ACTA BOT. ISL. 15: 61-79, 2011

Floristic and vegetational discontinuity along the frontal zone in southeastern Iceland

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ABSTRACT: The Icelandic coast is surrounded by water masses of widely different origins and characters, which are reflected in the benthic algal flora and vegetation. In the Southeast there is a sharp hydrographic boundary between approx. 64º24' N and 64º16' N, where the cold East Icelandic Current of Arctic origin meets warm and saline Atlantic water. This frontal zone is usually sharply defined but submitted to seasonal and annual translocations. A tongue of cold, low salinity water can extend even as far as to Mýrabugur in the South. This hydrographic boundary area creates widely different vegetation patterns along a relatively short shore-line of about 55 km. The flora and vegetation was studied on both sides of the frontal zone: on the little islet of Hrollaugseyjar (64º02' N and 16º00' W) and farther eastward at Stokksnes outside Skarðsfjörður (64º15' N and 14º58' W) and Hvalnes outside Lónsfjörður (64º24' N and 14º33' W). On Hrollaugseyjar a remnant of the warm boreal South Icelandic flora and vegetation was found with typical Atlantic floristic elements and low eulittoral belts of: *Mastocarpus stellatus*, *Corallina officinalis* and *Aglaothamnion sepositum*. Thirty-five characteristic Atlantic species disappeared along the distance to Stokksnes, where the benthic algal vegetation was impoverished both in species richness and the number of eulittoral belts. There is a sandy area between the two sites. Farther eastwards, at Hvalnes and Krossanes, the vegetation has become typical subarctic East Icelandic vegetation. This floristic and vegetational discontinuity is the most abrupt, not only in the Icelandic coastal area, but also in the entire northern North Atlantic, where it has no parallel.

INTRODUCTION

Distributional boundaries of marine organisms are an interesting tool from different aspects, first of all their relation to the fronts, where horizontal gradients of hydrographic parameters are large. There are, however, complex interactions between the oceanic circulation, climatic changes, hydrographic conditions and the distribution of pelagic and benthic marine organisms (MCCOY et al. 1986, BALL 1975, MANN & LAZIER 1991, LONGHURST 1998). Descriptive distributional data for benthic marine algae have been presented for both, the Mediterranean and the Atlantic (e.g. SETCHELL 1920, VAN DEN HOEK 1975, FURNARI 1984, ALVAREZ et al. 1988, KAIN & NORTON 1990, LÜNING 1990, PRUD'HOMME VAN REINE & VAN DEN HOEK 1990, RIBERA & BOUDERESQUE 1995). A sharp biotic transition in the distribution of benthic marine algae was also reported for the northern Indian Ocean by SCHILS and WILSON (2006).

Recently, BÁEZ et al. (2004) developed quantified methods based on biotic units for a few Mediterranean genera of benthic marine algae. MICHANEK (1979), VAN DEN HOEK (1975, 1982a, 1982b, 1984) and ADEY & STENECK (2001) treated broad scale boundaries in the North Atlantic and stressed the importance of temperature in biotic delimitations. The work of VAN DEN HOEK et al. (1990) was based on generalized isotherm maps.

In Iceland, centred between Greenland and Ireland in the northern North Atlantic, extreme variations in vegetation patterns were found within a relatively small area (MUNDA 1975, 1976a, 1978, 1983, 1992a, 1992b, 1992c, 1999a, 1999b). There are, however, both gradual transitions between the different vegetation types, as e.g. in the Southwest and Northeast (MUNDA 1987, 1992c), or sharp floristic and vegetational boundaries, as found in the Northwest and Southeast of Iceland (MUNDA 1975, 1992a, 1992b). These vegetational discontinuities reflect the varying hydrographic conditions around the Icelandic coast, which is surrounded by water masses of widely different origins and characters (e.g. EINARSSON 1969, STEFÁNSSON 1962, 1969, 1972, MALMBERG & STEFÁNSSON 1972, MALMBERG 1972, 1984, 1986, MALMBERG & KRISTMANNSSON 1992, SWIFT & AAGARD 1981, HANSEN 1985, KRAUSS 1986, 1995, DE BOER 1993, VALDIMARSSON & MALMBERG 1999), and occasionally also influenced by drift ice (SIGTRYGGSSON 1972).

On the shelf in southeastern Iceland, there is a sharp hydrographic boundary between 64° 24′ N and 64° 15′ N, where the cold East Icelandic Current of arctic origin meets warm and saline Atlantic water, conveyed by the Gulf Stream. This frontal zone, situated between Austurhorn (Hvalnes) and Vesturhorn (Stokksnes) (Fig. 1) is usually sharply defined, but submitted to annual and seasonal translocations (STEFÁNSSON 1972, MALMBERG 1972, 1984). A tongue of cold, low salinity water can extend as far south as to Mýrabugur.

This hydrographic boundary area creates widely different vegetation patterns along a relatively short coastline. Algological studies carried out on both sides of the frontal zone had revealed an abrupt floristic and vegetational discontinuity.

It deserves special attention because it is unique, not only for Iceland, but also for the entire northern North Atlantic, where it has no parallel.

The aim of the present contribution is a description of the species composition and vegetation patterns on both sides of the frontal zone.

Study area and hydrographic conditions

The study area was restricted to the extreme Southeast of Iceland, ranging from the small islands of Hrollaugseyjar (64° 02′ N and 16° 00′ W) over Stokksnes outside Skarðsfjörður (64° 15′ N and 14° 58′ W) and west of the frontal zone, to Hvalnes (64° 24′ N and 14° 33′ W) on its eastern edge (Fig. 1). Hrollaugseyjar is situated in Mýrabugur about 8 km offshore and 55 km from Stokksnes. The extension of the frontal zone itself is usually 28 km.

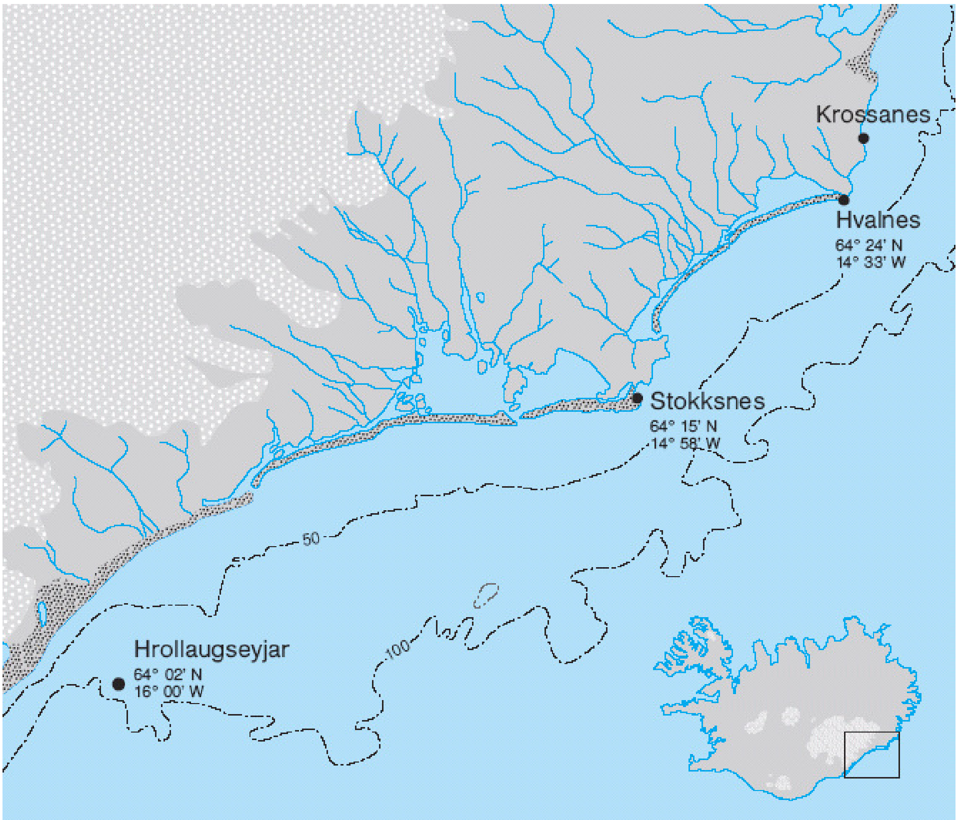

FIGURE 1. Map of the area in southeastern Iceland.

Temperature and salinity measurements were carried out during algal samplings, first during August/September 1968. They are presented in Table 1 together with ten years annual temperature averages after STEFÁNSSON (1969) and indicate a prevalence of warm Atlantic water west of the frontal zone, at Stokksnes and Hafnarnes (Vesturhorn) with relatively high summer temperatures and salinities. A temperature and salinity drop was recorded on the eastern side of the frontal zone, at Hvalnes (Austurhorn) for about 2.6° C and 1 psu respectively.

A further temperature decline was found farther eastwards.

Seasonal variations of water temperature at three characteristic spots in southeastern Iceland are presented in Fig. 2 following data given by STEFÁNS-

SON (1969). Mýrabugur is situated in the Atlantic water area of the Icelandic coast, and Vesturhorn (Stokksnes) and Austurhorn (Hvalnes) on either side of the frontal zone. There are some differences in the seasonal temperature variations between these localities. Around Vesturhorn and in Mýrabugur temperature maxima were recorded in July and August, but in August/ September at Austurhorn. Average yearly temperature minima were found between January and March around Austurhorn, and in January and February around Vesturhorn, while in Mýrabugur the yearly temperature minimum was limited to February.

TABLE 1. Temperature and salinity data in southeastern Iceland in August/September 1968. Annual temperature averages after STEFÁNSSON 1969.

Localities	**Temperature (°C)**	**Salinity (psu)**	**Mean annual temperature (°C)**
Mýrabugur			7.5
Hrollaugseyjar	10.1	34.7	
Vesturhorn			5.8
Stokksnes	8.5	34.2	
Hafnarnes	8.2	34.4	
Austurhorn			4.7
Hvalnes	5.8	33.4	
Krossanes	5.6	33.2	
Berufjörður (outer area)			4.0
Framnes	5.7	32.2	
Núpstangi	3.9	33.0	

The entire south Icelandic coast is, however, a sandy desert bare of algal vegetation. East of the Reykjanes Peninsula there are only the Vestmann Islands and some small skerries and shoals which offer support to benthic algae (e.g. Þrídrangar, Faxasker, Geirfuglasker). On the mainland, rocky grounds are restricted to Vík in Mýrdal and to the localities mentioned above, viz. Stokksnes/Hafnarnes and the surroundings of Hvalnes. Farther to the east, from Krossanes and northwards, the coast in mostly rocky. The coast-line between Hrollaugseyjar in Mýrabugur and Stokksnes is sandy and bare of algal vegetation. Along the frontal zone itself there are several land-locked fjords (Hornafjörður, Skarðsfjörður, Papafjörður and Lónsfjörður) which are separated from the open sea by bars, formed of basaltic sand, pebbles and gravel. Landward of the bars the fjords are covered by both alluvial sand and glacial deposits, and offer growth conditions to an atypical, estuarine vegetation of filamentous brown and green algae (MUNDA 1999a).

Floristic and vegetational differences were detected on the rocky substrate around Hrollaugseyjar, Stokksnes/Hafnarnes and Hvalnes.

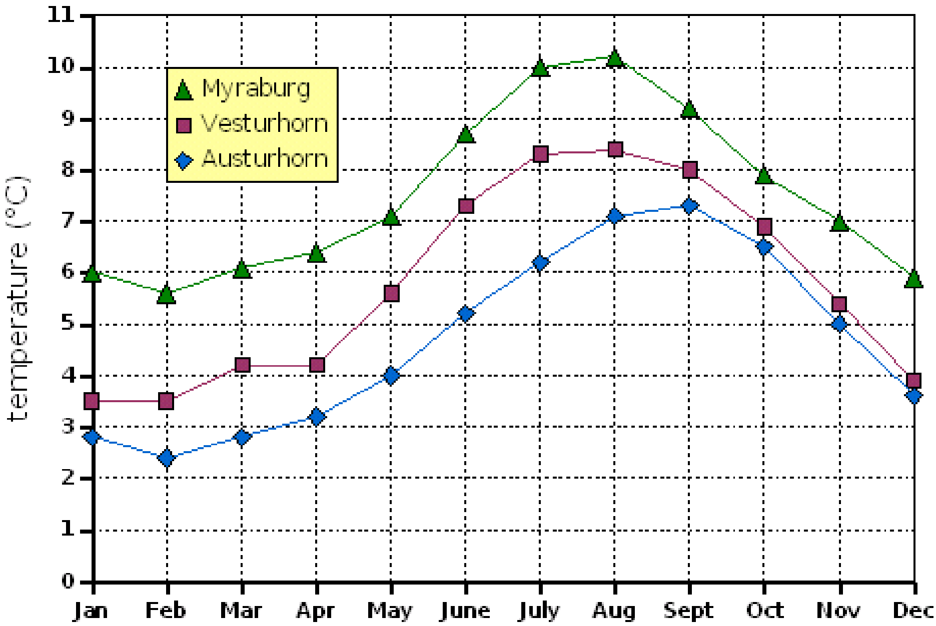

FIGURE 2. Seasonal variations of water temperature in southeastern Iceland (after STEFÁNSSON 1969) .

Oceanographic situation

Iceland belongs to the Atlantic Arctic Province (DIETRICH 1964, 1969, LONGHURST 1998), situated between the edge of the Greenland coastal currents and the Oceanic Polar Front, which crosses the ocean from Flemish Cap to the Faeroes. It includes the central part of the Labrador Sea, a broad zone towards the northeast of Iceland, and the central part of the Nordic Sea from Iceland to the Fram Strait. Different surface water masses cross this boreal zone of the North Atlantic. The surface circulation north of the Polar Front is dominated by a cyclonic gyre, while an anticlockwise subtropical one occurs in the south. Consequently this province has some characteristics of both, the Atlantic Drift and the polar water masses. The Oceanic Polar Front is, however, a conjunction between warm and salty subtropical water and cold, less saline polar water. It passes the east of Iceland and continues eastwards along the Icelandic Faeroe Ridge, and then northwards to Jan Mayen, and to the Mid-Atlantic Ridge (DIETRICH 1964, JOHANNESSEN 1986, VAN AKEN et al. 1991, VAN AKEN 1993).

A strong flow of cold, low salinity water forms a northern cyclonic gyre between the Labrador Sea and Iceland (KRAUSS 1986), and an arm of the North Atlantic Current penetrates into the Atlantic Arctic Province as the Irminger Current. The Oceanic Polar Front is thus associated with a wide eddy field and exchanges with Atlantic surface water from the south.

The circuit between Iceland and Jan Mayen feeds water to the East Icelandic Current (STEFÁNSSON 1962). In addition this current is mixed with water masses from the East Greenland Current, the North Icelandic Irminger Current, coastal water and the so-called North Icelandic Winter Water, which is formed on the north Icelandic shelf during winter.

The East Icelandic Current was an ice-free arctic current up to 1963. Later, especially between 1965 and 1970, it advanced farther southwestwards and developed into a polar current, transporting drift ice (MALMBERG 1969, 1972, 1984, MALMBERG & STEFÁNSSON 1972). The penetration of drift ice is a crucial factor influencing hydrographic conditions along the north and east Icelandic coasts (EINARSSON 1969, SIGTRYGGSSON 1972). Particularly severe ice conditions were found in the north and east Icelandic waters in the late sixties (1965, 1967, 1968) after a long ice-free period. During these years a tongue of cold water extended as far as to Mýrabugur. After this period ice conditions became less severe, but in the late seventies drift ice appeared again (MALMBERG 1984). Ice conditions influenced the annual translocations of the frontal zone. There were, however, strong climatic changes in the North Atlantic (DICKSON et al. 1975, FRAKES 1978), as a whole.

The shift of the characters and extension of the East Icelandic Current is, according to LAMB (1979) one of the most important aspects of these changes in the North Atlantic in recent and historical times.

The benthic algal flora and vegetation

Along boundary areas there are, however, differential species and common species. Essential are the dominant, canopy-forming ones as well as the undergrowth. Less important are the small epiphytes which are mainly ephemeral, fugitive species within the associations.

The bentic algal vegetation was studied on rocky slopes of the island of Hrollaugseyjar, at Stokksnes/Hafnarnes and Hvalnes and Krossanes on the mainland. The coast between Hrollaugseyjar and Stokksnes is sandy and vegetation-free and the same is true for the bars, separating land-locked fjords from the open sea (Suðurfjörur, Austurfjörur and Fjörur).

Hrollaugseyjar (Fig. 3A)

There are different growth conditions on the landward and seaward side of this rocky island.

Landwards, a complete fucoid zonation was found, ranging from *Pelvetia canaliculata* over *Fucus spiralis*, *F. vesiculosus* to *F. distichus* ssp. *edentatus* and *F. serratus*. *Ascophyllum nodosum* was found scattered and did not form a continuous belt. Seawards, the uppermost eulittoral was occupied by narrow belts of *Porphyra umbilicalis*, *Ulothrix* species and *Blidingia minima*, while fucoids were only represented by *Fucus distichus* ssp. *anceps* and *F. distichus* ssp. *edentatus*. In the lower eulittoral, algal belts characteristic of the South Icelandic coastal area (MUNDA 1976a) dominated, viz. *Mastocarpus stellatus*, *Corallina officinalis* and *Aglaothamnion sepositum*. In the tide pools, diverse warm-water algal associ-

TABLE 2. Floristic changes along the southeastern area of the Icelandic coast. A. Differential species

Species with distributional limit at Hrollaugseyjar	**Species joining east of the frontal zone**
Rhodophyta	
Florideophycidae; *Audouinella alariae* (Jónsson) Woelkerling, *Aglaothamnion scopulorum* (C.Ag.) Feldmann-Mazoyer, *Antithamnionella floccosa* (O.F. Müller) Whitick, *Aglaothamnion sepositum* (Gunn.) Maggs et Hommersand, *Aglaothamnion hookeri* (Dillw.) Maggs et Hommersand, *Callithamnion tetragonum* (With.) Gray, *Ceramium areschougii* Kylin, *Ceramium deslongchampsii* Chauvin ex Duby, *Ceramium nodulosum* (Lightf.) Ducluz., *Ceramium shuttleworthianum* (Kütz.) Silva, *Ceramium* sp., *Corallina officinalis* L., *Chondrus crispus* Stackh., *Cystoclonium purpureum* (Huds.) Batters, *Dilsea carnosa* (Schmidel) Kuntze, *Dumontia contorta* (Gmel.) Ruprecht, *Gloiosiphonia capillaris* (Huds.) Carm. ex Berkeley, *Lomentaria clavellosa* (Turn.) Gail., *Lomentaria orcadensis* (Harvey) Collins ex Taylor, *Mastocarpus stellatus* (Stackh.) Guiry, *Membranoptery alata* (Huds.) Stackh., *Phyllophora pseudoceranoides* (Gmel.) Newroth ex Taylor, *Phymatolithon purpureum* (Crouan et Crouan) Woelkerling, *Pterothamnion plumula* (Ellis) Nägeli, *Plocamium cartilagineum* (L.) Dixon, *Plumaria plumosa* (Huds.) Kuntze, *Polysiphonia lanosa* (L.) Tandy, *Polysiphonia fucoides* (Huds.) Grev.	**Bangiophycidae**; *Porphyra amplissima* (Kjellm.) Setchell et Hus., *Porphyra thulaea* Munda et Pedersen **Florideaphycidae**; *Pantoneura baerii* (Post. et Rupr.) Kylin, *Polysiphonia arctica* Harvey,
Phaeophyta	
Asperococcus fistulosus (Huds.) Hooker, *Desmarestia ligulata* (Lightf.) Lam., *Leathesia difformis* (L.) Aresch., *Fucus serratus* L., *Mesogloia vermiculata* (Smith) S.F. Gray, *Pelvetia canaliculata* (L.) Decne et Thur.	*Coilodesme bulligera* Strömfelt, *Laminaria nigripes* J. Ag., *Petalonia filiformis* (Batt.) Kuntze, *Ralfsia fungiformis* (Gunn.) Setchel et Gardner, *Sphacelaria arctica* Harvey,
Chlorophyta	
Cladophora rupestris Kütz.	*Blidingia chadefaudii* (Feldm.) Bliding, *Blidingia marginata* (C. Ag.) Dang., *Capsosiphon groenlandicus* (J. Ag.) Vinogradova, *Monostroma arcticum* Wittr.

TABLE 2 (continued). B. Common species. Subordinate in the vegetation westwards and outstanding eastwards of the frontal zone.

Rhodophyta	*Phaeophyta*	*Chlorophyta*
Florideophycidae; *Callophylis cristata* (C. Ag.) Kütz., *Clathromorphum circumscriptum* (Strömfelt) Foslie, *Coccotylus truncatus* (Pallas) Wynne et Heine, *Delesseria sanguinea* (Huds.) Grev., *Devaleraea ramentacea* (L.) Guiry, *Delesseria sanguinea* (Huds.) Grev., *Fimbrifolium dichotomum* (Lepech.) Hansen, *Lithothamnion glaciale* Kjellm., *Phycodrys rubens* (L.) Batters, *Ptilota gunneri* Silva, Maggs et Irvine, *Ptilota serrata* Kütz.	*Alaria esculenta* (L.) Grev., *Chordaria flagelliformis* (O. F. Müll.) J. Ag., *Desmarestia aculeata* (L.) Lam., *Dictyosiphon foeniculaceus* (Huds.) Grev., *Halosiphon tomentosus* (Lyngb.) Jaasund, *Petalonia fascia* (O. F. Müll.) Kuntze, *Petalonia zosterifolia* (Reinke) Kuntze, *Scytosiphon lomentaria* (Lyngb.) Link	*Acrosiphonia* spp., *Ulothrix* spp.

ations were found, like *Chondrus crispus, Corallina officinalis*, *Dumontia contorta*, *Ceramium* ssp., *Cystoclonium purpureum* and *Ahnfeltia plicata*, as the most outstanding.

Atlantic floristic elements, such as *Plumaria plumosa*, *Corallina officinalis*, *Membranoptera alata*, *Ceramium* species, *Phymatolithon purpureum* and *Polysiphonia fucoides,* were dominant also in the Fucacean undergrowth. Characteristic among the epiphytes was *Polysiphonia lanosa* on *Ascophyllum nodosum* plants.

In the upper sublittoral *Laminaria digitata* f. *stenophylla* was belt-forming. Several warm-water floristic elements were present also in the sublittoral, such as *Plocamium cartilagineum*, *Phyllophora pseudoceranoides*, *Desmarestia ligulata* and *Lomentaria* species. The benthic algal flora and vegetation of the island of Hrollaugseyjar is likely to represent the last outcrop of the warm boreal conditions, characteristic of the South Icelandic coastal area.

Stokksnes and Hafnarnes (Fig. 3 B, C)

The Atlantic vegetation pattern just described was abruptly changed around Stokksnes (Vesturhorn) on the western side of the frontal zone. The area between the two rocky sites is separated by a sandy extent, so that a precise delimitation between the two different vegetation types could not be estimated in full detail. No gradual transition could be observed, only a sharp boundary between the Atlantic and low-subarctic vegetation. Around Stokksnes and Hafnarnes all the typical Atlantic floristic elements were absent, and the vegetation extremely reduced (Table 2 A).

There was likewise a reduction in the number of the eulittoral algal belts, especially in heavily exposed steep rocky sites (Fig. 4).

A wide *Ulothrix* spp.-*Urospora penicilliformis* zone occupied the entire eulittoral slopes. Only *Acrosiphonia arcta* could be found in rocky fissures. With conditions of decreasing exposure, additional algal belts could join in the upper eulittoral, such as *Porphyra umbilicalis* and *Fucus distichus* ssp. *anceps* and *Acrosiphonia* species lower down. Such vegetation features are comparable to those found in highly exposed, steep rocky sites in the mid-East of Iceland (e.g. Munda 1983, 1992b). Where the slopes were rather moderate and medium exposed, several algal belts occupied the eulittoral, such as *Porphyra umbilicalis*, *Fucus spiralis*, *F. vesiculosus*, *F. distichus* ssp. *edentatus*, *Devaleraea ramentacea*, *Acrosiphonia* species and *Chordaria flagelliformis*.

In the upper sublittoral, *Laminaria digitata* f. *stenophylla* belts were replaced by belts of *Alaria esculenta*. Sublittorally, several species disappeared, e.g. *Desmarestia ligulata*, *Plocamium cartilagineum*, *Lomentaria* species, *Phyllophora pseudoceranoides*, *Polysiphonia fucoides* and *Membranoptera alata*.

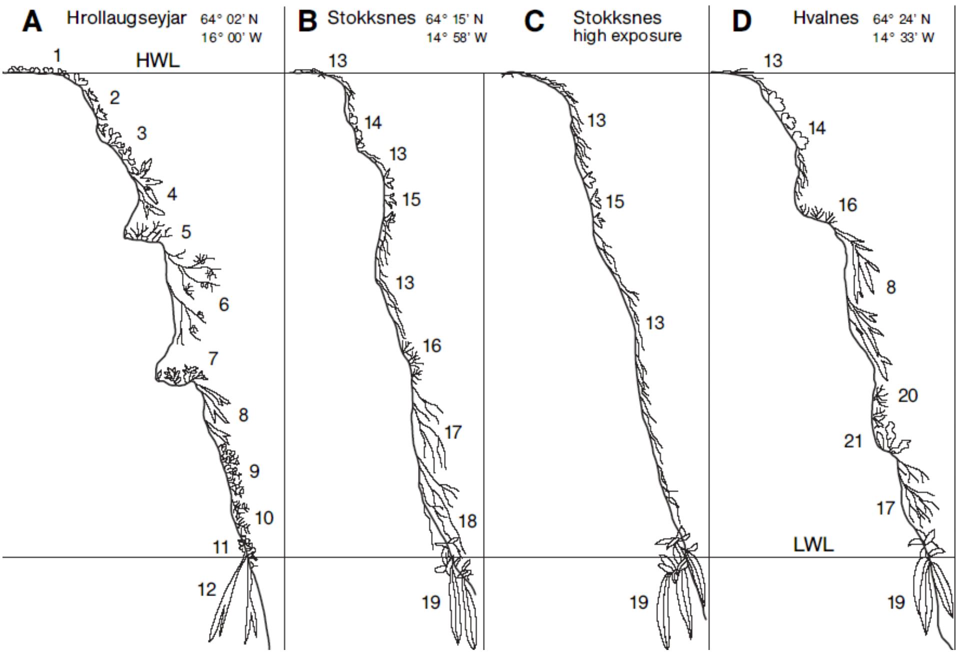

FIGURE 3. Patterns of algal zonation in southeastern Iceland.

Main species along the frontal zone: 1 – *Prasiola stipitata;* 2 – *Pelvetia canaliculata;* 3 – *Fucus spiralis;* 4 – *Fucus vesiculosus;* 5 – *Ahnfeltia plicata;* 6 – *Asophyllum nodosum* with *Polysiphonia lanosa;* 7 – *Chondrus crispus;* 8 – *Fucus distichus* ssp. *edentatus;* 9 – *Mastocarpus stellatus;* 10 – *Corallina officinalis;* 11 – *Aglaothamnion sepositum;* 12 – *Laminaria digitata* f. *stenophylla;* 13 – *Ulotrix* spp. -*Urospora penicilliformis;* 14 – *Porphyra umbilicalis;* 15 – *Fucus distichus* ssp. *anceps;* 16 – *Acrosiphonia* spp.; 17 – *Chordaria flagelliformis;* 18 – *Halosiphon tomentosus;* 19 – *Alaria esculenta;* 20 – *Devaleraea ramentacea;* 21 – *Palmaria palmata*

Eulittorally, *Pelvetia canaliculata* and *Fucus serratus* were absent from the vegetation. The same was true of the typical low-eulittoral algal belts, found in the Atlantic waters, such as those of *Mastocarpus stellatus*, *Corallina officinalis* and *Aglaothamnion sepositum*. The rather variegated tide pool vegetation still found around Hrollaugseyjar was absent at Stokksnes and farther eastwards. Where the eulittoral slopes were moderate several associations, characteristic of the subarctic East Icelandic coastal area, replaced the Atlantic ones. Noteworthy are belts of *Devaleraea ramentacea*, *Acrosiphonia* spp. and *Chordaria flagelliformis*. It seems likely, however, that the Atlantic *Mastocarpus stellatus* association is equivalent to the subarctic *Devaleraea ramentacea* one, *Corallina officinalis* mats to those of *Acrosiphonia* ssp., and *Chordaria flagelliformis*, which is belt forming lowermost in the eulittoral, to *Aglaothamnion sepositum* populations. In the tide pools, associations of *Devaleraea ramentacea*, *Palmaria palmata*, *Acrosiphonia* spp., *Chordaria flagelliformis*, diverse filamentous brown algae with the dominance of *Dictyosiphon foeniculaceus,* replaced the numerous red algal associations of Atlantic waters (e.g. *Chondrus crispus*, *Ahnfeltia plicata*, *Dumontia contorta*, *Ceramium* species, *Cystoclonium purpureum*).

In sites, where compact fucoid belts were present, e.g. around Brunnhorn outside Papafjörður, their undergrowth was also impoverished for several Atlantic floristic elements, such as *Plumaria plumosa*, *Membranoptera alata*, *Polysiphonia fucoides*, *Corallina officinalis*, *Ceramium* species, *Phymatolithon purpureum*. Only ubiquitous floristic elements were left, e.g. *Ralfsia verrucosa*, *Hildenbrandia rubra*, *Sphacelaria radicans* and a few crustose corallines.

The benthic algal vegetation on the western side of the frontal zone was thus extremely impoverished, with a simplified zonation pattern in most sites (Fig. 4). In spite of the abrupt floristic and vegetational changes it still represents a transitional area towards the typically subarctic vegetation of eastern Iceland.

Hvalnes (Fig. 3 D)

The rocky formations around Hvalnes (Austurhorn) outside Lónsfjörður offer support to a more variegated algal flora and vegetation than the surroundings of Vesturhorn.

In relatively protected sites a complete Fucacean zonation was found, ranging from *F. spiralis*, over *F. vesiculosus*, and *Ascophyllum nodosum* to *Fucus distichus* ssp. *edentatus*. In the lower eulittoral there were extensive mats of *Acrosiphonia* species, and the *Devaleraea ramentacea* belt, still unconspicous around Vesturhorn, was wide and prolific. *Chordaria flagelliformis* became outstanding in the vegetation, both in the lower eulittoral and in the tide pools. Around the eulittoral/sublittoral junction *Chordaria* belts were joined by *Halosiphon tomentosus*.

In this area, *Ralfsia fungiformis* joined the vegetation but was still unconspicuous. Farther northeastwards, it forms a typical subarctic association with

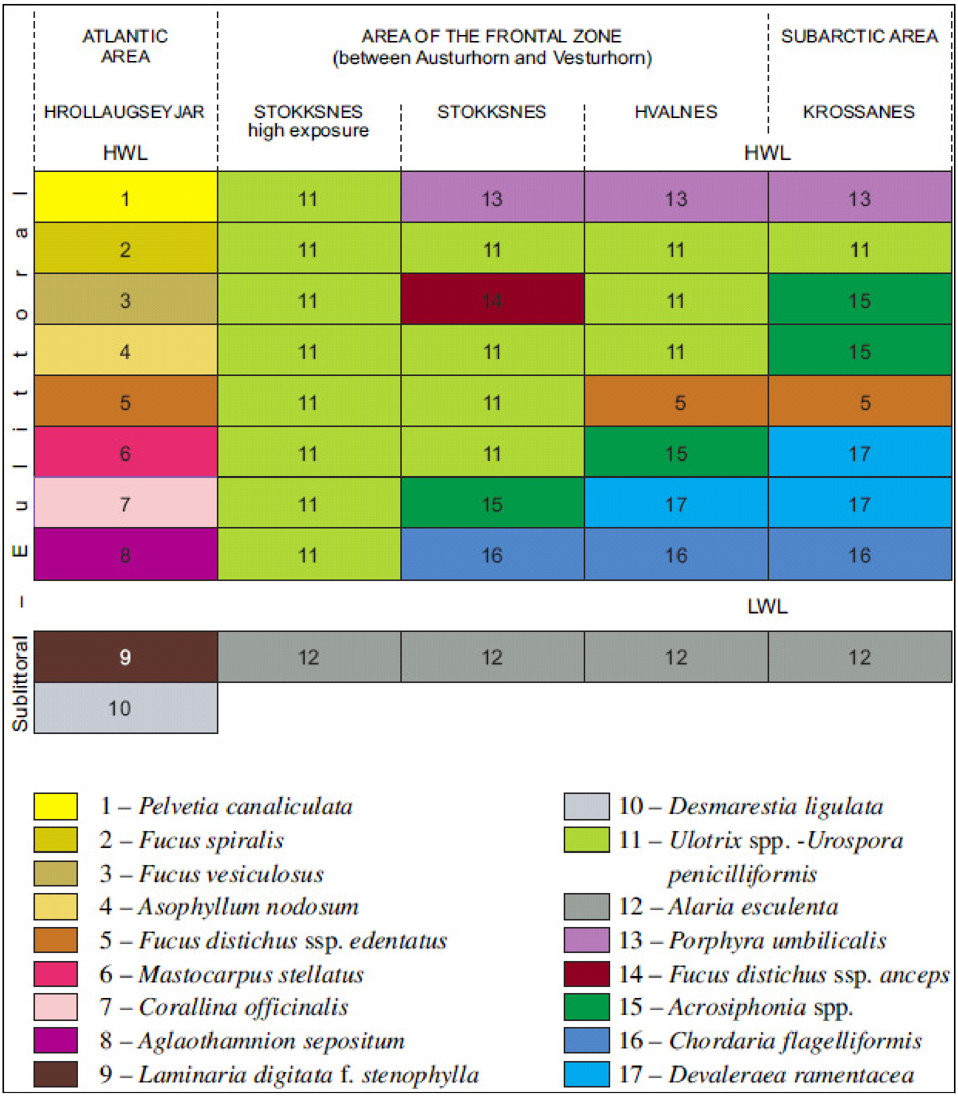

FIGURE 4. Main algal belts

Coilodesme bulligera in the tide pools. The latter species appeared only as far north as in Berufjörður.

In the uppermost eulittoral, belts of *Porphyra umbilicalis* and *Ulothrix* species were outstanding. Locally, in sheltered sites, *Blidingia minima* and *B. chadefaudii* were belt forming below the *Ulothrix* level. *Fucus spiralis* was rather rare.

The benthic algal vegetation north from Hvalnes was also studied, all the way over Krossanes to Mælifellsdalur, with sporadic observations up to Hafnarskjól outside Álftafjörður.

An increase in width of the *Ulothrix* spp.-*Urospora penicilliformis* belts was observed northwards along the East Icelandic coast, and the same was true of belts of *Devaleraea ramentacea*, *Chordaria flagelliformis*, *Acrosiphonia* species and *Alaria esculenta*.

A similar vegetation pattern was observed all the way up to Berufjörður. And it is first along the outer area of its northern coast that several typically subarctic species joined the vegetation (MUNDA 1999b), e.g. *Coilodesme bulligera*, *Pantoneura baerii*, *Porphyra thulaea*, *Turnerella pennyi*, *Polysiphonia arctica* and *Capsosiphon groenlandicus*.

The main algal belts in the southeastern area between Hrollaugseyjar and Krossanes are schematically presented in Fig. 4.

DISCUSSION AND CONCLUSIONS

Delimitations between floral districts, as reported for the North Atlantic, do not always coincide with the geographic latitude (e.g. VAN DEN HOEK & DONZE 1967, VAN DEN HOEK 1975, 1982a, b, 1984, MICHANEK 1987); but seem most pronounced within small areas where they are determined by the hydrographic conditions, like within the Icelandic coastal area (MUNDA 1975, 1992a, b, c). Strong hydrographic boundaries create significantly different biota. The frontal zone in southeastern Iceland is usually situated between Vesturhorn and Austurhorn, but is submitted, as mentioned, to wide annual translocations, first of all during severe ice years, as e.g. in 1967 and 1968, when the first algological studies in this area were carried out. As a response to the sharp hydrographic boundary and its southwest extension, thirty five typically Atlantic species were excluded from the vegetation at Stokksnes (Vesturhorn). It seems likely, however, that there is a temperature limit between Hrollaugseyjar and Stokksnes which causes the floristic turnover so that all the taxa with warm water affinities disappeared (Fig. 5). A list of the exclusive species, having their eastwards distributional limit around Hrollaugseyjar is presented in Table 2 A together with species which appear east of the frontal zone. Common species with an overall distributional pattern differ in their abundance and degree of cover. They can be subordinate on one side of the boundary and dominant on the other, as e.g. *Devaleraea ramentacea*, *Acrosiphonia* spp., *Chordaria flagelliformis* with *Halosiphon tomentosus*, *Dictyosiphon foeniculaceus*, *Scytosiphon lomentaria*, *Petalonia* species and *Alaria esculenta* (Table 2 B).

The islets of Hrollaugseyjar contains, however, all the typical Atlantic floristic elements, found along the South Icelandic coastal area (MUNDA 1976a). Floristic and vegetational differences versus Stokksnes (Vesturhorn) refer to the eulittoral- and tide pool associations, as well as to the Fucacean undergrowth and the upper sublittoral vegetation

Floristic changes comprise first of all Rhodophytan species. Most of them are canopy-forming in the lower eulittoral and in the tide pools. Vegetation-determining in Atlantic water areas of the Icelandic coast is first of all *Mastocarpus* *stellatus* (MUNDA 1977), which forms wide low-eulittoral belts. This cold-boreal species has a rather northerly distribution in the North Atlantic, e.g. in northern Norway (JAASUND 1965), the Faeroes (IRVINE 1982, PRICE & FARNHAM 1982), Shetland (IRVINE 1974), but is absent in southern Norway (SUNDENE 1953). In Iceland it forms low-eulittoral belts up to Hornbjarg (MUNDA 1977, 1992a) and occurs sporadically along the North Icelandic coast, to Melrakka-slétta. The second most outstanding Atlantic species is *Corallina officinalis*, which forms extensive belts or wide meadows lower down than *Mastocarpus*. It is likewise outstanding in the tide pools, and its distributional limit around Iceland is Vopnafjörður in the Northeast.

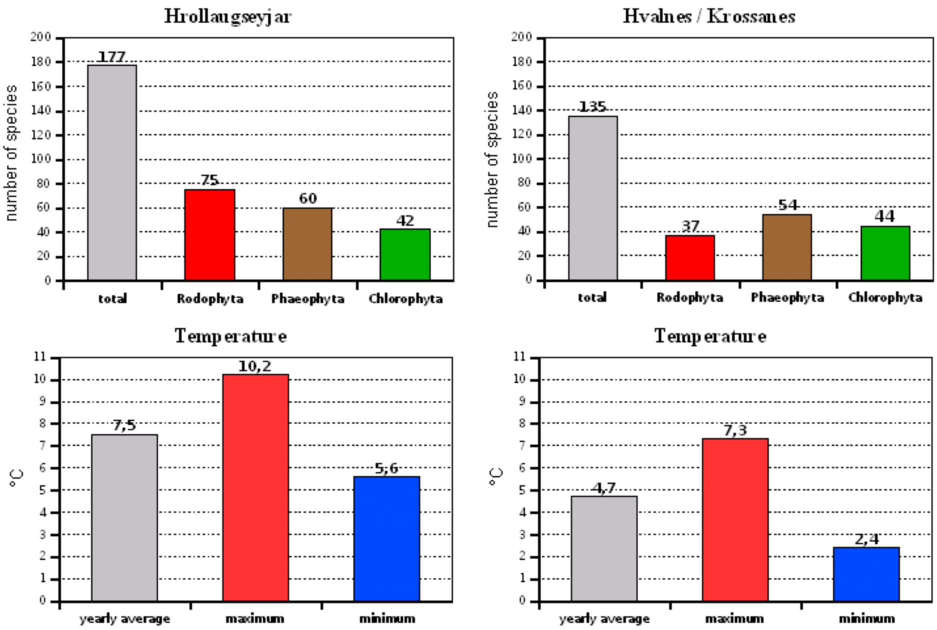

FIGURE 5. Number of species versus surface sea temperature in southeastern Iceland

The third conspicuous association-forming species in the lowermost eulittoral is *Aglaothamnion sepositum*, reaching up to Hornbjarg. All these typically Atlantic low eulittoral associations were found around Hrollaugseyjar (Table 3). In the tide pools several Atlantic floristic elements dominated here; but were absent eastwards at Stokksnes. Conspicuous is *Chondrus crispus*, a warm boreal species with a wide distributional pattern throughout the Atlantic, from Morocco to northern Norway (JAASUND 1965, MACFARLANE 1968, LILLY 1968). In Iceland, it has a narrower distribution than *Mastocarpus*, reaching only as far north as to the Snæfellsnes Peninsula (MUNDA 1987). Most of the conspicuous and association-forming tide pool species had their northwest distributional limit at Hornbjarg (MUNDA 1992a), as e.g. *Ahnfeltia*

TABLE 3. Changes of the main algal associations along the southeastern area of the Icelandic coast.

Hrollaugseyjar	**East of the frontal zone (Hvalnes/Krossanes)**
Upper eulittoral	
Pelvetia canaliculata	*Ulothrix* spp.-*Urospora penicilliformis*
Lower eulittoral	
Mastocarpus stellatus, *Corallina officinalis*, *Aglaothamnion sepositum*	*Devaleraea ramentacea*, *Acrosiphonia* spp., *Chordaria flagelliformis* with *Halosiphon tomentosus*
Tide pools	
Chondrus crispus, *Corallina officinalis*, *Dumontia contorta*, *Ahnfeltia plicata*, *Ceramium* spp., *Cystoclonium purpureum*	*Devaleraea ramentacea*, *Acrosiphonia* spp., *Dictyosiphon foeniculaceus*
Upper sublittoral	
Laminaria digitata f. *stenophylla*	*Alaria esculenta*
A survey of the main algal associations and floristic composition of the South and East Icelandic coastal areas was given by MUNDA (1976a, 1983, 1994).	

plicata, *Dumontia contorta*, while some were association forming also along the North Icelandic coastal area (*Corallina officinalis*, *Ceramium* species, *Cystoclonium purpureum*).

Low-eulittoral belts of *Mastocarpus stellatus* were replaced by belts of *Devaleraea ramentacea* eastwards of the frontal zone and all along the East and North Icelandic coastal areas (MUNDA 1976b). This circumpolar species is outstanding also in Greenland (LUND 1959, PEDERSEN 1976), Newfoundland and Labrador (WILCE 1959) and other subarctic areas.

Floristic changes along the hydrographic boundary area were less pronounced for the brown algae (Table 2A). *Leathesia difformis*, *Asperoccocus fistulosus* and *Mesogloia vermiculata* disappeared from the eulittoral, and *Desmarestia ligulata* sublittorally. Vegetational differences, centre, however, to the fucoid belts since both, *Pelvetia canaliculata* and *Fucus serratus* were absent. Conspicuous was also the shift from *Laminaria digitata* f. *stenophylla* belts in the upper sublittoral to *Alaria esculenta* ones, beside the absence of several sublittoral red algae, as e.g. *Lomentaria* species, *Plocamium cartilagineum* *Membranoptera alata*, *Polysiphonia fucoides*, *Phyllophora pseudoceranoides*.

The least floristic changes along the boundary area refer to the Chlorophyta. Only the disappearance of *Cladophora rupestris* is noteworthy. There are, on the other hand, pronounced vegetational changes regarding the increased width of the *Ulothrix* spp.-*Urospora penicilliformis* belts eastwards from Vesturhorn, and the dominance and extension of the *Acrosiphonia* spp. mats.

As contrast to Hrollaugseyjar with its variegated flora and vegetation, that of the surroundings of Stokksnes was extremely impoverished, not only floristically, but also regarding the zonation pattern. It was simplified and reduced to a wide *Ulothrix* spp.-*Urospora penicilliformis* belt (Fig. 4), reaching down to the *Alaria esculenta* zone. Farther eastwards, under less severe exposure conditions, additional algal belts were observed on rather moderate rocky slopes (e.g. *Porphyra umbilicalis*, *Fucus distichus* ssp. *anceps, F. distichus* ssp. *edentatus*, *Devaleraea ramentacea*, *Palmaria palmata*, *Chordaria flagelliformis*, *Acrosiphonia* spp.). These algal belts, characteristic of the arctic-water influenced East Icelandic coast, are well developed on the eastern side of the frontal zone. They resemble the Newfoundland and Labrador vegetation (WILCE 1959, MATHIESEN et al. 1969).

The area between Stokksnes and Hvalnes, viz. that of the frontal zone, could still be regarded as a transitional and atypical one, in spite of the profound floristic and vegetational changes taking place between Hrollaugseyjar and Stokksnes. The zonation pattern here was simplified (Fig. 4). The typical subarctic vegetation with wide eulittoral belts of *Devaleraea ramentacea*, *Acrosiphonia* spp. and *Chordaria flagelliformis* joined by *Halosiphon tomentosus*, first appeared north-eastwards of the frontal zone, between Hvalnes/ Krossanes and Berufjörður.

Several species, which were subordinate in the vegetation west of the frontal zone, became outstanding or even association forming eastwards. Noteworthy are *Ulothrix* species, *Devaleraea ramentacea*, *Palmaria palmata*, *Chordaria flagelliformis*, *Dictysiphon foeniculaceus*, *Petalonia* species, *Scytosiphon lomentaria* and *Acrosiphonia* species (Table 2B).

There was a loss of thirty five species between Hrollaugseyjar and Stokksnes on the western side of the frontal zone, but only 13 species gradually joined the vegetation on its eastern side (Table 2 A).

The number of species versus water temperatures is presented in Fig. 5. A decline in species number with decreasing average water temperatures was obvious, especially regarding the red algae component. At Hrollaugseyjar species of red algae were most numerous, but brown algae became the most numerous group eastwards of the frontal zone.

The delimitation between the typically Atlantic and the subarctic vegetation in southeastern Iceland can be explained by the temperature drop in the area of the frontal zone. A several years lasting westwards extension of cold, low salinity water masses, coinciding with severe ice seasons, obviously caused the floristic and vegetational impoverishment, found already around Stokksnes/ Hafnarnes, where the measured summer temperatures were still relatively high (Table 1) at the time of our field studies. The second, less pronounced boundary east of the frontal zone, separates the atypical, transitional vegetation pattern from the subarctic one, characteristic of the East Icelandic coastal area (MUNDA 1983, 1992 b). The floristic turnover in the eulittoral and upper sublittoral may reflect short-term temperature changes and translocations of the frontal zone, while deep-water crustose corallines indicate, following ADEY (1969), long-term water climate, with temperature minima and maxima as decisive.

Observations revealed, however, that the floristic and vegetational limit found in southeastern Iceland is the most abrupt and pronounced in the entire Northern North Atlantic, reflecting boundary conditions between Atlantic and arctic waters.

REFERENCES

ADEY, W.H. 1969. The distribution of crustose corallines on the Icelandic coast. — Scientia Islandica 1: 16-25.

ADEY, W.H. & STENECK, R.S. 2001. Thermogeography over time creates biogeographic regions: a temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. — Journal of Phycology 37: 677-698.

ALVAREZ, M., GALLARDO, T., RIBERA, M. & GOMEZ-GARETA, A. 1988. A reassessment of the Northern Atlantic seaweed biogeography. — Phycologia 27: 221-233.

BÁEZ, J.C., FEAL, R., VARGAS, J.M. & FLORES-NOYA, A. 2004. A biogeographical analysis of the genera *Audouinella* (Rhodophyta), *Cystoseira* (Phaeophyceae) and *Cladophora* (Chlorophyta) in the western Meditearranean Sea and the Adriatic Sea. — Phycologia 43: 404-415.

BALL, I.R. 1975. Nature and formulation of biogeographic hypothesis. — Systematic Zoology 24: 407-430.

DE BOER, C.J. 1993. Water mass distribution in the Iceland Basin calculated with an optical parameter analysis. — ICES C.M. 1993/ C: 16.

DICKSON, R.R., LAMB, H.H., MALMBERG, S.-A. & COOLENBROOK, J.M 1975. Climate reversal in the northern North Atlantic. — Nature 256: 479-482.

DIETRICH, G. 1964. Oceanic Polar Front survey in the North Atlantic. — In: ODISHAW, H. (ed.). Research in Geophysics, Vol. 2: Solid Earth and Interface Phenomena, pp. 291-308.— MIT Press, Cambridge.

DIETRICH, G. 1969. Atlas of the hydrography of the northern Atlantic Ocean. Based on the Polar Front survey of the International Geographical Year, winter and summer 1958. — International Council for the Exploration of the Sea, Hydrographic Service. Copenhagen. 140 pp.

EINARSSON, T. 1969. The ice in the North Polar Basin and the Greenland Sea and general causes of occasional approach of ice to the coast of Iceland. — Jökull 19: 2-6.

FRAKES, L.A. 1978. Climates throughout geological times. — Elsevier, Amsterdam. 310 pp.

FURNARI, G. 1984. The benthic marine algae of southern Italy. Floristic and geobotanic considerations. — Webbia 38: 349-369.

HANSEN, B. 1985. The circulation of the northern part of the Northeast Atlantic. — Rit Fiskideildar 9: 110-126.

IRVINE, D.E.G. 1974. The marine vegetation of the Shetland Isles. — In: GOODIER, R. (ed.) The natural environment of Shetland, pp. 107-113. — The Nature Conservancy Council, Edinburgh.

IRVINE, D.E.G. 1982. Seaweeds of the Faroes l. The flora. — Bulletin of the British Museum, Natural History (Botany series) 10: 109-131.

JAASUND, E. 1965. Aspects of the marine algal vegetation of North Norway. — Botanica Gothoburgensia 4: 1-174.

JOHANNESSEN, O.M. 1986. Brief overview of the physical oceanography. — In: HURDLE, B.G. (ed.). The Nordic Seas, pp. 103-127.— Springer Verlag, New York.

KAIN, J.M. & NORTON, T. 1990. Marine ecology. — In: COLE, K.M. & SHEATH, R.G. (eds.). Biology of the red algae, pp. 377-422. Cambridge University Press, Cambridge.

KRAUSS, S.W. 1986. The North Atlantic Current. — Journal of Geophysical Research 91: 5061-5074.

KRAUSS, W. 1995. Currents and mixing in the Irminger Sea and in the Iceland Basin. — Journal of Geophysical Research 100: 10851-10871.

LAMB, H.H. 1979. Climatic variations and changes in the wind and ocean circulation. The Little Ice Age in the northeast Atlantic. — Quaternary Research 11: 1-20.

LILLY, G.R. 1968. Some aspects of the ecology of Irish moss *Chondrus crispus* (L.) Stack., in Newfoundland waters. — Fisheries Research Board of Canada. Technical report no. 43: 1-44.

LONGHURST, A. 1998. Ecological geography of the sea. — Academic Press, San Diego. 398 pp.

LUND, S. 1959. The marine algal vegetation of East Greenland. II. Geographical distribution. — Meddelelser om Grønland 156: 1-170.

LÜNING, K. 1990. Seaweeds: their environment, biogeography and ecophysiology. — John Wiley & Sons, Inc., New York. 527 pp .

MACFARLANE, C.I. 1968. *Chondrus crispus* Stackhouse – a synopsis. — Nova Scotia Research Foundation. Seaweed division: 1-47.

MALMBERG, S.-A. 1969. Hydrographic changes in the waters between Iceland and Jan Mayen in the last decade. — Jökull 19: 30-43.

MALMBERG, S.-A. 1972. Annual and seasonal variations in the East Icelandic Current between Iceland and Jan Mayen. — In: KARLSSON, T. (ed.) Sea ice. Proceedings of an International Conference Reykjavík, Iceland.— National Research Council 4: 42-54.

MALMBERG, S.-A. 1984. Hydrographic conditions in the East Icelandic Current and sea ice in the North Icelandic Waters, 1970-1980. — Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 185: 170-178.

MALMBERG, S.-A. 1986. The ecological impact of the East Greenland Current on the North Icelandic waters. — NATO ASI series, Vol G7: 389-404.

MALMBERG, S.-A. & KRISTMANNSSON, S.S. 1992. Hydrographic conditions in Icelandic water 1980-1989. — ICES Marine Science Symposia 195: 76-92.

MALMBERG, S.-A. & STEFÁNSSON, U. 1972. Recent changes in the water masses of the East Icelandic Current. — Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 162: 185-200.

MANN, K.H. & LAZIER, J.R.N. 1991. Dynamics of marine ecosystems. Biological-physical interactions in the oceans. — Blackwell Science Publishing, New York. 470 pp.

MATHIESEN, A.C., DAVES, C.J. & HUMM, H.J. 1969. Contributions to the marine algae of Newfoundland. — Rhodora 71: 110-159.

MCCOY, E.D., BELL, S.S. & WALTERS K. 1986. Identifying biotic boundaries along environmental gradients. — Ecology 67: 749-759.

MICHANEK, G. 1979. Phytogeographic provinces and seaweed distribution. — Botanica Marina 22: 375-391.

MUNDA, I.M. 1975. Hydrographically conditioned floristic and vegetation limits in Icelandic coastal waters. — Botanica Marina 18: 223-235.
MUNDA, I.M. 1976a. Some aspects of the benthic algal vegetation of the South Icelandic coastal area. — Research Institute Neðri Ás, Hveragerði, Iceland. Bulletin 25: 1-69.
MUNDA, I.M. 1976b. The distribution of the *Halosaccion ramentaceum* (L.) J. Ag. associations in the Icelandic coastal area and their hydrographically conditioned variations. — Botanica Marina 19: 179-162.
MUNDA, I.M. 1977. The structure and distribution of the *Gigartina stellata* (Stackh.) Batters and *Chondrus crispus* Stackh. associations in Icelandic waters. — Botanica Marina 20: 291-302.
MUNDA, I.M. 1978. Survey of the benthic algal vegetation of the Dýrafjördur, Northwest Iceland. — Nova Hedwigia 2: 281-402.
MUNDA, I.M. 1983. Survey of the benthic algal vegetation of the Reydarfjördur as a typical example of the East Icelandic vegetation pattern. — Nova Hedwigia 37: 545-640.
MUNDA, I.M. 1987. Characteristic features of the benthic algal vegetation along the Snaefellsnes Peninsula (Southwest Iceland). — Nova Hedwigia 44: 399-448.
MUNDA, I.M. 1992a. Hornstrandir – a conspicuous area of vegetation shift in the extreme northwest of Iceland. — Acta Botanica Islandica 11: 17-88.
MUNDA, I.M. 1992b. The gradient of the benthic algal vegetation along the eastern Icelandic coast. — Acta Phytogeographica Suecica 78: 131-141.
MUNDA, I.M. 1992c. Gradient of the seaweed vegetation along the North Icelandic coast, related to hydrographic conditions. — Hydrobiologia 242: 133-147.
MUNDA, I.M. 1999a. The bentic algal vegetation of land-locked fjords in southeastern Iceland. — Hydrobiologia 393: 169-180.
MUNDA, I.M. 1999b. Survey of the benthic algal vegetation of the Berufjördur, southeastern Iceland. — Nova Hedwigia 69: 473-516.
PEDERSEN, P.M. 1976. Marine benthic algae from southernmost Greenland. — Meddelelser om Grønland 199: 1-80.
PRICE, J.H. & FARNHAM, W.F. 1982. Seaweeds of the Faroes 3. Open shores. — Bulletin of the British Museum, Natural History (Botany series) 10: 153-225.
PRUD'HOMME VAN REINE, W.F. & VAN DEN HOEK, C. 1990. Biogeography of Macaronesian seaweeds. — Courier Forschungsinstitut Senckenberg 129: 55-73.
RIBERA, M.A & BOUDERESQUE, F. 1995. Introduced marine plants with special reference to macroalgae. Mechanisms and impact. — In: ROUND, F.E. & CHAPMAN, D.J. (eds.). Progress in phycological research, pp. 187-268.— Biopress, London.
SCHILS, T. & WILSON, S.C. 2006. Temperature threshold as a biogeographic barrier in northern Indian Ocean macroalgae. — Journal of Phycology 42: 749-757.
SETCHELL, V.A. 1920. The temperature interval in geographical distribution of marine algae. — Science 45: 197-204.
SIGTRYGGSSON, H. 1972. An outline of sea-ice conditions in the vicinity of Iceland — Jökull 22: 1-11.
STEFÁNSSON, U. 1962. North Icelandic waters. — Rit Fiskideildar 1: 1-269.
STEFÁNSSON, U. 1969. Sjávarhiti á siglingaleið umhverfis Ísland. — In: EINARSSON, M.Á. (ed.). Hafísinn, pp. 131-149.— Almenna bókafélagið, Reykjavík.

STEFÁNSSON, U. 1972. Near-shore fluctuations of the frontal zone southeast of Iceland. —Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 162: 201-205.

SUNDENE, O. 1953. The algal vegetation of the Oslofjord. — Norske Videnskaps-Akademi i Oslo. Skrifter. I. Matematisk-Naturvitenskapelige Klasse 2: 1-244.

SWIFT, J.H. & AAGARD, K. 1981. Seasonal transitions and water mass formation in the Iceland and Greenland Seas. — Deep-Sea Research A 28: 1107-1129.

VALDIMARSSON, H. & MALMBERG S.-A. 1999. Near surface circulations in Icelandic waters derived from satellite tracked drifters. — Rit Fiskideildar 16: 23-39.

VAN AKEN, H.M. 1993. Current measurements in the Iceland Basin. — ICES C.M. 1993/ C : 11.

VAN AKEN, H.M., QUADFASEL, D. & WARPAKOWSKI, A. 1991. The Arctic Front in the Greenland Sea during February 1989: Hydrographic and biological observation. — Journal of Geophysical Research 96: 4739-4750.

VAN DEN HOEK, C. 1975. Phytogeographic provinces along the coasts of the northern Atlantic Ocean. — Phycologia 14: 317-330.

VAN DEN HOEK, C. 1982a. Phytogeographic distribution groups of benthic marine algae in the North Atlantic Ocean. — Helgoländer wissenschaftliche Meeresuntersuchungen 35: 153-214.

VAN DEN HOEK, C. 1982b. The distribution of benthic marine algae in relation to the temperature regulation of their life histories. — Biological Journal of the Linnean Society 18: 81-144.

VAN DEN HOEK, C. 1984. World-wide longitudinal and latitudinal seaweed distribution patterns and their possible causes as illustrated by the distribution of Rhodophytan genera. — Helgoländer wissenschaftliche Meeresuntersuchungen 38: 227-257.

VAN DEN HOEK, C. & DONZE, M. 1967. Algal phytogeography of the European Atlantic coast. — Blumea 15: 63-89.

VAN DEN HOEK, C., BREEMAN, A.M. & STAMM, W.T. 1990. The geographic distribution of seaweed species in relation to temperature: present and past. — In: BEUKEMA, J.J., WOLF, W.J. & BROUNS, J.J.W.M. (eds.). Expected effects of climatic change on marine coastal ecosystems, pp. 55-67.— Kluwer Academic Publishers, Dordrecht.

WILCE, R.T. 1959. The marine algae of the Labrador Peninsula and northwest Newfoundland (ecology and distribution). — Bulletin of the National Museum of Canada 158: 1-103.

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