ACTA BOT. ISL. 14: 103-159, 2004

The Structure and Distribution of Fucacean Associations in the Icelandic Coastal Area

Ivka Maria Munda

Centre of Scientific Research, Slovene Academy of Science and Arts,

Novi trg. 2, Sl 1000 Ljubljana, Slovenia

ABSTRACT: The structure, floristic composition, local and regional distribution of Fucacean associations in the Icelandic coastal area is described on the basis of field studies. Attention was paid to the stratification, floristic composition and biomass of the fucoid settlements, as well as their zonal position in dependence on the inclination and exposure of the eulittoral slopes. Within the fjords and in local estuaries the influence of the salinity factor was also observed. The regional distribution around Iceland is likely a function of the varying hydrographic conditions around the coast, causing pronounced floristic and vegetational discontinuities along boundary areas between different water masses.The high-level fucoid *Pelvetia canaliculata* is limited to the South and Southwest of Iceland, and the low-level *Fucus serratus* only to some spots along the southern coast. *Fucus vesiculosus*, *Ascophyllum nodosum* and *Fucus distichus* (sensu Powell) exhibit an overall distributional pattern around the coast, while *Fucus spiralis* is more frequent and prolific in the South and Southwest than in the rest of the area.

KEYWORDS: Fucacean associations, Icelandic coast, regional distribution, zonation, floristic composition, stratification, biomass

INTRODUCTION

Dense eulittoral settlements of fucoids are characteristic of boreal shores on both sides of the Atlantic. They form conspicuous associations and are usually zoned along environmental gradients, corresponding to their physiological responses to desiccation and interactions with other organisms (cf. DRING & BROWN 1982). Rocky shores represent, however, a physiological gradient with optimum conditions for benthic algae in the lowermost eulittoral, and stressful ones at its terrestrial end (BÉRARD-THERRIAULT & CARDINAL 1973, SCHONBECK & NORTON 1978, 1979, 1980, DAVIDSON & PEARSON 1996). Along the shores of the North European mainland as well as the British Isles, Shetland, Orkneys and the Faeroes, the distributional pattern of the fucoid associations is rather uniform (e.g. PRINTZ 1926, GIBB 1950, SUNDENE 1953, JORDE & KLAVESTAD 1963, JAASUND 1965, PRICE &

FARNHAM 1982, TITTLEY et al. 1982, RUSSEL 1974). Around Iceland, which has a central position in the northern North Atlantic, and is surrounded by water masses of widely different origins and characters (STEFÁNSSON 1962, 1972, MALMBERG 1984, 1985, MALMBERG & KRISTMANSSON 1992) their distribution proved to be uneven.

The high-level fucoid *Pelvetia canaliculata* (Gmel.) Decn. et Thur. is association-forming in the South and Southwest of Iceland. It has, however, its transatlantic distributional limit here. The second high-level association of *Fucus spiralis* L. occurs lower down the eulittoral than *Pelvetia*. It is most prolific and widespread in the South and Southwest, and subordinate in the vegetation elsewhere in Iceland. *Fucus serratus* L. forms the lowermost Fucacean association and has a scattered distribution along the South Icelandic coastal area: on the Vestmann Islands, around the Reykjanes Peninsula, reaching as far north as to Reykjavík. This Fucacean association has a discontinuous distribution throughout the North Atlantic, being common along the North European mainland, and the British Isles, but absent at the Faeroes. It reappears again in the Canadian Maritime Provinces. *Fucus vesiculosus* L. is, on the other hand, common and widespread all around Iceland. Its association occurs in several variants, dependent on the degree of exposure, salinity conditions and competition with other fucoids. In low-salinity areas it is usually codominant with *Fucus ceranoides* L. The latter forms an association also for itself in innermost fjord areas and local estuaries, penetrating into fresh water.

Ascophyllum nodosum (L.) Le Jol. is association-forming in the mid eulittoral of semi-exposed rocky sites all around Iceland, first of all in middle fjord areas. Its maximum frequency and widest extension of its stands was found in the South and Southwest, while it is relatively rare in the North and East. *Fucus evanescens* C. Ag. and *Fucus distichus* L. (sensu RICE & CHAPMAN 1985) are best represented in the North and East. The four subspecies of *Fucus distichus* L. emend. Powell form, however, distinct associations which are spatially separated and differ in their floristic composition, physiognomy and zonal position. For this reason it seemed appropriate to retain Powell's concepts in the present ecologically descriptive contribution (POWELL 1957a, b, 1963) in spite of later numerical/ morphometric analyses within the *Fucus distichus* complex (RICE & CHAPMAN 1985, RICE et al. 1985). In the present context the reduction of four taxa into two could be misleading. Studies of MCLACHLAN et al. (1971), MCLACHLAN (1974), SIDEMAN & MATHIESON (1983a, b, 1985) indicated that differences between the four subspecies are genetically based. These authors accepted them as ecotypes.

In northern and eastern Iceland, where *Pelvetia canaliculata* is absent and *Fucus spiralis* rare, *Fucus distichus* ssp. *anceps* occupies the upper eulittoral of highly exposed rocky sites, while *Fucus distichus* ssp. *distichus* covers tide pools of different eulittoral levels.

It is noteworthy that associations of *Halidrys siliquosa* (L.) Lyngb. and *Himanthalia elongata* (L.) Gray, still found on the Faeroes, do not extend as far as to Iceland.

Studies of the Icelandic Fucacean associations are based on field observations and collections during consecutive years between 1963 and 1980. Scattered data were included into vegetational surveys of Icelandic fjords (MUNDA 1978, 1980, 1983, 1994, 1997, 1999a, b), and open coast-lines (MUNDA 1976a, 1977a, 1985, 1987, 1992a, b). The present paper presents, on the other hand, a general overview about their regional and zonal distribution, floristic composition, ecological implications, structure and biomass, while previous informations were given by JÓNSSON (1910, 1912). Later a quantitative study was carried out by HANSEN & INGÓLFSSON (1993) in the eastern fjords.

METHODS

The benthic algal vegetation of different areas around the Icelandic coast was studied along vertical transects, from the level of the littoral fringe / or terrestrial level to the upper sublittoral. Attention was paid to the zonation patterns, stratification of the algal settlements and their floristic composition. Regarding the Fucacean associations their vertical and horizontal distribution was followed within the fjords and along open shores. The implications of salinity, degree of exposure, configuration of the coastal slopes and of the neighbouring vegetation were considered. Most Fucacean associations are four-layered, comprising the undergrowth, companions species, the dominant species and its epiphytes.

The number of species within these strata is presented. Species composition and estimates of their relative abundance are based on qualitative field observations and collections. The same scale as in previous contributions was used (e.g. Munda 1976b, l977b): M- abundant, A-relatively abundant, R-rare, RR-very rare, S-single specimens. In the floristic lists for the individual associations all the species are named, although there are regional differences in their occurrence within the strata. These differences in floristic composition of the Fucacean associations are presented separately in the Table I.

Some quantitative estimates of the fresh weight biomass were carried out simultaneously with algal samplings. 1/4 and 1/8 m^2 frames were used, within which the algal growth was harvested and weighted. The biomass data refer only to the dominant fucoids, and represent averages of 5 to 10 parallel measurements. They are expressed as g/m^2 of fresh weight.

Field studies were carried out in different areas of the Icelandic coast during consecutive years, between 1963 and 1981. They refer to summer and autumn months, viz. July/August to October.

THE STUDY AREAS

The coastal areas investigated around Iceland are signed on the map (Fig. 1). In southern Iceland, which is prevailingly a sandy desert, bare of algal vegetation,

the coast-line between the rivers Ölfusá and Thjórsá was studied in detail, as well as the Reykjanes Peninsula and the Vestmann Islands. Between the two big southern rivers, there are wide, moderately sloping lava rocks, which offer support to extensive eulittoral Fucacean fields, as the most obvious physiognomic feature of this area. The Reykjanes Peninsula is formed by compact, locally steep lava rocks and is exposed to strongest surf. Depending on the shore topography, a whole spectrum of intertidal habitats can be found along the same transects and, as a consequence, a wide variety of zonation patterns. The South Icelandic coast is influenced by the inflowing NE Atlantic water masses. The maximum yearly temperature averages are found in the middle of the South Icelandic coast, with minimal seasonal amplitudes, and a temperature decrease westwards, towards Reykjanes (MALMBERG 1962, STEFÁNSSON 1962, 1969). In the Southwest of Iceland, within the Faxa Bay, three widely different areas were studied: Borgarfjörður as an example of an Atlantic-water influenced fjord, with a considerable freshwater influx; the open sandy-muddy Mýrar area, which is split into small islets and skerries; and the Snæfellsnes Peninsula, deviding the Faxa Bay from Breiðafjörður. The greater part of this peninsula, which has a central position in western Iceland, belongs to the basaltic Plateau, and is built of Tertiary flood basalts, which underly Pleistocene rocks. Snæfellsjökull is a recent volcano, and the coastal slopes around it are a complex mixture of lavas of Pleistocene and Holocene origin (THORODDSEN 1891, ÁSKELSSON 1938, SIGURÐSSON

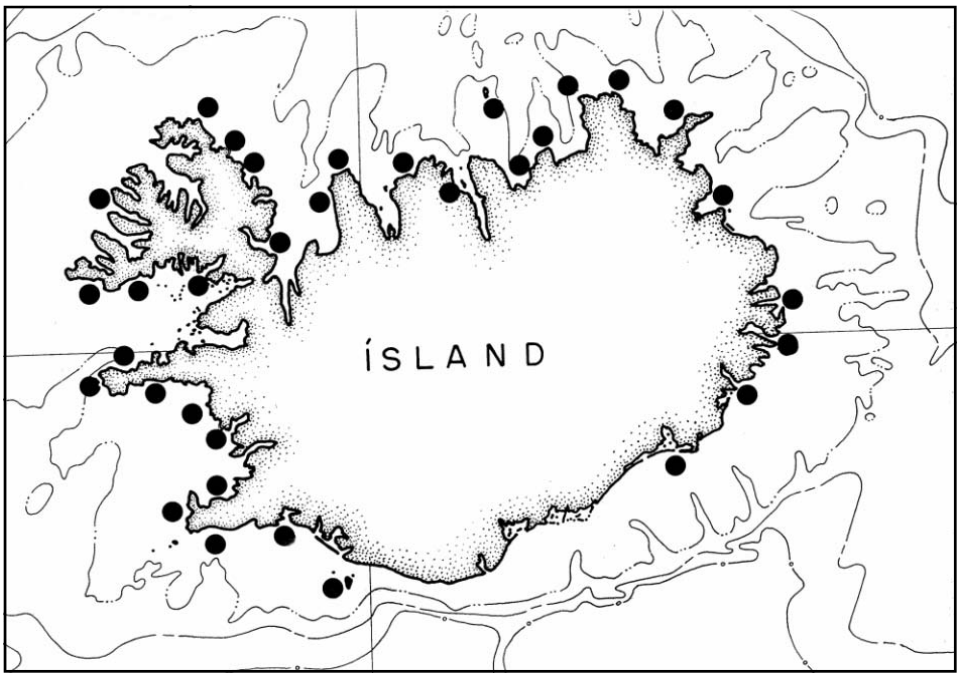

FIGURE 1. Map of Iceland with the investigated areas.

1966). Both, the geological structure and hydrographic position of the Snæfellsnes Peninsula profoundly influence the benthic algal vegetation, which is an intermediate between the warm boreal of southern Iceland, and the cold boreal one, found farther northwards along the NW peninsula, up to Hornbjarg.

In the Northwest of Iceland there are two major areas, which differ regarding the exposure conditions, hydrographic parameters and substrate configurations. The Barðaströnd coast faces Breiðafjörður and is relatively protected, with wide sandy extenses in between rocky formations. The eastern Barðaströnd coast was studied on the line from Reykhólar to Þorskafjörður. Here there are flat and and wide eulittoral rocky surfaces, covered by extensive Fucacean fields, like in the South. The western Barðaströnd coast, observed between Siglunes and Rauðadalur, is prevailingly sandy, with rocky formations in between. Sandy and rocky slopes can follow each other also along the same vertical transects.

The second major area of the northwestern peninsula is turned seawards, and is totally exposed to oceanic conditions. It is split into numerous long and narrow fjords, which follow almost regular tectonic lines and were formed in the

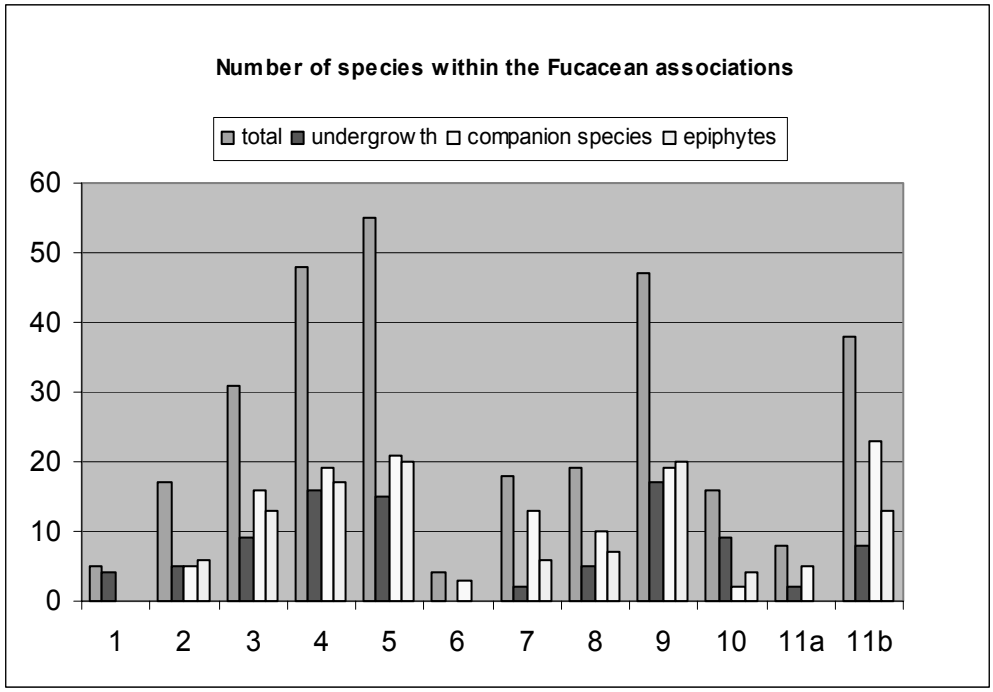

FIGURE 2. Number of species within the Fucacean associations. Associations: 1 - *Pelvetia canaliculata.* 2 - *Fucus spiralis.* 3 - *Fucus vesiculosus.* 4 - *Ascophyllum nodosum.* 5 - *Fucus serratus.* 6 - *Fucus ceranoides.* 7 - *Fucus vesiculosus — Fucus ceranoides.* 8 - *Fucus distichus* ssp. *evanescens.* 9 - *Fucus distichus* ssp. *edentatus.* 10 - *Fucus distichus* ssp. *anceps.* 11 - *Fucus distichus* ssp. *distichus,* A - uppermost pools, B - lower pools.

past by ice erosion and sinking of the sea floor. Here sporadic observations were carried out within the fjords and along open coast-lines between them. Only Dýrafjörður was studied in detail from the innermost estuary and outwards. Attention was paid to the gradual formation of fucoid belts along the fjord coast in dependence on salinity and exposure conditions (MUNDA l978). The north-western peninsula is still under the influence of warm Atlantic water, carried northwards by the Irminger Current. In the extreme Northwest, around Hornbjarg, conspicuous hydrographic changes profoundly influence the benthic algal vegetation (MUNDA 1975, 1992a). These vegetational changes were studied along the heavily exposed Hornstrandir coast. The entire north Icelandic coastal area, between Hornbjarg in the west, and Melrakkaslétta in the east, was studied only along open shores, such as Skagaströnd, Fljót outside Skagafjörður, Ólafsfjörður, the Tjörnes Peninsula, Melrakkaslétta and the island of Grímsey. The only fjord investigated here was Steingrímsfjörður in the Húnaflóa Bay (MUNDA 1992b, 1997).

The north Icelandic coast is, however, a mixing area of different primary and secondary water masses, with a gradual cooling in the eastwards direction (STEFÁNSSON 1962, 1969). Its benthic algal vegetation shows affinities to the sub-arctic one of eastern Iceland, also regarding the Fucacean associations.

Eastern Iceland is influenced by cold water masses of arctic origin, carried by the East Icelandic Current. It enters the Icelandic coastal area north of Melrakkaslétta and Langanes, and meets warm Atlantic water in the Southeast (STEFÁNSSON 1972, MALMBERG & STEFÁNSSON 1972, MALMBERG l984). The sub-arctic vegetation of eastern Iceland was studied mainly within the fjords, such as Mjóifjörður, Reyðarfjörður, Berufjörður, and land-locked fjords in the Southeast (MUNDA 1983, 1992 c, 1994, 1999 a, b).

FUCACEAN ASSOCIATIONS

PELVETIA CANALICULATA

Regional distribution

This high-level Fucacean association is most luxuriant in the South of Iceland in the rocky upper eulittoral. It is frequent along the coast-line between the rivers Ölfusá and Þjórsá, around the Reykjanes Peninsula, on the Vestmann islands, in Vík í Mýrdal, and was also found on the little island of Hrollaugseyjar in the Southeast. In the Southwest its distribution is rather scattered. It was found in the outer areas of Hvalfjörður and Borgarfjörður. Along the sandy-muddy Mýrar area it has a patchy distribution on the small islets and skerries, but is again rather frequent around the Snæfellsnes Peninsula, where it covers sheltered sides of rocky formations and boulders. It is still present on some of the Breiðafjörður islands, but not as far north as the Barðaströnd coast. The density and vertical extension of the *Pelvetia canaliculata* association declines in the

northwards direction. Its regional distribution limits correspond, however, with those of the *Chondrus crispus* association (MUNDA 1977 b) and are tentatively temperature-conditioned.

Zonal position

Pelvetia canaliculata occupies sheltered rocky slopes in the uppermost eulittoral, the level of the littoral fringe and penetrates locally into the terrestrial level. The association is dense and prolific in the upper eulittoral, where 5 to 12 cm long plants are usual. The density of the settlements and the size of the dominant fucoid declines towards the uppermost eulittoral. At the level of the littoral fringe *Pelvetia* plants are up to 4 cm long, whereas at the terrestrial level extremely reduced, 1 to 2 cm long specimens are found scattered at the edges of bogs and among grass meadows (cf. RUGG & NORTON 1987). The association is usually followed lower down the eulittoral by *Fucus spiralis*.

Structure and composition

The *Pelvetia canaliculata* association is floristically poor and usually only two-layered. Only exceptionally *Ectocarpus fasciculatus* is found in the epiphytic cover of the dominant fucoid. As mentioned, the highest density of the association was found in the upper eulittoral, whereas at the level of the littoral fringe and at the terrestrial level, the association has a scattered appearence.

Upper eulittoral

I stratum (undergrowth):	*Ulothrix* spp.	M
	Urospora penicilliformis	M
	Blidingia minima	A
	Enteromorpha intestinalis	R
II stratum (companion species):	-	
III stratum (dominant):	*Pelvetia canaliculata*, dense growth	
IV stratum (epiphytes):	*Ectocarpus fasciculatus*	S

Littoral fringe

I stratum (undergrowth):	*Ulothrix* spp.	A
	Rhizoclonium tortuosum	R
II stratum (companion species)	-	
III stratum (dominant):	*Pelvetia canaliculata*, scattered growth of small plants	

Terrestrial level

I stratum (undergrowth):	*Rhizoclonium tortuosum*	A
	Prasiola stipitata	R

III stratum (dominant):	*Pelvetia canaliculata*, single, dwarf plants, scattered growth

FUCUS SPIRALIS

Regional distribution

This Fucacean association is distributed all around the Icelandic coast, and is most prolific, with the widest vertical extension, in the South and Southwest (especially around the Reykjanes Peninsula). Its vertical extension is notably reduced in the Northwest, where it still forms continuous, narrow belts on moderately exposed rocks. In the North and East of Iceland it is subordinate in the vegetation and exhibits a patchy distribution, being mostly replaced by other high-level associations. Similar conditions were reported for the Norwegian coast, where it is prolific in the West (JORDE & KLAVESTAD 1963), and present only as narrow belts farther north (PRINTZ 1926, JAASUND 1965). In the fjords *Fucus spiralis* usually joins the vegetation in their middle areas, farther out from the innermost estuaries than *Fucus vesiculosus* and *Ascophyllum nodosum*. In outer fjord areas it is subordinate or absent, found only in the shelter of protruding rocks and boulders, or as fringing high-level tide pools, colonized by *Enteromorpha* species. Like in northern Norway (JAASUND 1965) it reappears on highly exposed rocky slopes of open coast-lines.

Zonal position

Fucus spiralis forms a high-level association in sheltered or semi-exposed rocky sites. In the South and Southwest its zonal position is between *Pelvetia canaliculata* and *Fucus vesiculosus*, while in the rest of the Icelandic coastal area it follows lower down than belts of either *Porphyra umbilicalis*, *Ulothrix* spp.-*Urospora penicilliformis*, *Blidingia* species or *Enteromorpha intestinalis*. In eastern Iceland it is, on the other hand, frequently situated below a mixed association of dwarf brown and green algae (*Petalonia filiformis*, dwarf *Scytosiphon lomentaria*, *Isthmoplea sphaerophora*, dwarf *Pylaiella littoralis*, *Blidingia* species). Lower down the eulittoral follow either *Fucus vesiculosus* or *Ascophyllum nodosum*. In highly exposed rocky sites in the East it is locally found above the *Fucus distichus* ssp. *anceps* association.

Structure and composition

The association is floristically poor and occasionally only two-layered. In its undergrowth there are intruders from other high-level associations together with crustose floristic elements.

I stratum (undergrowth):	*Hildenbrandia rubra*	M
	Phymatolithon lenormandii	R
	Ralfsia verrucosa	M
	Ulothrix spp.	A

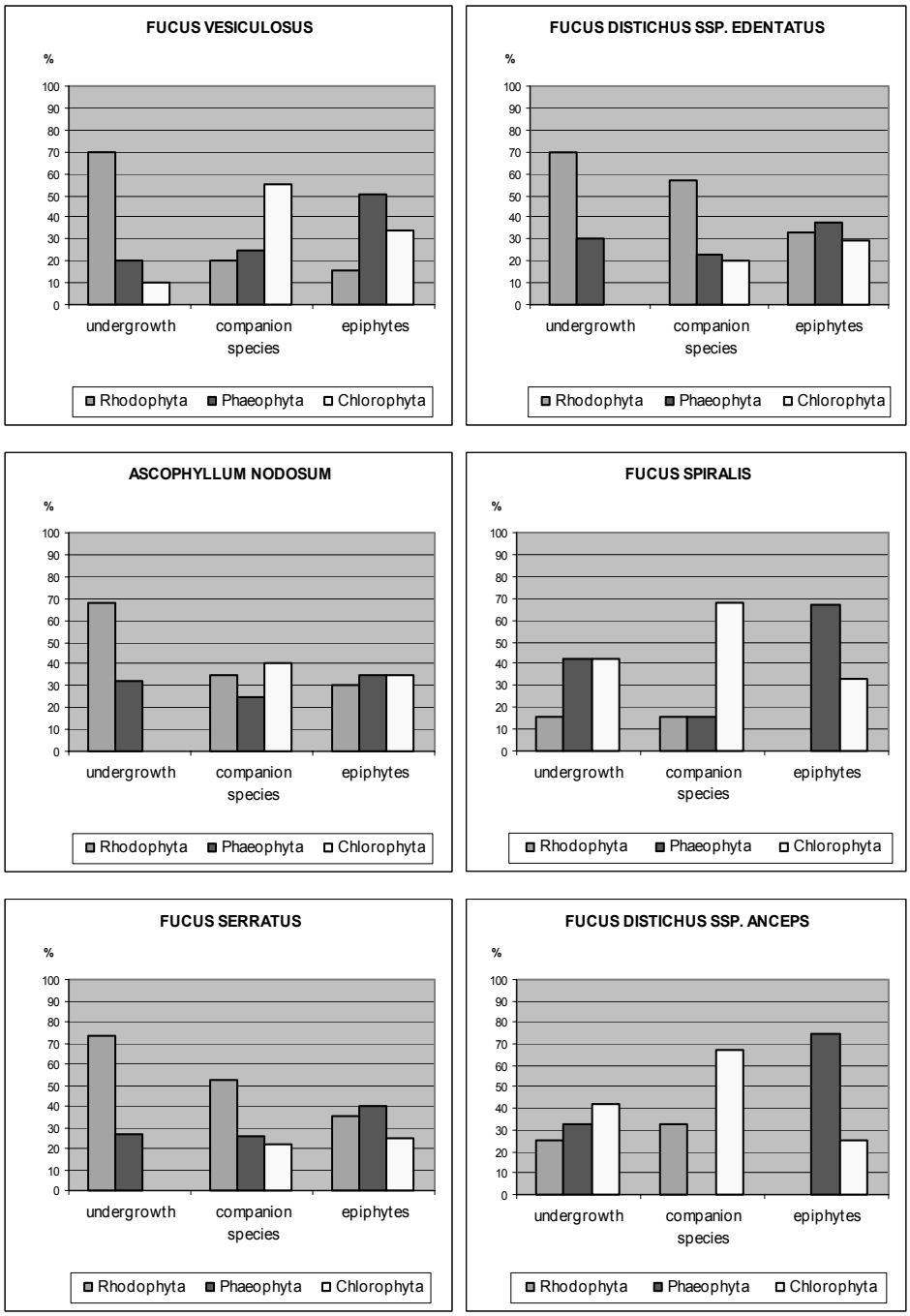

FIGURE 3. Percentage floristic composition of Fucacean associations.

	Urospora penicilliformis	A
	Blidingia minima	R
in the North and East also:	*Petalonia filiformis*	A
	Pylaiella littoralis	R
	dwarf *Scytosiphon lomentaria*	R
	Isthmoplea sphaerophora	RR
	Blidingia marginata	R
	Blidingia chadefaudii	RR
II stratum (companion species):	*Porphyra umbilicalis*	R
	Pylaiella littoralis	A
	Ulva lactuca	R
	Enteromorpha intestinalis	R
	Enteromorpha clathrata	RR
	Enteromorpha prolifera	R
III stratum (dominant):	*Fucus spiralis*	
IV stratum (epiphytes):	*Elachista fucicola*	R
	Ectocarpus fasciculatus	A
	Ectocarpus siliculosus	R
	Spongonema tomentosum	R
	Spongomorpha aeruginosa	R
	Enteromorpha spp.	A

FUCUS VESICULOSUS

Regional distribution

This association is common and widespread all around Iceland, occupying a whole range of habitats. It occurs in several variants, dependent on salinity and exposure conditions, the inclination of the substrata as well as neighbouring vegetation. On gently sloping rocky surfaces in the South and Southwest it occupies wide surfaces, and the dominant species is mostly represented as f. *sphaerocarpa* J. Ag. Wide *Fucus vesiculosus* fields are likewise common in middle areas of most Icelandic fjords. In inner fjord areas the association appears already in the oligohalinikum, where it has a patchy distribution, sometimes together with *Fucus ceranoides*. Its further distribution along the fjord coasts is controlled by salinity conditions. In eastern Iceland *Fucus vesiculosus* occurs mostly in narrow belts. There f. *vadorum* Aresch. dominates over f. *sphaerocarpa*, along with several intermediate forms, while in exposed habitats the var. *evesiculosus* Cotton is usual.

Zonal position

The *Fucus vesiculosus* association belongs to the mid-eulittoral. It is usually situated below *Fucus spiralis* or other high-level belts, such as *Porphyra umbilicalis*, *Ulothrix* spp., *Blidingia minima* or *Enteromorpha intestinalis*. Exceptionally the

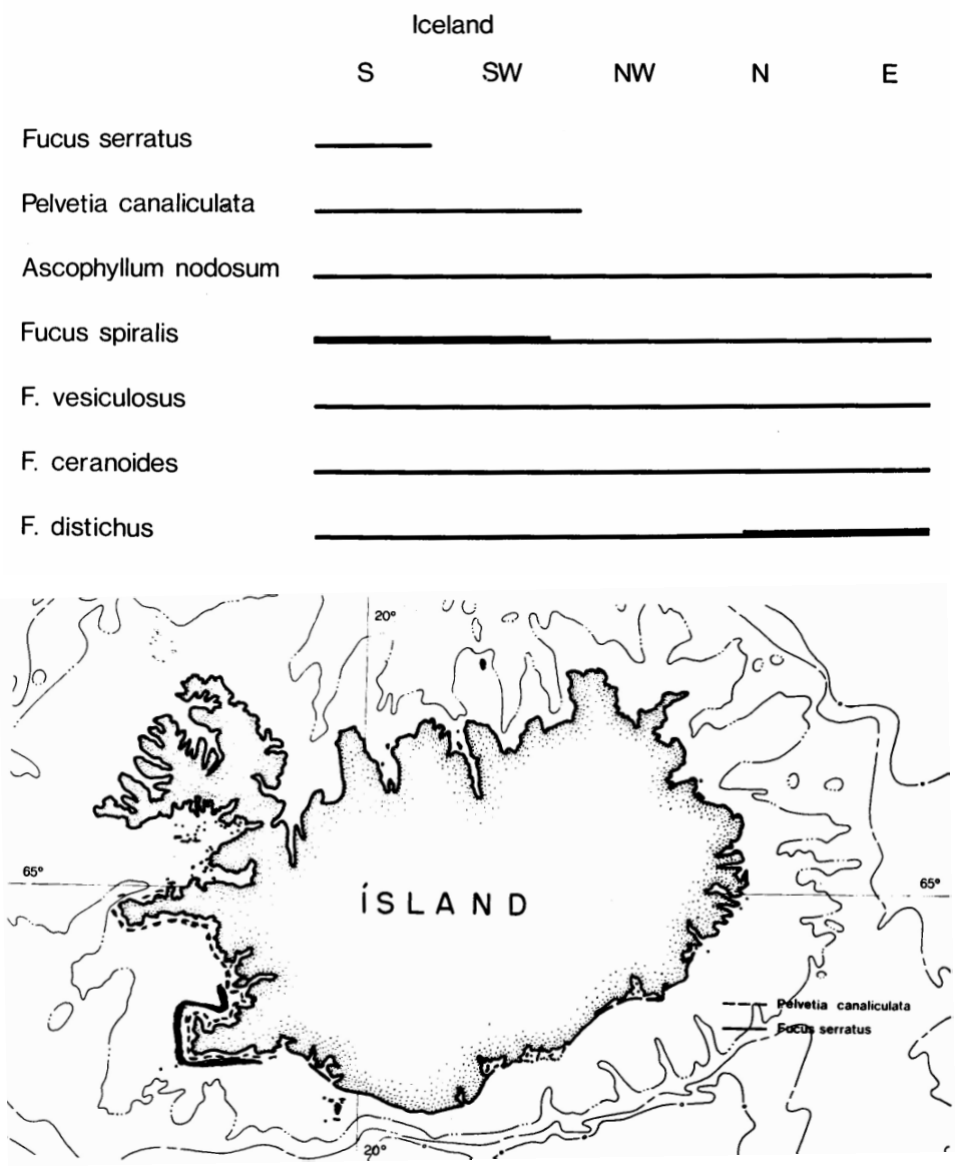

FIGURE 4. Distribution of Fucacean Associations in Iceland.

eulittoral vegetation starts immediately with *Fucus vesiculosus*. Downwards this association limits to *Ascophyllum nodosum* or *Fucus distichus* ssp. *edentatus*/ or *evanescens*. It may even overlap with these associations. In estuarine habitats it touches downwards a mixed association of diverse brown and green filamentous algae (cf MUNDA 1978, 1983).

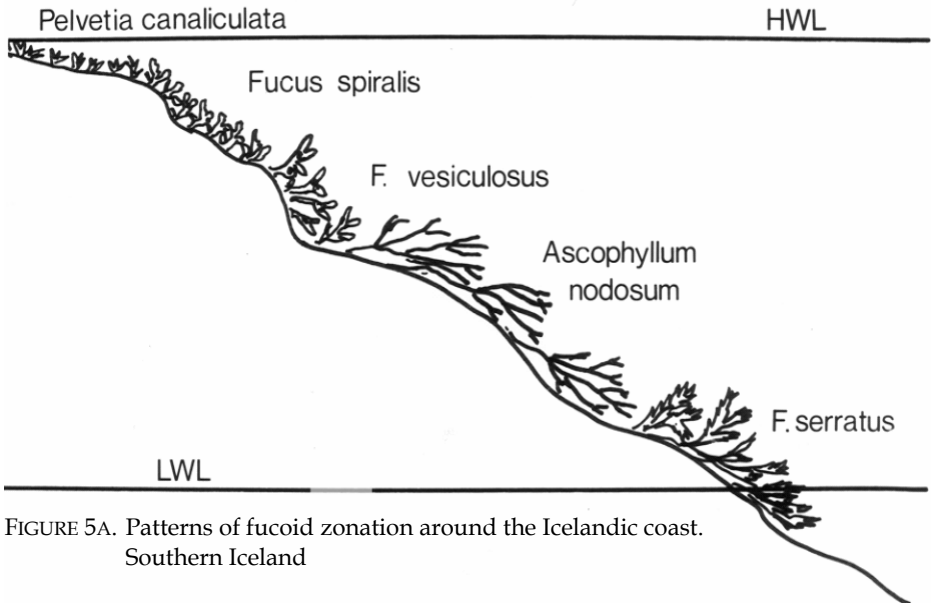

FIGURE 5A. Patterns of fucoid zonation around the Icelandic coast. Southern Iceland

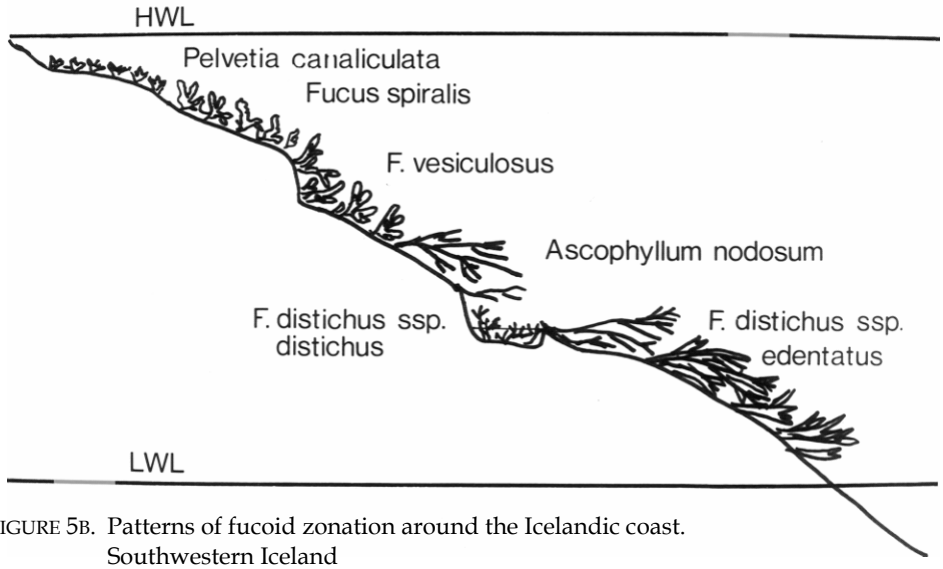

FIGURE 5B. Patterns of fucoid zonation around the Icelandic coast. Southwestern Iceland

Structure and composition

This association is floristically richer than the two high-level ones, and usually four-layered. Its undergrowth, companion species and epiphytes vary greatly as responses to the regional ecology, as well as to local conditions. A conspicuous difference in floristic composition within all the strata is found in dependence on

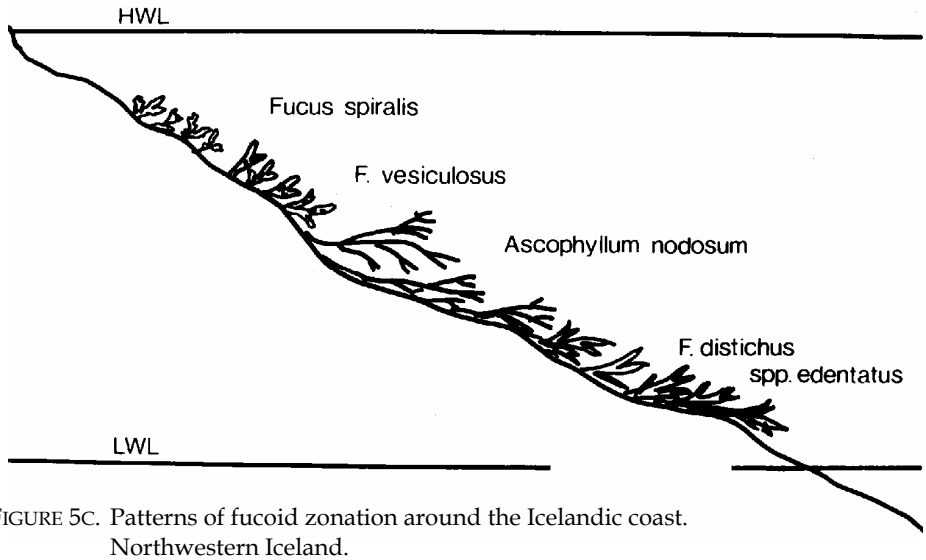

FIGURE 5C. Patterns of fucoid zonation around the Icelandic coast. Northwestern Iceland.

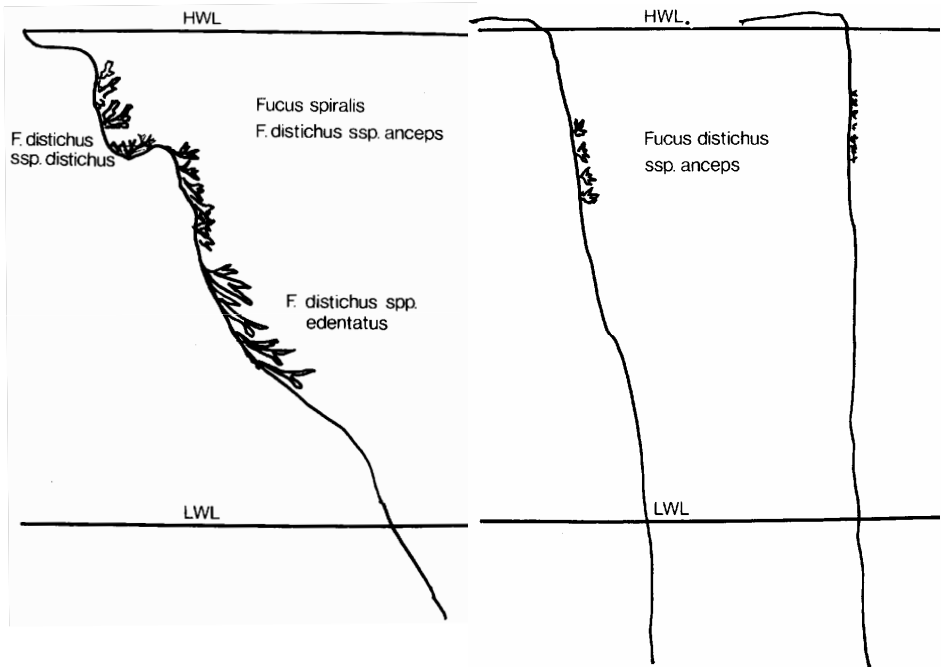

FIGURE 5D and E. Patterns of fucoid zonation around the Icelandic coast.
d: Northern and eastern Iceland.
e: Northern and eastern Iceland — highly exposed sites.

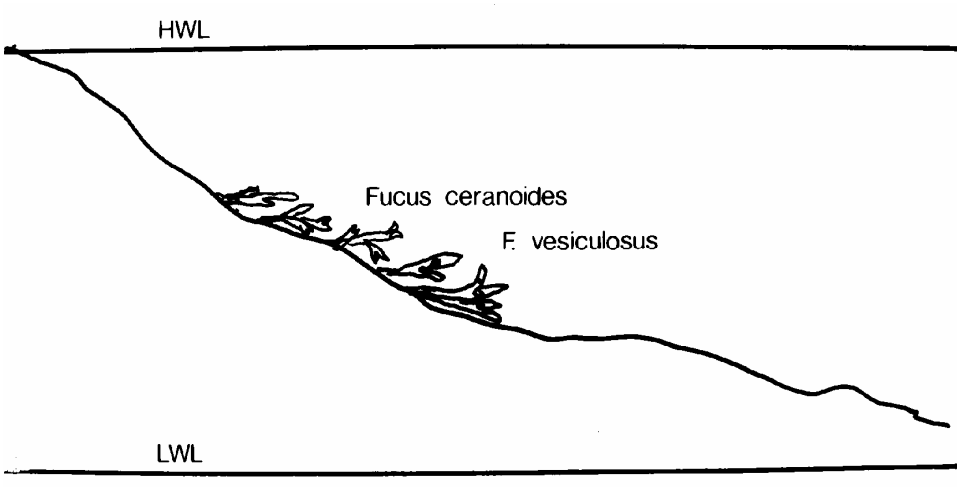

FIGURE 5F. Patterns of fucoid zonation around the Icelandic coasts. Estuaries.

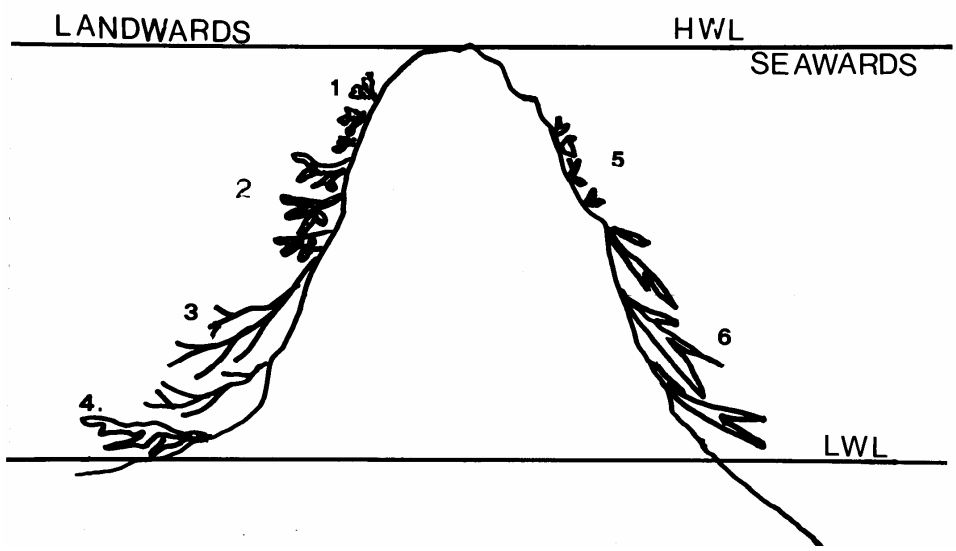

Figure 6. Patterns of fucoid zonation on seawards and landwards sides of rocky formations within the fjords: 1: *Fucus spiralis*. 2: *Fucus vesiculosus*. 3: *Ascophyllum nodosum*. 4: *Fucus distichus* ssp. *evanescens*. 5: *Fucus distichus* ssp. *anceps*. 6: *Fucus distichus* ssp. *edentatus*.

hydrographic conditions, viz. Atlantic-water ones up to Hornbjarg on the one side, and subarctic ones on the other, along with intermediate conditions in the

North. As it was mentioned, the extreme Northwest of Iceland represents a sharp floristic and vegetational limit, conditioned by hydrographic discontinuities in this area (MUNDA 1975, 1992a).

In the fjords a salinity-dependent gradient in floristic composition was obvious, from the head of the fjord and outwards, along with a morphocline of the dominant species. Green algae dominate within the association in the inner fjord areas.

Average floristic composition around Iceland:

I stratum (undergrowth):	*Hildenbrandia rubra*	M
	Phymatolithon lenormandii	A
	Phymatolithon polymorphum	R
	Phymatolithon laevigatum	RR
	Clathromorphum circumscriptum	A
	Rhodochorton purpureum	R
	Polysiphonia stricta	AA
	Ralfsia verrucosa	M
	Sphacelaria radicans (on sand-covered rocks)	R
	Acrosiphonia sp.	RR
II stratum (companion species):	*Ceramium nodulosum*	A
	Ceramium areschougii	A
	Porphyra purpurea	R
	Porphyra abyssicola	RR
	Pylaiella littoralis	M
	Ectocarpus siliculosus	M
	Dictyosiphon foeniculaceus	R
	Spongonema tomentosum	R
	Ulva lactuca	A
	Monostroma grevillei	R
	Monostroma undulatum	RR
	Enteromorpha intestinalis	M
	Enteromorpha prolifera	A
	Enteromorpha compressa	R
	Enteromorpha clathrata	RR
	Cladophora rupestris	R
	Spongomorpha aeruginosa	RR
	Acrosiphonia grandis	A
	Acrosiphonia arcta	R
III stratum (dominant);	*Fucus vesiculosus* f. *sphaerocarpa*, f. *vadorum*, var. *evesiculosus*, intermediate estuarine forms	
IV stratum (epiphytes):	*Ceramium nodulosum*	A
	Porphyra leucosticta	R

Elachista fucicola	A
Ectocarpus fasciculatus	R
Ectocarpus siliculosus	A
Spongonema tomentosum	A
Dictyosiphon foeniculaceus	R
dwarf *Ulva lactuca*	R
Spongomorpha aeruginosa	RR
Enteromorpha intestinalis	A
Enteromorpha prolifera	R

On sand-covered rocks a floristic impoverishment was found within all the strata. The undergrowth was depleted of crustose floristic elements and represented only by *Sphacelaria radicans* and *Acrosiphonia* species. In eastern Iceland the association was changed, and depleted of Atlantic floristic elements, such as e.g. *Ceramium* species, *Porphyra leucosticta*, *Cladophora rupestris*, *Phymatolithon polymorphum*.

It is noteworthy, that several species were common to the strata of the epiphytes and companion species, as e.g. *Ectocarpus siliculosus*, *Pylaiella littoralis*, *Dictyosiphon foeniculaceus*, *Ulva lactuca*, *Enteromorpha* and *Ceramium* species.

ESTUARINE VARIANT: CODOMINANT FUCUS VESICULOSUS — FUCUS CERANOIDES

Regional distribution and zonal position

In estuarine habitats all around Iceland, in oligo- and mixo-mesohaline areas, both fucoids form mixed stands. They appear side by side in widely different growth forms, which make taxonomic distinctions difficult. The relative amounts of the two codominant fucoids vary from spot to spot in the estuaries.

In innermost fjord areas and in local estuaries, the benthic algal vegetation is not yet distributed into distinct zones, but exhibits a patchy distribution. Benthic algae are attached to pebbles and gravel. The entire estuaries are totally emerged during low tides. Conditions of lowered salinities, with wide fluctuations during the tides, coincide with conditions of extreme shelter and soft substrata of sand/mud.

There is, however, a complexity of sources for morphological variations of the two estuarine fucoids and their intermediate forms.

Structure and composition

Along the estuaries, which represent unstable environments, the structure and floristic composition of Fucacean associations is submitted to wide and unpredictable variations.

Average floristic composition:

Figure 7. Fucus vesiculosus association.

I stratum (undergrowth):	*Hildenbrandia rubra*	RR
	Blidingia minima	A
II stratum (companion species):	*Porphyra purpurea*	M
	Pylaiella littoralis	A
	Ectocarpus siliculosus	A
	Dictyosiphon chordaria	M
	Dictyosiphon foeniculaceus	R
	Ulva lactuca	A
	Cladophora flexuosa	RR
	Monostroma obscurum	R
	Monostroma grevillei	R
	Enteromorpha ahlneriana	M
	Enteromorpha intestinalis	M
	Enteromorpha prolifera	A
III stratum (dominants):	*Fucus vesiculosus* in vesiculated and evesiculated, variable growth forms - *Fucus ceranoides*	
IV stratum (epiphytres):	*Elachista fucicola*	R
	Pylaiella littoralis	M
	Ectocarpus siliculosus	A
	Ectocarpus fasciculatus	R

Monostroma grevillei	R
Enteromorpha intestinalis	A
Enteromorpha prolifera	A
Enteromorpha clathrata	RR

FUCUS CERANOIDES

In marginally brackish situations both fucoids form a mixed association. Close to river outlets, on the other hand, *Fucus ceranoides* occurs for itself as the pioneer Fucacean association in the oligohalinikum.

Regional distribution and zonal position

The association is distributed all around Iceland in suitable habitats close to river outlets. The dominant species exhibits a patchy distribution and is usually attached to small stones, lying on soft substrata of sand/mud. Locally it penetrates high up into the river outlets, and is influenced by fresh water during a part of the tidal cycle.

Structure and composition

The association is usually only two-layered, lacking both the undergrowth and epiphytes.

I stratum (undergrowth):	-	
II stratum (companion species):	dwarf *Pylaiella littoralis*	M
	dwarf *Dictyosiphon chordaria*	M
	Enteromorpha intestinalis	R
III stratum (dominant):	*Fucus ceranoides*	
IV stratum (epiphytes):	-	

ASCOPHYLLUM NODOSUM

Ascophyllum nodosum is one of the dominant fucoids on North Atlantic shores (BAARDSETH 1970). In Iceland it forms the main Fucacean association, with the widest extension and highest biomass yield (MUNDA 1964a, 1976a).

Regional distribution

The association is distributed all around Iceland, but most prolific in the South and Southwest: on moderately sloping lava rocks between the rivers Ölfusá and Thjórsá; and along the eastern Barðaströnd coast, where 1 to 2 km wide *Ascophyllum* fields extend into the sea. It is less abundant in the North and East, but covers wide extenses in middle fjord areas all around Iceland. In outer fjord areas and along open coast lines it usually gives way to the *Fucus distichus* ssp. *edentatus* association.

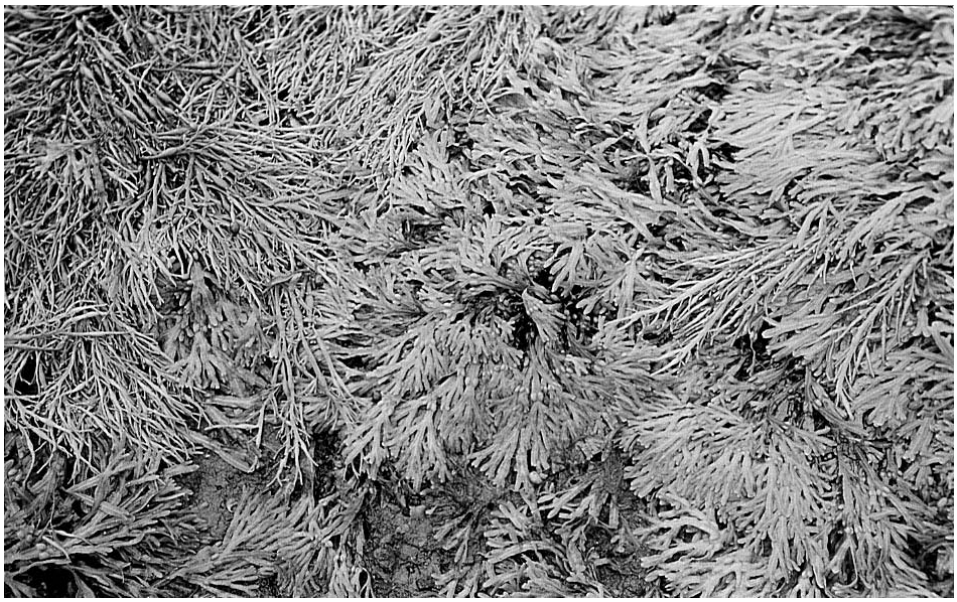

Figure 8. Ascophyllum nodosum association below Fucus vesiculosus.

Zonal position

The *Ascophyllum nodosum* association belongs to the mid-eulittoral, and is usually situated lower down than *Fucus vesiculosus*. Enclaves of *Ascophyllum* were locally found in between *Fucus vesiculosus* fields, as e.g. in Steingrímsfjörður (MUNDA 1997), or even an inversion of the two mid-eulittoral associations was observed. On some boulders the Fucacean vegetation could start directly with *Ascophyllum*, below *Ulothrix - Urospora* belts. Downwards this association limits to that of *Fucus serratus* in the South, or to *Fucus distichus* ssp. *edentatus* elsewhere in Iceland. In the fjords, *Ascophyllum nodosum* joins the vegetation farther out than *Fucus vesiculosus*, avoiding extreme estuarine environments. It occurs as narrow belts in inner fjord areas, as well as along outer, exposed shores but is absent under extreme surf conditions.

Structure and composition

In comparison with *Fucus vesiculosus*, the *Ascophyllum nodosum* association is floristically enriched, and always four-layered. In the South, Southwest and Northwest Atlantic floristic elements are richly represented within all the strata. The hydrographic discontinuity in the extreme Northwest of Iceland (STEFÁNSSON 1949, 1962) is reflected in the floristic composition and physiognomy of the *Ascophyllum nodosum* association, which gets impoverished in the North, and even more in the East.

Floristic composition all around Iceland:

I stratum (undergrowth):	*Hildenbrandia rubra*	M
	Phymatolithon lenormandii	M
	Phymatolithon polymorphum	R
	Phymatolithon laevigatum	R
	Lithothamnion sp.	R
	Clathromorphum circumscriptum	A
	Rhodochorton purpureum	A
	Polysiphonia stricta	A
	Plumaria plumosa	A
	Membranoptera alata	R
	dwarf *Palmaria palmata*	R
	Ralfsia verrucosa	M
	Ralfsia fungiformis	R
	Sphacelaria radicans	R
	Sphacelaria nana	RR
	Sphacelaria plumosa	RR
II stratum (companion species):	*Palmaria palmata*	M
	Rhodomela lycopodioides	R
	Ceramium nodulosum	A
	Ceramium areschougii	RR
	Cystoclonium purpureum	R
	Porphyra purpurea	R
	Porphyra abyssicola	A
	Pylaiella littoralis	M
	Ectocarpus siliculosus	A
	Dictyosiphon foeniculaceus	M
	Scytosiphon lomentaria	A
	Chordaria flagelliformis	R
	Ulva lactuca	A
	Acrosiphonia grandis	A
	Acrosiphonia arcta	R
	Acrosiphonia sonderi	A
	Cladophora rupestris	M
	Monostroma grevillei	RR
	Monostroma undulatum	RR
	Enteromorpha spp.	R
III stratum (dominant):	*Ascophyllum nodosum*	
IV stratum (epiphytes):	*Polysiphonia lanosa*	M
	Ceramium nodulosum	A
	Ceramium areschougii	R

Porphyra miniata	RR
Porphyra abyssicola	R
Elachista fucicola	M
Ectocarpus fasciculatus	R
Ectocarpus siliculosus	A
Pylaiella littoralis	A
Dictyosiphon foeniculaceus	A
Spongonema tomentosum	RR
dwarf *Ulva lactuca*	RR
Monostroma grevillei	R
Acrosiphonia sp.	RR
Spongomorpha aeruginosa	A
Enteromorpha spp.	A

Local and regional differences in the floristic composition of the *Ascophyllum nodosum* association were obvious within all the strata. In the undergrowth, *Plumaria plumosa*, *Membranoptera alata* and *Phymatolithon polymorphum* were absent in the North and East where *Ralfsia fungiformis*, *Clathromorphum circumscriptum* and *Lithothamnion* sp. dominate.

Cystoclonium purpureum and *Ceramium* species, still found within this association in northern Iceland, were absent along the arctic-water influenced eastern coast, where filamentous brown algae determine its physiognomy. The most conspicuos regional difference is obvious in the epiphytic cover of *Ascophyllum*. Its obligatory epiphyte *Polysiphonia lanosa* reaches only as far as to Hornbjarg. This epiphyte contributes essentially to the physiognomy and biomass of the *Ascophyllum* association (MUNDA 1976a, 1978, 1980), but is absent in innermost fjord areas, sheltered bays and inlets.

FUCUS SERRATUS

Regional distribution

This association has a rather discontinuous distribution in southern Iceland, found at the Vestmann Islands, in Vík í Mýrdal and around the Reykjanes Peninsula, northwards from Garðskagi and up to Reykjavík.

Zonal position

Fucus serratus represents the lowermost Fucacean association in Iceland and is usually situated below *Ascophyllum nodosum* or *Fucus distichus* ssp. *edentatus*. Downwards the eulittoral it touches *Laminaria* stands, either *Laminaria saccharina* or *Laminaria digitata* f. *stenophylla*. At its lower edges it can also mingle with the *Mastocarpus stellatus* and/or *Corallina officinalis* associations.

Structure and composition

The association is floristically rich and four-layered. It includes many Atlantic floristic elements.

I stratum (undergrowth):	*Hildenbrandia rubra*	M
	Phymatolithon lenormandii	A
	Phymatolithon polymorphum	A
	Phymatolithon rugulosum	RR
	Phymatolithon laevigatum	R
	Lithothamnion sp.	R
	Rhodochorton purpureum	M
	Polysiphonia stricta	A
	Membranoptera alata	M
	Plumaria plumosa	A
	dwarf *Palmaria palmata*	RR
	Ralfsia verrucosa	M
	Sphacelaria radicans	A
	Sphacelaria nana	R
	Sphacelaria plumosa	RR
II stratum (companion species):	*Palmaria palmata*	M
	Rhodomela lycopodioides	M
	Mastocarpus stellatus	A
	Corallina officinalis	A
	Ceramium nodulosum	M
	Ceramium areschougii	M
	Ceramium strictum	R
	Ceramium shuttleworthianum	RR
	Polysiphonia fucoides	R
	Cystoclonium purpureum	R
	Porphyra abyssicola	R
	Porphyra miniata	RR
	Asperococcus fistulosus	RR
	Pylaiella littoralis	A
	Ectocarpus siliculosus	M
	Dictyosiphon foeniculaceus	R
	Chordaria flagelliformis	RR
	Scytosiphon lomentaria	R
	Acrosiphonia arcta	R
	Acrosiphonia grandis	A
	Acrosiphonia sp.	RR
	Cladophora rupestris	A
III stratum (dominant):	*Fucus serratus*	
IV stratum (epiphytes):	*Ceramium nodulosum*	M
	Ceramium areschougii	A
	Rhodomela lycopodioides	A

Polysiphonia stricta	R
Audouinella virgatula	RR
Porphyra abyssicola	R
Porphyra miniata	R
Pylaiella littoralis	M
Ectocarpus fasciculatus	A
Ectocarpus siliculosus	A
Dictyosiphon foeniculaceus	R
Chordaria flagelliformis	R
Spongonema tomentosum	R
Elachista fucicola	A
Asperococcus fistulosus	R
dwarf *Ulva lactuca*	RR
Spongomorpha aeruginosa	A
Acrosiphonia sp.	R
Monostroma grevillei	R
Monostroma undulatum	RR

FUCUS DISTICHUS ASSOCIATIONS

The four subspecies of *Fucus distichus* L. emend. Powell form distinct associations, which are treated separately in accordance to their distribution, floristic composition, physiognomy, and ecological implications.

FUCUS DISTICHUS SSP. EVANESCENS

Regional distribution

This subspecies of *Fucus distichus* is association-forming in sheltered and estuarine habitats, such as inner fjord areas, land-locked bays and inlets all around Iceland, but most frequently in the North and East. In the fjords it joins the vegetation somewhat farther out than *Fucus vesiculosus*, and is usually found in the meso- and polyhalinikum. The dominant fucoid appears in huge, up to 1 m long specimens of a considerable width (2 to 4 cm).

Zonal position

The association is situated lower down the eulittoral than *Fucus vesiculosus* or *Ascophyllum nodosum*. It is found on moderately sloping rocky platforms, or on stones and pebbles lying on soft substrata. At its lower edges it touches an association of diverse filamentous brown and green algae, characteristic of inner fjord areas, or a mixed association of codominant *Pylaiella littoralis* – *Acrosiphonia* spp. (cf. MUNDA 1978, 1983).

Structure and composition

The association is floristically poor and occasionally only three-layered.

I stratum (undergrowth):	absent on soft grounds	
	on sand-covered rocks:	
	Sphacelaria radicans	R
	Acrosiphonia sonderi	R
	on rocks:	
	Hildenbrandia rubra	A
	Phymatolithon lenormandii	R
	Ralfsia verrucosa	A
II stratum (companion species):	*Porphyra purpurea*	M
	Pylaiella littoralis	M
	Dictyosiphon foeniculaceus	M
	Dictyosiphon chordaria	A
	Ectocarpus siliculosus	A
	Ulva lactuca	M
	Enteromorpha intestinalis	A
	Enteromorpha prolifera	A
	Enteromorpha ahlneriana	RR
	Enteromorpha clathrata	R
III stratum (dominant):	*Fucus distichus* ssp. *evanescens* - giant growth forms	
IV stratum (epiphytes):	*Elachista fucicola*	A
	Pylaiella littoralis	M
	Ectocarpus fasciculatus	A
	Ectocarpus siliculosus	A
	Dictyosiphon foeniculaceus	A
	dwarf *Ulva lactuca*	R
	Enteromorpha spp.	A

FUCUS DISTICHUS SSP. EDENTATUS

Regional distribution

The association is common and widespread all around the coast, but most outstanding in the North and East of Iceland. It replaces the above described association in outer fjord areas, and is frequent also along open coast-lines, on moderately sloping rocky surfaces.

Zonal position

The association belongs to the mid- and lower eulittoral, and is usually situated lower down than *Fucus vesiculosus* or *Ascophyllum nodosum*. On rocky slopes depleted of *Ascophyllum*, the two *Fucus* species could cover wide eulittoral surfaces. On exposed rocky slopes with an uneven configuration, it can follow lower down than the *Fucus distichus* ssp. *anceps* association, covering moderately sloping rocks. At lower edges this association touches diverse low-level belts,

such as those of *Mastocarpus stellatus* or *Corallina officinalis* in Atlantic water regions of Iceland, and of *Devaleraea ramentacea*, *Chordaria flagelliformis* and *Acrosiphonia* spp. in the North and East. In the South, it locally limits to the *Fucus serratus* association.

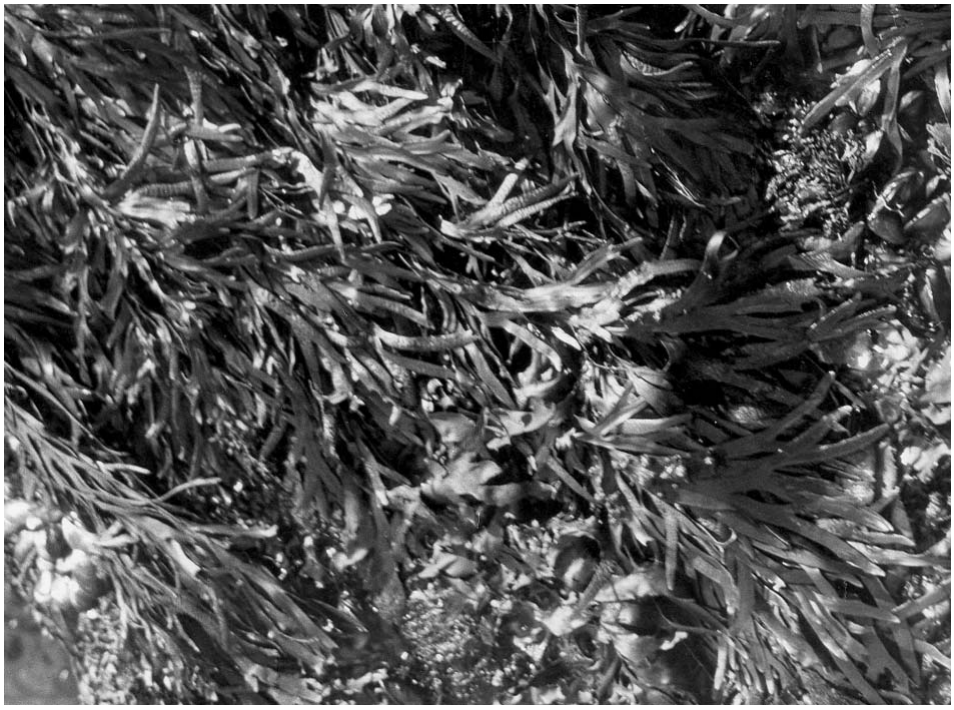

FIGURE 9. *Fucus distichus* ssp. *edentatus* association.

Structure and composition

The floristic diversity within this association is high, and there are pronounced regional differences. Diverse low-level floristic elements penetrate into its first and second stratum.

I stratum (undergrowth):	*Hildenbrandia rubra*	M
	Phymatolithon lenormandii	A
	Phymatolithon polymorphum	R
	Phymatolithon laevigatum	R
	Phymatolithon rugulosum	RR
	Clathromorphum circumscriptum	M
	Lithothamnion sp.	
	Rhodochorton purpureum	R
	Membranoptera alata	A
	Plumaria plumosa	R

	Polysiphona stricta	A
	dwarf *Palmaria palmata*	
	Ralfsia verrucosa	M
	Ralfsia fungiformis	M
	Sphacelaria radicans	R
	Sphacelaria nana	RR
	Sphacelaria plumosa	RR
II stratum (companion species):	*Palmaria palmata*	M
	Devaleraea ramentacea	M
	Rhodomela lycopodioides	A
	Cystoclonium purpureum	A
	Mastocarpus stellatus	RR
	Corallina officinalis	R
	Ceramium nodulosum	A
	Ceramium areschougii	R
	Ceramium strictum	RR
	Ceramium shuttleworthianum	RR
	Polysiphonia fucoides	R
	Porphyra miniata	RR
	Chordaria flagelliformis	R
	Dictyosiphon foeniculaceus	A
	Ectocarpus siliculosus	A
	Scytosiphon lomentaria	R
	Petalonia fascia	RR
	Ulva lactuca	R
	Acrosiphonia grandis	A
	Acrosiphonia arcta	R
	Acrosiphonia sonderi	R
	Cladophora rupestris	M
III stratum (dominant):	*Fucus distichus* ssp. *edentatus*	
IV stratum (epiphytes):	*Porphyra abyssicola*	R
	Porphyra miniata	RR
	Ceramium nodulosum	M
	Ceramium areschougii	A
	Rhodomela lycopodioides	R
	dwarf *Palmaria palmata*	RR
	Elachista fucicola	A
	Pylaiella littoralis	R
	Ectocarpus fasciculatus	R
	Ectocarpus siliculosus	RR
	Chordaria flagelliformis	RR
	Spongonema tomentosum	A

Asperococcus fistulosus	RR
dwarf *Ulva lactuca*	RR
Enteromorpha spp.	R
Spongomorpha aeruginosa	A
Monostroma grevillei	RR
Acrosiphonia sp.	R

Several floristic elements are found only in Atlantic water regions of Iceland (e.g. *Polysiphonia fucoides*, *Membranoptera alata*, *Plumaria plumosa*, *Mastocarpus stellatus*, *Corallina officinalis*, *Asperococcus fistulosus*, *Cladophora rupestris*). *Ceramium* species and *Cystoclonium purpureum*, still present in the North, are absent in eastern Iceland, where brown algae predominate as epiphytes and companions species; and *Ralfsia fungiformis* and *Clathromorphum circumscriptum* in the undergrowth.

FUCUS DISTICHUS SSP. ANCEPS

Regional distribution

The *Fucus distichus* ssp. *anceps* association is relatively rare in the South and Southwest, but frequent in the North and East of Iceland, in outer fjord areas and along open, steep, and highly exposed shores.

Zonal position

The association belongs to the upper and mid-eulittoral. Under extreme surf conditions it is translocated to the uppermost eulittoral as the only Fucacean association left. Where the slopes are moderate or even horizontal lower down the eulittoral, it can touch the *Fucus distichus* ssp. *edentatus* association. Both Fucacean associations can, however, follow each other along the same vertical transects, dependent on the configuration of the rocks. Such broken zonation patterns were rather common along the eastern coast.

The most usual zonal position of this association is between belts of *Ulothrix* spp. - *Urospora penicilliformis* or *Porphyra umbilicalis* and diverse low-level associations, such as *Devaleraea ramentacea*, *Chordaria flagelliformis*, *Acrosiphonia* spp.

Structure and composition

The association is floristically poor. In its undergrowth species from the uppermost eulittoral are also found as a result of a downwards extension of their belts.

I stratum (undergrowth):	*Hildenbrandia rubra*	M
	Polysiphonia stricta	R
	crustose corallines	RR
	Ralfsia verrucosa	M
	dwarf *Pylaiella littoralis*	R
	dwarf *Scytosiphon lomentara*	R
	Petalonia filiformis	A

FIGURE 10. *Fucus distichus* ssp. *anceps* assotiation.

	Ulothrix spp.	A
	Urospora penicilliformis	A
	Blidingia minima	M
	Blidingia marginata	R
	Blidingia chadefaudii	RR
II stratum (companion species):	*Porphyra umbilicalis*	R
	Acrosiphonia arcta	R
	Acrosiphonia sonderi	R
III stratum (dominant):	*Fucus distichus* ssp. *anceps* (morphocline in relation to exposure, extremely reduced specimens under conditions of high surf)	
IV stratum (epiphytes):	*Elachista fucicola*	A
	Spongonema tomentosum	R
	Ectocarpus fasciculatus	RR
	Spongomorpha aeruginosa	RR

Under conditions of extreme surf, the epiphytic cover is absent along with a floristic impoverishment within all the strata.

FUCUS DISTICHUS SSP. DISTICHUS

Fucus distichus ssp. *distichus* is adapted to constant submersion and is association-forming in tide pools of different eulittoral levels. Its autecology was studied by EDELSTEIN & MCLACHLAN (1975), and its populations by several authors, as e.g. RUSSELL (1974), ANG (1991), ANG & DE WREEDE (1992).

In Iceland a morphocline of the dominant species was obvious in dependence on the position of the pools in the eulittoral slopes. In the uppermost pools the plants are reduced, narrow, slender and mostly sterile, while in the lowermost pools and lagoons they become robust, broader, and of a considerable size (up to 25 cm in length).

Regional distribution and zonal position

The association has a discontinuous distribution around Iceland, being most frequent in the North and East. In Atlantic water regions the tide pools are mostly occupied by red algae (e.g. by *Chondrus crispus*, *Ahnfeltia plicata*, *Corallina officinalis*, *Ceramium* species, *Cystoclonium purpureum*, *Dumontia contorta*). In eastern Iceland, on the other hand, a whole system of *Fucus distichus* ssp. *distichus* inhabited tide pools was usually found along the eulittoral slopes, from the littoral fringe down to the upper sublittoral (MUNDA, 1981).

Structure and composition

There are notable differences in the floristic composition and physiognomy of the association in dependence on the position of the pools. In uppermost pools, the association is floristically poor, lacking epiphytes, and the number of species increases towards the lower pools and lagoons.

Pools at the level of the littoral fringe:

I stratum (undergrowth):	*Hildenbrandia rubra*	RR
	Cyanobacteria	M
II stratum (companion species):	*Ectocarpus siliculosus*	RR
	Blidingia minima	R
	Enteromorpha intestinalis	M
	Enteromorpha prolifera	RR
	Enteromorpha clathrata	R
III stratum (dominant):	*Fucus distichus* ssp. *distichus* in reduced growth forms	
IV stratum (epiphytes):	-	

Eulittoral pools

Average floristic composition:

I stratum (undergrowth):	*Hildenbrandia rubra*	M
	Phymatolithon lenormandii	M
	Phymatolithon polymorphum	R

Figure 11. *Fucus vesiculosus* - *Fucus distichus* ssp. *edentatus* fields — outer fjord area.

Figure 12. Rocky promontories in a middle fjord area.

	Clathromorphum circumscriptum	A
	Lithothamnion sp.	R
	Ralfsia verrucosa	M
	Ralfsia fungiformis	A
	Sphacelaria radicans	R
II stratum (companion species):	*Palmaria palmata*	A
	Rhodomela lycopodioides	R
	Devaleraea ramentacea	M
	Ceramium nodulosum	M
	Corallina officinalis	A
	Cystoclonium purpureum	R
	Porphyra miniata	RR
	Porphyra purpurea	RR
	Ectocarpus siliculosus	A
	Dictyosiphon foeniculaceus	A
	Chordaria flagelliformis	M
	Pylaiella littoralis	A
	Scytosiphon lomentaria	A
	Petalonia fascia	RR
	Stictyosiphon tortilis	RR
	Punctaria plantaginea	RR
	Eudesme virescens	RR
	Coilodesme bulligera	M
	Chaetomorpha melagonium	A
	Chaetomorpha capillaris	RR
	Cladophora oblitterata	RR
	Ulva lactuca	A
	Enteromorpha compressa	R
	Enteromorpha linza	S
	Enteromorpha intestinalis	A
	Enteromorpha prolifera	A
	Acrosiphonia grandis	A
	Acrosiphonia arcta	R
	Acrosiphonia sonderi	R
III stratum (dominant):	*Fucus distichus* ssp. *distichus* in different growth forms	
IV stratum (epiphytes):	*Ceramium nodulosum*	R
	Porphyra miniata	R
	Pylaiella littoralis	A
	Ectocarpus fasciculatus	A
	Ectocarpus siliculosus	A
	Elachista fucicola	A

Dictyosiphon foeniculaceus	A
Chordaria flagelliformis	RR
Spongonema tomentosum	A
Spongomorpha aeruginosa	A
dwarf *Ulva lactuca*	R
Monostroma grevillei	R
Enteromorpha spp.	R

There are, however, pronounced regional differences within this association from low-eulittoral pools. In eastern Iceland *Ralfsia fungiformis* and *Clathromorphum circumscriptum* are dominant in the undergrowth, while *Phymatolithon polymorphum* is absent. In Atlantic water regions, *Phymatolithon* species are well represented, and red algae are conspicuous among the companion species (e.g. *Ceramium* spp., *Cystoclonium purpureum*, *Corallina officinalis*). In eastern Iceland, on the other hand, filamentous brown algae dominate within this association, determining its physiognomy, and the admixture of the subarctic species *Coilodesme bulligera* is noteworthy.

The exceeding polymorphism of the dominant fucoid relates to the ambient conditions, viz. the position of the pools in the eulittoral slopes. In splash pools, transitional forms towards *Fucus distichus* ssp. *anceps* were observed. In spite of such form gradations the two subspecies of *Fucus distichus* are likely to be distinct, and form separate associations.

Regional differences in floristic composition between the individual Fucacean associations are presented separately in Table I-A, I-B, and I-C. They are, however, most pronounced within the low-level associations, which touch intermediate low-level belts, separating fucoids from the Laminarians.

DISTRIBUTION OF FUCACEAN ASSOCIATIONS WITHIN ICELANDIC FJORDS – SALINITY AND EXPOSURE IMPLICATIONS

In Icelandic fjords studied in the West and East of Iceland (MUNDA 1978, l980, 1983, 1994, 1997, 1999a, b) a salinity-induced gradient in the appearence of Fucacean associations was obvious like in the Norwegian fjords (e.g. JORDE & KLAVESTAD 1963, JORDE 1966).

In innermost estuaries, *Fucus ceranoides* was the pioneer Fucacean association, appearing as scattered growth of reduced specimens. Next to it, in the oligo- and partly mesohalinikum, a mixed association of *Fucus vesiculosus* and *Fucus ceranoides* appeared, within which both fucoids exhibited widely different growth forms, both regarding the width of the thalli and form of the receptacles. Species delimitation within the complex of estuarine fucoids remained unclear, and measurements of morphometric characters of the estuarine material were carried out (MUNDA, unpublished data: Report to the Icelandic Research Foundation Reykjavík, 1980).

The next association appearing along the fjord coasts in the mesohalinikum, was that of *Fucus vesiculosus*, still as floristically poor, with *Enteromopha* species,

TABLE 1A. Species composition of Fucacean associations in Iceland—Rhodophyta.
• - common to the strata of companion species and epyhytes.

Associations	Pelvetia canaliculata		Fucus spiralis				Fucus vesiculosus				Fucus vesiculosus – F. ceranoides			Ascophyllum nodosum				Fucus distichus ssp. edentatus				Fucus distichus ssp. evanescens				Fucus distichus ssp. anceps			Fucus distichus ssp. distichus				Fucus serratus
Species:	S	SW	S	SW	NW	NE	S	SW	NW	NE	SW	NW	NE	S	SW	NW	NE	S	SW	NW	NE	S	SW	NW	NE	SW	NW	NE	S	SW	NW	NE	S
Rhodophyta																																	
Rhodophyceae																																	
Bangiophycidae																																	
Porphyra abyssicola Kjellm •								X	X	X				X	X	X	X		X	X	X												X
P. leucosticta Thur.									X																								
P. miniata (C.Ag.) C.Ag. •																	X			X	X										X	X	X
P. purpurea (Roth.) C.Ag.									X	X	X	X	X		X	X	X					X	X	X	X						X	X	
P. umbilicalis (L.) Kütz.					X	X																					X	X					
Florideophycidae																																	
Audouinella virgatula (Harvey) Batters																																	X
Ceramium areschougii Kylin •							X	X	X					X	X	X		X	X	X									X	X	X		X
Ceramium nodulosum (Lightf.) Ducluz. •							X	X	X					X	X	X		X	X	X									X	X	X		X
C. shuttleworthianum (Kütz.) Rabenhorst																		X	X														X
C. strictum Harv.																		X															X
Clathromorphum circum-scriptum (Huds.) Batters								X	X	X					X	X	X	X	X	X	X						X	X	X	X	X	X	
Corallina officinalis L.																		X	X	X									X	X	X		X
Cystoclonium purpureum (Huds.) Batters														X	X	X		X	X	X									X	X	X	X	X
Devaleraea ramentacea (L.) Guiry																			X	X	X										X	X	
Hildenbrandia rubra (Sommerf.) Menegh.			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lithothamnion sp.															X	X	X							X	X					X	X	X	X
Mastocarpus stellatus (Stackh. in With) Guiry																		X	X														X
Membranoptera alata (Huds.) Stackh.														X	X	X		X	X	X													X
Palmaria palmata (L.)Kuntze•														X	X	X	X	X	X	X	X								X	X	X	X	X
Phymatolithon laevigatum (Foslie) Foslie							X	X	X					X	X	X		X	X	X													X
Ph. lenormandii (Aresch.) Adey			X	X	X	X	X	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Ph.polymorphum (L.) Foslie							X	X	X					X	X			X	X										X	X			X
Ph. rugulosum Adey																			X	X													X
Plumaria plumosa (Huds.) Kuntze														X	X	X		X	X	X													X
Polysiphonia fucoides (Huds.) Grev.														X				X															X
P. lanosa (L.) Tandy														X	X	X																	
P. stricta (Dillw.) Grev •								X	X	X				X	X	X	X	X	X	X	X					X	X	X		X	X	X	X
Rhodochorton purpureum (Lightf.) Rosenv.							X	X	X	X				X	X	X	X	X	X	X	X							X		X	X		X
Rhodomela lycopodioides (L.) C. Ag. •														X	X	X	X		X	X	X								X	X	X	X	X

TABLE I B. Species composition of Fucacean associations in Iceland – Phaeophyta.
● – common to the strata of companion species and epiphytes

Associations	Species:	Pelvetia canaliculata S	Pelvetia canaliculata S W	Fucus spiralis S W	Fucus spiralis N W	Fucus spiralis N E	Fucus vesiculosus S W	Fucus vesiculosus N W	Fucus vesiculosus N E	Fucus vesiculosus-F. ceranoides S W	Fucus vesiculosus-F. ceranoides N W	Fucus vesiculosus-F. ceranoides N E	Ascophyllum nodosum S W	Ascophyllum nodosum N W	Ascophyllum nodosum N E	Fucus distichus ssp. edentatus S W	Fucus distichus ssp. edentatus N W	Fucus distichus ssp. edentatus N E	Fucus distichus ssp. evanescens S W	Fucus distichus ssp. evanescens N W	Fucus distichus ssp. evanescens N E	Fucus distichus ssp. anceps S W	Fucus distichus ssp. anceps N W	Fucus distichus ssp. anceps N E	Fucus distichus ssp. distichus S W	Fucus distichus ssp. distichus N W	Fucus distichus ssp. distichus N E	Fucus distichus ssp. distichus S	Fucus serratus S
	Phaeophyta																												
	Phaeophyceae (Fucophyceae)																												
	Asperococcus fistulosus (Huds.) Hook ●															X													
	Chordaria flagelliformis (O.F. Müll.) J.Ag. ●												X		X	X	X	X	X		X					X	X	X	
	Coilodesme bulligera Strömf.																												
	Dictyosiphon chordaria Aresch.																		X	X	X								
	D. foeniculaceus (Huds.) Grev. ●									X			X	X	X	X	X	X	X	X	X					X	X	X	X
	Ectocarpus fasciculatus Harvey		X				X	X	X	X	X		X	X	X		X	X	X	X	X			X		X	X	X	X
	E. siliculosus (Dillw.) Lyngb.●						X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X		X	X	X	X
	Elachista fucicola (Vell.) Aresch.			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				X	X	X	X	X
	Eudesme virescens (Carm.ex Harv.) J.Ag. ●																												
	Isthmoplea sphaerophora (Harv.) Kjellm.					X																X							
	Petalonia fascia (O.F.Müll.) Kuntze																X												
	P. filiformis (Batt.) Kuntze					X																X	X						
	Punctaria plantaginea (Roth). Grev.																								X	X			
	Pylaiella littoralis (L.) Kjellm. ●			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X		X	X	X	X
	Ralfsia verrucosa (Aresch.) J. Ag.			X	X	X	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X
	R.fungiformis (Gunn.) Setch.et Gardn.														X						X								
	Scytosiphon lomentaria (Lyngb.) Link.					X		X	X	X	X	X	X	X	X	X	X	X					X	X		X	X	X	
	Spongonema tomentosum (Huds.) Kütz. ●				X	X	X	X	X				X	X	X	X	X	X				X	X			X	X	X	
	Sphacelaria nana Näg.ex Kütz.													X	X		X	X											
	S. radicans (Dillw.) C.Ag.						X	X					X	X	X	X	X	X	X	X	X					X			
	S. plumosa Lyngb.													X	X		X	X											
	Stictyosiphon tortilis (Rupr.) Reinke																												

TABLE I C. Species composition of Fucacean associations in Iceland – Chlorophyta.
● – common to the strata of companion species and epiphytes.

Associations	Species	Pelvetia canaliculata S	Pelvetia canaliculata W	Fucus spiralis S	Fucus spiralis W	Fucus spiralis N	Fucus spiralis E	Fucus vesiculosus S	Fucus vesiculosus W	Fucus vesiculosus N	Fucus vesiculosus E	Fucus vesiculosus-F. ceranoides N	Fucus vesiculosus-F. ceranoides E	Fucus vesiculosus-F. ceranoides W	Fucus vesiculosus-F. ceranoides S	Ascophyllum nodosum S	Ascophyllum nodosum W	Ascophyllum nodosum N	Ascophyllum nodosum E	Fucus distichus ssp. edentatus S	Fucus distichus ssp. edentatus W	Fucus distichus ssp. edentatus N	Fucus distichus ssp. edentatus E	Fucus distichus ssp. evanescens S	Fucus distichus ssp. evanescens W	Fucus distichus ssp. evanescens N	Fucus distichus ssp. evanescens E	Fucus distichus ssp. anceps S	Fucus distichus ssp. anceps W	Fucus distichus ssp. anceps N	Fucus distichus ssp. anceps E	Fucus distichus ssp. distichus S	Fucus distichus ssp. distichus W	Fucus distichus ssp. distichus N	Fucus distichus ssp. distichus E	Fucus serratus S
	Chlorophyta																																			
	Chlorophyceae																																			
	Acrosiphonia arcta (Dillw.) J.Ag.									X						X	X	X															X	X	X	X
	Acrosiphonia centralis (Lyngb) Kjellm.									X	X					X	X	X																		
	Acrosiphonia grandis Kjellm.									X	X					X	X	X															X	X	X	X
	Acrosiphonia sonderi (Kütz.) Kornm.									X	X					X	X	X															X	X	X	X
	Acrosiphonia sp. ●										X							X																		X
	Blidingia chadefaudii (Felrm.) Bliding																					X								X						
	B. marginata (C.Ag.) Dang.																						X							X						
	Blidingia minima (Näg.ex Kütz.) Kylin			X	X							X	X	X										X	X					X						
	Chaetomorpha capillaris (Kütz.) Börg.																																X	X	X	X
	Ch.melagonium Kütz.																																X	X	X	X
	Cladophora flexuosa (Müll.) Kütz.												X	X																						
	Cl. oblitterata Söderstr.																																X	X	X	X
	Cl. rupestris (L.) Kütz.									X	X					X	X	X																		
	Enteromorpha clathrata (Roth.) Grev. ●							X	X	X	X																						X	X	X	X
	E. compressa (L.) Grev.								X	X																										
	E. ahlneriana Bliding																																X	X	X	X
	E. intestinalis (L.) Nees. ●			X	X	X	X	X	X	X	X					X	X	X	X																	
	E. linza (L.) J.Ag.																																X	X	X	X
	E. prolifera (Müll.) J.Ag. ●																																			
	E. spp. ●			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X														X	X	X	X
	Monostroma grevillei (Thur.) Wittr. ●																																			
	M. undulatum Wittr. ●										X																						X	X	X	X
	Monostroma obscurum (Kütz.) J. Ag.																																			
	Prasiola stipitata (Suhr.) in Jessen	X																																		
	Rhizoclonium tortuosum (Dillw.) Kütz.	X	X																																	
	Spongomorpha aeruginosa (L.) Hoek. ●			X	X	X	X	X	X	X	X							X	X			X	X													
	Ulothrix spp.	X	X	X	X	X	X																						X	X	X	X				
	Urospora penicilliformis (Roth.) Aresch.	X	X	X	X	X	X																													
	Ulva lactuca L. ●				X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Ulva lactuca and *Porphyra purpurea* as the main companion species. The estuarine forms of *Fucus vesiculosus* were mostly evesiculated or poorly vesiculated. Even farther out the fjord coasts, *Fucus distichus* ssp. *evanescens* appeared lower down than *Fucus vesiculosus*, and next to it *Ascophyllum nodosum*. In the polyhalinikum, and outwards the fjord coast *Fucus spiralis* joined the Fucacean vegetation. In middle fjord areas, under normally high salinity conditions, a regular sequence of fucoid belts was usual, ranging from *Fucus spiralis*, over *Fucus vesiculosus* and *Ascophyllum nodosum* to *Fucus distichus* ssp. *evanescens*. There we dealt usually with moderate, almost horizontal rocky slopes, which offer support to wide Fucacean fields.

From the head of the fjords and outwards, exposure conditions gradually increase and the littoral slopes are prevailingly steep, interrupted by boulders, islets, small peninsulas and rocky promontories. In the outer fjord areas *Fucus distichus* ssp. *evanescens* was replaced by the usual low-level association of *Fucus distichus* ssp. *edentatus*, while *Ascophyllum nodosum* gradually disappeared. There wide fields of *Fucus vesiculosus* and *Fucus distichus* ssp. *edentatus* were found on moderately sloping rocks, whereas where the slopes are steep or even vertical, *Fucus distichus* ssp. *anceps* appeared as the only Fucacean association left in extreme environments.

A scheme of the distribution of Fucacean associations within the fjords is presented in Table II. It is noteworthy, however, that in the subarctic fjords of eastern Iceland fucoids appeared closer to the innermost estuaries than in fjords of Atlantic water regions. There estuarine associations of ephemeral algae were interimposed between the freshwater area and the first fucoids.

FIGURE 13. Fruiting estuarine fucoids.

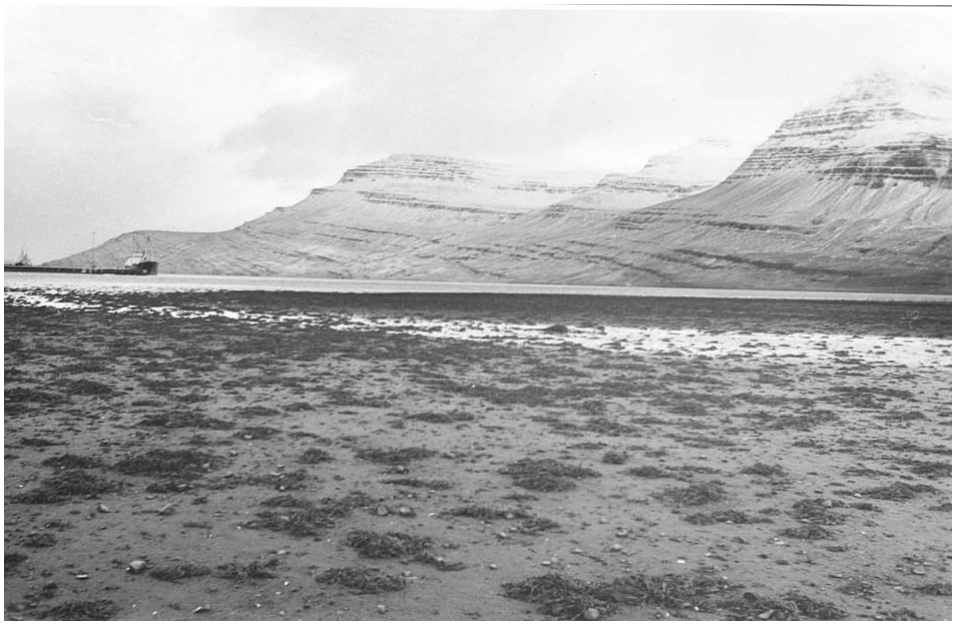

FIGURE 14. Scattered fucoid vegetation in an inner, estuarine fjord area.

Within the fjords a further implication of the exposure factor was obvious on small rocky promontories, islets and boulders. A different fucoid zonation was, however, found on the seawards and landwards-sides of such rocky formations (Figure 6). Landwards a complete zonation from *Fucus spiralis*, over *Fucus vesiculosus*, *Ascophyllum nodosum*, and *Fucus distichus* ssp. *evanescens* was found,

TABLE II. Distribution of Fucacean associations within Icelandic fjords.

Associations	innermost estuaris	inner areas	middle areas	outer areas	outermost sites
Fucus seranoides	+ +				
Fucus vesiculosus – F. ceranoides	+	+			
Fucus vesiculosus		+ + +	+ + +	+ +	
Ascophyllum nodosum		+	+ + +	+	
Fucus distichus ssp. *evanescens*		+ +	+ + +		
Fucus distichus ssp. *edentatus*				+ + +	
Fucus distichus ssp. *anceps*				+	+ +
Fucus spiralis			+ + +	+ + +	

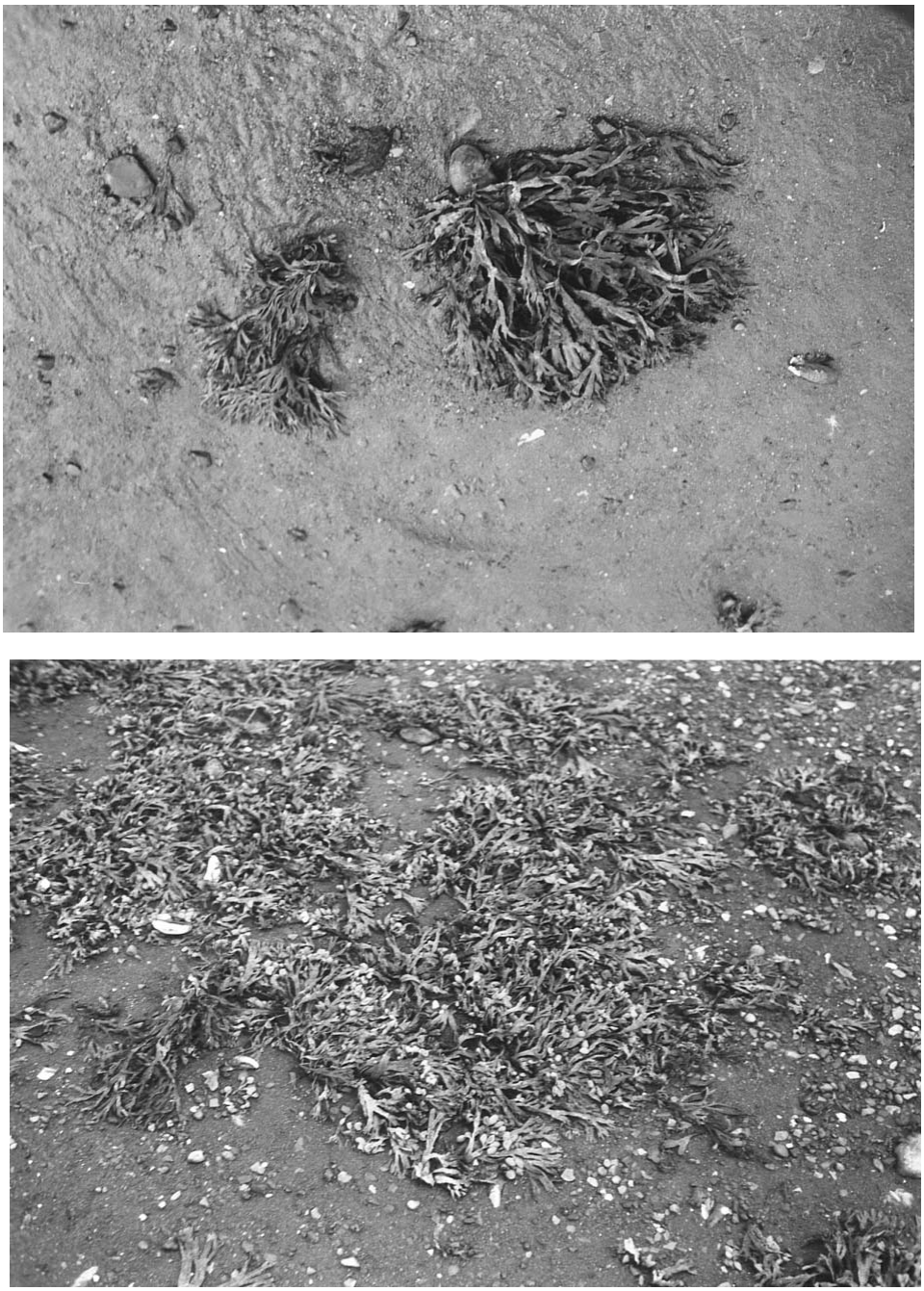

FIGURE 15 A and B. Details from the estuaries.

whereas seawards belts of *Fucus distichus* ssp. *anceps* and *Fucus distichus* ssp. *edentatus* dominated. Under high exposure, the seaward sides of rocks and boulders were colonized only by the *Fucus distichus* ssp. *anceps* association.

NUMBER OF SPECIES

The number of species recorded within Fucacean associations is presented in Fig. 2, and the percentage contribution of the red, brown and green algae within the strata in Fig. 3. The data are based on repeated field observations during summer and autumn months of consecutive years, and present thus an overview about the structure of the individual associations during this part of the year.

Several species were common to the strata of the companion species and epiphytes, what was taken into account when estimating their total numbers.

It was obvious, that the total number of species within the associations increases from the upper towards the lower eulittoral levels. The high level associations (*Pelvetia canaliculata*, *Fucus spiralis*, *Fucus distichus* ssp. *anceps*) were floristically poor and occasionally only two-layered. The same was true for the estuarine associations (*Fucus ceranoides*, codominant *Fucus vesiculosus* - *F. ceranoides*, *Fucus distichus* ssp. *evanescens*). In the latter case salinity conditions dictate the species composition and physiognomy of the associations. Within the fjords a salinity-induced gradient in the number of species was found from the oligotowards the polyhalinikum (MUNDA, 1978, 1983, 1997) cf. "the fjord effect" (JORDE & KLAVESTAD 1963).

Within the mid- and low-eulittoral Fucacean associations the number of species was notably increased in comparison with the high-level ones, and the highest floristic diversity was usual among the companion species (associations of *Fucus vesiculosus*, *Ascophyllum nodosum*, *Fucus serratus*, *Fucus distichus* ssp. *edentatus*).

As repeatedly mentioned, the four subspecies of *Fucus distichus* form separate associations, obviously determined by physical differences connected with the degree of exposure and inclination of the substrata. *Fucus distichus* ssp. *evanescens*, which is association-forming in protected and also estuarine habitats is floristically poor. An about three times higher number of species was recorded for the *Fucus distichus* ssp. *edentatus* association, which belongs to the lower eulittoral of moderately exposed shores. Under high or extreme exposure conditions, the *Fucus distichus* ssp. *anceps* association dominates the upper- and mid-eulittoral, and exhibits a low number of species along with a reduced stratification. The fourth subspecies of *Fucus distichus* is association-forming in tide pools of different eulittoral levels. In high-lying pools the association is floristically poor, whereas the highest number of species was found in the lowermost pools and lagoons. Two extreme examples are presented in Fig. 2, the number of species being four to five times higher in the low- than in the high-lying pools.

The floristic composition incl. number of species of the high-level and estuarine Fucacean associations proved to be rather uniform all around Iceland. Within the mid- and low eulittoral associations regional differences in floristic composition became obvious, and the same was true for the above mentioned tide pool association. This relates first of all to a reduction in the number of species in eastern Iceland, where all the typical Atlantic floristic elements are absent from the vegetation.

Looking at the percentage floristic composition of the main Fucacean associations (Fig. 3) several differences in their structure became obvious. Within the two mid-eulittoral associations, *Fucus vesiculosus* and *Ascophyllum nodosum*, the highest percentage of red algae was found in their undergrowth, followed by brown algae, while green algae were in minority in the *Fucus vesiculosus* association, and absent in the *Ascophyllum nodosum* one. Among the companion species relationships were just the opposite, revealing a pronounced dominance of green algae within both associations. In the stratum of the epiphytes brown algae dominated within the *Fucus vesiculosus* association. It is noteworthy, that the percentage of red algae in the epiphytic cover of *Ascophyllum* was twice as high as of *Fucus vesiculosus*.

Within the two low-level associations, *Fucus serratus* and *Fucus distichus* ssp. *edentatus*, both the undergrowth and companion species were in percentage dominated by the red algae component, and the epiphytic cover by the brown one, green algae being in minority within all the strata. It was obvious, however, that the red algae component gets more outstanding lower down the eulittoral.

In both high-level associations, considered from this point of view, green algae were outstanding among the companion species, while in the epiphytic cover brown algae dominated and red algae were absent.

BIOMASS EVALUATIONS

The fresh weight biomass of some Fucacean associations was evaluated at some characteristic spots within the fjords and along open shores. The data presented in Table III refer only to the fucoid species, and are averages of 10 to 15 measurements, expressed as g fresh weight/m^2.

The average biomass of the Fucacean associations decreased from the lower towards the upper eulittoral. The lowermost values were found for *Pelvetia canaliculata* stands at the terrestrial level, where scattered and reduced specimens were found. The biomass increased towards the upper eulittoral, where about 10 times higher values were usual. *Fucus spiralis* exhibited higher biomass values than *Pelvetia*, along with some regional variations. The highest biomass within this association was found in southern Iceland, and a gradual decrease from the Southwest, over the Northwest and North to the East.

The dominant mid-eulittoral associations of *Fucus vesiculosus* and *Ascophyllum nodosum* were rather rare along open shores. Therefore their biomass was evaluated first of all within the fjords in the West and East. *Fucus vesiculosus*

exhibited the highest biomass values in middle fjord areas. Within the western fjords its biomass was rather low in inner, estuarine areas, while the opposite was found in the eastern fjords. There fucoids appear in dense stands closer to the innermost estuaries than in the West. *Ascophyllum nodosum* showed rather uniform biomass values in inner fjord areas all around Iceland, and increases farther out the fjord coasts. In eastern Iceland the highest biomass values of *Ascophyllum* were found in the middle fjord areas, whereas in the West a gradual increase towards the outer fjord regions was observed. Extensive streches of rich fucoid vegetation, suitable for commercial harvesting are, however, restricted to some well defined areas in the South and Southwest of Iceland, where *Ascophyllum* dominates in 1 to 2 km broad fields (coast-line between the rivers Ölfusá and Thjórsá, and the eastern Barðaströnd coast). Previously (Munda 1964 a) the quantiuty and chemical composition of *Ascophyllum nodosum* was estimated there, revealing an average fresh weight biomass of 6300 g/m², while the maximum recorded weight was 12 000 g/m².

TABLE III. Biomass evaluations within Fucacean associations.
(g fresh weight / m^2 - averages of 10 to 15 measurements).

	South	Southwest	Northwest	East	Southeast
Pelvetia canaliculata					
upper eulittoral	561-780	350-428			
littoral fringe	172-215				
terrestrial level	43-70				
Fucus spiralis	1860-3400	980-2700	386-1560	370-560	1268-1530
Fucus vesiculosus					
open coasts	4070-6487	2500-6000			
in fjords: inner areas		1600	1230	3200	2950
middle areas			6349	6220	5800
outer areas		5520	5400	1256	1080
Ascophyllum nodosum					
open coasts	6806-8700	3490-5700			
in fjords: inner areas		2800	3780	3150	3500
middle areas			6780	5990	6280
outer areas		5760	7650	4570	3600
Fucus serratus	6500-8276				
Fucus distichus ssp. *edentatus*		6800-8100	6430-7000	5510-6830	5100-6450
Fucus *distichus* ssp. *anceps*			387-786	910-1376	530-920
Fucus ceranoides					
estuaries	950-1005				

High biomass values were found also for the low level fucoid associations, *Fucus serratus* from southern Iceland, and *Fucus distichus* ssp. *edentatus* from the North and East. Some biomass evaluations were carried out also for the surf-adapted *Fucus distichus* ssp. *anceps* association, which locally penetrates into the upper eulittoral. Its biomass obviously decreases with increasing exposure conditions.

DISCUSSION

The fucoid vegetation of sheltered shores around Iceland is structured into distinct zones along vertical gradients, but exhibits pronounced regional differences. In the South and Southwest of Iceland a complete sequence of fucoid belts is found, ranging from *Pelvetia canaliculata*, over *Fucus spiralis*, *Fucus vesiculosus* and *Ascophyllum nodosum* to *Fucus serratus* (South) and/or *Fucus distichus* ssp. *edentatus*. There are likewise wide variations in the sequence of fucoid belts as related to the exposure conditions and inclinations of the eulittoral slopes. *Pelvetia canaliculata* reaches only as far north as to the Snæfellsnes Peninsula (MUNDA 1975, 1987), while *Fucus spiralis* gets subordinate in the vegetation of the North and East, where also *Ascophyllum nodosum* is relatively rare along open coast-lines. There *Fucus distichus* ssp. *edentatus* is the dominant fucoid, forming locally mixed fields with *Fucus vesiculosus*. Highly exposed sites are colonized by *Fucus distichus* ssp. *anceps* as the only fucoid under extreme stress conditions.

These regional discontinuities and disjunct distribution of fucoids along with some other benthic macroalgae is obviously conditioned by the varying hydrographic conditions around Iceland, which has a central position in the North Atlantic. It belongs partly to the North Atlantic Subarctic Province (JOHANESSEN 1986, LONGHURST 1998), which is a complex hydrographic region, influenced by the North Atlantic Current waters (KRAUSE 1986). The greater part of the Icelandic coast is surrounded by warm Atlantic water masses, carried northwards by the Irminger Current. In the extreme Northwest a pronounced hydrographic discontinuity occurs, due to the diminished inflow of Atlantic water into the North Icelandic coastal area, and mixing with cold water from the East Greenland Current (STEFÁNSSON 1949, 1962). The northeastwards flowing Irminger Current (DIETRICH 1957, MALMBERG 1985) gets gradually cooled and diluted during its passage over the insular shelf. It meets the cold East Icelandic Current, which is of arctic origin, north of Melrakkaslétta. In the extreme Northeast, there is, however, a second hydrographic mixing area.

The entire east Icelandic coast is influenced by cold, low-salinity water, carried southwards by the East Icelandic Current. It is as such considered as belonging to the North Atlantic Arctic Province (DIETRICH 1964, JOHANESSEN 1986, LONGHURST 1998), which is situated on the edge of the Greenland coastal currents, and the Oceanic Polar Front. It crosses the ocean diagonally from Flemish Cap to the Faeroes, and includes the central part of the Labrador Sea and of the

Nordic Sea, including eastern Iceland. It extends then farther north to the Fram Strait.

In the Southeast there is a well marked frontal zone, separating warm and saline Atlantic water from the colder and diluted one, carried by the East Icelandic Current. It is submitted to seasonal and annual translocations, dependent on climatic changes and ice conditions (STEFÁNSSON 1972, MALMBERG & STEFÁNSSON 1972, DICKSON et al. 1975, MALMBERG 1984).

The described hydrographic boundaries are reflected in more or less pronounced floristic and vegetational limits in the Northwest, Northeast and Southeast of Iceland (MUNDA 1975, 1992a, b, c), which refer also to the structure and floristic composition of the Fucacean associations. In this connection it seems interesting that KALVAS & KAUTSKY (1998) found significant morphological differences between populations of *Fucus vesiculosus* from southern and western Iceland on the one side, and from northern and eastern on the other. They outlined a hypothesis of long-distance dispersal of mature, reproductive thalli by the Irminger Current and/or the East Icelandic Current as possible links to Newfoundland on the one side, and the Barents Sea on the other. A more plausible interpretation for the named morphological differences are, however, the regning ecological conditions, viz. higher water temperatures and larger tidal range in the South and West than in the North and East.

Mid-eulittoral fucoids, *Fucus vesiculosus* and *Ascophyllum nodosum*, are association-forming all around Iceland, but with certain regional differences in their floristic composition, physiognomy and vertical extension. In the South and Southwest, where there are wide Fucacean fields, *Fucus vesiculosus* appears mainly as f. *sphaerocarpa*. Within the fjords widely different morphs were found, tending towards f. *vadorum*, along with evesiculated forms within estuaries and in exposed sites. Morphological variations of the dominant fucoids, which highly influence the physiognomy of the associations, can be both, salinity- and exposure conditioned (JORDAN & VADAS 1972, RUSSELL 1979, RUSSELL & FIELDING 1981, BÄCK 1992, 1993, KAUTSKY et al. 1992, KALVAS & KAUTSKY 1993). The *Fucus vesiculosus* association is usually found higher up the eulittoral than that of *Ascophyllum nodosum*, but at its lower limit the two associations may overlap (Fig. 8). Within the fjords, the *Fucus vesiculosus* association appears closer to the innermost estuaries than *Ascophyllum nodosum*. In the oligo-and mesohalinikum an estuarine association of codominant *Fucus vesiculosus* and *Fucus ceranoides* was usual. Under low salinity conditions wide form variations were observed regarding the width of the thalli, and form and size of the receptacles, from small rounded, over narrow and oblong to heavy and forked ones (cf. RUSSEL 1979). As contrast to observations of JORDAN & VADAS (1972) estuarine fucoids in Iceland were mainly evesiculated. A distinction between narrow, evesiculated forms of *Fucus vesiculosus* and *Fucus ceranoides* seemed frequently unpossible. Although experiments conducted by KHFAJI & NORTON (1979) indicated differences in behaviour of the two fucoids towards salinity, previous transplantation

experiments of *Fucus vesiculosus* f. *vadorum* into estuaries (MUNDA 1964b) put the distinction between the two species into doubt.

The mid-eulittoral Fucacean association of *Ascophyllum nodosum* is best represented in Atlantic water regions of Iceland. It has, in general, a wide distribution in the entire North Atlantic, reaching from Baffin Bay to the White Sea (ZINOVA 1953), and to Portugal in the South. In many areas its homogenous stands encouraged industrial harvesting (BAARDSETH 1970, NEILL 1979, KESER et al. 1981, TOPINKA et al. 1981, COUSENS 1981, 1984), as it is also the case in southwestern Iceland. Its concentrated stands were studied in detail previously in southern Iceland (MUNDA 1964a). In Atlantic water regions of Iceland *Ascophyllum* bears a heavy load of its obligatory epiphyte *Polysiphonia lanosa*, which determines the physiognomy of the association, and locally contributes more than 30% to its biomass. The presence/absence of this epiphyte is the main distinguishing character between the south and west, and north and east association of *Ascophyllum*. Further floristic differences refer to the undergrowth and companion species, since Atlantic floristic elements have their distributional limits in the hydrographic boundary areas in the Northwest (*Membranoptera alata*, *Plumaria plumosa*), and Northeast (*Cystoclonium purpureum*, *Ceramium* species, *Corallina officinalis*) as examples.

The *Fucus vesiculosus* association is floristically poorer than the *Ascophyllum nodosum* one, and exhibits consequently less pronounced regional variations in its floristic composition and structure. In inner and middle fjord areas green and brown algae predominate within both mid-eulittoral associations, whereas farther out along the fjord coasts a shift towards the red algae component became obvious. A sandy layer, covering the rocks, locally greatly influences the benthic fjord vegetation, sand preventing the attachment of a continuous understorey. Under such conditions only *Sphacelaria radicans* and *Acrosiphonia* species were left.

The least regional differences were observed for the high-level associations, which are floristically poor. They endure under stress conditions and physical factors are first of all important for their structure and vertical extension (cf. HAWKINS & HARTNOLL 1985). The regionally restricted *Pelvetia canaliculata* association penetrates locally into the terrestrial level, and its upper distributional limit seems determined by its resistence to desiccation (SCHONBECK & NORTON 1978, 1979, 1980, BÉRARD-THÉRRIAULT & CARDINAL 1973, RUGG & NORTON 1987). The *Fucus spiralis* association, although found all around Iceland, is best represented in warm-water regions, viz. the South and Southwest, where dense settlements with a wide vertical extension and relatively high biomass are found. In the North and East it appears as narrow belts over a wide range of habitats, from sheltered to rather exposed ones, where it is occasionally situated higher up than *Fucus distichus* ssp. *anceps*. A similar exposure-conditioned distributional pattern was found also at the Faeroes (BÖRGESEN 1902, 1905, PRICE & FARNHAM 1982) and the North of Norway (JAASUND 1965). A phenotypic plastic-

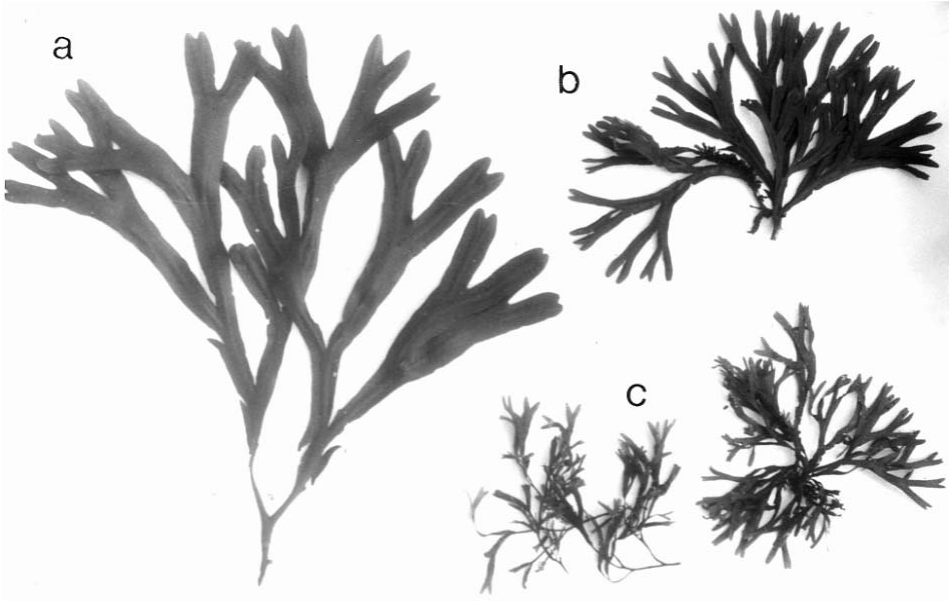

FIGURE 16. A: *Fucus distichus* ssp. *edentatus*. B: *Fucus distichus* ssp. *anceps*. C: *Fucus distichus* ssp. *distichus*.

ity in relation to exposure was also observed, like in other areas (BÖRGESEN 1902, KRISTENSEN 1958, JAASUND 1965). The ecology and growth forms of *Fucus spiralis* were, however, studied in different areas, as e.g. by NIEMECK & MATHIESON 1976, ROBERTSON 1987, NEILL et al. 1987, CHAPMAN 1989, 1990, ANDERSON & SCOTT 1998, SCOTT et al. 2001.

The low-level Fucacean associations of Iceland are floristically rich within all the strata. The lowermost one, *Fucus serratus*, penetrates locally into the upper sublittoral, and can also overlap with the low level associations of *Mastocarpus stellatus* and *Corallina officinalis*. As mentioned in the introduction, *Fucus serratus* has an irregular and scattered distribution throughout the North Atlantic. It is common and widespread along the Norwegian coast (PRINTZ 1926, SUNDENE 1953, JORDE & KLAVESTAD 1963, JORDE 1966, JAASUND 1965), the British Isles (e.g. GIBB 1950, KNIGHT & PARKE 1950), the Netherlands and the island of Helgoland in the North Sea (van den HARTOG 1959), reaching southwards to the north of Spain (ARRONTES 1993). Found at the Shetlands and Orkneys, it is absent at the Faeroes (BÖRGESEN 1902, IRVINE 1982) and rare in Iceland. It is found again at the Canadian Maritime Provinces (EDELSTEIN et al. 1972/73, DALE 1982), where its distributional pattern had recently changed. ROBINSON (1903) postulated that *Fucus serratus* was introduced from Europe possibly around the turn of the 19th century. It might be possible that it was introduced also to Iceland by shipping (cf. van den HOEK 1987).

A further low-level association is that of *Fucus distichus* ssp. *edentatus*. Although found all around the Icelandic coast, it has a rather northerly distributional pattern and occurs in narrow belts in Atlantic-water regions of Iceland, but is outstanding in the vegetation of the North and East. It has in general a wide distributional pattern in the northern North Atlantic, such as the Barents Sea and White Sea (ZINOVA 1953), the Norwegian coast, the Shetlands (RUSSELL 1974), western Sweden, Greenland (ROSENVINGE 1893, LUND 1959, PEDERSEN 1976) as well as Atlantic coasts of North America and Canada (WILCE 1959, SIDEMAN & MATHIESON 1985). This association exhibits pronounced regional variations in Iceland, touching intermediate algal belts which separate fucoids from the Laminarians (*Mastocarpus stellatus* and *Corallina officinalis* up to Hornbjarg, and *Chordaria flagelliformis*, *Acrosiphonia* spp. and *Devaleraea ramentacea* in the North and East).

The *Fucus distichus* ssp. *evanescens* association is restricted to sheltered and also low-salinity habitats. It is floristically poor and exhibits negligible regional variations around Iceland. According to POWELL (1957a) it is a best of all subspecies of *Fucus distichus* adapted to arctic and subarctic growth conditions, having a wide circumpolar distribution, such as the Siberian Polar Sea, northern Russia, Barents Sea, Novaja Zemlja (ZINOVA 1953), Svalbard (SVENDSEN 1959), Jan Mayen, Greenland (LUND 1959) as well as the American Polar Sea, Bering Sea, Northern Canada and North America (WILCE 1959). Under arctic growth conditions smaller and narrower plants were reported by ZINOVA (1953).

The *Fucus distichus* ssp. *anceps* association is, to the contrast, found only in highly and extremely exposed habitats, most frequently in northern and eastern Iceland. It was described by different names, e.g.: by JÓNSSON (1910, 1912) for Iceland and for the Faeroes, Norway, Shetland and Greenland (ROSENVINGE 1893, LUND 1959, BÖRGESEN 1905, JORDE & KLAVESTAD 1963, JAASUND 1965, RUSSELL 1974). With increasing surf conditions an upwards translocation of this association was found, along with a size reduction of the dominant fucoid. Several authors had correlated the size of *Fucus distichus* plants with exposure (BÖRGESEN 1902, JÓNSSON 1903, POWELL 1957a, b, SCHONBECK & NORTON 1980) In Iceland, dwarf 1 to 2 cm high plants were found on the island of Grímsey under extreme surf conditions (MUNDA l977a).

The genetic distinction of this subspecies of *Fucus distichus* was studied by SIDEMAN & MATHIESON (1980). It has a rather northerly distribution, such as the Barents Sea, White Sea, the Norwegian coast, Ireland, Shetlands, Orkneys, the Faeroes and possibly also Svalbard. SVENDSEN (1959) reported *Fucus distichus* as the only fucoid species for Svalbard. There the small eulittoral forms may represent the ssp. *anceps*, while larger forms belong there to the sublittoral.

All the non-tide pool populations of *Fucus distichus* were studied from different aspects by SIDEMAN & MATHIESON (1983b, 1985), THOM (1983), ANG (1991), ANG & DE WREEDE (1983).

FIGURE 17. *Fucus distichus* ssp. *distichus* from uppermost tide pools.

The *Fucus distichus* ssp. *distichus* association is, on the other hand, found in tide pools of different eulittoral levels, most frequently in the North and East of Iceland (MUNDA 1981, 1983). Form-variations are, however, the widest within this subspecies of *Fucus distichus*. It was studied in detail by MCLACHLAN et al. (1971) and EDELSTEIN & MCLACHLAN (1975). The size of the plants increases gradually from the upper towards the lower pools. A wide northerly distribution of this subspecies of *Fucus distichus*, as reported by POWELL (1957a), includes the entire Norwegian coast, the Shetlands, Faeroes, Greenland, the Kara Sea, White Sea, Barents Sea as well as Atlantic coasts of Canada and North America.

The wide variations in form and size within the *Fucus distichus* complex observed in Icelandic waters initiated also numerical studies of some morphometric characters on material from the Reyðarfjörður and the island of Grímsey off North (unpublished data-Munda: Report to the Icelandic Research Foundation, Reykjavík, 1980). From the data obtained a morphological continuum between the extreme forms was found throughout the fjord coast: from huge plants belonging to ssp. *evanescens* (inner and middle fjord areas), to extremely reduced ones from the outer areas, belonging to ssp. *anceps*. Such gradual transitions between forms within the *Fucus distichus* complex were reported also by other authors (e.g. ROSENVINGE 1893, BÖRGESEN 1902, JÓNSSON 1903, SVENDSEN

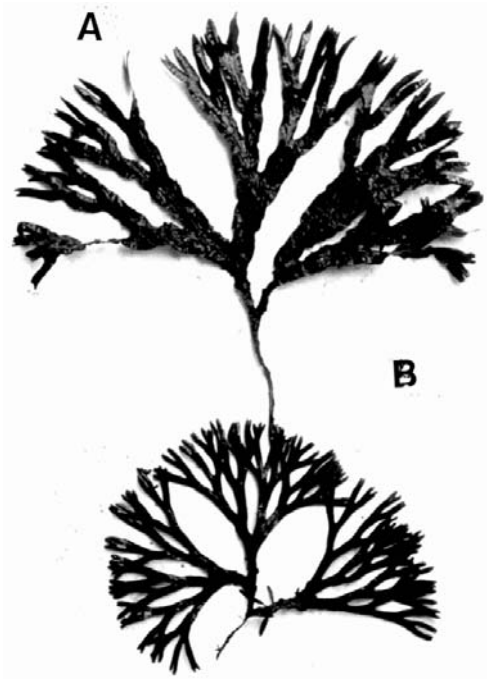

Figure 18. A: *Fucus distichus* ssp. *evanescens*; B: transitional form between ssp. *edentatus* and ssp. *anceps*.

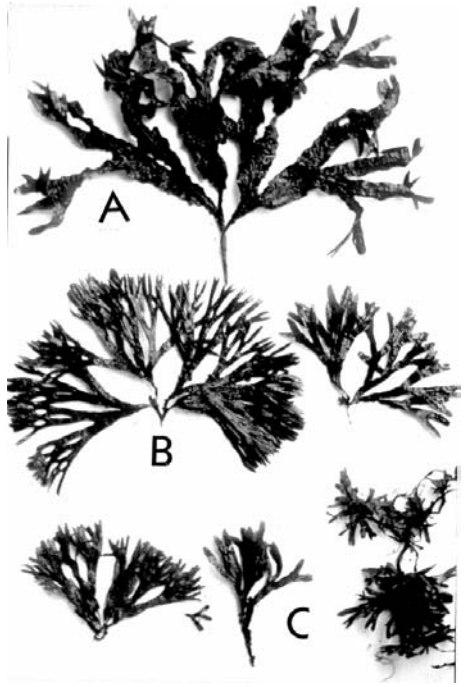

Figure 19. A: *Fucus distichus* ssp. *evanescens* (broad form); B: transistional forms towards ssp. *anceps*; C: reduced specimens from exposed sites.

1959, TAYLOR 1962, SCHONBECK & NORTON 1980), and are likely exposure conditioned. Some authors had proved, however, that the different forms are genetically based (MCLACHLAN et al. 1971, SIDEMAN & MATHIESON 1983a, 1985).

As outlined in the introduction Powell's concept (POWELL 1957a, b) of four subspecies of *Fucus distichus* was retained in the present ecologically descriptive contribution, in spite of the transitional forms observed under field conditions. They form, however, spatially separated associations with pronounced differences in their structure, floristic composition and physiognomy.

On the basis of qualitative observations and collections eleven Fucacean associations were recognized for the Icelandic coastal area. They exhibit an uneven distribution around the coast as well as conspicuous differences in their floristic composition and physiognomy between Atlantic and subarctic regions of Iceland (Table I A-C). All the field studies were carried out during summer and autumn months of consecutive years, and we have thus no insight into the year-round floristic changes within these associations.

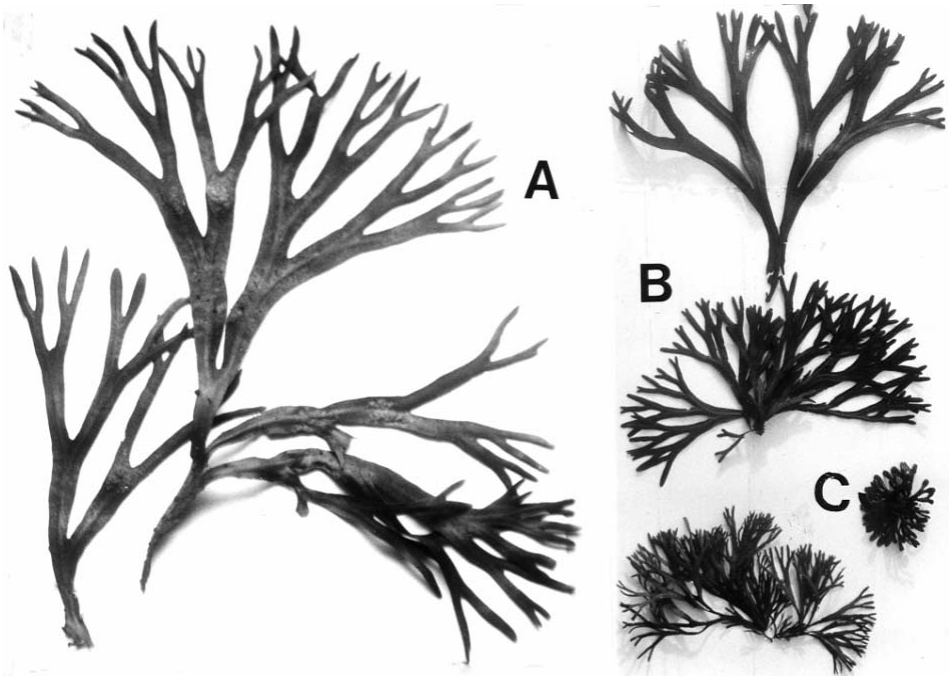

FIGURE 20. Form and size transitions between A: *Fucus distichus* ssp. *edentatus* and B: ssp. *anceps*; C: extremely reduced specimen from highly exposed sites (Grímsey).

ACKNOWLEDGEMENT

Field work in the Icelandic coastal area was supported by yearly grants from the Icelandic Research Foundation (Vísindasjóður), Reykjavík.

REFERENCES

ANG, P.O. 1991. Natural dynamics of a *Fucus distichus* (Phaeophyceae, Fucales) population. — Mar. Ecol. Progr. Ser. 78: 71-85.

ANG, P.O. & DE WREEDE, R.E. 1993. Simulation and analysis of the dynamics of a *Fucus distichus* (Phaeophyceae, Fucales) population. — Mar. Ecol. Progr. Ser. 93: 253-265.

ANDERSON, C.I.H. & SCOTT, G.W. 1998. The occurrence of different morphotypes within a population of *Fucus spiralis*. — J. Mar. Biol. Assoc. U.K. 78: 1003-1006.

ARRONTES, J. 1993. The nature and distributional boundary of *Fucus serratus* on the north shore of Spain. — Mar. Ecol. Progr. Ser. 93: 183-193.

ÁSKELSSON, J. 1938. Quartärgeologische Studien auf Island. — Meddr. Dansk Geol.Forening 9: 300-319.

BAARDSETH, E. 1970. Synopsis of biological data on the knobbed wrack *Ascophyllum nodosum*. — FAO Fish. Synopsis 38. Rev.I.

BÉRARD-THÉRRIAULT, L. & A. CARDINAL. 1973. Importance de certains facteurs écologiques à la désiccation des Fucacées (Phaeophyceae). — Phycologia 12 : 14-52.

BÖRGESEN, F. 1902. Marine Algae. — In: E. Warming (ed.) Botany of the Faeroes based on Danish Investigations. Part II: 339-532.

BÖRGESEN, F. 1905. The algae vegetation of the Faeroese coasts with remarks on the phytogeography. — In: E. Warming (ed.) Botany of the Faeroes based on Danish investigations. Part III: 683-834.

BÄCK, S. 1992. Effects of salinity on growth of Baltic and Atlantic *Fucus vesiculosus*. — Brit. Phycol. Journ. 237: 39-47.

BÄCK, S. 1993. Morphological variation of northern Baltic *Fucus vesiculosus* along the exposure gradient. — Ann. Bot. Fenn. 30: 275-283.

CHAPMAN, R.A.O. 1989. Abundance of *Fucus spiralis* and ephemeral seaweeds in a high eulittoral zone: effects of grazers, canopy and substratum type. — Mar. Biol. 102: 565-572.

CHAPMAN, R.A.O. 1990. Competitive interactions between *Fucus spiralis* L. and *Fucus vesiculosus* L. (Fucales, Phaeophyta). — Hydrobiologia 204: 205-209.

COUSENS, R. 1981. Variation in annual production by *Ascophyllum nodosum* (L.) Le Jolis with the degree of exposure to wave action. — Proc. Int. Seaweed Symp 10: 253-258.

COUSENS, R. 1994. Estimation of annual production by the intertidal brown alga *Ascophyllum nodosum* (L.) Le Jolis. — Bot. Mar. 27: 217-227.

DALE, M. 1982. Phytosociological structure of seaweed communities and the invasion of *Fucus serratus* to Nova Scotia. — Can. J. Bot. 60: 2652-2658.

DAVIDSON, I.R. & PEARSON, G.A. 1996. Stress tolerance in intertidal seaweeds. — J. Phycol. 32: 197-211.

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

DIETRICH, G. 1957. Schichtung und Zirkulation der Irminger See im Juni l955. — Ber. Deutsche Komm. Meeresforsch. 14 (4): 255-312.

DIETRICH, G. 1964. Oceanic polar front survey. — Res. Geophys. 2: 291-308.

DRING, M.J. & BROWN, F.A.. 1982. Photosynthesis of intertidal brown algae during and after periods of emersion: a renewed search for physiological causes of zonation. — Mar. Ecol. Progr. Ser. 8: 301-308.

EDELSTEIN, T. & MCLACHLAN, J. 1975. Autecology of *Fucus distichus* ssp. *distichus* (Phaeophyceae, Fucales) in Nova Scotia, Canada. — Mar. Biol. 30: 305-324.

EDELSTEIN, T., GREENWELL, M., BIRD, C.J. & MCLACHLAN, J. l972/73. Investigations of marine algae of Nova Scotia .X. Distribution of *Fucus serratus* and some other species of *Fucus* in the Maritime Provinces. — NS Inst. Sci. 27: 33-42.

GIBB, D.C. 1950. A survey of the common fucoid algae on Scotish shores. — Journ. Ecol. 27: 364-382.

HANSEN, J.R. & INGÓLFSSON, A.. 1993. Patterns of species composition of rocky shore communities in sub-arctic fjords in eastern Iceland. — Mar. Biol. 117: 469-481.

HARTOG, C. VAN DEN. 1959. The epilithic algal communities occurring along the coasts of the Netherlands. — Wentia: 1-241.

HAWKINS, S.J. & HARTNOLL, R. G. 1985. Factors determining the upper limits of intertidal canopy-forming algae. — Mar. Ecol. Progr. Ser. 20: 265-271.

HOEK, C. VAN DEN. 1987. The possible significance of long-range dispersal for the biogeography of seaweeds. — Helgol. Meeresunters. 41: 261-272.

IRVINE, D.E.G. 1982. Seaweeds of the Faroes. l. The flora. — Bull. Br. Mus. Nat. Hist. Bot. 10 (3): 109-131.

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

JOHANESSEN, O.M. 1986. Brief overview of the physical, oceanography. — In: Hurdle, B.G. (ed.). The Nordic Seas: 103-127. Springer Verlag, Berlin.

JÓNSSON, H. 1903. The Marine Algae of Iceland. II. Phaeophyceae. — Bot. Tidskrift 25 (2): 141-195.

JÓNSSON, H. 1910. Om algevegetationen ved Islands kyster. — Bot. Tidskrift 30: 223-328.

JÓNSSON, H. 1912. The Marine Algal Vegetation. — The Botany of Iceland. I: 1-186.

JORDAN, A.J. & VADAS, R.L. 1972. Influence of environmental parameters on intraspecific variation in *Fucus vesiculosus*. — Mar. Biol. 14 (3): 248-252.

JORDE, I. 1966. Algal associations of a coastal area south of Bergen, Norway. — Sarsia 23: 1-52.

JORDE, I. & KLAVESTAD, N. 1963. The natural history of the Hardangerfjord. The benthonic algal vegetation. — Sarsia 9: 1-99.

KALVAS, A & KAUTSKY, L. 1993. Geographical variation in *Fucus vesiculosus* morphology in the Baltic and North seas. — European Journ. Phycol. 28: 85-91.

KALVAS, A. & KAUTSKY, L. 1998. Morphological variation in *Fucus vesiculosus* populations along temperature and salinity gradients in Iceland. — J. Mar. Biol. Ass. U.K. 78: 985-1001.

KAUTSKY, H., KAUTSKY, L., KAUTSKY N., KAUTSKY U. & LINDBLAD C. 1992. Studies on the *Fucus vesiculosu*s community in the Baltic Sea. — Acta Phytogeogr. Suecica 78: 33-48.

KESER, M., VADAS, R.L. & LARSON, B.R. 1981. Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting conditions in Maine, USA. — Bot. Mar. 24: 29-38.

KHFAJI, A.K. & NORTON T.. 1979. The effects of salinity on the distribution of *Fucus ceranoides*. — Estuarine Coastal Mar. Sci. 8: 433-439.

KNIGHT, M. & PARKE, M.. 1950. A biological study of *Fucus vesiculosus* and *Fucus serratus*. — J. Mar. Biol. Ass. U.K. 29: 439-514.

KRAUSE, W. 1986. The North Atlantic Current. — J. Geophys. Res. 91: 5061-5074.

KRISTENSEN, I. 1958. Surf influence on the thallus of fucoids and the rate of desiccation. — Sarsia 34: 69-82.

LONGHURST, A.G. 1998. Ecological Geography of the Sea. — Academic Press San Diego-London. 398 pp.

LUND, S. 1959. The marine algae of East Greenland. II. Geographical distribution. — Meddr. Grønland 156 (2): 1-72.

MALMBERG, S.A. 1962. Schichtung und Zirkulation in den südislandischen Gewässern. — Kieler Meeresforsch. 18: 3-28.

MALMBERG, S.A. 1984. Hydrographic conditions in the East Icelandic Current and sea ice in north Icelandic waters, 1970-1980. — Rapp. Réun. Cons. Int. explor. Mer 185: 170-178.

MALMBERG, S.A. 1985. The water masses between Iceland and Greenland. — Rit Fiskideildar 9: 127-140.

MALMBERG, S.A. & STEFÁNSSON, U.. 1972. Recent changes in the water masses of the East Icelandic Current. — Rapp. Réun. Cons. Int. Explor. Mer 162: 195-200.

MALMBERG, S.A. & KRISTMANNSSON, S.. 1992. Hydrographic conditions in Icelandic waters. 1980-1989. — ICES Marine Science Symposium 195: 75-92.

MCLACHLAN, J. 1974. Effects of temperature and light on the growth and development of embryos of *Fucus edentatus* and *Fucus distichus* subsp. *distichus*. — Can. Journ. Bot. 52: 943-951.

MCLACHLAN, J., CHEN, L.C.M. & EDELSTEIN, T.. 1971. The culture of four species of *Fucus* under laboratory conditions. — Can. Journ. Bot. 49: 1463-1469.

MUNDA, I.M. 1964a. The quantity and chemical composition of *Ascophyllum nodosum* (L.) Le Jol. along the coast between the rivers Ölfusa and Thjórsá (Southern Iceland). — Bot. Mar. 7 (l/4): 76-89.

MUNDA, I.M. 1964b. Observations of variations in form and chemical composition of *Fucus ceranoides* L. — Nova Hedwigia 8: 405-414.

MUNDA, I.M. 1975. Hydrographically conditioned floristic and vegetation limits in Icelandic coastal waters. — Bot. Mar. 18: 223-235.

MUNDA, I.M. 1976a. Some aspects of the benthic algal vegetation of the South Icelandic coastal area. — Res. Inst. Neðri Ás, Hveragerði, Iceland. Bull. 25: 1-69.

MUNDA, I.M. 1976b. The distribution of the *Halosaccion ramentaceum* (L.) J. Ag. associations in the Icelandic coastal area and their hydrographycally conditioned variations. — Bot. Mar. 19: 161-182.

MUNDA, I.M. 1977a. The benthic algal vegetation of the island of Grímsey (Eyjafjarðarsýsla, North Iceland). — Res. Inst. Neðri Ás, Hveragerði, Iceland. Bull. 28: 1-69.

MUNDA, I.M. 1977b. The structure and distribution of the *Gigartina stellata* (Stackh.) Batters and *Chondrus crispus* Stackh. associations in Icelandic waters. — Bot. Mar. 20: 291-301.

MUNDA, I.M. 1978. Survey of the benthic algal vegetaton of the Dýrafjörður, Nortwest Iceland. — Nova Hedwigia. 29(1/2): 281-403.

MUNDA, I.M. 1980. Survey of the benthic algal vegetation of the Borgarfjörður, Southwest Iceland. — Nova Hedwigia 32 (1/2): 855-927.

MUNDA, I.M. 1981. Tide pool associations of benthic algae in Icelandic waters. — Proc. 10th internat. Seaweed Symp. Gothenbourg 1980: 327-332.

MUNDA, I.M. 1983. Survey of the benthic algal vegetation of the Reyðarfjöðurr as a typical example of the East Icelandic vegetation pattern. — Nova Hedwigia. 37: 545-460.

MUNDA, I.M. 1985. General survey of the benthic algal vegetation along the Barðaströnd coast (Breiðafjörður, West Iceland). — Res. Inst. Neðri Ás, Hveragerði, Iceland. Bull. 44: 1-62.

MUNDA, I.M. 1987. Characteristic features of the benthic algal vegetation along the Snaefellsnes Peninsula (Southwest Iceland). — Nova Hedwigia. 44(3/4): 399-448.

MUNDA, I.M. 1992a. Hornstrandir — a conspicuous area of vegetation shift in the extreme Northwest of Iceland. — Acta Bot. Isl. 11: 17-88.

MUNDA, I.M. 1992b. Gradient in seaweed vegetation patterns along the North Icelandic coast, related to hydrographic conditions. — Hydrobiologia 242(3): 133-147.

MUNDA, I.M. 1992c. The gradient of the benthic algal vegetation along the eastern Icelandic coast. — Acta Phytogeogr. Suecica 78: 131-141.

MUNDA, I.M. 1994. The benthic algal vegetation of the Mjóifjörður, Eastern Iceland. — Netherlands Journal of Aquatic Ecology 28(1) : 35-49.

MUNDA, I.M. 1997. Survey of the benthic algal vegetation of the Steingrímsfjörður (Húnaflói, North Iceland). — Nova Hedwigia. 64 (3/4): 567-612.

MUNDA, I.M. 1999a. Survey of the benthic algal vegetation of the Berufjörður, southeastern Iceland. — Nova Hedwigia 69 (3/4): 473-516.

MUNDA, I.M. 1999b. The benthic algal vegetation of land-locked fjords in southeastern Iceland. —Hydrobiologia 393: 169-180.

NEILL, F.X. 1979. Sobre la biologia de *Ascophyllum nodosum* (L.) Le Jol., en Galicia. III. Biometria, crescimiento y produccion. — Inv. Pesq. 43: 501-518.

NEILL, F.X., JIMENEZ, C. & FERNANDEZ, J.A.. 1987. The forms of *Fucus spiralis* L. on the Canary Islands: discriminant and canonical analysis applied to define a new form. — Bot. Mar. 30: 27-32.

NIEMECK, R. & MATHIESON, A.C. 1976. An ecological study of *Fucus spiralis* L. — J. Exp. Mar. Biol. Ecol. 24: 33-48.

PEDERSEN, P.M. 1976. Marine, benthic algae from southernmost Greenland. — Meddr. Grønland 199 (3): 1-80.

POWELL, H.T. 1957a. Studies in the genus *Fucus* L. I. *Fucus distichus* L. emend. Powell. — J. Mar. Biol. Ass. U.K. 36: 407-432.

POWELL, H.T. 1957b. Studies in the genus *Fucus* L. II. Distribution and ecology of forms of *Fucus distichus* L. emend. Powell in Britain and Ireland. — J. Mar. Biol. Ass. U.K. 36: 663-693.

POWELL, H.T. 1963. Speciation in the genus *Fucus* and related genera. — In: Harding J.P. & Tebble, N.T. (eds.). Speciation in the Sea: 63-77.

PRICE, J.H. & FARNHAM, W.F. 1982. Seaweeds of the Faroes. 3. Open shores. — Bull. Br. Mus. Nat. Hist. (Bot). 10 (3): 153-225.

PRINTZ, H. 1926. Die Algenvegetation des Trondheimfjordes. — Skr. Norske Vidensk. Akad. Oslo, Mat. Nat. Kl. 5: 1-274.

RICE, E.L. & CHAPMAN, A.R.O. 1985. A numerical taxonomic study of *Fucus distichus* (Phaeophyta). — Journ. Mar. Biol. Ass. U.K. 65: 433-459.

RICE, E.L., KENCHINGTON, T.J. & CHAPMAN, R.A.O. 1985. Intraspecific, geographic-morphological variation patterns in *Fucus distichus* and *Fucus evanescens*. — Mar. Biol. 88: 207-215.

ROBERTSON, B. 1987. Reproductive ecology and canopy structure of *Fucus spiralis* (L.). — Bot. Mar. 30: 475-482.

ROBINSON, C.B. 1903. The distribution of *Fucus serratus* in America. — Torreya 3: 132-134.

ROSENVINGE, K.L. 1893. Grönlands Havalger. — Meddr Grönland 3: 765-98l.

RUGG, D.A. & NORTON, T.A. 1987. *Pelvetia canaliculata*, a seaweed that shuns the sea. — In: Crawford, R.M.M. (ed.). Plant life in aquatic and amphibious environment: 347-358.

RUSSELL, G. 1974. *Fucus distichus* communities in Shetland. — J. Appl. Ecol. 11: 679-684.

RUSSELL, G. 1979. Heavy receptacles in estuarine *Fucus vesiculosus*. — Estuarine and Coastal Mar. Sci. 9: 659-661.

RUSSELL, G. 1987. Spatial and environmental components of evolutionary changes: interactive effects of salinity and temperature on *Fucus vesiculosus* as an example. — Helgol. Meeresunters. 41: 371-376.

RUSSELL, G. & FIELDING A.H. 1981. Individuals, populations and communities. — Bot. Monogr. 17: 393-420.

SCHONBECK, M. & NORTON, T.A. 1978. Factors controlling the upper limits of fucoid algae on the shore. — Journ. Exp. Mar. Biol. Ecol. 31: 303-313.

SCHONBECK, M. & NORTON, T.A. 1979. Drought hardening in the upper shore seaweeds *Fucus spiralis* and *Pelvetia canaliculata*. — Journ. Ecol. 67: 687-696.

SCHONBECK, M. & NORTON, T.A. 1980. The effects on intertidal fucoid algae of exposure to air under various conditions. — Bot. Mar. 23: 141-147.

SIDEMAN, E.J. & MATHIESON, A.C. 1980. Morphological variation within and between natural populations of non-tide pool *Fucus distichus* (Phaeophyta) in New England. — J. Phycol. 21: 250-257.

SIDEMAN, E.J. & MATHIESON, A.C. 1983a. Ecological and genecological distinction of a high-intertidal dwarf form of *Fucus distichus* (L.) Powell. — J. Exp.. Mar. Biol. Ecol. 72: 171-188.

SIDEMAN, E.J. & MATHIESON, A.C. 1983b. The growth, reproductive phenology and longevity of non-tide pool *Fucus distichus* (L.) Powell in New England. — J. Exp. Mar. Biol. Ecol. 68: 111-127.

SIDEMAN, E.J. & MATHIESON, A.C. 1985. Morphological variation within and between natural populations of non-tide pool *Fucus distichus* (Phaeophyta) in New England. — J. Phycol. 21: 250-257.

SIGURÐSSON, H. 1966. Geology of the Setberg areas, Snæfellsnes. Western Iceland. — Soc. Sci. Islandica. Greinar 4: 53-135.

SCOTT, G.W., HULL, S.L., HORNBY, S.E., HARDY, C.F. & OWENS, J.P. 2001. Phenotypic variation in *Fucus spiralis* (Phaeophyceae): morphology, chemical phenotype and their relationship to the environment. — Eur. J. Phycol. 35: 43-50.

STEFÁNSSON, U. 1949. Influx of Atlantic water North of Iceland. — Ann. Biol. 5: 16-18.

STEFÁNSSON, U. 1962. North Icelandic waters. — Rit Fiskideildar 3: 1-269.

STEFÁNSSON, U. 1969. Sjávarhiti á siglingaleið umhverfis Ísland. In: Einarsson, M.Á. (ed.): Hafísinn: 131-149.

STEFÁNSSON, U. 1972. Near-shore fluctuations of the frontal zone southeast of Iceland. — Rap. Proc. Réun. Cons. Int. Explor. Mer 162: 201-205.

SUNDENE, O. 1953. The algal vegetation of the Oslofjord. — Norske Vidensk. Akad. Avh. 2: 1-244.

SVENDSEN, P. 1959. The algal vegetation of Spitsbergen. — Norsk Polarinstitut Skrifter 116: 1-47.

TAYLOR, W.R. 1962. Marine algae of the Northeastern coast of North America. — Ann Arbor: 1-509.

THORODDSEN, TH. 1891. Geologiske Iaktagelser paa Snæfellsnes og Omegnen av Faxa Bugten i Island. Kong. Svensk. Akad. Avh. 17.

THOM, R.M. 1983. Spatial and Temporal Patterns of *Fucus distichus* ssp. *edentatus* (de la Pyl.) Pow. (Phaeophyceae, Fucales) in central Puget Sound. — Bot. Mar. 26: 471-486.

TITTLEY, I., FARNHAM, W.F. & GRAY, P.W.G. 1982. Seaweeds of the Faroes. 2. Sheltered fjords and sounds. — Bull. Br. Mus. Nat. Hist. (Bot.) 10 (3): 133-151.

TOPINKA, J.A., TUCKER, L. & KORJEFF, W. 1981. The distribution of fucoid macroalgal biomass along central coastal Maine. — Bot. Mar. 24: 311-319.

WILCE R.T. 1959. The marine algae of the Labrador Peninsula and northwest Newfoundland (ecology and distribution). — Bull. Nat. Mus. Canada 158: 1-103.

ZINOVA, A.D. (1953). Opredelitelj byrih vodoroslej severnih morej SSSR. — Akad. Nauk Moskva-Leningrad: 1-224.

Note: During printing of the present work, the generic name of *Enteromorpha* was changed to *Ulva* following: Hayden H.S., Blomster, J., Maggs, C.A., Silva, P.C. Stanhope, M.J., & Waaland, R. (2003). Linnaeus was right all along: *Ulva* and *Enteromorpha* are not distinct genera. Eur. J. Phycol. 38: 277-294.