Response to Wave Exposure by Littoral Species in the Faroe Islands

Hvussu djórasløg í føroyskum firðum laga seg eftir aldubrotum

Grethe Bruntse[1], Tor Eiliv Lein[2], Ruth Nielsen[3] and Karl Gunnarsson[4]

1: Grethe Bruntse, Kaldbak Marine Biological Laboratory, FO-180 Kaldbak, Faroe Islands (present address: Kolstrup 44E, 6200 Aabenraa, Denmark). E-mail: Gbruntse@hotmail.com

2: Tor Eiliv Lein, Department of Fisheries and Marine Biology, University of Bergen, N-5020 Bergen, Norway. Tlf.: +47 5558 4480, Fax: +47 5558 4450, E-mail: tor.lein@ifm.uib.no

3: Ruth Nielsen, The Botanical Museum and Library, University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen K, Denmark. Tlf.: +45 3532 2185, Fax: +45 3532 2186, E-mail: ruthn@bot.ku.dk

4: Karl Gunnarsson, Marine Research Institute, Skúlagøtu 4, Reykjavík, Iceland. Tlf.: +354 552 0240, Fax: +354 5623790, E-mail: Karl@hafro.is

Úrtak

Henda kanning lýsir plantu- og djórasamfeløgini á klettastrondum niður á dýpi, har plantuvøksturin heldur uppat. Vit nýttu telduforritið Expon og resiprokka algoritmu til at kanna, hvussu 23 ymisk sløg laga seg eftir styrki á aldubrotum (polynomial) á 146 støðum. Av 7 ymiskum umhvørvisligum faktorum tykjast aldubrot at vera orsøk til meginpartin av frávikum í savnaða tilfarinum, tá ið ein fyribils korrespondansu-analysa (CCA) varð gjørd. Signifikant aftursvar góvu *Aglaothamnion setositum, Alaria esculenta, Coralina officinalis, Fucus distichus* ssp. *anseps, Himanthalia elongata, Mastocarpus stellatus, Polysiphonia stricta* og *Porphyra umbilicalis,* sum mest eru at finna á teimum ábærastu støðunum, og *Ascophyllum nodosum, Cladophora rupestris, Pelvetina canaliculata, Verrucaria mucosa, Littorina obtusata* og *Nucella lapillus,* sum vóru vanligast á kyrrustrondum, og eisini *Semibalanus balanoides,* ið mest er av á miðalbardum strondum. Ein lívfrøðiligur stigi í mun til aldubrotsstyrki varð gjørdur út frá rásmyndum fyri hesi 15 sløgini. Stigin er galdandi fyri klettastrendur, har ið munurin millum flóð og fjøru er er meira enn 40 í miðal, og kann nýtast at forklára útbreiðslu av ráðandi og ofta fyrikomandi sløgum fram við strendurnar. Harumframt verður í strikumyndum lýst loddrætt útbreiðsla av plantu- og djóralívi á strondum, sum vórðu vald eftir styrki á aldubrotum. Okkara kanningar samsvara við aðrar kanningar av útbreiðslu av plantum og dýrum fram við føroysku strendurnar. Um samanborið verður við úrslit frá bretsku oyggjunum og suðurvesturstrond Noregs, er størsti munurin, at *Laminaria digitata* og *Alaria esculenta* eru at finna á vardum strondum, at tættur vøkstur av *Fucus serratus* ikki er at finna, og at fleiri sløg eru at finna á øllum strondum, sama hvussu ábært har er.

Abstract

This investigation describes the rocky shore communities in the littoral zone of the Faroe Islands and their response to wave exposure. We utilised the Expon software and its reciprocal algorithm to develop response functions (polynomials) to wave exposure for species based on the abundance of 23 dominant species at 146 stations. Among the seven environmental factors analysed, wave exposure explained most of the variance in the data set according to a preliminary correspondence analysis (CCA). A significant response to wave exposure was obtained for *Aglaothamnion sepositum, Alaria esculenta, Corallina officinalis, Fucus distichus* ssp. *anceps, Himanthalia elongata, Mastocarpus stellatus, Polysiphonia stricta* and *Porphyra umbilicalis,* predominantly found on exposed shores; for *Ascophyllum nodosum, Cladophora rupestris, Pelvetia canaliculata, Verrucaria mucosa, Littorina obtusata* and *Nucella lapillus,* predominantly found on sheltered shores; and *Semibalanus balanoides,* with the greatest abundance on moderately exposed shores. A biological exposure scale was developed for the area based on the response curves for these 15 species. The scale is valid for rocky shores in the Faroe Islands with mean tidal amplitude larger than 0.40 m, and can be used to account for the distribution of dominant and frequently occurring species in the littoral zone. This is supplemented with diagrams illustrating the vertical distribution and abundance of species at localities selected to represent different wave exposure. Our studies confirm the descriptions of the distribution of littoral organisms in earlier works about the Faroe Islands. Compared to the British Isles and the south-west coast of Norway, the most striking differences are the abundant growth of *Laminaria digitata* and *Alaria esculenta* on sheltered shores, the lack of dense populations of *Fucus serratus* and the frequent occurrence of many species over the whole exposure range.

Introduction

Previous studies of the littoral marine algae and invertebrates of the Faroe Islands have focused either on the occurrence of species and their distribution or on qualitative descriptions of communities (Børgesen, 1902; 1905; Lemche, 1929; Stephensen, 1929; Spärck and Thorsen, 1933; Høpner Petersen, 1968; Irvine, 1982; Price and Farnham, 1982; Tittley *et al.*, 1982).

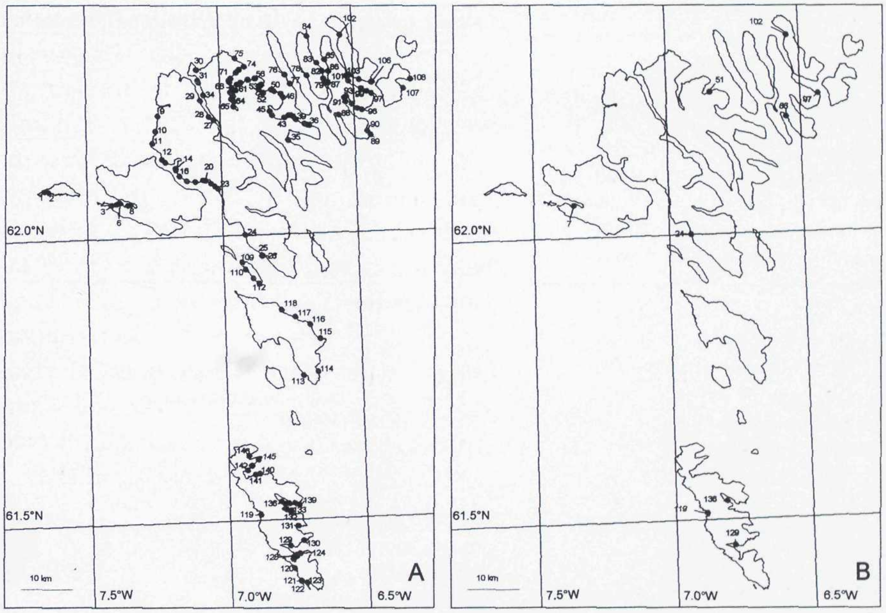
Wave action is known to affect plant and animal communities on rocky shores, but wave exposure is difficult to calculate from physical data in areas of complicated bathymethric conditions. Several researchers have developed scales for assessment of exposure based on species composition changes in relation to wave exposure (e.g. Crisp and Southward, 1958; Ballantine, 1961; Dalby *et al.*, 1978). There is a risk of the reasoning becoming circular when biological aspects are interpreted in terms of biological exposure values, as pointed out by Raffaelli and Hawkins (1996). However, when used with caution, such scales may be useful in describing changes in rocky shore communities in relation to wave exposure, provided it is the predominant environmental variable. In the present work, a biological exposure scale is developed for the hard-bottom communities of the Faroe Islands. The scale is used to account for the distribution of dominant and frequently occurring species in the littoral zone. This is supplemented with information on the vertical distribution and abundance of species at nine localities selected to have different wave exposure values.

Study Area

The Faroe Islands is situated in the North Atlantic between 61°33' and 62°40'N and 6°25' and 7°68'W (Fig. 1). A major part of the shoreline consists of basaltic bedrock. The tidal amplitude varies within short geographical distances, being virtually non-existent in the Tórshavn area (not included in our study), and reaching approximately 2.5 m in the outer parts of the islands to the west. Water temperature ranges from a monthly average of 6°C in February to 10°C in October and air temperature from 4°C in February to 11°C in August (Lysgaard, 1969; Hansen, 1997).

Materials and Methods

The exposure scale was developed according to the technique described by Dalby *et al.* (1978) and calculated utilising Expon software (Årrestad and Lein, 1993). The technique uses a reciprocal algorithm to develop, alternately, response functions (polynomials) for species in relation to



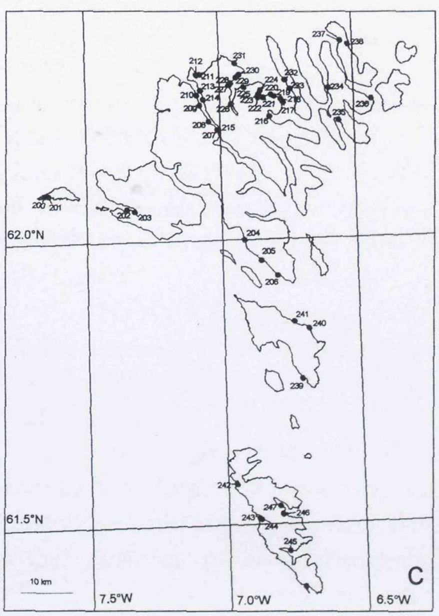


Fig. 1. The Faroe Islands, sites for studies of the littoral communities. A: The 146 stations where an abundance of the 23 dominant species was observed. B: The nine selected stations where the vertical distribution of species was recorded. C: The 48 localities where frequently occurring algae were collected. Stations on each island are numbered in anticlockwise sequences.

Mynd 1. Støðirnar, har ið strandarsamfeløgini vórðu kannað. A: Støðir, har ið nógv var til av teimum valdandi (dominerandi) sløgunum. B: Tær 9 støðirnar, har loddrætt útbreiðsla hjá teimum ymsu sløgunum varð staðfest. C: Tær 48 støðirnar, har ið innsavningar vórðu gjørdar av vanliga fyrikomandi algum. Kanningarstøðirnar eru talsettar móti urinum, fyri hvørja oyggj sær.

Lichens / Skónir	
70	> 80% cover
60	50 - 80% cover
50	20 - 50% cover
40	1 - 20% cover
30	Big, separated patches
20	Small, separated patches
10	Only 1 - 2 patches

***Patella spp.* and *Littorina spp.* / Fliður og kúvingar**	
70	> 200 pr m^2
60	100 - 200 pr m^2
50	50 - 100 pr m^2
40	10 - 50 pr m^2
30	1 - 10 pr m^2
20	1 - 10 pr m^2
10	< 1 pr m^2

Algae / Algur	
70	> 90% cover
60	50 - 90% cover
50	20 - 50% cover
40	5 - 20% cover
30	Les than 5%, zone clear
20	Single plants, zone unclear
10	Only 1 - 2 plants

Other snails / Aðrir sniglar	
70	> 100 pr m^2
60	50 - 100 pr m^2
50	10 - 50 pr m^2
40	1 - 10 pr m^2, locally sometimes more
30	< 1 pr m^2, locally sometimes more
20	Always less than 1 pr m^2
10	< 1 pr 10 m^2

Barnacles / Gjar	
70	More than 5 pr cm^2
60	3 - 5 pr cm^2
50	1 - 3 pr cm^2
40	10 - 100 pr dm^2
30	1 - 10 pr dm^2
20	1 - 100 pr m^2
10	Less than 1 pr m^2

Mussles / Skeljadýr	
70	> 80% cover
60	50 - 80% cover
50	20 - 50% cover
40	Big patches, but less than 20% cover
30	Many single individuals or small patches
20	Single individuals, no patches
10	< 1 pr m^2

Table 1. *Scales of abundance for different groups of littoral organisms according to Årrestad and Lein (1993). Values are comparable with "Abundance Scale" from Dalby et al. (1978). 70: extra abundant; 60: super abundant; 50: abundant; 40: common; 30: frequent; 20: occasional; 10: rare.*

Talva 1. Nøgd av ymiskum plantu/djórabólkum eftir Årestad og Lein (1993). Virðini kunnu samanberast við "Abundance scale" hjá Dalby o.ø. (1978). 70: alráðandi, 60: ovurvanlig, 50: sera vanlig, 40: vanlig, 30: rættiliga vanlig, 20: av og á, 10: sjáldsom.

wave exposure and exposure values for stations. The method is based on the fact that species respond differently to wave exposure (Dalby *et al.*, 1978) and the assumption that wave action is the strongest physical factor influencing the species abundance. For each station, the data input comprises abundance values for species and an approximate exposure value ('first exposure value' – FEV). In total, data from 146 stations were compiled. The abundance of the following 23 dominant species was recorded: The algae *Aglaothamnion sepositum* (Gunnerus) Maggs & Hommers., *Alaria esculenta* (L.) Grev., *Ascophyllum nodosum* (L.) LeJol., *Cladophora rupestris* (L.) Kütz., *Corallina officinalis* L., *Fucus distichus* L. ssp. *anceps* (Harv. & Ward ex Carruthers) Powell, *F. evanescens* C. Agardh, *F. spiralis* L., *F. vesiculosus* L., *Himanthalia elongata* (L.) Gray, *Laminaria digitata* (Huds.) J.V. Lamour., *L. saccha-*

rina (L.) J.V. Lamour., *Mastocarpus stellatus* (Stackh. in With.) Guiry in Guiry *et al.*, *Palmaria palmata* (L.) Kuntze, *Pelvetia canaliculata* (L.) Decne. & Thur., *Polysiphonia stricta* (Dillwyn) Grev., *Porphyra umbilicalis* (L.) J. Agardh; the lichen *Verrucaria mucosa* Wahlenb.; and the invertebrates *Littorina obtusata* (L., 1758), *Mytilus edulis* L., 1758, *Nucella lapillus* (L., 1758), *Patella vulgata* L., 1758, and *Semibalanus balanoides* (L., 1767). These species were easy to recognise and quantify according to a defined abundance scale (Table 1) and did not show bio-geographic boundaries within the area.

The 146 stations were selected to cover the main islands and the range of wave exposure (Fig. 1A). Many stations were reached from the sea by use of a Zodiac. Areas with unstable boulders and stones, or a tidal amplitude less than 0.40 m were not included in the study. With small tidal amplitude, the atmospheric pressure has a relatively large effect on the water level, thereby causing irregular exposure to air and often prolonged desiccation. This may have greater and more varied effects on the structure of the biota of these shores than wave action. For each station, a physical exposure (PE) value was calculated by using the percentage of wind (W) stronger than 15 m/sec and fetch to the nearest point of land in each of 32 sectors. The fetch was rated in three categories: local effect: 0.5 - 7.5 km (multiplier 1), fjord effect: 7.5 - 100 km (multiplier 10); ocean effect: >100 km (multiplier 100) (Sjøtun *et al.*, 1993). The calculated values were transposed into a scale from 1 (exposed) to 8 (sheltered) for use as first exposure values (FEV) in Expon.

A station was defined as an area of the coast with a length of 8 m and a vertical distribution from the lowest water level to the upper limit of the 23 dominant species listed above. The height of a station was divided into equal intervals, each corresponding to 1/10 of the mean tidal amplitude in the area. The abundance of each species was recorded at the interval where it had its highest value, according to the simplified method described and tested by Kruskopf and Lein (1998). The abundance scales used were originally defined by Crisp and Southward (1958) and further modified by Ballantine (1961), Dalby *et al.* (1978) and Årrestad and Lein (1993) (Table 1). Also recorded at each station were substrate, slope, aspect of shore, tidal amplitude, tidal current and topography using scales defined in Bruntse *et al.* (in press). Rock pools and backsides of boulders, etc. with local shelter were avoided. The major part of the fieldwork was carried out during July - September 1995, May - November 1996 and May - October 1997.

Before running Expon, the data were subjected to a correspondence analysis (CA) and canonical correspondence analysis (CCA) (Ter Braak, 1986) to assess the importance of exposure (FEV) and the other recorded environmental variables. Canonical correspondence analysis (CCA) is a technique specifically designed to examine relationships between species and environmental factors (Ter Braak, 1986; Ter Braak and Verdonschot, 1995). Following the

CCA, species response polynomials were developed using Expon by the reciprocal process described by Dalby *et al.* (1978). The recorded abundance of each species and the FEV for each station were applied to generate the first polynomials. From these first polynomials new exposure values for each station were calculated. These are values where the observed abundance for each species and the estimated abundance fit best for all species. In the Expon algorithm, mean residuals (sum of square residuals/number of species) were plotted for all possible 1/4 steps on the biological exposure scale (0-9). The new exposure values selected corresponded to the minimum, mean residual values. The reciprocal algorithm was continued until only 2.7% of the stations changed by less than 1/4 of a step on the exposure scale. This is within the requirement of less than 10% recommended by Årrestad and Lein (1993) and Kruskopf and Lein (1998). The final species response polynomials were then fitted and the estimated abundance for each species listed for each biological exposure value (BEV) from 0 (exposed) to 9 (sheltered). Handling of missing data, 0-values, and the polynomial regression solution were adapted or slightly modified from Dalby *et al.* (1978) as given by Årrestad and Lein (1993).

Diagrams illustrating the abundance of the 23 dominant species and other species, which covered more than 1% of the area, were made of nine stations representing different categories of exposure (Fig. 1 B). The abundance was recorded at intervals of 12.5 cm from the upper limit of *Semibalanus balanoides* to the lowest water level. The records were correlated to MLWS (mean low water spring) according to the tide table for the Faroe Islands (Anon., 1996) and the air pressure. The slope of the shore was measured in 25-cm vertical steps by use of a surveyor's level and a staff.

General collections of algae were made at 49 localities, from the low-water level to as high up as marine algae were found (Fig. 1C). These localities were grouped into three categories of exposures: exposed (0-2.75), moderately exposed (3-5.75) and sheltered (6-9), based on the calculated biological exposure values (BEV). The relation between BEV and the physical exposure value (PE) (linear regression, BEV = -1.02 lnPE+7.01, $R^2 = 0.56$) was used to estimate exposure for localities not included in the calculation of the biological exposure scale (Fig. 1 B, C). Each collection covered a shore length of 8-50 m, which did not always correspond exactly to the stations used for the development of the biological exposure scale. An effort was made to collect all species from all microhabitats. Only species of Bangiophyceae, Fucophyceae and Chlorophyceae, which were found at a minimum of 33% of the localities within any one exposure group, are presented. Herbarium specimens are deposited at the Botanical Museum, Copenhagen; the Marine Research Institute, Reykjavík and the Natural History Museum, Tórshavn.

Results

The area studied was heterogeneous in respect to several physical factors. It is important when analysing species response to a single environmental factor, such as wave exposure, that this factor has the strongest influence on the data. The data matrix, therefore, was tested using CCA. This preliminary test showed that wave exposure (FEV) was closely related to axis 1, which explained 21.0% of the species variance. Cumulative percentage variance of axes 1-4 was 24.4%, indicating that the other recorded variables included in the analysis were of little importance. Therefore, FEV was the strongest of the physical variables known to influence species abundance. Further examination of the unexplained variance (in correspondence analysis) did not suggest that other unknown factors were of major importance. Species response to wave exposure and biological exposure values (grade) (BEV) for each station (Table 2) were then calculated using Expon (Årrestad and Lein, 1993).

The abundance of 15 dominant species showed a significant correlation (polynomial regression, $P<0.05$) with wave exposure (BEV) and response polynomials were obtained (Fig. 2). The abundance value for each of the 15 species at different biological exposure values (grade) (BEV), the level of significance, and the R^2 value (coefficient of determination) are shown in Table 3. *Porphyra umbilicalis*, *Polysiphonia stricta*, *Fucus distichus* ssp. *anceps* and *Cladophora rupestris* were stable in their response to wave exposure as shown by the high R^2 values. *Ascophyllum nodosum* and *Verrucaria mucosa* have low R^2 values (Table 3). These species have a patchy occurrence and were missing at several stations where they were expected to occur. Eight of the 23 dominant species examined did not show an unequivocal response to changes in wave exposure. These were not included in the final Expon calculation, but were later plotted against the biological exposure value (BEV) for each station (Fig. 3). *Laminaria digitata*, *Palmaria palmata*, and *Patella vulgata* had a more or less even distribution throughout the exposure range, whereas *Fucus spiralis* and *F. evanescens* were only found on the moderately exposed to sheltered coasts, and *L. saccharina* and *F. vesiculosus* only on sheltered coasts. Even though some of these species seemed to respond to change in wave exposure, the species response polynomials were not significant probably because of a patchy distribution of these species and/or the influence of some physical factors or biological interactions not accounted for in this study.

Abundance of species in relation to height on the shore is shown in Fig. 4, A-I. The MLWS and MHWS are indicated on the diagrams for comparison. The identified species, with a frequency of occurrence of at least 33% in any one of the three exposure groups, are listed in Table 4.

The species predominantly found on exposed coasts were *Aglaothamnion sepositum*, *Alaria esculenta*, *Himanthalia elongata*, *Polysiphonia stricta* and *Porphyra umbilicalis*. Most species found at these localities extended high above MHWS (Fig. 4, A-D). *Fucus distichus* ssp. *anceps* was not recorded at any of the profiles given in Fig. 4, but was found elsewhere at exposed localities (Fig. 2) in association with *P. umbilicalis*. *Lomentaria articulata* occurred

St.no	StF	PE	FEV	BEV
1	sta 165	132.2	1	1.00
2	sta 166	188.0	1	0.75
3	sta 65	14.0	4	5.50
4	sta 64	53.5	2	4.50
5	sta 63	1.9	7	5.75
6	sta 62	2.1	7	6.75
7	sta 60	41.1	2	7.00
8	sta 59	1.7	7	8.50
9	sta 158	307.3	1	2.50
10	sta 157	309.0	1	0.75
11	sta 156	283.0	1	1.00
12	sta 68	17.5	4	6.00
13	sta 67	4.6	5	7.00
14	sta 121	3.3	6	7.00
15	sta 122	4.4	5	8.25
16	sta 123	4.4	5	8.75
17	sta 124	5.2	4	7.75
18	sta 125	4.6	5	6.25
19	sta 126	5.2	4	2.75
20	sta 127	6.2	4	2.75
21	sta 128	20.3	3	2.00
22	sta 129	46.1	2	1.75
23	sta 130	73.4	2	1.75
24	sta 7	104.3	1	0.50
25	sta 6	39.0	3	4.25
26	sta 5	16.8	4	2.50
27	sta 58	1.3	8	9.00
28	sta 79	1.2	8	9.00
29	sta 80	1.6	7	9.00
30	sta 1	47.2	2	3.25
31	sta 72	42.1	2	4.50
32	sta 73	42.1	2	4.25
33	sta 74	42.1	2	5.00
34	sta 76	4.3	5	8.75
35	sta 70	11.8	4	4.00
36	sta 102	1.7	7	4.00
37	sta 103	3.3	6	4.50
38	sta 104	14.6	4	4.75
39	sta 105	9.6	4	7.00
40	sta 106	10.6	4	3.75
41	sta 107	3.8	6	4.25
42	sta 108	4.8	5	6.75
43	sta 109	3.2	6	7.00
44	sta 110	1.4	8	5.50
45	sta 111	1.7	7	6.75
46	sta 81	18.7	4	4.50
47	sta 82	17.3	4	3.25
48	sta 83	17.3	4	2.75
49	sta 84	31.0	3	2.75
50	sta 85	26.1	3	3.00

St.no	StF	PE	FEV	BEV
51	sta 92	3.9	6	4.50
52	sta 91	3,0	6	6.50
53	sta 90	1.8	7	5.50
54	sta 88	1.8	7	5.75
55	sta 89	2.6	6	6.25
56	sta 95	46.4	2	3.00
57	sta 96	46.4	2	3.25
58	sta 93	26.6	3	4.25
59	sta 94	26.6	3	4.75
60	sta 101	15.5	4	4.25
61	sta 66	4.7	5	5.00
62	sta 115	3.7	6	3.75
63	sta 114	4.3	5	6.25
64	sta 113	1.1	8	7.50
65	sta 120	0.3	8	9.00
66	sta 119	0.8	8	7.25
67	sta 118	1.8	7	5.25
68	sta 117	2.4	7	5.25
69	sta 116	3.1	6	3.50
70	sta 75	3.0	6	3.75
71	sta 100	4.0	6	3.00
72	sta 99	4.0	6	2.75
73	sta 98	4.4	5	2.25
74	sta 97	4.4	5	1.75
75	sta 2	73.1	2	1.75
76	sta 86	78.0	2	2.50
77	sta 87	33.8	3	2.00
78	sta 19	4.1	5	4.00
79	sta 20	1.7	7	8.50
80	sta 47	1.5	7	7.00
81	sta 48	1.4	8	7.25
82	sta 49	8.4	4	6.50
83	sta 50	23.2	3	1.50
84	sta 169	59.8	1	1.25
85	sta 51	4.5	5	3.00
86	sta 52	4.3	5	5.25
87	sta 53	3.9	6	8.00
88	sta 32	21.2	3	6.50
89	sta 36	153.7	1	4.25
90	sta 37	32.4	3	4.50
91	sta 38	11.0	4	4.25
92	sta 30	0.4	8	7.00
93	sta 31	4.3	5	6.50
94	sta 33	4.5	5	3.25
95	sta 34	4.6	5	5.25
96	sta 35	71.2	2	4.50
97	sta 43	11.0	4	5.25
98	sta 44	2.6	6	4.25
99	sta 45	1.7	7	5.25
100	sta 46	1.6	7	6.00

St.no	StF	PE	FEV	BEV
101	sta 22	2.4	7	6.75
102	sta 21	84.3	2	0.75
103	sta 39	4.6	5	6.50
104	sta 40	3.8	6	5.25
105	sta 41	37.8	3	3.00
106	sta 42	43.5	2	3.50
107	sta 167	144.1	1	0.75
108	sta 168	152.3	1	0.75
109	sta 152	269.7	1	2.25
110	sta 153	338.4	1	0.25
111	sta 154	257.2	1	1.25
112	sta 155	190.3	1	0.75
113	sta 163	96.7	2	0.50
114	sta 162	129.2	1	1.00
115	sta 71	47.9	2	5.25
116	sta 161	71.0	2	3.50
117	sta 160	67.0	2	4.00
118	sta 159	41.8	2	3.25
119	sta 15	283.8	1	2.00
120	sta 13	354.3	1	4.00
121	sta 12	451.3	1	3.00
122	sta 11	439.4	1	1.25
123	sta 14	234.4	1	2.25
124	sta 133	13.2	4	2.00
125	sta 132	4.2	5	6.25
126	sta 131	4.3	5	7.00
127	sta 135	0.6	8	9.00
128	sta 134	1.7	7	6.00
129	sta 151	3.8	6	6.00
130	sta 150	44.3	2	3.00
131	sta 149	11.9	4	6.25
132	sta 17	0.4	8	7.50
133	sta 146	2.0	7	8.75
134	sta 147	3.2	6	3.50
135	sta 18	0.6	8	9.00
136	sta 148	1.0	8	9.00
137	sta 143	4.8	5	6.25
138	sta 144	25.2	3	4.25
139	sta 145	20.3	3	5.25
140	sta 140	26.7	3	3.50
141	sta 141	22.3	3	1.25
142	sta 136	24.5	3	4.50
143	sta 138	34.7	3	1.75
144	sta 137	34.7	3	2.25
145	sta 139	30.5	3	1.75
146	sta 142	13.8	4	2.25

St.no	StB	(=St.no)	BEV
200	F971784	1	1.00
201	F971783	2	0.75
202	F971781,F971764	6	6.75
203	F951288,F951289		4.70
204	F971759,F971768	24	0.50
205	F951174,F961352,F961624	26	2.50
206	F951142,F961349		9.00
207	F951183		8.25
208	F961686	28	9.00
209	F961687	29	9.00
210	B041564		8.00?
211	B071565		3.00
212	F961353		3.25
213	F971771,F971765		7.00
214	F961684	34	8.75
215	F961682		7.5
216	F951297	45	6.75
217	F961688	46	4.50
218	F961689	47	3.25
219	F961690	49	2.75
220	F961691	50	3.00
221	F971766,F971773	51	4.50
222	F961696	53	5.50
223	F951280,F951281		7.00
224	F961697	54	5.75
225	F951187		4.25
226	F951272	66	7.25
227	F961683	70	3.75
228	F961703	71	3.00
229	F961702	72	2.75
230	F961701	73	2.25
231	F940034,F961350,F961351	75	1.75
232	F961692	76	2.50
233	F961693	77	2.00
234	F961657	87	8.00
235	F971762,F971777	88	6.50
236	F971779,F971763	97	5.25
237	F971761,F971775	102	0.75
238	F940035		3.00
239	F971723	113	0.50
240	F971721	116	3.50
241	F971720	117	4.00
242	F940016		2.00?
243	F971760	119	2.00
244	F961364		9.00
245	F971767,F971850	129	6.00
246	F940024		5.00
247	F971851,F971756	136	9.00

Table 2. *Comparison between exposure values for the various stations. PE (physical exposure value), FEV (first exposure value), BEV (biological exposure value), StF (Fig. 1A) and StB (Fig. 1C) (original station numbers).*

Talva 2. Samanbering av ábærisstigum fyri tær ymisku støðirnar. PE: Alisfrøðiligur áabærisstigi. BEV: Lívfrøðiligur ábærisstigi. StF (mynd 1A) og StB (mynd 1B) tey upprunaligu støðnumrini.

in dense populations on moderately exposed shores (Fig. 4, C-F).

The species only or predominantly found on sheltered coasts were *Ascophyllum nodosum*, *Cladophora rupestris*, *Pelvetia canaliculata* and *Verrucaria mucosa*. Associated with these were *Polysiphonia lanosa* and *Littorina obtusata* with the endozoic *Tellamia contorta*. Other species occurring mainly on sheltered coasts were *Chondrus crispus*, *Chordaria flagelliformis*, *Enteromorpha compressa*, *Fucus vesiculosus*, *Nucella lapillus* and *Pilayella littoralis* (Figs. 2, 3, Table 4). Most species recorded on sheltered shores did not extend much above the MHWS (Fig. 4, F-I).

A number of species occurred at all grades of wave exposure. Among them were *Corallina officinalis* and *Mastocarpus stellatus,* although their greatest abundance was observed on exposed coasts. *Semibalanus balanoides* was also found at all exposure grades, but had the greatest abundance on moderately exposed coasts (Fig. 2). *Palmaria palmata* was found in almost equal abundance throughout the whole exposure range (Fig. 3), but sometimes had a patchy occurrence and was often observed in large and dense stands in paths of running water. *Patella vulgata* was observed in numbers of 50 - 100 individuals per m^2 in most areas. Other species frequently found at all exposure grades were *Acrochaetium secundatum*, *Acrosiphonia arcta*, *Blidingia minima*, *Ceramium nodulosum*, *Enteromorpha intestinalis*, *E. linza* and *Ulva lactuca* (Table 4).

By coincidence, *Balanus balanus* (L., 1758), *Gibbula cineraria* (L., 1758), *Littorina saxatilis* (Olivi, 1792) and *Ceramium pallidum* (Naegeli ex Kuetz., Maggs & Hommers.) occurred at some of the localities selected for observation of vegetation profiles, but were not among the dominant species or frequently occurring algae.

Discussion

The major advantage of biological exposure scales is that the abundance of long-lived species represents an integration of conditions over many years, thus reflecting all local physical factors and biological interactions (Raffaelli and Hawkins, 1996). The reciprocal algorithm used in Expon for the development of the final species polynomials assigns exposure values to the stations based on the abundance of dominant species. The changes in the exposure grade during the process may be interpreted as effects of local conditions on wave exposure, as long as the influence of other environmental variables (e.g. instability of the substrate) is negligible. As a consequence of this, the final species polynomials based on the biological exposure values (BEV) may better reflect the effects of exposure on the littoral species than similar curves based on physical exposure values (PE). Some localities on the open shore of the Faroe Islands had a lower or higher BEV than would be expected from PE calculations, as is also indicated by the relatively low regression coefficient (0.56). Local bathymetric conditions or wave refraction, not accounted for in the calculations of PE, can explain some of the differences. Other factors not included in our data set may also have contributed to the species variation, as

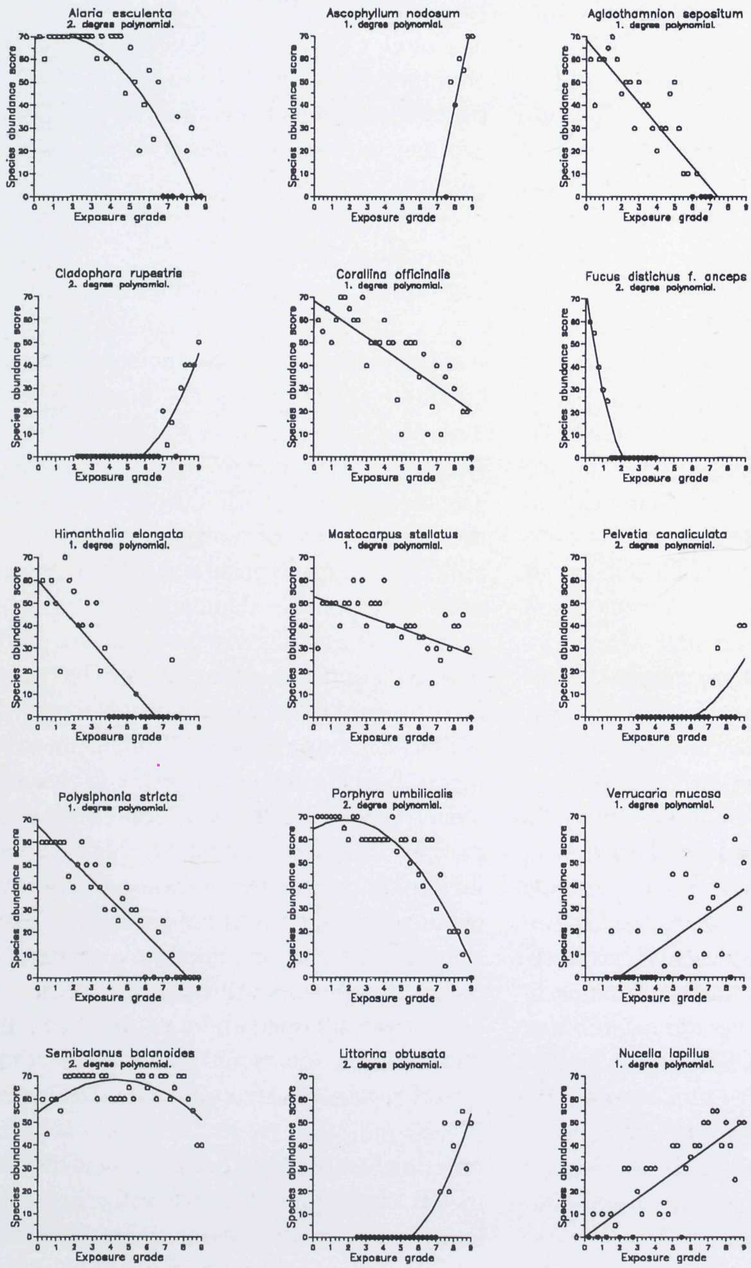


Fig. 2. Response polynomials of 15 dominant species, which are correlated (P<0.05) to wave exposure. X-axis: Biological exposure value (grade) (BEV) (0: exposed; 9: sheltered). Y-axis: Species abundance values as given in Table 1.

Mynd 2. Response polymialir fyri 15 sløg, sum mest var til av, í mun til aldubrot (P<0.05). X-ásin: Lívfrøðiliga virðið á brotunum (stig) (BEV) (0: ábært, 9: í lívd). Y-ásin: Virðið á nøgd av sløgum, sum nevnd verða á Talvu 1.

	Exposed								Sheltered			
Biological exposure grade												
	0	1	2	3	4	5	6	7	8	9	P	R^2
Aglaothamnion sepositum	65	55	50	40	30	20	10	0	0	0	***	0,759
Alaria esculenta	65	70	65	65	55	50	35	25	5	0	***	0,775
Ascophyllum nodosum	0	0	0	0	0	0	0	0	35	70	*	0,017
Cladophora rupestris	0	0	0	0	0	0	0	10	25	40	***	0,836
Corallina officinalis	65	60	55	50	45	40	35	30	25	20	***	0,557
Fucus distichus f. anceps	70	25	0	0	0	0	0	0	0	0	***	0,940
Himanthalia elongata	55	50	40	30	20	10	5	0	0	0	***	0,679
Mastocarpus stellatus	50	50	45	40	40	35	35	30	30	25	***	0,325
Pelvetia canaliculata	0	0	0	0	0	0	0	0	10	25	**	0,442
Polysiphonia stricta	65	55	50	40	35	25	15	10	0	0	***	0,876
Porphyra umbilicalis	60	65	65	65	60	55	45	35	20	5	***	0,846
Verrucaria mucosa	0	0	0	5	10	15	20	25	30	35	***	0,386
Littorina obtusata	0	0	0	0	0	0	0	15	30	50	***	0,790
Nucella lapillus	0	5	10	15	20	25	30	35	45	50	***	0,632
Semibalanus balanoides	50	60	60	65	65	65	65	60	55	50	***	0,350

Table 3. *Abundance value for each of the 15 dominant species at different biological exposure values (BEV). P = level of significance; *** < 0.001 ; ** < 0.01; * < 0.1,* R^2 *= coefficient of determination.*

Talva 3. Nøgdarstig fyri hvørt av teimum 15 sløgunum, sum mest var til av, í mun til lívfrøðiliga stigan, ið er gjørdur í mun til styrki av aldubrotum (BEV). P = signifikansur. *** < 0.001, ** < 0.01, * < 0.1. R2 = ásetingarstuðul

the total explained variance in the CCA analyses was less than 25%. Examples of such factors that may have increased variance in our data include the local influence of rainwater, heterogeneous texture of the substrate, and biological interactions.

The biological exposure scale is relative and directly applicable only to the area where it was developed, although some cautious comparisons can be made with other areas. Species polynomials have been established with the same method for several areas of the Norwegian coast (Dalby *et al.*, 1978; Årrestad and Lein, 1993; Kruskopf and Lein, 1997). In the Norwegian studies, some species showed slightly different distribution patterns from one area to another, *i.e.,* some showed a gradient from south to north. Compared to the western coast of Norway, Sogn and Fjordane County (Kruskopf and Lein, 1997), the response polynomials developed for the Faroe Islands were similar for *Corallina officinalis* and *Verrucaria mucosa*, whereas, they were slightly different for other species. *Alaria esculenta, Mastocarpus stellatus, Ceramium schuttleworthianum, Aglaothamnion sepositum,* and to a lesser degree, *Himanthalia elongata* seemed to grow in more sheltered sites in the Faroe Islands than in Sogn and Fjordane. Price and Farnham (1982) made similar observations when comparisons were made with English shores.

The climate of the Faroe Islands is strictly oceanic with little difference in winter and summer temperatures and high humidity caused by frequent rain and fog. Therefore, the effect of desiccation on littoral algae is less profound than in areas further

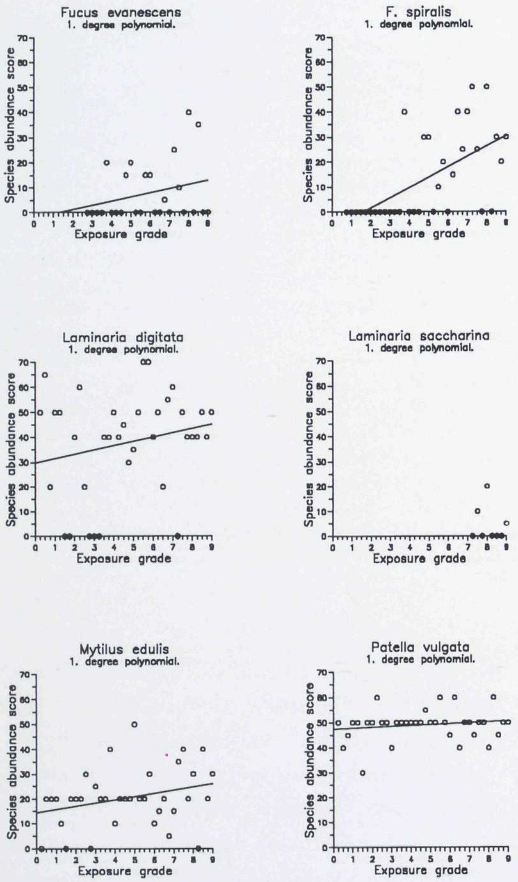


Fig. 3. Tendency lines for dominant species not included in the final Expon calculation. X-axis: Biological exposure value (grade) (BEV) (0: exposed; 9: sheltered). Y-axis: Species abundance values as given in Table 1.

Mynd 3. Rák hjá sløgum, sum nógv var til av, sum ikki vórðu tikin við í endaligu Expon útrokningini. X-ásin: Lívfrøðiligi ábærisstigin (BEV) (=: sera ábært, 9: í kyrru). Y-ásin: Stigi fyri fyrikomu av teim ymsu sløgunum sum í talvu 1.

south. As a consequence of this and the consistent strong water movement on the shores of the Faroe Islands, the species with non-peripheral distribution in the Faroe Islands, according to the arguments of Price and Farnham (1982), will appear in abundance and even colonise areas with marginally tolerable environmental conditions. Hence, organisms that are commonly accepted as indicators for strong water movement in England are less reliable indicators in the Faroe Islands.

Another explanation could be the special effects of environmental factors on individual species. The upper lethal temperature limit of *Alaria esculenta* is 16°C during summer (Sundene, 1962). It is possible that growth in more sheltered sites in Sogn and Fjordane County in western Norway is restricted by this factor, as the mean monthly temperature reaches 14.6°C in summer (Midttun, 1975) compared to 10°C in the Faroe Islands. The growth pattern observed in West Finnmark in the northern

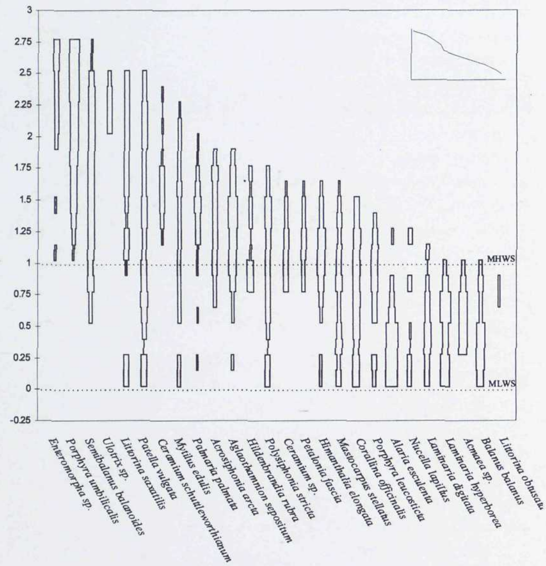
Exposure group	E	M	S
Bangiophyceae			
Acrochaetium secundatum (Lyngb.) Naegeli	2	2	3
Aglaothamnion sepositum (Gunnerus) Maggs & Hommers.	3	3	1
Bangia atropurpurea (Roth) C.Agardh	1	2	1
Ceramium nodulosum (Lightf.) Ducluz.	3	2	3
C. shuttleworthianum (Kuetz.) Rabenh.	3	2	1
Chondrus crispus Stackh.	1	1	2
Corallina officinalis L.	3	3	1
Lomentaria articulata (Huds.) Lyngb.	1	2	1
Mastocarpus stellatus (Stackh. in With.) Guiry in Guiry et al.	3	3	3
Membranoptera alata (Huds.) Stackh.	2	2	2
Palmaria palmata (L.) Kuntze	3	3	3
Phycodrys rubens (L.) Batters	2	1	1
Plocamium cartilagineum (L.) P.S.Dixon	2	1	1
Polysiphonia brodiaei (Dillwyn) Spreng.	1	2	1
P. lanosa (L.) Tandy	0	0	3
P. stricta (Dillwyn) Grev.	3	3	2
Porphyra leucosticta Thur. in LeJol.	2	2	2
P. purpurea (Roth) C.Agardh	1	1	2
P. umbilicalis (L.) J.Agardh	3	3	3
Rhodochorton purpureum (Lightf.) Rosenv.	2	1	2
Fucophyceae			
Alaria esculenta (L.) Grev.	3	3	1
Ascophyllum nodosum (L.) LeJol.	0	0	3
Chordaria flagelliformis (O.F.Muell.) C.Agardh	1	1	2
Ectocarpus fasciculatus Harv.	3	2	1
Elachista fucicola (Velley) Aresch.	2	1	3
Fucus distichus (L.) f. anceps	2	1	1
F. evanescens C.Agardh	1	1	2
F. spiralis L.	2	2	3
F. vesiculosus L.	1	1	3
Himanthalia elongata (L.) Gray	3	2	1
Laminaria digitata (Huds.) J.V.Lamour.	3	2	2
L. hyperborea (Gunnerus) Foslie	2	1	1
Pelvetia canaliculata (L.) Decne & Thur.	0	1	3
Petalonia fascia (O.F.Muell.) Kuntze	2	2	1
Pilayella littoralis (L.) Kjellm.	1	0	3
Scytosiphon lomentaria (Lyngb.) Link	2	1	1
Chlorophyceae			
Acrosiphonia arcta (Dillwyn) J.Agardh	3	3	3
Blidingia minima (Naegeli ex Kuetz.) Kylin	3	3	2
Chaetomorpha melagonium (F.Weber & D.Mohr) Kuetz.	2	2	1
Cladophora rupestris (L.) Kuetz.	2	2	3
Enteromorpha compressa (L.) Nees	0	0	2
E. intestinalis (L.) Nees	3	3	3
E. linza (L.) J.Agardh	2	2	2
Monostroma grevilleï (Thur.) Wittr.	3	1	2
Prasiola stipitata Suhr in Jess.	2	2	1
Rhizoclonium riparium (Roth) Harv.	2	2	2
Tellamia contorta Batters	0	0	2
Ulva lactuca L.	2	2	3
Ulvaria fusca (Postels & Rupr.) Rupr.	2	2	2

Table 4. *Frequently occurring algae that were found at a minimum of 33% of the localities in any one of three exposure groups. These were defined according to the biological exposure values (BEV) into E (exposed = 0-2.75), M (moderately exposed = 3-5.75), and S (sheltered = 6-9). Occurrences of species in % of localities within each exposure group are given as 1 = 1-33%, 2 = 34-66%, 3 = 67-100%.*

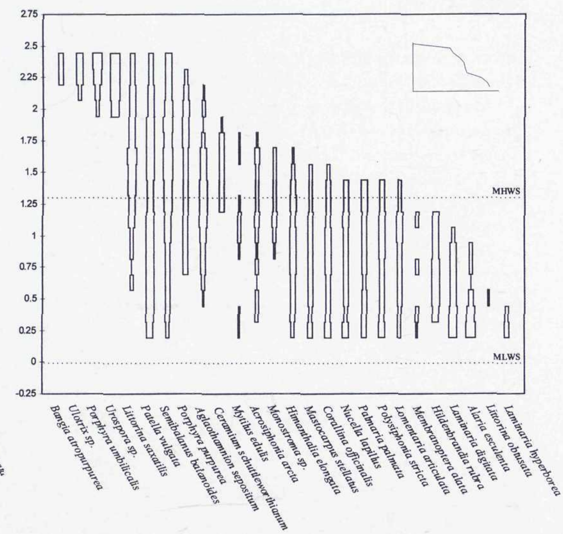
Talva 4. Algur, ið ofta koma fyri og funnar á minst 33% av støðunum, bólkaðar í trý, eftir hvussu ábært har er. Bólkarnir eru skipaðir eftir lívfrøðiliga stiganum (BEV), har E røkkur frá 0 til 2,75, M frá 3-5,75 og S 6-9. Fyrikoma av teim ymsu sløgunum í prosentum: 1 = 1-33%, 2 = 34-66%, 3 = 67-100%.

part of Norway, which has a mean summer temperature in August of 10.4°C (Midttun, 1975), actually resembled observations in the Faroe Islands (Årrestad and Lein, 1993).

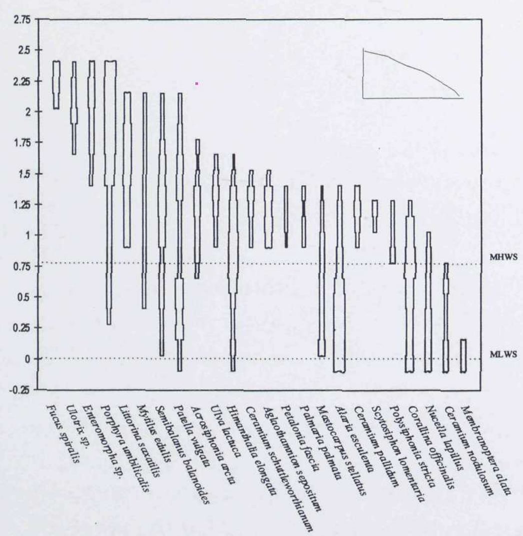
On the moderately exposed shores of the Faroe Islands, *Lomentaria articulata* grows gregariously, as also recorded by Børgesen (1905). The distribution of this species, which is rare on the west coast of Norway (Haugen, 1968), appears to be correlated with the relatively warm Atlantic water in



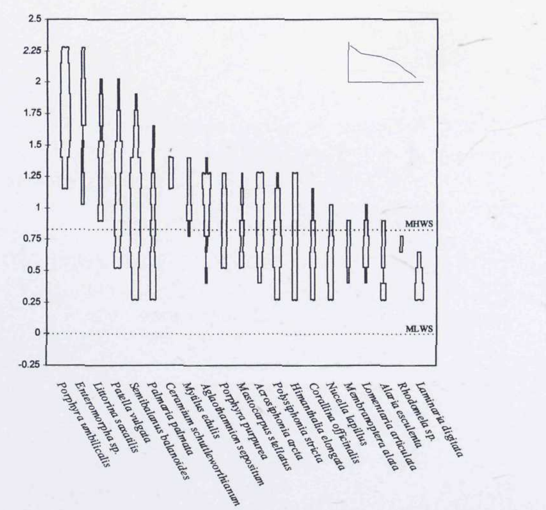
A. Station 24. Biological exposure grade = 0.5. *Porphyra umbilicalis* upper limit: 3.9 m above MLWS.



C. Station 119. Biological exposure grade = 2. *Porphyra umbilicalis* upper limit: 4.3 m above MLWS.

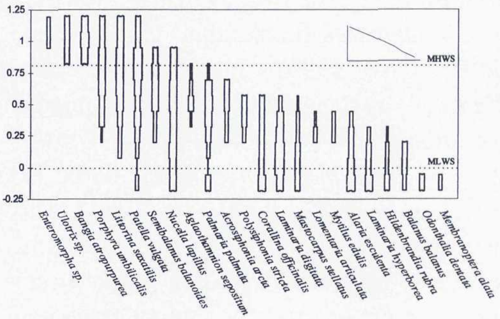


B. Station 102. Biological exposure grade = 0.75. *Porphyra umbilicalis* upper limit: 3.4 m above MLWS.



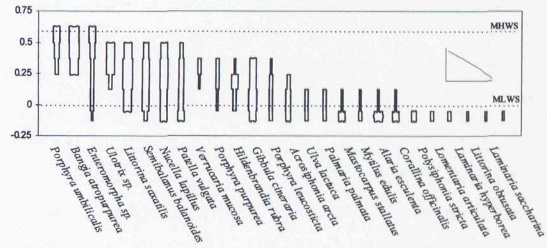
D. Station 51. Biological exposure grade = 4.5. *Porphyra umbilicalis* upper limit: 2.7 m above MLWS.

Fig. 4. *(p. 194-195) Profiles for littoral species from nine localities (A-J) selected to have different wave exposure. Widths of the columns correspond to the abundance scale values given in Table 1. Shore profile is inserted in upper right corner of each diagram. MHWS = mean high water spring, MLWS = mean low water spring. Locality numbers as in Fig. 1B.*

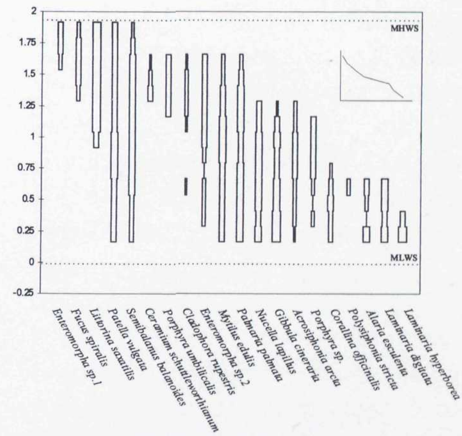


E. Station 97. Biological exposure grade = 5.25. *Porphyra umbilicalis* upper limit: 1.5 m above MLWS.

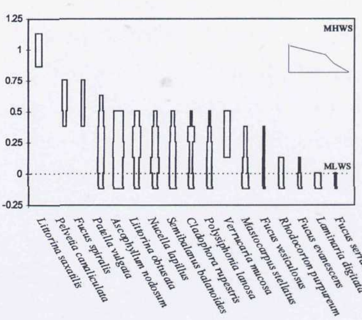
F. Station 129. Biological exposure grade = 6.



G. Station 88. Biological exposure grade = 6.5. *Porphyra umbilicalis* upper limit: 0.8 m above MLWS.



H. Station 7. Biological exposure grade = 7. *Porphyra umbilicalis* upper limit: 1.7 m above MLWS.



I. Station 136. Biological exposure grade = 9.

Mynd 4. Yvirlit yvir fyrikomu av litteralu sløgunum á 9 støðum (A-J), ið eru valdar eftir, hvussu ábært har er. Breidd á súlunum samsvarar við fyrikomustigan í talvu 1. Hallið á lendinum er tilskilað ovast høgrumegin á hvørjari mynd sær. MHWS = miðal mysingsflíð. MLWS = miðal mysingsfjøra. Nummar á støðunum sum í mynd 1 B.

the winter (>4.5°C) and the moderately high summer temperatures (<15°C) (Midttun, 1975; Lein *et al.*, 1999). In western Norway (Sogn and Fjordane County), it is found under a dense cover of *Ascophyllum nodosum* on sheltered shores (Boye, 1896; Lein, pers. obs.). In the British Isles, *L. articulata* also seems to prefer shady places when growing in the littoral zone (Irvine, 1983). Haugen (1968), however, reported dense populations of *L. articulata* epiphytic on *Corallina officinalis* at an exposed shore further north in Norway (Nord-Trøndelag County) where mean summer temperatures are below 13°C (Midttun, 1975).

This growth pattern may indicate that *L. articulata* is favoured by the oceanic climate in the Faroe Islands.

Other species were also observed in different growth patterns than found on most other NE Atlantic shores. *Laminaria digitata* was observed in abundance and was common throughout exposure grades in the Faroe Islands, whereas it was scarce in sheltered areas in Norway (Kruskopf and Lein, 1997; Årrestad and Lein, 1993). On north-west European coasts, amongst the fucoids, *Fucus serratus L.* normally grows lowest on the shore and above the laminarians (Connor *et al.*, 1996; Jorde, 1966). *F. serratus* is very rare, however, in the Faroe Islands. It is possible that in the Faroe Islands, *L. digitata* occupies the space taken by *F. serratus* on other coasts, thereby reaching a broader distribution and greater abundance on sheltered shores. *Fucus serratus* was reported in abundance along most of the Faroese coasts by Landt (1800), but since then has not been recorded until recently (Lyngbye, 1819; Børgesen, 1905; Irvine, 1982). The species was observed at a few sheltered localities within one fjord in 1997. The plants were fertile in August with both male and female plants present. A contrasting situation exists in Iceland where *Fucus serratus* has an abrupt northern distribution border in south-west Iceland. North of this limit, *Ascophyllum nodosum,* which normally grows immediately above *F. serratus*, extends its vertical distribution to cover the area occupied by *F. serratus.*

Effects of biological factors such as herbivory and predation are known to have a large influence on species distribution and the abundance of fucoid algae (for reviews, see Chapman 1995). Predation may also change along the gradient of wave exposure as demonstrated by Robles (1997). The absence of *Littorina littorea* in the Faroe Islands (see Spärck and Thorson (1933), who mentioned only three finds of single individuals during the 1800s) is probably an important factor for the abundance of some species, compared to other North Atlantic shores were it is an important grazer (Lein, 1980). In the Faroe Islands, *Patella vulgata* seems to be the most important grazer and was found throughout the exposure scale in large numbers. In Norway, it is generally abundant on moderately exposed shores, but is found in smaller numbers on both exposed and sheltered shores (Dalby *et al.*, 1978). The response curve for *P. vulgata* in Sogn and Fjordane County, however, resembles the even distribution observed in the Faroe Islands (Kruskopf and Lein, 1997). Hartnoll and Hawkins (1985) demonstrated the tremendous effect of grazing by *Patella* on semi-exposed shores in the Isle of Man. Further experiments are needed to evaluate the ecological influence of *P. vulgata* on the development and structure of littoral communities in the Faroe Islands.

The species list (Table 4) reflects the heterogeneity of the exposed localities. Crevices in cliff faces gave shelter to species such as *Rhizoclonium riparium* and *Cladophora rupestris*, which otherwise are more frequently found in sheltered localities (Fig. 2). Localised shelter may also explain the occurrence of *Fucus spiralis* and

Pelvetia canaliculata on moderately exposed shores.

Our study of the littoral flora confirms descriptions made by Børgesen (1905) and Price and Farnham (1982). Our findings agree with the general pattern of distribution seen in similar areas of neighbouring shores in western Norway (*e.g.* Jorde, 1966; Nerland, 1973; Sivertsen, 1981), Iceland (Hansen and Ingolfsson, 1993) and the northern part of the British Isles (Irvine, 1974; Connor *et al.*, 1996). Compared to other shores, the most striking features unique to the littoral zone of the Faroe Islands appear to be 1) the abundant growth even on sheltered shores of *Laminaria digitata* and *Alaria esculenta*, 2) the lack of dense populations of *Fucus serratus,* and 3) the frequent occurrence of many species over the whole exposure range.

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