Dominant Species Abundance Related to Environmental Factors on Rocky Shores in the Faroe Islands

Títtleikin av vanligastu føroysku dýra- og tarasløgunum á klettastrond í mun til ymisk umhvørvisviðurskifti

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Úrtak

Upplýsingar um títtleikan av 22 dýra- og tarasløgum av 168 harðbotnsstøðum í sjóvarmálanum í Føroyum vóru kannaðar við kanóniskari korrespondansuanalysu (CCA) og líkum kanningarháttum. Kanningarnar vístu, at alduábæri hevði størsta týdningin, meðan onnur viðurskifti so sum lendi og hvar á firðinum støðirnar lógu eisini sýntust at hava týdning, møguliga í lutfalli til ávirkan teirra í sambandi við alduábæri. Kanningarnar vístu eisini, at flóð og fjøra eins og streymur høvdu eina ávísa ávirkan, meðan lendishall, horving og vernd á staðnum ikki høvdu nakra ávirkan. Úrslitini bendu eisini á aðra ókenda orsøk til frábrigdið í úrslitunum. Víst varð, at lívfrøðiligi ábærisstigin, sum Bruntse o.a. (1999 b) gjørdu úr somu dátum, líkist fyrstu ás í 'Detrended' -korrespondansuanalysuni (DCA). Hesar kanningar stuðla metingini av, at tann lívfrøðiligi ábærisstigin í høvuðsheitum endurspeglar alduábærið.

Abstract

Abundance data on 22 species at 168 intertidal sites with hard substrate in the Faroe Islands were analysed using Canonical Correspondence Analysis (CCA) and related ordination techniques. Wave exposure was shown to be the single most important factor. Substrate type and the position in fjords were the other major variables, possibly related to their effects on exposure. Current and tidal amplitude had minor effects. No effects were detected from slope, aspect, or local protection. The results also indicated the presence of an unknown factor responsible for some of the variation. The biological exposure scale, which was developed by Bruntse *et al.* (1999b) and based on the same data, was shown to resemble the first axis in Detrended Correspondence Analysis (DCA). The present analyses supported the interpretation that the biological scale mainly reflects wave exposure.

Introduction

Bruntse *et al.* (1999a,b) explored the response to wave exposure of intertidal organisms in the Faroe Islands. They developed a biological exposure scale (cf. Dalby *et al.*, 1978) that was valid for rocky shores with mean tidal amplitude larger than 0.4 m using Expon software (Årrestad and Lein, 1993). Significant response curves were obtained for 15 of the 23 dominant species that were investigated. Biological zonation patterns were also described. The results confirmed earlier qualitative descriptions of the distribution of littoral organisms in the Faroe Islands, and comparisons were made with the British Isles and the southwest coast of Norway.

The biological exposure scale technique utilises a reciprocal algorithm to develop, alternately, response functions (polynomials) for species abundance in relation to wave exposure and exposure values for stations (Bruntse *et al.*, 1999b). The method relies on the presence of one factor, typically wave exposure, causing most of the species variation. To test this assumption, the data must be analysed by other methods, often Canonical Correspondence Analysis (e.g. in Kruskopf and Lein, 1997; Bruntse *et al.*¸ 1999a), and/or the results may be compared to other studies of the species response to the given factor.

Biological factors such as grazing and predation are well known to have large effects on the distribution of littoral species on local as well as larger spatial scales (Underwood and Chapman, 1996; Chapman, 1995). Bruntse *et al.* (1999b) discussed possible effects on the littoral community of competition between species of algae and of grazing by *Patella*. The main aim of our study, however, was to use in part the same data set to investigate the relative importance of wave exposure and other abiotic environmental factors on rocky shore communities in the Faroe Islands and to analyse the nature of the unexplained variation. The species response curves developed using Expon by Bruntse *et al.* (1999b) were interpreted in view of the new analyses. In addition, the data from the stations

Table 1. *Species used in the analysis and their abbreviations as used in Figs. 1-5.*

	Algae
Agl sep	*Aglaothamnion sepositum* (Gunnerus) Maggs & Hommers.
Alaria	*Alaria esculenta* (L.) Grev.
Asco	*Ascophyllum nodosum* (L.) LeJol.
Clad ru	*Cladophora rupestris* (L.) Kütz.
Corall	*Corallina officinalis* L.
F dis an	*Fucus distichus* L. ssp. *anceps* (Harv. & Ward ex Carruthers) Powell
F evan	*F. evanescens* C. Agardh
F spir	*F. spiralis* L.
F ves	*F. vesiculosus* L.
Him el	*Himanthalia elongata* (L.) Gray
La dig	*Laminaria digitata* (Huds.) J.V. Lamour.
Masto	*Mastocarpus stellatus* (Stackh. in With.) Guiry in Guiry *et al.*
Palm	*Palmaria palmata* (L.) Kuntze
Pelv	*Pelvetia canaliculata* (L.) Decne. & Thur.
Pol str	*Polysiphonia stricta* (Dillwyn) Grev.
Porph	*Porphyra umbilicalis* (L.) J. Agardh
	Lichen
Verr	*Verrucaria mucosa* Wahlenb.
	Invertebrates
Li obt	*Littorina obtusata* (L., 1758)
Myt ed	*Mytilus edulis* L., 1758
Nucel	*Nucella lapillus* (L., 1758)
Patel	*Patella vulgata* L., 1758
Semiba	*Semibalanus balanoides* (L., 1767)

with tidal amplitude 0.4 m or less, which were left out of the analysis by Bruntse *et al.* (1999b), were explored.

Methods

Stations and data registration

The data set comprises abundance data of hard-bottom littoral organisms from 168 sites in the Faroe Islands, as given in Bruntse *et al.* (1999b). The data from each station were collected from an 8 m wide transect running from the upper to the lower part of the littoral zone. A sub zone for each species, in which maximum abundance occurred (approximately 1/10th of the tidal amplitude), was selected and the abundance estimated on a semi-quantitative (ordinal) scale. The scale was modified from Dalby *et al.* (1978). Only species that were observed in at least 10% of the sites were included in the analyses. These are listed in Table 1. This sampling method is designed to investigate species distributions along environmental gradients at intermediate spatial scales (e.g. in the Faroe Islands) and should only with great care be used for the analysis of biological interaction and environmental variability on smaller scales (e.g. within single station areas, see Discussion). For details on the study area and sampling methodology, see Bruntse *et al.* (1999b).

Environmental variables

The environmental variables included in the analyses are listed in Table 2. The exposure variable is calculated by using the frequency of wind stronger than 15 m/s and fetch to the nearest point of land in each of 32 sectors. This variable is equal to the

Table 2. *Environmental variables, their range, mean values and skewness for the 159 rocky shore sites with tidal amplitude larger than 0.4 m.*

Variable	Definition	Range	Mean	Skewness
Exposure	Index based on map- and wind data. (1=lowest, 8=highest wave exposure)	(1,2,…, 8)	4.7	-0.1
Substrate	1=bedrock; 2=boulders; 3=stones/rocks	(1, 2, 3)	1.1	3.8
Fjord index	=D/W for fjord stations, where D=distance to open coast and W=width of fjord opening. =0 for open coast stations.	(0-9.0)	0.8	2.9
Current	1=no known strong current; 2=strong tidal current	(1, 2)	1.2	1.3
Slope	1=<30°; 2=30-60°; 3=>60°	(1, 2, 3)	1.3	1.7
Tide	Mean tidal amplitude (cm)	(60-200)	107	0.8
Aspect	1=N, 2=E, 3=W, 4=S	(1, 2, 3, 4)	2.4	0.0
Local protection	1=no sheltering effect 2=physical shelter (skerry, foreland etc.)	(1, 2)	1.1	2.2

FEV values of Bruntse *et al.* (1999b), except that the scale is inverted so that high values signify high exposure. The shore aspect variable is coded to reflect expected differences in amounts of sunlight received (Table 2).

Numerical methods

Canonical Correspondence Analysis (CCA) was used to examine the relationships between species and environmental factors. CCA is an ordination technique that maximises the dispersion of species centroids (the weighted averages of the different species) along axes that are constrained to be linear combinations of the environmental variables (ter Braak, 1986; ter Braak and Verdonschot, 1995). The method is based on a unimodal response model (e.g. ter Braak, 1995). If the community variation is within a narrow range, linear ordination methods (Principal Component Analysis and Redundancy Analysis) are appropriate because most species are behaving monotonically over the observed range (ter Braak and Prentice, 1988). The gradient length of the first axis in Detrended Correspondence Analysis (DCA), measured in standard deviation units of turnover (SD), indicates which method to use. For gradients less than about 1.5-3 SD, the approximations involved in weighted averaging (used in CCA, DCA and Correspondence Analysis, CA) become worse (ter Braak and Prentice, 1988). The first DCA axis for the present data set was 2.9 SD, giving no clear indication of which model to apply. The weighted-averaging methods were chosen since with this data the main DCA axis explained a higher percentage of the species data than the main axis in Principal Component Analysis.

The eigenvalue of an axis in CCA is a measure of the amount of variation explained by it. The total variance is given by the sum of all unconstrained eigenvalues in a Correspondence Analysis (CA). The importance of an environmental variable in the ordination may be expressed by the amount of variance (referred to as inertia) attributable to it. If the environmental variables are inter-correlated, the correlation of each variable with the major canonical axes may better indicate its significance (ter Braak, 1986; ter Braak and Verdonschot, 1995). This can be shown in an ordination diagram in which each environmental variable is shown as a vector from the origin (centre) to a point (x, y), in which x and y approximate the correlation between the variable and two given canonical axes. The species centroids can be shown in the same diagram, and each centroid can be projected to either canonical axis or any environmental variable to find the species' weighted average score on the axis or variable (ter Braak and Verdonschot, 1995). In the analyses, the environmental variables of importance were selected by a "forward selection" procedure. The method ranks the variables in importance and selects them one by one starting with the one that would add the most inertia if included. For each step, the significance of the new variable was tested using the Monte Carlo Permutation Test (999 unrestricted permutations), and the variable was included if significant at a 5% level. The marginal effect of each variable, which includes effects due to correlation with other variables, was determined using the variance extracted by CCA with the given variable entered as the only environmental variable. The unique effect of each variable, which only includes variance that cannot be extracted by the other variables, was determined using the variance extracted by partial CCA, in which the given variable was entered as the only environmental variable and all other variables were entered as co-variables.

In order to explore the variation unaccounted for by the CCA, Partial Correspondence Analysis (partial CA) was used with the previously selected environmental variables entered as co-variables. In order to view all variation in the species data independently of the estimated environmental

Table 3. *Canonical Correspondence Analysis (CCA) for rocky shore communities in the Faroe Islands, showing eigenvalues, extracted percentage variance of species data and species-environment relations for the first four canonical axes.* Inertia: *weighted variance of species data.* Marginal effect: *inertia explained by each variable if selected as the only variable.* Unique effect: *inertia explained by each variable if the other variables are entered as co-variables. The variables of importance were selected by the* 'forward selection' *procedure, by which the variables were selected one by one in sequence and included if significant at a 5% level. The data comprise 22 species at 159 sites with tidal amplitude larger than 0.4 m.*

Axis	1	2	3	4
Eigenvalue	0.262	0.018	0.009	0.007
Cumulative extracted variance (%) of species data	29.2	31.3	32.3	33.1
- of species – environment relation	87.6	93.8	96.9	99.2

	Inertia	%
Total inertia (sum of all unconstrained eigenvalues)	0.898	100
Variance explained by environmental variables (sum of all canonical eigenvalues)	0.299	33
Unexplained variance	0.599	67

Variable	Marginal effect (percentage of total inertia)	Unique effect (percentage of total inertia)	Forward selection (percentage of total inertia added)
Exposure	19 *	8 *	19 *
Substrate	14 *	7 *	9 *
Fjord index	13 *	2 *	3 *
Current	2 *	1 *	1 *
Slope	2 *	1	-
Tide	1 *	2 *	2 *
Local protection	1	0	-
Aspect	1	1	-

* Significant at a 5% level (Monte Carlo permutation test, 999 unrestricted permutations)

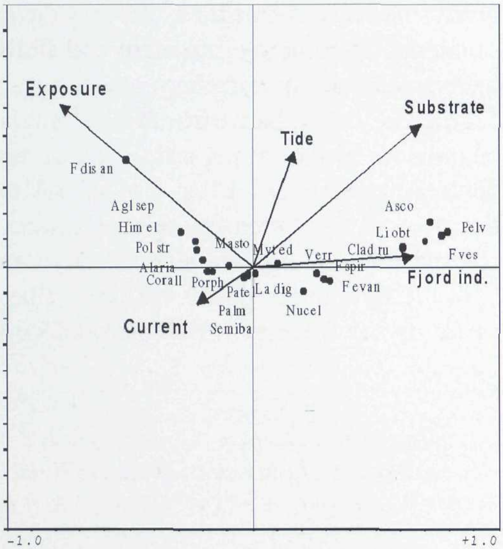

Fig. 1. Canonical Correspondence Analysis (CCA) for rocky shore communities in the Faroe Islands: ordination diagram of species and environmental variables for canonical axes 1 (horizontal) and 2 (vertical), displaying 31% of the inertia (= weighted variance) in species abundances and 92% of variance in the species—environment relation. The eigenvalues of axes 1 and 2 are 0.26 and 0.02, respectively. The environmental variable vectors are pointing in the directions of increased wave exposure, substrate *category (stones/rocks>boulders>bedrock),* fjord index *(increasing into fjords), tidal* currents *and* tide *(tidal amplitude). The data comprise 159 sites with tidal amplitude larger than 0.4 m. Species names are given in full in Table 1.*

variables, Detrended Correspondence Analysis (DCA) was used. Detrending-by-segments (Hill and Gauch, 1980) was done due to the "arch effect" if Correspondence Analysis (CA) was used. The first DCA axis reflects the main trend in the data. Species response curves, showing the abundance of each species along this axis, were then constructed. Abundance values were plotted against site scores on the axis and the response curves were fitted using a Generalised Linear Model, assuming Gaussian distributions in the species data. These curves were compared to the response curves obtained by Bruntse *et al.* (1999b) using Expon. Nine of the sites, with tidal amplitude 0.4 m or less, exhibited a unique pattern that differed from the other stations and, thus, were explored separately with DCA. DCA was chosen as a method in order to compare the results with those obtained for the other sites.

The analyses were carried out with the *Canoco for Windows* 4.0 Package (ter Braak and Smilauer, 1997-1999).

Results

Effects of environmental factors at sites with tidal amplitude larger than 0.4 m

In the Canonical Correspondence Analysis (CCA, Table 3), the first axis explained 29% of the species variation, and each of the consequent axes explained only 2.1, 1.0 and 0.8% of the species variation, respectively (eigenvalues of the two, first axes were 0.26 and 0.02). The focus of the interpretation, therefore, will be on the first axis. In the forward selection of variables (Table 3), wave exposure appeared to be the most important variable, explaining 19% of the species variance, followed by substrate and fjord index. Each of these variables had marginal effects explaining more than 10% of the species data. The unique effects of wave exposure and substrate explained 7-8% of the species data, while the unique effect of the fjord index only explained 2%. Each of the following variables – current, slope, tidal amplitude, aspect, and local protection – was able to explain 1-2% of the species data, if selected as the only factor (i.e. marginal effects). Of these, only current and tidal amplitude had significant unique effects, and were selected in the forward selection. Slope was entered both as a continuous (shown) and a categorical variable (i.e. as three variables, not shown), neither of which were significant in the forward selection. The weighted correlation between the variables and the first canonical axis (Table 4) confirmed this ranking of the variables in importance. Wave exposure, substrate, and fjord index were all highly correlated with the axis (correlation coefficients -0.64, 0.56 and 0.53, respectively). These environmental variables, however, correlated with each other (Table 4). In particular, wave exposure and fjord index were highly correlated (correlation coefficient -0.47), partly due to similarities in the definitions, which may explain the low unique effect of the fjord index. Due to the correlations, it may be difficult to separate the effect of each variable.

In the ordination plot of the CCA (Fig. 1), the species were mainly dispersed along the first axis. The species at the left in the plot were most likely found at high wave exposure, bedrock substrate and/or at the open coast. These species included *Fucus distichus* ssp. *anceps*, *Aglaothamnion sepositum, Himanthalia elongata, Polysiphonia stricta, Alaria esculenta, Corallina officinalis*, *Porphyra umbilicalis,* and *Masto-*

Table 4. *Weighted correlation matrix for environmental variables and axes in Canonical Correspondence Analysis (CCA) and Detrended Correspondence Analysis (DCA) for 159 rocky shore sites with tidal amplitude larger than 0.4 m in the Faroe Islands.*

Exposure	1							
Substrate	-0.21	1						
Fjord index	**-0.47**	0.20	1					
Current	0.18	-0.16	**-0.32**	1				
Slope	0.15	-0.15	-0.03	-0.04	1			
Tide	0.13	0.03	0.15	-0.17	0.03	1		
Local protection	-0.03	0.11	0.09	-0.17	-0.18	0.01	1	
Aspect	0.14	0.08	0.05	-0.12	0.00	0.07	0.07	1
CCA axis 1	**-0.64**	**0.56**	**0.53**	-0.18	-	0.14	-	-
CCA axis 2	0.29	0.25	0.02	-0.07	-	0.20	-	-
CCA axis 3	0.03	0.02	-0.20	**0.37**	-	0.14	-	-
CCA axis 4	0.04	-0.13	0.28	0.20	-	-0.02	-	-
DCA axis 1	**0.68**	**-0.52**	**-0.53**	0.16	-	-0.12	-	-
DCA axis 2	-0.28	0.24	0.13	0.01	-	0.11	-	-
DCA axis 3	0.16	-0.15	-0.05	0.20	-	0.03	-	-
DCA axis 4	-0.04	0.00	0.15	**-0.32**	-	-0.04	-	-
	Expo.	Substr.	Fjord i.	Current	Slope	Tide	Loc. pr.	Aspect

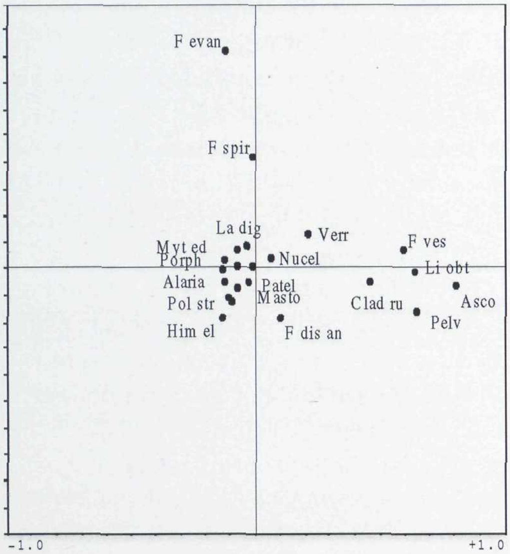

Fig. 2. Partial Correspondence Analysis (partial CA) for rocky shore communities in the Faroe Islands, showing the variation unaccounted for by the variables selected in the CCA (cf. Fig. 1), i.e. exposure, substrate, fjord index, current and tide. The diagram shows the species and ordination axes 1 (horizontal) and 2 (vertical), which explain 26% of the total inertia (= weighted variance) in species abundances. The eigenvalues of axes 1 and 2 are 0.16 and 0.08, respectively. Species names are given in full in Table 1.

carpus stellatus. The species at the right were most likely found in conditions at the opposite end of the scale, i.e. low exposure, stony or bouldery substrate and/or within fjords. These included *Pelvetia canaliculata, F. vesiculosus, Ascophyllum nodosum, Littorina obtusata, Cladophora rupestris, F. evanescens, F. spiralis, Verrucaria mucosa,* and *Nucella lapillus*. Species near the centre were either favoured by intermediate levels of these environmental factors, or they were found in a wide range of conditions. These included *Semibalanus balanoides, Palmaria palmata, Patella vulgata, Laminaria digitata,* and *Mytilus edulis.* In the partial Correspondence Analysis (partial CA), with the environmental variables entered as co-variables, the two first axes explained 17% and 8%, respectively, of the total species variation (eigenvalues 0.16 and 0.08). In the ordination plot (Fig. 2) *Ascophyllum nodosum, Pelvetia canaliculata, Littorina obtusata, Fucus vesiculosus* and *Cladophora rupestris* formed one group with high scores on the first axis, while the other species had scores much closer to zero. The same group of species was conspicuous on the CCA plot. Partly due to this, the species sequences along the two first axes in the partial CA plot reflected their sequences along the corresponding axes in the CCA plot (Spearman's Rank Correlation Coefficients, $r_s = 0.67$ and -0.76, respectively, between the two first-axes and between the two second-axes, $p<0.01$ for both correlations). This is an unusual result. One possible explanation might be that the same pattern that was shown in the CCA was repeated at a different scale, i.e. that different sequences of sites or groups of sites yielded similar sequences of species centroids. Another explanation might be that the environmental variables estimated the underlying factor(s) imperfectly, and that the partial CA reflected the unexplained part of the same pattern, i.e. that there was one main underlying sequence of sites reflected in both plots. This might also occur if an unknown factor, not correlated to the environmental variables,

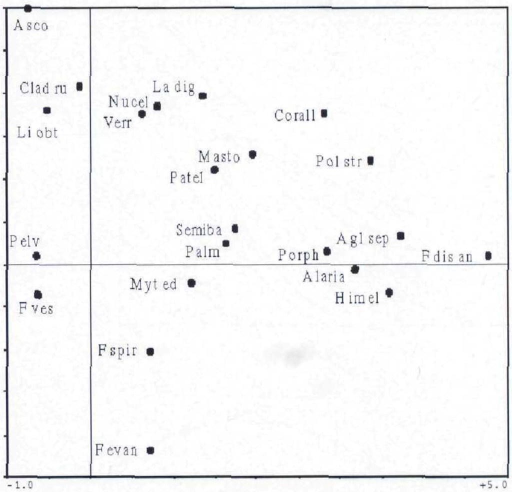

Fig. 3. Detrended Correspondence Analysis (DCA) for rocky shore communities in the Faroe Islands: diagram of species and ordination axes 1 (horizontal) and 2 (vertical), explaining 52% of the inertia (= weighted variance) in species abundances. The eigenvalues of axes 1 and 2 are 0.40 and 0.07, respectively. The data comprise 159 sites with tidal amplitude larger than 0.4 m. Species names are given in full in Table 1.

caused a similar species response as the environmental variables.

In the Detrended Correspondence Analysisis (DCA), wherein the axes were not constrained by the environmental variables, the first axis explained 45% of the species variation and the second axis 7% (eigenvalues 0.40 and 0.07). The sequence of the species along the first axis (Fig. 3) resembled their sequence along the first axes in the CCA and in the partial CA plots (r_s = -0.99 and -0.71, respectively, $p<0.01$ for both). This suggested the presence of one strong trend in the data, which was reflected in the first axis in each of the three plots. It also implied imperfect estimations of the underlying factor(s) by the environmental variables, or possibly, an unknown factor causing a similar species pattern. The high correlations between some of the environmental variables and the first CCA axis as well as the first DCA axis (Table 4) suggested, however, that these variables were in fact important to explain the observed pattern. The DCA may provide the best representation of the major trend in the data since it does not depend on imperfect variables and since it seems to reflect the same major trend as found by the CCA.

The species sequence along the second DCA axis was correlated with the species sequences along the second and the third axes in the partial CA (r_s = 0.43 and 0.63, $0.01<p<0.05$ and $p<0.01$, respectively). It was not significantly correlated with species sequences along any of the CCA axes. The site scores along the axis were weakly correlated with the wave exposure index (negatively, correlation coefficient -0.28) and the substrate index (positively, correlation coefficient 0.24) (Table 4).

Biotic factors

Biotic factors such as grazing, predation and competition are known to play important roles in intertidal communities. This study has been designed to focus on extrinsic, physical factors. Other sampling designs or experimental methods would have been better suited to study the effects of the biotic factors. However, to see to what extent the abundances of the predator *Nucella lapillus* and the grazers *Patella vulgata* and *Littorina obtusata* could explain the other

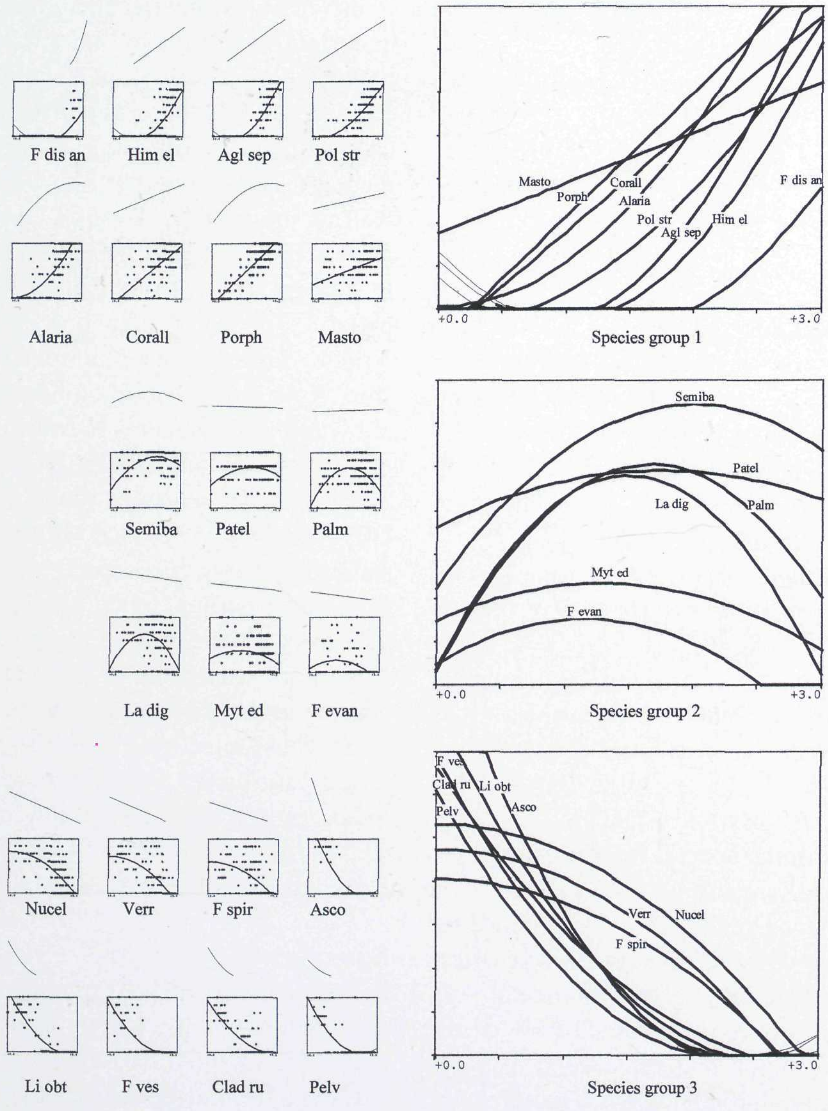

Fig. 4. *The diagrams within the small frames show the abundance of each species as a function of site score on the first axis in DCA for rocky shore sites in the Faroe Islands (cf. Fig. 3). Curves are fitted using a Generalised Linear Model (GLM) and assuming Gaussian distribution of the variables. The curves may be divided into three groups, which are shown in the large frames to the right. The figures above the small frames show the mirror images of the species response curves developed using the biological exposure scale methodology (Expon) on the same data by Bruntse et al. (1999b). The y-axes represent species abundance on a semi-quantitative scale from 0 (bottom of diagrams) to 70 (top of diagrams). Species names are given in full in Table 1.*

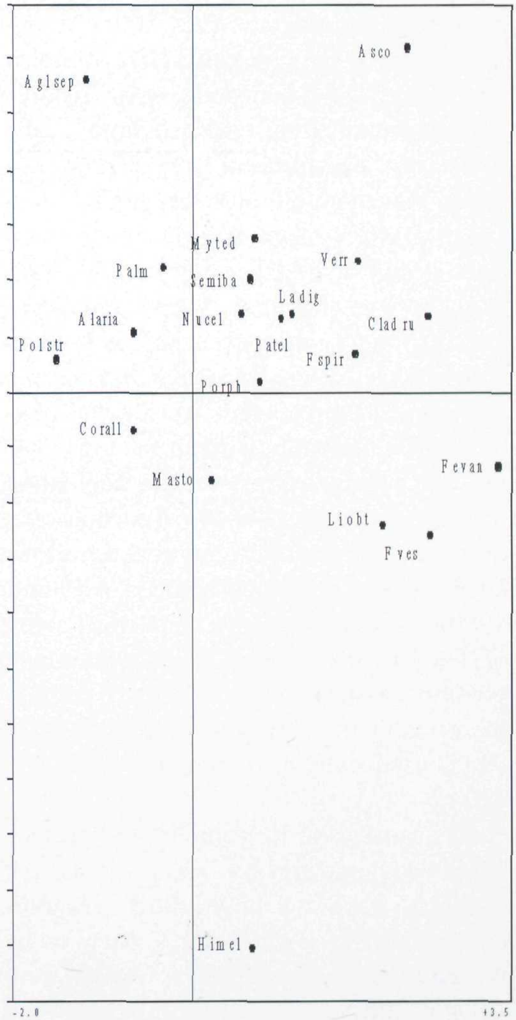

Fig. 5. Detrended Correspondence Analysis (DCA) of nine sites with tidal amplitude 0.40 m or less in the Faroe Islands: diagram of species and ordination axes 1 (horizontal) and 2 (vertical), explaining 44% of the inertia (= weighted variance) in species abundances. The eigenvalues of axes 1 and 2 are 0.29 and 0.09, respectively. Species names are given in full in Table 1.

species abundances, a partial CCA was done with the previously selected environmental variables entered as co-variables and the abundances of the predators/grazers entered as environmental variables. *Littorina* abundance explained 16% of the previously unexplained variance of the other species (eigenvalue 0.107), while *Patella* and *Nucella* each explained 1-2% (eigenvalues 0.012 and 0.011, respectively, marginal effects). The large effect of *Littorina* appeared mainly to be due to a positive association between this species and *Ascophyllum, Fucus vesiculosus, Pelvetia* and *Cladophora*, whose centroids all had high scores on the *Littorina* vector in the ordination diagram (not shown). As noted above, these species also formed a clear group in the partial CA plot (Fig. 2). The other species centroids were clustered around the centre of

Table 5. *Weighted correlation matrix for environmental variables and ordination axes 1 and 2 in Detrended Correspondence Analysis (DCA) for nine rocky shore sites with tidal amplitude 0.40 m or less in the Faroe Islands.*

	Expo.	Substr.	Fjord i.	Current[1]	Slope	Tide[1]	Loc. pr.	Aspect
DCA axis 1	-0.14	0.57	0.92	-	0.05	-	0.23	0.69
DCA axis 2	0.49	-0.20	-0.02	-	0.58	-	0.05	-0.28

[1] Variable has the same value at all sites.

the ordination diagram, thus failing to demonstrate any large negative effect of *Littorina* on any of the included species living at the same station, but not necessarily at the same level. The apparent large effect of *Littorina* was therefore probably not due to a negative effect of grazing, but rather to it often occurring together with certain species. However, grazing may be a secondary explanation for this coexistence, as *L. obtusata* is known to use *Ascophyllum nodosum* as the main food source (Watson and Norton, 1987), probably without having a significant negative effect on the population level of the host. It is also probable that juvenile *L. obtusata* use microalgae on the algal surface as a food source (Williams, 1990), thus reducing the epiphytic growth on the host plant. Such interactions might possibly explain some of the variation extracted by the first axis in the partial CA, and consequently also along the first DCA axis.

As seen by the low amount of variance explained, grazing by *Patella* was not shown to have any large effect. *Semibalanus* and *Mytilus*, which are predated on by *Nucella*, had their centroids near the zero value of the *Nucella* vector, thus failing to demonstrate any predation effect.

When interpreting these results, two points should be kept in mind. First, the scaling: Significant effects of grazing and predation might have been detected more locally than on 8 m stretches of shoreline. Second, the sampling method, by which only the abundance of a species was recorded for the horizontal zone where it was most abundant: Recording of total abundance might have been more sensitive to grazing and predation effects. The results suggest, however, that on an intermediate scale the maximal abundances of the investigated species were not strongly affected by grazing by *Littorina* or *Patella* or predation by *Nucella*, except possibly indirectly by *Littorina* grazing.

Species abundance curves

Considering the earlier discussion, the species abundance curves along the first DCA axis may be assumed to represent the species responses to the main environmental factor(s). All species abundance curves, except those for *Mytilus edulis, Palmaria palmata* and *Patella vulgata,* were significant at a 5% level, but the test is only suggestive, as the ordinal abundance data hardly fit a Gaussian distribution pattern. As Fig. 4 shows, the species may be divided into three main groups. The first group increased in abundance with increasing site scores on the first DCA axis. The second group, as evidenced by the curves, seemed to have the highest abundance at intermediate scores on the first DCA axis. The plots for the individual species revealed, however, that several of these species were found at variable abundance at all, or nearly all, axis scores. The group, therefore, includes species with no clear response to the factors underlying the axis. The shapes of the curves for these species appear somewhat arbitrary. The third group decreased in abundance with increasing site scores on the first DCA axis. The groups were nearly the same as those identified by the CCA plot (see above).

Table 6. *The distribution of species along the first axis in Detrended Correspondence Analysis (DCA) in the Faroe Islands (cf. Fig. 3) compared to the species' responses to wave exposure, according to quantitative interpretations of other authors' descriptions (Börgesen, 1902; 1905; Connor et al., 1996), see text. The rankings are from high to low exposure, based on the weighted centres of the tabulated distributions. ES = Extremely Sheltered. VS = Very Sheltered. S = Sheltered. ME = Moderately Exposed. E = Exposed. VE = Very Exposed. EE = Extremely Exposed.*

	Faroe I. DCA	Faroe I. (Børgesen, 1903)				British Isles (Connor *et al.*, 1996)							
	Rank	S	ME	E	Rank	ES	VS	S	ME	E	VE	EE	Rank
Fucus distichus ssp. *anceps* [1]	1			X	1							x	1
Aglaothamnion sepositum [2]	2			X	1								
Himanthalia elongata [3]	3		x	X	4				x	x			5
Polysiphonia stricta [4]	4	x	X	X	10								
Alaria esculenta [5]	5		x	X	4				x	x			5
Porphyra umbilicalis [6]	6		x	X	4			x	x	x	x	x	4
Corallina officinalis	7	x	x	X	9				x	x	x	x	2
Mastocarpus stellatus [7]	8		x	X	4	x	x	x	x	x	x		12
Semibalanus balanoides	9					x	x	x	x	x	x	x	9
Palmaria palmata [8]	10		x	X	4			x	x	x	x		5
Patella vulgata	11					x	x	x	x	x	x	x	9
Laminaria digitata [5]	12			X	1				x	x			5
Mytilus edulis	13					x	x	x	x	x	x	x	9
Nucella lapillus	14								x	x	x	x	2
F. spiralis [9]	15	x	X		12	x	x	x	x				15
F. evanescens [10]	16	x	X		12								
Verrucaria mucosa	17					x	x	x				x	14
Cladophora rupestris	18	X	X	X	11	x	x	x					18
Littorina obtusata	19					x	x	x	x				15
F. vesiculosus	20	X			16	x	x	x	x	x	x		12
Pelvetia canaliculata	21	X	X		14	x	x	x	x				15
Ascophyllum nodosum	22	X	x		15	x	x	x					18

1 Børgesen: *Fucus inflatus* f. *disticha*
2 Børgesen: *Callithamnion arbuscula*
3 Børgesen: *Himanthalia lorea*
4 Børgesen: *Polysiphonia urceolata*
5 Connor *et al.*: maximum abundance is 'Occasional'
6 Børgesen: *Porphyra umbilicalis* f. *umbilicalis*
7 Børgesen: *Gigartina mamillosa*
8 Børgesen: *Rhodymenia palmata*
9 Forma *nana* not included
10 Børgesen: *Fucus inflatus* f. *edentata*

Effects of environmental factors at sites with tidal amplitude 0.4 m or less

In the DCA of the nine stations with tidal amplitude 0.4 m or less (Fig. 5 and Table 5), axes 1 and 2 explained 33% and 10%, respectively, of the species data (eigenvalues 0.29 and 0.09). The sequence of species along the first axis was similar to that along the first DCA axis of the other stations (Spearman's Rank Correlation Coefficient, $r_s=-0.85$, $p<0.01$). This axis was not correlated, however, with the wave exposure index (correlation coefficient –0.14), but it did correlate with the fjord index (correlation coefficient 0.92), aspect (correlation coefficient 0.69), and substrate (correlation coefficient 0.57). This may have been the reason why these stations did not fit in the canonical ordination with the others, wherein wave exposure was revealed as the most important variable. The second axis was correlated with slope (correlation coefficient 0.58) and wave exposure index (correlation coefficient 0.49).

Discussion

Effects of environmental factors at sites with tidal amplitude larger than 0.4 m

The interpretation of some variables other than wave exposure should be done with some caution. The location of the various stations was based on a stratified strategy by which the entire geographical area was covered and included different environmental factors, one of which was exposure to wave action. If too many environmental variables had been included in the stratification determination, however, the stations would be no longer representative of the environmental conditions in the Faroes, and the effects of the major factors might have been wrongly estimated. As a consequence, some variables did not have a balanced distribution across stations (Table 2), which led to some arbitrariness when attributing effects to these factors. This applied particularly to the substrate variable where only 12 of the 159 stations had substrate other than bedrock. Most of the non-bedrock stations were situated in relatively sheltered locations, as reflected in the negative correlation between substrate and wave exposure (Table 4), which further complicated the interpretation of the substrate variable.

Wave exposure is well known as a potential structuring factor for rocky shore communities (e.g. Lewis, 1964). Table 6 demonstrates that the first axis in Detrended Correspondence Analysis (DCA) for stations with tidal amplitude larger than 0.4 m reflected to a considerable degree the species responses to wave exposure described by other authors. The sequence of species along the axis was correlated to the species occurrence in relation to wave exposure in the Faroe Islands following Börgesen's (1902; 1905) description (Spearman's Rank Correlation Coefficient, $r_s=0.79$, $p<0.01$), and to their responses to wave exposure in the British Isles following the classification ($r_s=0.79$, $p<0.01$) of Connor *et al.* (1996). Börgesen (1902; 1905) made a thorough description of the algal flora in the Faroe Islands, but the quantitative interpretation is ours. The tabulated distribution in the British Isles is based on the Connor *et al.* (1996) classification of marine biotopes. Species noted as frequent, common, abundant, or super abundant in biotopes on eulittoral or supralittoral rock (not including rockpools) are marked in the table for the exposure interval in which the biotopes occur. Since quantitative descriptions of individual species responses to wave exposure was not the purpose either of Börgesen (1902; 1905) or Connor *et al.* (1996), our interpretation is, thus, somewhat subjective and should be considered with caution.

Assuming that wave exposure was the main structuring factor at the sites with tidal amplitude larger than 0.4 m, the effects of the substrate and fjord variables seen in the Canonical Correspondence Analysis (CCA) may have been partly due to the correlation of these variables with the exposure variable. There was, however, some added effect from these variables, particularly from the substrate variable, that could not be attributed to the wave exposure variable. Some of this added effect might still have been connected to wave exposure. A high substrate index signified boulders, or, less commonly, stones (only one station). Provided these were stable, they might provide some shelter from wave action. The wave-modifying effect of the substrate appears plausible, particularly at low wave exposure levels that occur at most of the bouldery or stony sites.

The unique effect of the fjord index may also be explained partly by wave exposure. On the open coast, there may have been more effects generated by reflected or deflected waves, or small islets may have provided less shelter than they would have in fjords. These factors would lead to underestimation of the exposure at some open coast stations by the wave exposure index, which might be corrected by the fjord index.

The substrate and fjord factors may have had other effects, but these were not detected unequivocally in the present analysis. A high substrate index may signify reduced stability of the substrate as well as heterogeneity with respect to light conditions, risk of desiccation, etc. A high fjord index may indicate greater temperature variation or, perhaps less likely, reduced salinity. The stability of the substrate did not seem to be reflected in the species pattern in any obvious way. In particular, the high score of *Ascophyllum nodosum* along the substrate vector could be difficult to explain. It is a species that may need several years to reach maturity and is considered to require stable substrate (Baardseth, 1970). The fjord effect is difficult to untangle from that of wave exposure due to the high correlation between the variables.

It seemed most likely that wave exposure was the main structuring factor behind the first axis in the DCA and the CCA, as well as in the partial CA, for the stations with tidal amplitude larger than 0.4 m. This was supported by the results of the forward selection of variables in the CCA and the correlation between the variables and the axes in CCA and DCA, which suggested that wave exposure was the most important variable. This conclusion is further supported by the conformance with descriptions made by other authors, and by the possibility of explaining the effects of the

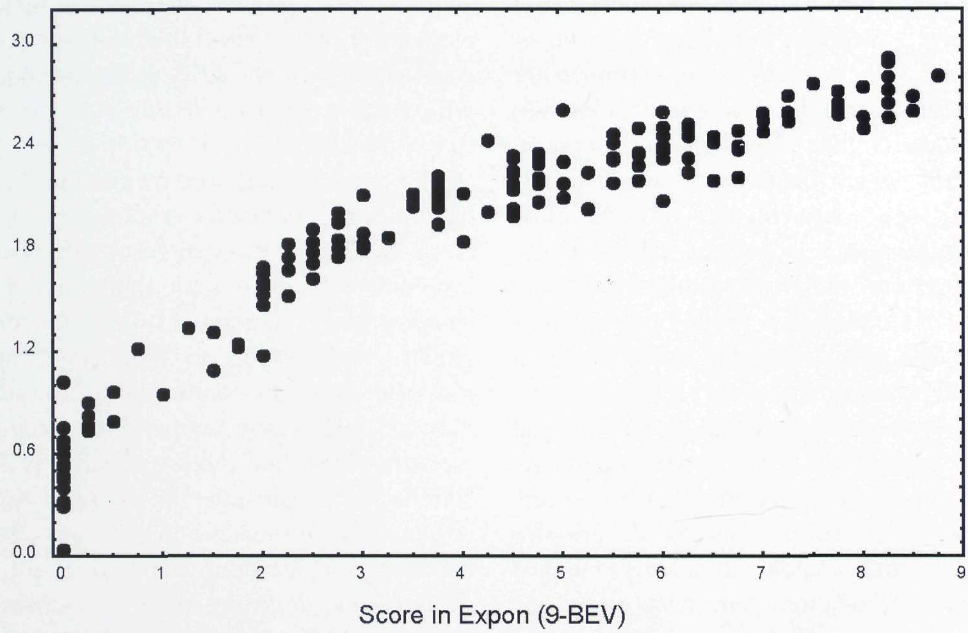

Fig. 6. The relationship between site scores on the first axis in DCA (cf. Fig. 3) and their scores in Expon (9-Biological Exposure Value) found by Bruntse et al. (1999b) for rocky shore sites in the Faroe Islands. The correlation coefficient is 0.93.

substrate and fjord indices, at least partly, through effects on wave exposure.

Tidal amplitude and current apparently had only modest effects on the species composition at sites with tidal amplitude larger than 0.4 m. Considering the large variation in tidal range and current conditions within the Faroe Islands, this was of particular interest.

Slope, aspect and local protection were not shown to have any effects. In a comparable analysis from Finnmark, northern Norway (Stige and Lein, *unpublished data*), slope was shown to have a modifying effect on wave exposure. Sites with slopes approaching 45° seemed to experience added effects of wave exposure compared to sites with less slope. The results were not directly comparable, however. In contrast to the present study, in Finnmark only stations with slopes less than 45° were included and the slope was measured in degrees and not as a categorical variable (cf. Table 2). The effect seen in Finnmark would, therefore, not be detected as easily in the present study.

The wedge shape of the species centroids in the DCA plot for sites with tidal amplitude larger than 0.4 m implied that at low wave exposure levels another factor was of importance. This was not reflected in the CCA plot, and the axis was only weakly correlated with any environmental variable (negatively with the exposure index and positively with the substrate index). The interpretation of this axis may only be speculated. It may have reflected a different aspect of exposure, for instance a different time aspect, than the first axis. From the species plot, it seemed that the axis may have reflected life-history patterns, with temporally stable, long-lived species such as *Ascophyllum nodosum* and *Corallina officinalis* at the top of the diagram, and temporally more variable and potentially opportunistic species such as *Fucus evanescens* at the bottom of the diagram. This might be connected to the particular histories of the sites, but needs further exploring.

Biotic factors

The results indicated that direct effects of grazing by *Littorina* or *Patella*, or predation by *Nucella* could not explain any large part of the variation in the ordination. However, as already pointed out, such interactions may surely have occurred, as known from experimental studies elsewhere (see e.g. Hartnoll and Hawkins, 1985; Chapman, 1995), but their effects were not pronounced with the scale and sampling method used. Indirect effects of grazing could not be ruled out as a possible explanation for some of the variation. If so, these effects caused a similar species pattern to that caused by wave exposure. It was not possible to say to what extent competition between species influenced the observed patterns. The degrees of distributional overlaps along the gradient were indicated by the distances between the species centroids in the DCA plot (Fig. 3) as well as by comparisons of the plots of species abundances versus site scores on the first DCA axis (Fig. 4). For instance, the centroids of *Fucus distichus* ssp. *anceps* and *Ascophyllum nodosum* were distanced far apart in the DCA plot, suggesting little distributional overlap, which was further confirmed by the plots of their abundances along the first DCA axis, from which it seemed that the two species did not occur together at all. Such patterns might be induced both by extrinsic factors such as wave exposure as well as by interactions between the species, or perhaps most likely, by a combination of both. Experimental studies are needed to discern the causative factors for the distributions.

Species abundance curves

Considering the discussion of the factors influencing the first DCA axis for sites with tidal amplitude larger than 0.4 m, it seems reasonable to interpret the plots of species abundance versus site scores on the axis as the species responses to wave exposure. The three groups identified were, thus, (1) species that increase in abundance with increasing exposure, (2) species with abundance optimums at intermediate exposure or with no clear response to exposure, and (3) species that increase in abundance with decreasing exposure.

Comparison with and interpretation of the biological exposure scale methodology

The species abundance curves of the first and third group resembled those developed using the biological exposure scale methodology (Expon) by Bruntse *et al.* (1999b). The exact shape of the curves differed, but they generally depicted the same trends. For the second group, the curves did not resemble each other, again demonstrating that the curves for these species must be interpreted with considerable caution. In Fig. 6, the site scores on the first DCA axis and on the biological exposure scale developed by Expon are plotted against each other. The high correlation coefficient (0.93) demonstrates that the two techniques arranged the sites quite similarly. The relationship does not appear to be first-order linear, however, which may partly explain differences in curve shapes between the methods. For instance, DCA separated sites with low exposure more than Expon. Most of the differences in the curves between the methods, however, probably depended on the curve fitting procedures. In Expon, the polynomial order was chosen subjectively, and lower order polynomials were preferred since they tend to stabilise the iterations. In the curve fitting to the DCA plot, the default option of Canodraw 3.1 (in: ter Braak and Smilauer, 1997-1999) was chosen, in which the polynomial order was chosen automatically based on a significance test.

The high correlation between site scores on the biological exposure scale and on the first DCA axis implied that the DCA could be used to interpret the biological exposure scale for the present data. This would not necessarily be the case for other data sets. Expon can model bimodal responses, as long as they can be approximated by second- or higher-order polynomial functions, while DCA basically relies on an unimodal response model (e.g. ter Braak, 1995).

The results suggested that the species response curves developed for dominant species on hard substrates in the Faroe Islands by Bruntse *et al.* (1999b) did reflect the species responses to wave exposure, which appeared to be the single most important factor structuring the species composition. The first DCA axis, and, thus, probably also the biological exposure scale, was also influenced by substrate and fjord index. The effects of these variables on wave exposure could at least partly explain this influence. Further, the high amount of species variation accounted for by the first DCA axis (45%) suggested that the biological exposure scale reflected a large proportion of the species variation.

Effects of environmental factors at sites with tidal amplitude 0.4 m or less

The nine sites with tidal amplitude 0.4 m or less were all from the fjord area to the north of Tórshavn. The area was atypical in other respects than tidal range. Four of the sites were cliffs with slope more than 60°, and two of the sites were stony beaches. Only three sites had the "typical" bedrock substrate with slope less than 60°. The sequence of species centroids along the first DCA axis for these sites resembled that for the other sites, but the axis was mainly correlated with the fjord index in contrast to the exposure index. Further, aspect was highly correlated with the axis. These results should be interpreted with caution due to the low number and the limited geographical range of the sites. It is possible that fjord effects and aspect were more important in this area than at other places in the Faroe Islands. However, the resemblance of the ordination plot to that for the other stations suggested that the same factor was underlying the first axis in both ordinations. For the nine stations all situated in one fjord system, the fjord index may have been a more reliable estimator of exposure than the exposure index. The apparent effect of aspect may have been due to a positive correlation with the fjord index — in that there happened to be more south-oriented stations farther into the fjord.

Acknowledgements

The field investigations were part of the FARCOS project, supported by Amerada Hess, BP, Conoco, Mobil, Phillips Petroleum and Texaco and of the large BioFar 2 project, supported by the Carlsberg Foundation. The data treatment was conducted at the Marine Biological Station, University of Bergen, partly financed by Alpha Environmental Consultants, NoBaLes (Norwegian Barents Sea Exploration Co-operation) and OLF (the Norwegian Oil Industry Association). We are also grateful to Dr. Eivind Oug and Prof. H. John B. Birks, who helped to improve our understanding of the statistical methods involved and to cand. scient. Mikaela Kruskopf for comments on the manuscript.

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