water samples), Zechman & Mathieson

(1985) obtained young plants of 22 to 28 taxa from inshore water samples taken at one point of the New Hampshire coast (USA). Here, again, *Blidingia minima*, *Enteromorpha* spp., various "Chaetophoraceae" and filamentous browns were predominant. Only once was a young *Laminaria*-sporophyte obtained over their whole period of sampling (five times in the period August 1980–July 1981). They also sampled, on one occasion (Nov. 1981), offshore waters at distances of 8, 16 and 24 km from the coast. These samples produced plantlets of only 5, 11 and 1 species, respectively. *Enteromorpha* spp., "Chaetophoraceae" and brown algal filaments were again predominant. Only *Enteromorpha* was sampled from the farthest point. Their study also included estuarine waters but these are not considered here. In both above-cited studies, the composition of the seaweed disseminules in the near-shore waters differed widely from that of the seaweed floras on the nearby rocks with their predominance of brown and red algal species.

Amsler & Searles (1980) collected seaweed disseminules on plastic and glass slides which were left for 8 to 9 days in 20 m deep water 30 km off the coast of North Carolina. They were then cultured into recognizable stages. The upper layers of the water column produced "Chaetophoraceae", *Enteromorpha* spp. and small Bangiophycidae (*Erythrotrichia* and *Erythrocladia*). The *Enteromorpha* spores were 35 km from the nearest sizable population of this genus. Slides left near the rocky bottom (with a diversified seaweed flora) also collected spores of Florideophycidae.

Do the observations in the three above-cited papers have any relevance for the topic of long-range dispersal over thousands of kilometers? Perhaps they suggest that easy and early colonizers such as *Blidingia* and *Enteromorpha* have more chance for long-range dispersal by spores than other species. Further, these studies tend rather to discount the role of planktonic seaweed stages in long-range dispersal. However, these studies do not, of course, consider a realistic time scale (10 000 to 1 000 000 years for the establishment of a flora; see first paragraph of this paper). Further, the volumes of water filtered (200–500 ml) in the first two papers are minute.

Actually, our conclusion must be that there is not any evidence available for either supporting or discounting the role of planktonic stages of seaweeds in long-range dispersal.

#### LONG-RANGE DISPERSAL BY DRIFT ALGAE: EVIDENCE IS AVAILABLE

In discussions on long-range dispersal of seaweeds, the role of floating algae is generally stressed. This is understandable, as drift algae have been observed all over the world, often at great distances from the nearest shores (cf. Oltmanns, 1923; Boergesen, 1905; Norton & Mathieson, 1983).

Enormous amounts of seaweed are thrown upon the Netherlands' shores especially during autumnal gales. Stegenga & Mol (1983) give a few remarks which are relevant to our topic of long-range dispersal. Only few algae drift as a result of their own floating capability. These are *Fucus vesiculosus*, *F. spiralis*, *Ascophyllum*, *Cystoseira* spp., *Hali-drys siliquosa*, *Himanthalia elongata*. Other species drift only if they grow attached to other floating substrates, such as wood, cork, plastic etc, and also to other floating algae. In general, the material is in good condition; it is often reproductive. Most of the material is of southern origin, coming from the coasts of Normandy, Brittany or S. England (a distance of ca 500 to 800 km). The algae were probably several months underway.



In this context, it is relevant to recall that many benthic seaweeds do not need attachment to solid substrates. Especially in calm fjords and bays, loose lying vegetation of many different species may flourish on shallow sediment bottoms (Norton & Mathieson, 1983). However, this vegetation (which should not be confused with the floating vegetation of shallow eutrophic lagoons) sinks to the bottom; it does not float at the surface, and this draws attention to the point already raised that only a limited number of algal species do actually float.

In the tropical and subtropical Atlantic Ocean, the floating populations of *Sargassum natans* and *S. fluitans* would seem to be particularly effective carriers of other algae from one coast of the ocean to the other. Woelkerling (1975) describes their epiphytes. About forty amphiatlantic, tropical-to-warm temperate species are recorded. Typical examples are *Cladophora dalmatica*, *C. laetevirens*, *C. socialis*, *Crouania attenuata*, *Herposiphonia secunda*, *H. tenella*, *Heterosiphonia wurdemannii*, *Hypoglossum tenuifolium*. *Colpomenia sinuosa*, which floats easily, has been also found among the Sargassums.

*Ascophyllum nodosum* and *Fucus vesiculosus* are regularly recorded in the Sargasso Sea; they come from more northern latitudes. They bear northern algae as epiphytes (Woelkerling, 1975). Floating *Ascophyllum* plants were found near the equator off the coast of W. Africa by John (1974). The specimens collected were, according to John, healthy and reproductive! These plants must have travelled at least 5500 km (which would take ca 430 days at a speed of 13 km d<sup>-1</sup>).

Børgesen (1908) argues that the seaweed flora of the Faeroes was re-established after the last glaciation mainly by floating algae. He mentions *Fucus serratus* as a species lacking on the Faeroes but which would be expected there. He thinks that this is related to the species' lack of floating capability.

In conclusion, there is convincing circumstantial evidence that drifting algae could be an important agent in long-range dispersal of benthic seaweeds. However, the majority of algae cannot float, and they can only be transported by other floating algae or other floating objects.

#### LONG-RANGE DISPERSAL BY OTHER FLOATS

Jokiel (1984) reports on a few anecdotic records of long-range dispersal across the Pacific Ocean (20 000 to 40 000 km): (1) A glass net float from Japan, bearing a coral colony of *Pocillopora*, was recorded at Hawaii; this had bridged 7000 km. (2) A piece of floating pumice from San Benedicto Island, Mexico, was also recovered at Hawaii. It also bore a colony of the coral *Pocillopora*. This had reached Hawaii in 264 days (4800 km at 18 cm s<sup>-1</sup>).

The author comments that two events in 4 to 5 years equals 400 000 times per million years! Other records of rafting pumice are cited in this paper. For instance, pumice of the Krakatao eruption which drifted 8500 km across the Indian Ocean in ca 1 year.

Again, there is circumstantial evidence that rafts may function as agents in long-distance dispersal.

#### EVIDENCE AGAINST LONG-RANGE DISPERSAL OF SEaweEDS

The question is apparently not whether long-range dispersal exists or not. It evidently does. Floating is probably an important agent for long-range dispersal, but we

don't actually know anything about the role of spores. One wonders whether big calcareous corallines could ever reach oceanic islands as a floating alga. I don't think so. Spores are needed here, or perhaps juvenile stages growing attached to floating algae. Rather, the question should be: how important is long-range dispersal?

Let us assume for the sake of argument that all algal species, given enough time, could freely disperse to all coasts of the world and settle where they find favourable conditions. One would expect the coasts of the world's oceans to be inhabited by the same latitudinally changing floras. This is not the case; the Atlantic and Pacific Oceans and within these oceans their W and E shores, and their southern hemisphere and northern hemisphere parts harbour different floras. Their differences are much more pronounced than their resemblances even on the generic level (van den Hoek, 1984; Joosten & van den Hoek, 1986). Apparently, long-range dispersal is ineffective for most species of algae.

Introduced alien algae are sometimes cited as examples for the rapid dispersal capabilities of seaweeds. A famous example is *Sargassum muticum*, a Japanese species which was probably introduced together with Japanese oysters. It was first reported from S. England (vicinity of Portsmouth) in 1973, and has spread since along the coasts of the British Channel to reach the Netherlands coasts in 1977, and Norway in 1984 (albeit as floating plants) (Farnham, 1980; Critchley et al., 1983; Prud'homme van Reine, 1977; Rueness, 1985). Of course, this example demonstrates the highly effective dispersal of this species by floating vegetative branches along more or less uninterrupted shores (Deysher & Norton, 1982). The monoecious nature and the rapid growth of this species are probably also essential for its high dispersal capability.

The success of *S. muticum* as an invader also suggests (as do other introduced species) that many seaweeds are potentially capable of establishing themselves on foreign coasts where they have so far not occurred. Apparently there are considerable obstacles to their free dispersal. As soon as man has helped algae to overcome the obstacles to their dispersal, some algae can be quite successful along shores with favourable conditions. A recent example is the successful establishment of the Japanese Laminariales algae *Undaria pinnatifida*, and *Laminaria japonica* in the Étang de Thau, along the French Mediterranean coast. *Undaria* is in the process of spreading beyond the Étang de Thau where these species were probably introduced with Japanese oyster breed (Boudouresque et al., 1985). Other "alien" algae are less successful than *Sargassum muticum* in dispersing from their first point of introduction. An example is *Grateloupia doryphora*, a Pacific species discovered in 1969 in the Solent region of southern England and which in 1978 had not yet spread beyond this region (Farnham, 1980).

The vectors for the above "artificial" long-range dispersal of seaweeds are not precisely known. Introduced shellfish, ship hulls and ballast water are likely candidates (Farnham, 1980; Carlton, 1985).

#### LITERATURE CITED

- Amsler, C. D. & Searles, R. B., 1980. Vertical distribution of seaweed spores in a water column offshore of North Carolina. – *J. Phycol.* 16, 617–619.
- Anderson, E. K. & North, W. J., 1966. In situ studies of spore production and dispersal in the giant kelp, *Macrosystis*. – *Proc. int. Seaweed Symp.* 5, 73–86.

- Ardré, F., 1970. Contribution à l'étude des algues marines du Portugal. I. La flore. – *Portugaliae Acta Biol.* 10, 1–423.
- Ardré, F., 1971. Contribution à l'étude des algues marines du Portugal. II. Écologie et chorologie. – *Bull. Cent. Étud. Rech. scient., Biarritz* 8, 359–574.
- Baardseth, E., 1941. The marine algae of Tristan da Cunha. – *Results Norw. scient. Exped. Tristan da Cunha* 9, 1–174.
- Børgesen, F., 1908. Botany of the Faeröes. P. 3. The algae-vegetation of the Faeröese coasts, with remarks on the phytogeography. – *Nordisk Forl., Copenhagen*, 683–834.
- Boudouresque, C. F., Gerbal, M. & Knoepffler-Péguy, M., 1985. L'algue japonnais *Undaria pinnatifida* (Phaeophyceae, Laminariales) en Méditerranée. – *Phycologia* 24, 364–366.
- Brown, J. H. & Gibson, A. C., 1983. Biogeography. Mosby, St. Louis, 643 pp.
- Brown, A. C. & Jarman, N., 1978. Coastal marine habitats. In: *Biogeography and ecology of southern Africa*. Ed. by M. J. A. Werger. Junk, The Hague, 2, 1239–1277.
- Carlton, J. T., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. – *Oceanogr. mar. Biol.* 23, 313–371.
- Chamberlain, Y. M., 1965. Marine algae of Gough Island. – *Bull. Brit. Mus. nat. Hist. (Bot.)* 3, 175–232.
- Chamberlain, Y., Holdgate, M. W. & Wace, N., 1985. The littoral ecology of Gough Island, South Atlantic Ocean. – *Téthys* 11, 302–319.
- Critchley, A. T., Farnham, W. F. & Morrell, S. L., 1983. A chronology of new European sites of attachment for the marine brown alga, *Sargassum muticum*, 1973–1981. – *J. mar. biol. Ass. U.K.* 63, 799–811.
- Dayton, P. K., 1973. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. – *Ecology* 54, 433–438.
- Deysher, L. & Norton, T. A., 1982. Dispersal and colonization in *Sargassum muticum* (Yendo) Fensholt. – *J. exp. mar. Biol. Ecol.* 56, 179–195.
- Donze, M., 1968. The algal vegetation of the Ria de Arosa (NW Spain). – *Blumea* 16, 159–183.
- Farnham, W. F., 1980. Studies on aliens in the marine flora of southern England. In: *The shore environment*. Ed. by J. H. Price, D. E. G. Irvine & W. F. Farnham. Acad. Press, London, 2, 875–914.
- Hoek, C. van den, 1975. Phytogeographic provinces along the coasts of the northern Atlantic Ocean. – *Phycologia* 14, 317–330.
- Hoek, C. van den, 1984. World-wide latitudinal and longitudinal seaweed distribution patterns and their possible causes, as illustrated by the distribution of rhodophyten genera. – *Helgoländer Meeresunters.* 38, 227–257.
- Hoek, C. van den & Donze, M., 1967. Algal phytogeography of the European Atlantic coasts. – *Blumea* 15, 63–89.
- Hommersand, M. H., 1986. The biogeography of the South African marine red algae: a model. – *Botanica mar.* 29, 257–270.
- Hruby, T. & Norton, T. A., 1979. Algal colonization on rocky shores in the Firth of Clyde. – *J. Ecol.* 67, 65–77.
- Irvine, D. E. G., 1982. Seaweeds of the Faroes. I: The flora. – *Bull. Br. Mus. nat. Hist. (Bot.)* 10, 109–131.
- John, D. M., 1974. New records of *Ascophyllum nodosum* (L.) Le Jol. from the warmer parts of the Atlantic Ocean. – *J. Phycol.* 10, 243–244.
- Jokiel, P. L., 1984. Long distance dispersal of reef corals by rafting. – *Coral Reefs* 3, 113–116.
- Jones, W. E. & Babb, M. S., 1968. The motile period of swimmers of *Enteromorpha intestinalis* (L.) Link. – *Br. phycol. Bull.* 3, 525–528.
- Jónsson, S., 1966. Le commencement du peuplement benthique des côtes rocheuses de Surtsey, la nouvelle île volcanique dans l'Atlantique Nord. – *C. r. hebdom. Séanc. Acad. Sci., Paris* 262, 915–916.
- Jónsson, S., 1970. Meeresalgen als Erstbesiedler der Vulkaninsel Surtsey. – *Schr. naturw. Ver. Schlesw.-Holst. (Sonderb.: Surtsey Island, natürliche Erstbesiedlung [Ökogenese] der Vulkaninsel)*, 21–28.
- Joosten, A. M. T. & Hoek, C. van den, 1986. World-wide relationships between red seaweed floras, a multivariate approach. – *Botanica mar.* 29, 195–214.

- Kain, J. M., 1964. Aspects of the biology of *Laminaria hyperborea*. III. Survival and growth of gametophytes. – J. mar. biol. Ass. U.K. 44, 415–433.
- Kühnemann, O., 1972. Bosquejo fytogeografico de la vegetacion marina del litoral Argentino. – Physis, B. Aires 31, 117–142.
- McIntyre, A., 1976. The surface of the ice-age earth. – Science, N.Y. 191, 1131–1137.
- McIntyre, A. & Kipp, N. G., 1976. Glacial North Atlantic 10 000 years ago: a CLIMAP reconstruction. – Mem. geol. Soc. Am. 145, 43–76.
- 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, 77–90.
- Moss, B. L., Tovey, D. & Court, P., 1981. Kelps as fouling organisms on North Sea platforms. – Botanica mar. 24, 207–209.
- Nielsen, P. H., 1983. Geology and crustal structure of the Faeroe Islands. A review. 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, 77–90.
- Norton, T. A. & Mathieson, A. C., 1983. The biology of unattached seaweeds. – Progr. phycol. Res. 2, 333–386.
- Oltmanns, F., 1923. Morphologie und Biologie der Algen. Fischer, Jena, 3, 1–538.
- Papenfuss, G. F., 1964. Catalogue and bibliography of antarctic and subantarctic benthic marine algae. – Antarc. Res. Ser. 1, 1–76.
- Pickard, G. L. & Emery, W. J., 1982. Descriptive physical oceanography. Pergamon Press, Oxford, 249 pp.
- Printz, H., 1926. Die Algenvegetation des Trondhjemsfjordes. – Skr. norske VidenskAkad. (Kl. 1) 5, 1–274.
- Prud'homme van Reine, W. F., 1977. Japans bessenwier aan onze kust. – Zeepaard 37, 58–63.
- Rueness, J., 1977. Norsk Algeflora. Universitetsforl., Oslo, 266 pp.
- Rueness, J., 1985. Japans drivtang – *Sargassum muticum* – biologisk forensning av europeiske farvann. – Blyttia 43, 71–74.
- Sarnthein, M., Thiede, J., Pflaumann, U., Erlenkeuser, H., Fütterer, D., Koopmann, B., Lange, H. & Seibold, E., 1982. Atmospheric and oceanic circulation patterns off northwest Africa during the past 25 million years. In: Geology of the northwest African continental margin. Ed. by U. von Rad, K. Hinz, M. Sarnthein & E. Seibold. Springer, Berlin, 545–604.
- Scheltema, R. S., 1971. The dispersal of the larvae of shoal-water benthic invertebrate species over long distances by ocean currents. In: Fourth European Marine Biology Symposium. Ed. D. J. Crisp. Cambridge Univ. Press, Cambridge, 7–28.
- Schmidt, O. C., 1931. Die marine Vegetation der Azoren in ihren Grundzügen dargestellt. – Bibliothca bot. 102, 1–116.
- Schmincke, H.-U., 1982. Volcanic and chemical evolution of the Canary Islands. In: Geology of the northwest African continental margin. Ed. by U. von Rad, K. Hinz, M. Sarnthein & E. Seibold. Springer, Berlin, 273–306.
- Seagrief, S. C., 1984. A catalogue of South African green, brown and red marine algae. – Mem. bot. Surv. S. Afr. 47, 1–72.
- Stegenga, H. & Mol, I., 1983. Flora van de Nederlandse zeeieren. Koninkl. Ned. Natuurhist. Ver., Hoogwoud, Netherlands, 263 pp.
- Thiede, J. & Eldholm, O., 1983. Speculations about the paleodepth of the Greenland-Scotland Ridge during late Mesozoic and Cenozoic times. In: Structure and development of the Greenland-Scotland Ridge. Ed. by M. H. Bott, S. Saxov, M. Talwani & J. Thiede. Plenum Press, New York, 445–456.
- Thorson, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates. – Meddr. Kommn Danm. Fisk. – og Havunders. (Ser. Plankton) 4 (1), 1–523.
- Vermey, G. J., 1978. Biogeography and adaptation. Patterns of marine life. Harvard Univ. Press, Cambridge, Mass., 332 pp.
- Woelkerling, W. J., 1975. On the epibiotic and pelagic Chlorophyceae, Phaeophyceae, and Rhodophyceae of the Western Sargasso Sea. – Rhodora 77 (809), 1–40.
- Zechmann, F. W. & Mathieson, A. C., 1985. The distribution of seaweed propagules in estuarine, coastal and offshore waters of New Hampshire, USA. – Botanica mar. 28, 283–294.