

A multivariate study of biotic and abiotic relationships in a subtidal algal stand

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ABSTRACT: The distribution patterns of dominant macrophytes (*Gelidium sesquipedale*, *Saccorhiza polyschides* and *Laminaria ochroleuca*) in relation to local abiotic conditions (depth, sediment loading and substrate topography) were investigated in a commercial stand of *G. sesquipedale* off Cape Espichel, Portugal, using principal component analysis. Observed patterns were analysed using multiple regression models to assess the strength of the relationship between *G. sesquipedale* and the different biotic and abiotic factors. Both multivariate and multiple regression analyses revealed significant positive relationships between *G. sesquipedale* cover and substrate slope, and negative relationships among *G. sesquipedale*, sediment loading and *S. polyschides* density. The main effects of these variables on the abundance of *G. sesquipedale* are of the same relative magnitude. Within the depth range studied (0 to 18 m), *S. polyschides* abundance was the only variable correlated with depth. The only interaction significantly correlated with *G. sesquipedale* local distribution was that between *L. ochroleuca* density and depth. Data suggest that steep slopes and reduced sediment loading favour *G. sesquipedale* development. On the contrary, *S. polyschides* dominated in shallow zones with low slope surfaces and high sediment loading. *L. ochroleuca* by itself was not significantly correlated to the distribution of *G. sesquipedale*, but its interaction with depth suggests that at greater depths it dominates *G. sesquipedale*. This is supported by analysis of the correlations between the 3 species in shallow versus deeper zones. Potential mechanisms are discussed for the significant relationships found, and testable causal hypotheses are suggested.

INTRODUCTION

Patterns of species distribution and abundance are determined by a complex interaction of biotic and abiotic factors. The specific processes that structure many macroalgal assemblages are poorly understood, particularly in the subtidal zone. Most studies have been done in the intertidal, on plant-herbivore interactions (Schiel & Foster 1986). Several abiotic and biotic factors have been proposed to shape the local distribution of seaweeds, with light generally considered as having the most important direct effect (Lobban et al. 1985, Lüning 1990). The complex fluid dynamics resulting from the interaction of water motion with depth and the topographic characteristics of substratum also have an important effect on the physical

stress acting on plants (Vogel 1981, Koehl 1986, Denny 1988), on the assimilation of nutrients and on the settling and development of algal spores (Vadas et al. 1990, and reviews by Lobban et al. 1985 and Lüning 1990). Other major processes determining the patterns of distribution and abundance of algal species include intra- and interspecific competition (see review in Paine 1990).

The causal mechanisms that determine the patterns of species distribution can only be detected by experimentation (Underwood 1986). However, efficient design of experiments will require extensive preliminary analyses of observational data; numerical descriptive studies may play an important role in determining which hypotheses to test experimentally (James & McCulloch 1990). Multivariate methods have been extensively used in vegetation science to expose trends and patterns of co-distribution of species and environmental factors, and to generate hypothesis of

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community-environment interactions (Gauch 1982, Greig-Smith 1983, Gittins 1985, Ter Braak 1987).

Marine ecologists, unlike terrestrial ecologists, have not used numerical methods extensively (see review in Kautsky & Van der Maarel 1990). Applications of these methods to the study of biotic and environmental relationships in phyto-benthic communities were carried out early by Neushul (1967), who related clusters of similar seaweed species with depth and substrate type along transects. Lindström & Foreman (1978) analysed the seaweed communities of British Columbia, Canada, to determine major environmental factors related with the species composition. Kautsky & Van der Maarel (1990) recently correlated environmental factors of the Baltic Sea, such as depth, bottom type, slope, wave exposure and amount of sediment on the bottom, with the patterns of species distribution.

Depth (light), substrate topography, sedimentation and competition have all been identified as important factors influencing the local distribution of seaweeds (Lobban et al. 1985, Schiel & Foster 1986, Lüning 1990). Field correlations and laboratory studies have provided single factor explanations outlining the general relationships between abiotic and biotic environment and stand abundance, but the effects of interactions are largely unknown. Simple correlations among species distribution and abiotic factors or occurrence of other species have been the most common approach used to identify relationships in the subtidal zone (Schiel & Foster 1986).

Gelidium sesquipedale (Clem.) Born. et Thur. is a clonal red alga which grows in the subtidal by the continuous production of upright fronds from a small, prostrate system of colorless axes (Dixon 1958, Fan 1961). The value of understanding the causes of variation in its abundance is enhanced by its commercial importance. This species is harvested by divers along the Portuguese coast for the extraction of agar. Portugal is the third-largest producer of *G. sesquipedale* and is the fifth in agar production (Santos & Duarte 1991).

The ecological patterns of *Gelidium sesquipedale* distribution, as in most species of this genus (Santelices 1991), indicate that abundant populations occur in habitats of high water motion with steep slopes and low sediment loading. Interspecific competition with canopy-forming kelps, is likely to be an important process structuring its distribution and abundance as Montalva & Santelices (1981) have shown for *G. chilense*. Along the coasts of Spain and Portugal, *G. sesquipedale* forms high-density, nearly monospecific stands, or grows underneath the canopy of the kelps *Saccorhiza polyschides* (Lightf.) Batt., *Laminaria ochroleuca* Pyl. and *Cystoseira* spp. (Saldanha 1974, Melo & Santos 1979, Gorostiaga 1990).

This study addresses 2 questions concerning the biotic and abiotic relationships in a commercial *Gelidium sesquipedale* stand: (1) is the distribution of *G. sesquipedale* correlated with kelp abundance, depth, sediment loading and substrate topography, and (2) what is the strength of the relationship between *G. sesquipedale* distribution and the biotic and abiotic factors? I used multivariate and multiple regression techniques respectively to answer these questions. Two specific objectives were pursued with the second analysis. The first was to investigate the importance of each abiotic and biotic factor inasmuch as they act independently. The second was to assess the extent to which interactions between abiotic and biotic factors explain variation in *G. sesquipedale* abundance.

METHODS

The commercial stand of *Gelidium sesquipedale* studied is located off the north shore of Cape Espichel, Portugal (Fig. 1). Sampling was done from 24 September to 8 October 1986. Eighteen transects, averaging 325 m in length, were laid out along 6.6 km of coast, following the point-transect method of Pringle & Semple (1983). The southernmost 13 transects were 200 m apart in an area of high harvest effort. The northern 5 transects were 800 m apart, in an area where harvest effort was lower. Quadrats of 50 × 50 cm were sampled every 10 m along the transects. Systematic sampling was used rather than random sampling because it is more effective to describe variability in spatial patterns of communities (see review in Gauch 1982).

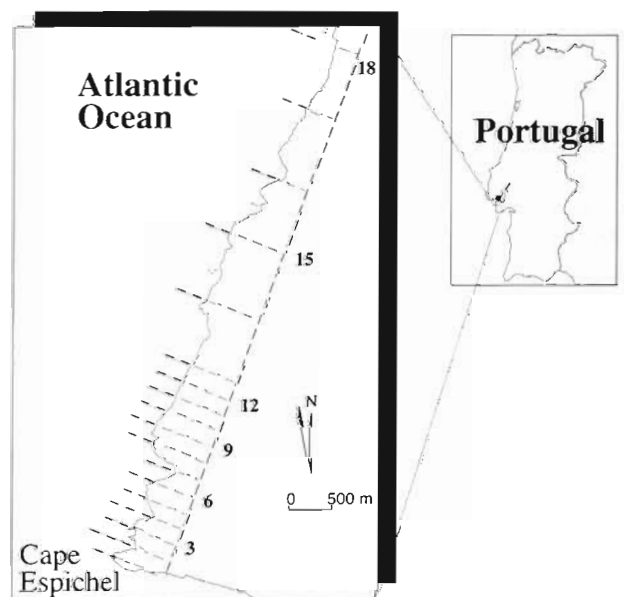


Fig. 1. Cape Espichel, Portugal, showing locations of transects

Estimates of subtidal seaweed abundances generally have high variances (Schiel & Foster 1986). They reflect contagious distributions of species and high sampling errors caused by diving constraints. Consequently, larger samples are required to detect significant relationships. To sample this large area, a fast (and low cost) non-destructive sampling method was selected rather than the more time-consuming biomass sampling. The quadrat density of the 2 kelp species present in the zone, *Saccorhiza polyschides* and *Laminaria ochroleuca*, was recorded. *Gelidium sesquipedale* density is very difficult to measure non-destructively because this species occurs in high-density mats of algal tufts. Its abundance was assessed by visually estimating its cover (%) inside the quadrats (Pielou 1981, Dethier 1984). To assess the reliability of the visual estimates in describing the general abundance of the species, the number of 1 m transect marks in contact with *G. sesquipedale* tufts was also recorded and compared to visual estimates.

The geological characteristics of the area (Zbyszewski et al. 1965, Ramalho 1971) define a gradient of bottom topography and sedimentation that may play an important role in structuring the subtidal algal community. The bed's south edge (Fig. 1, Transects 1 to 6) topography is characterized by parallel strata oriented WSW-ENE, inclined at 60°. Northward, the strata crop out at 35° and 25° NNE, to almost horizontal (Ramalho 1971, Rey 1972). The north edge of the area is characterized by patches of rock and sand. Depth, substratum topography and sediment loading were measured in each quadrat. Substratum inclination and the sediment load were rated using a 1 to 3 scale for slope (1: horizontal, 2: sub-vertical and 3: vertical) and 1 to 4 scale for silt (1: no sediment to 4: heavy sediment loading). The number of 1 m transect marks in contact with sand patches was also recorded to investigate the relationship between the amount of sediment over the rock and transect sand cover. Quadrats that laid on sand were not included in the analysis. A total of 510 quadrats was sampled.

Ordination. Data analyses were done using SYSTAT 5.1 for Macintosh (Wilkinson 1989). The data's underlying structure was investigated using a principal component analysis (PCA) (see Morrison 1976 and Hair et al. 1987 for a description and application of the method and James & McCulloch 1990 for a discussion of its limitations in ecology). To improve the detection of non-linear relationships, *Gelidium sesquipedale* cover data were transformed to $\arcsin\sqrt{x}$ and kelp density was transformed to $\sqrt{x + 0.5}$ (Sokal & Rohlf 1969).

As each of the original variables was measured on different scales, PCA was performed on the correlation matrix rather than on the variance-covariance matrix. Furthermore, this work focuses on the correlation structure of the variables rather than on their variance structure.

Significant principal components were selected by plotting the eigenvalues against the components (Cattell 1966), to detect when the amount of specific and error variance begin to dominate the shared variance among variables (Hair et al. 1987). The zone where the slope of the curve begins to flatten indicates the maximum number of components to extract. The selected components were then rotated by varimax rotation, which redistributed variance from earlier to subsequent factors (Hair et al. 1987). This technique is generally used to facilitate the ecological interpretation of the component pattern.

PCA biplots. The original data matrix of all abiotic and biotic variables was transformed using PCA into a rank 2 matrix by varimax rotation on 2 principal components. This matrix contains the scores of all quadrats for the 2 principal components. A biplot of variable loading vectors and site scores on the principal components was done to make the main features of the data easier to see (Ter Braak 1983). Variable vectors with an angle close to 0° have high positive correlation, angles close to 90° show no correlation and angles toward 180° indicate high negative correlation. Longer vectors show positions of more significance.

Model development. The objective of this regression analysis was to assess the relative statistical importance of variables and their interactions, rather than to select the 'best' subset of predictors. Random sampling is necessary to use multiple regression analysis to make predictions (see James & McCulloch 1990 for a review of the problems in constructing multiple regression models in ecology). The criteria I used to judge statistical importance are nevertheless the same as those used to select a subset of predictors (cf. Hocking 1976, Mosteller & Tukey 1977, Seber 1977, Draper & Smith 1981, Henderson & Velleman 1981). First, a full regression model containing all variables and interactions was built and both the *t*-values and partial *F*-values of variables were computed. Reduced models were then constructed, using partial correlations of variables as the selection criteria for the candidates to be included. The significance of partial correlations, *t*-values and partial *F*-values of variables was analysed. The coefficient of determination, R^2 , and the error mean square, MSE, of reduced models were compared with those of the full model to assess their prediction ability.

PCA transformation of variables for regression model. PC transformation can be regarded in the same manner as any other transformation that is used to prepare variates for regression. Massy (1965) compared this approach with classical least-squares multiple regressions and concluded that the PC regression method is useful in exploratory studies of complex relations between variables. One reason for transforming

a set of variables into principal components is that PCA substitutes orthogonal linear combinations of variables for original variables, removing any multicollinearity among them, while maintaining the original structure of the data (Morrison 1976). This is particularly important in ecological studies because the original independent variables are often highly correlated with each other. Another advantage resulting from the uncorrelated variables is that the relative importance of predictors in a model is easier to assess, because the order of entering them into the regression does not affect the regression coefficients.

PCA was performed on the original variables excluding *Gelidium sesquipedale* using a correlation matrix. The 5 component axes were rotated using varimax rotation, so that each component could be mainly identified with 1 variable. Five component scores for each individual quadrat were then calculated. Component scores associated with each quadrat (each representing 1 variable) represent a conservative reparameterization of the original data that does not alter the multidimensional geometric relationships among quadrat samples, but allows a more efficient means of describing these relationships in terms of

biotic and abiotic factors (Moloney 1989). A multiple regression model was then constructed, regressing transformed *G. sesquipedale* cover values against the PC scores associated with each quadrat.

RESULTS

Distribution patterns of species and abiotic factors

Fig. 2 shows the distribution patterns of the dominant macrophytes and abiotic factors. Transect averages of biotic and abiotic factors variation along the *Gelidium sesquipedale* commercial bed are shown. *G. sesquipedale* transect cover using the point transect method is compared with the eyeball quadrat estimates. Although transect cover absolute values were generally higher than quadrat cover values, the patterns of variation of the species cover along the bed were similar for both methods ($r = 0.89$, $p < 0.0001$). *G. sesquipedale* cover gradually decreased within the study site from south to north, whereas *Saccorhiza polyschides* density had the opposite distribution pattern. *Laminaria ochroleuca* density showed no distinct trend. However, the significance of trends can not be assessed from the graphs because with systematic sampling there is no indication of the precision of the mean (standard error) and no possibility of assessing of its difference from the mean in another area (Greig-Smith 1983).

Besides the natural depth gradient perpendicular to the shore line, an overall depth gradient parallel to the coast was apparent, where average depth decreases northward (Fig. 2). Also, the topographic characteristics of the coast determine that quadrat mean slope decreased northward. In contrast, both the amount of sediment over the rock and transect sand cover increase northward. The deposition of sediments over the rock and its effect on the abrasion of fronds is variable with time, and is not considered in the observations. However, transect sand cover is correlated ($r = 0.71$, $p = 0.001$) with the amount of siltation inside the quadrats (Fig. 2); plants near sand patches should be more subjected to the effects of siltation.

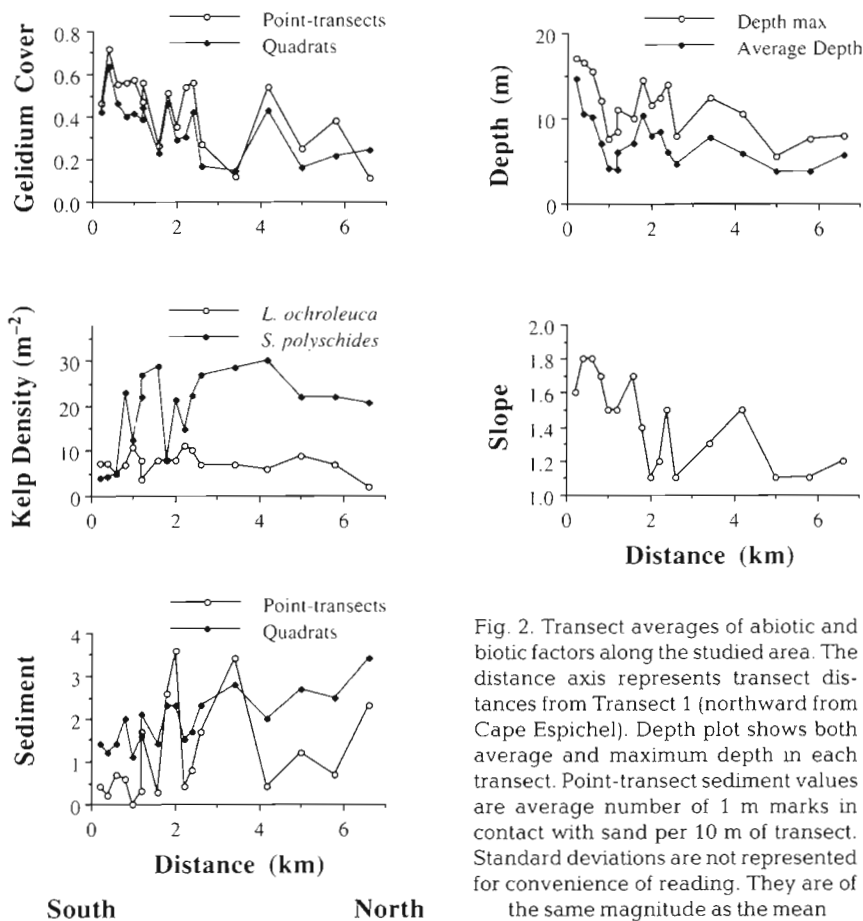


Fig. 2. Transect averages of abiotic and biotic factors along the studied area. The distance axis represents transect distances from Transect 1 (northward from Cape Espichel). Depth plot shows both average and maximum depth in each transect. Point-transect sediment values are average number of 1 m marks in contact with sand per 10 m of transect. Standard deviations are not represented for convenience of reading. They are of the same magnitude as the mean

Principal component analysis

Three PCs were selected for interpretation, based on the analysis of the plot of the eigenvalues against the components (see 'Methods'). Table 1 shows their loadings before and after varimax rotation. They represent the correlation between each original variable and the component. To decide which loadings to interpret, correlation coefficients were tested for significance, using Bonferroni's correction for multiple comparisons. All values of Table 1 greater than 0.24 (bold text) are significantly different from zero ($p < 0.001$). However, in PCA the level at which a loading is significant should decrease with the number of variables, and should increase from the first factor to the last (Hair et al. 1987). Based on this, the correlation coefficients higher than 0.40, 0.50 and 0.60 respectively for the first, second and third principal components were considered for interpretation (values marked 'a' in Table 1).

Computation of the first unrotated component extracts a linear combination of variables that accounted for 36% of the total relationship among variables. It is the single best summary of linear relationships among variables, and therefore it represents the gradient structure of data: *Gelidium sesquipedale* cover, substratum slope and depth were higher where *Saccorhiza polyschides* density and siltation were lower (and vice versa). The second unrotated component explains 18% of total relationship. It suggests that *Laminaria ochroleuca* density was higher in deeper zones.

Varimax rotation of the 3 principal components show that the strongest interrelationships of variables were among *Gelidium sesquipedale* cover, silt and slope. The first rotated component's loadings suggest that this species was more abundant in inclined zones with

low siltation. To a lesser degree, data structure suggests that *Saccorhiza polyschides* density was lower in such zones. The second principal component suggests that *S. polyschides* was more abundant in shallow zones.

PCA biplots

The original data matrix of all abiotic and biotic variables was transformed by PCA into a rank 2 matrix, by performing a varimax rotation of the 2 principal components. The 2 principal components explained 54.6% of total data relationships. Fig. 3 shows the biplot of the variable loadings vectors and the quadrat sample scores. *Gelidium sesquipedale* cover is highly positively correlated with substratum slope, and both are negatively correlated with siltation and, to a lesser degree, with *Saccorhiza polyschides* density. *Laminaria ochroleuca* density and depth are negatively correlated with *S. polyschides* abundance. To make the graph clearer, only the site scores of the first 3 transects of the south edge of the area studied and the last 6 transects (Transects 13 to 18) of the north edge are shown. There is a defined separation of both clusters of samples. The southern cluster is characterized by higher abundance of *G. sesquipedale* and *L. ochroleuca*, and higher substratum slopes and depth. The northern cluster shows higher *S. polyschides* densities and higher siltation (Fig. 3).

Full regression model

All the original variables except *Gelidium sesquipedale* were transformed by PCA and varimax-rotated. Each original variable value was replaced by the PC score with which that variable was highly correlated (Table 2). A full regression model was then constructed using as predictors all possible main effects and interactions. Table 3 shows the predictor coefficients of the full model. Variables with non-significant t - and partial F -tests are not presented. Non-significant variables do not contribute to the understanding of regressor variability when all predictors are included in the model.

Partial F -tests were computed for all predictors to examine their significance and their relative importance in explaining the variance of *Gelidium sesquipedale* abundance (Table 3). At this stage, both

Table 1. Variable loadings of first 3 principal components before and after varimax rotation. Correlations in bold text are significantly different from zero ($p < 0.001$). Gel, Sac and Lam: abundances of *Gelidium sesquipedale*, *Saccorhiza polyschides* and *Laminaria ochroleuca* respectively

Variables	Unrotated			Rotated		
	PC1	PC2	PC3	PC1	PC2	PC3
Gel (% cover)	0.73^a	0.38	0.07	-0.82^a	0.11	0.01
Sac (density)	-0.68^a	0.24	0.28	0.39	-0.65^a	0.14
Lam (density)	0.29	-0.70^a	0.57	0.02	0.13	-0.94^a
Slope (1 to 3 scale)	0.67^a	0.35	-0.13	-0.72^a	0.24	0.15
Silt (1 to 4 scale)	-0.67^a	-0.12	-0.48	0.71^a	0.06	0.43
Depth (m)	0.44^a	-0.52^a	-0.58	0.01	0.89^a	-0.04
Proportion of relationship explained	0.36	0.18	0.16	0.31	0.22	0.19
Cumulative proportion	0.36	0.54	0.70	0.31	0.53	0.72

^a Biologically significant loadings (see text)

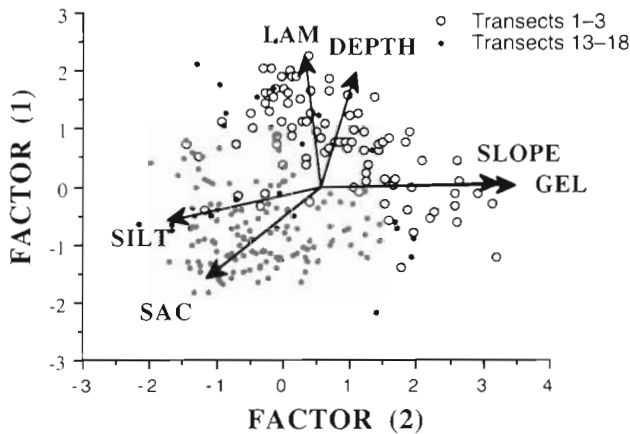


Fig. 3. Biplot of the variable loadings vectors and the quadrat sample scores. Only the scores of Transects 1 to 3 and 13 to 18 are shown. GEL: *Gelidium sesquipedale*; LAM: *Laminaria ochroleuca*; SAC: *Saccorhiza polyschides*

the t -values and the partial F -values indicate that the most important variables and interactions may be Slope, Sac, Silt, Slope \times Lam, Lam \times Depth and Slope \times Lam \times Depth \times Silt. However, the partial F -values in the full model also reflect the effects of all factors and interactions that are not significant in the regression, which can distort that judgement.

Table 2. Correlations among principal components (PC) rotated by varimax and original variables. Each rotated component is highly related with only 1 variable (bold text)

Variables	PC1	PC2	PC3	PC4	PC5
Slope	-0.974	0.016	0.084	0.129	0.164
Lam	0.014	-0.989	0.053	0.077	0.110
Depth	-0.082	-0.054	0.983	0.154	0.033
Sac	0.130	0.081	-0.160	-0.970	-0.097
Silt	0.164	0.116	-0.034	-0.095	-0.974

Table 3. Values from full regression model of all variables (see Table 1) and interactions. Variables shown have highly significant ($p < 0.001$) t - and partial F -tests. Variables with non-significant t - and partial F -tests are not included. Dependent variable: Gel; N = 496, $R^2 = 0.465$, adj. $R^2 = 0.430$, SE of estimate = 0.335

Variable	Coefficient	SE	Std coef.	t	p (2 tail)	F	p
Constant	0.601	0.016	0.000	37.777	0.000		
Slope	0.145	0.017	0.319	8.409	0.000	70.716	0.000
Sac	-0.166	0.018	-0.356	-9.425	0.000	88.833	0.000
Silt	-0.130	0.018	-0.288	-7.273	0.000	52.901	0.000
Sl \times La	-0.011	0.019	-0.023	-0.580	0.562	35.797	0.000
La \times De	-0.089	0.018	-0.197	-4.987	0.000	24.868	0.000
Sl \times La \times De \times Si	-0.102	0.027	-0.175	-3.730	0.000	13.911	0.000
Analysis of variance							
Source	SS	df	MS	F -ratio	p		
Regression	45.351	31.000	1.463	13.024	0.000		
Residual	52.117	464.000	0.112				

Reduced model development

A reduced model was constructed in steps. First, correlations between *Gelidium sesquipedale* and all predictor candidates were computed. The most highly correlated variable, Silt ($r = -0.373$), was regressed on *G. sesquipedale*. Then, partial correlations of the remaining variables with *G. sesquipedale* were computed to determine how much of its variation not explained by Silt can be accounted for by each of the other predictors.

Variables were entered into the equation one by one, each time choosing the variable with the highest partial correlation after the previous ones had been fixed. The magnitudes of the partial correlations show that after the effect of Silt is removed, the most important variable was Slope ($r = 0.34$) followed by Sac ($r = -0.35$) and Lam \times Depth ($r = -0.26$). The partial correlations of these selected variables are significantly different from zero with a probability $p < 0.001$ (Bonferroni correction for multiple correlations).

After this, there was a marked reduction in the significance of partial correlations. The next highest partial correlations, Sac \times Silt ($r = 0.15$) and the fourth order interaction Slope \times Lam \times Depth \times Silt ($r = -0.14$), were not significantly different from zero ($p < 0.05$, Bonferroni corrected). This indicates that these variables were not important in explaining the variation of *Gelidium sesquipedale* distribution, though they significantly contributed to the full model as indicated by their significant t - and partial F -values (Table 3). Including the next highest partial correlations (Sac \times Silt, Slope \times Lam \times Depth \times Silt, Lam \times Silt and Slope \times Depth) in the reduced model, raises the adjusted coefficient of determination to $R^2 = 0.41$ (Table 4). The mean-square error of this prediction model is 0.117, not much higher than that of the full model, where MSE = 0.112. This shows that the residual variance left after regression is almost the same in both models.

Table 4. Reduced regression model of *Gelidium sesquipedale* cover (Gel). See Table 1 for variables. N = 496, R² = 0.418, adj. R² = 0.408, SE of estimate = 0.341

Variable	Coefficient	SE	Std coef.	t	p (2-tail)	F	p
Constant	0.600	0.015	0.000	39.034	0.000		
Silt	-0.147	0.016	-0.326	-8.947	0.000	80.041	0.000
Sac	-0.147	0.016	-0.315	-8.931	0.000	79.766	0.000
Slope	0.136	0.016	0.300	8.586	0.000	73.719	0.000
La × De	-0.088	0.016	-0.194	-5.524	0.000	30.515	0.000
Sa × Si	0.055	0.016	0.122	3.442	0.001	11.847	0.001
La × Si	0.049	0.018	0.098	2.684	0.008	7.202	0.009
Si × La × De × Si	-0.054	0.020	-0.092	-2.618	0.009	6.855	0.008
Si × De	-0.040	0.016	-0.091	-2.591	0.010	6.711	0.010
Analysis of variance							
Source	SS	df	MS	F-ratio	p		
Regression	40.709	8	5.089	43.662	0.000		
Residual	56.758	487	0.117				

The marked drop in the *F*-values from the first to the second set of predictors (Lam × Depth = 30.5 to Sac × Silt = 11.8; Table 4) indicates that although the new predictors are useful in explaining additional variance in the dependent variable, their relative importance is much lower. Residual plots of the prediction model do not show any strong deviations from normality. The normal probability plot of the residuals do not deviate strongly from a straight line, suggesting that the regression does not violate assumptions.

Siltation, *Saccorhiza polyschides* and substratum slope are the main variables explaining the variation of *Gelidium sesquipedale* cover. Their relative importance is not distinguishable because their standardized regression coefficients were not significantly different from each other. Interaction effects were weaker than main effects of Silt, Slope and Sac. *Laminaria ochroleuca* and depth did not significantly explain *G. sesquipedale* variability when considered separately, but have a negative effect when they act together. Significant relationships were not detected between depth and *G. sesquipedale*.

DISCUSSION

The relative importance of the determinants of seaweed distribution vary with scale. On a broad geographical scale, temperature and day length determine the boundaries of species distribution through plant mortality or inhibition of growth or reproduction (Breeman 1988, Lüning 1990). On a local scale, light, water motion, substrate topography, sedimentation and competition appear to be the determinants of the zonation observed along the depth gradient (Lobban et al. 1985, Schiel & Foster 1986, Kain & Norton 1990).

This study shows that the amount of sediments over the rocky bottom, its slope and *Saccorhiza polyschides* density have the strongest relationships with *Gelidium sesquipedale* cover in the study area. Both PC and multiple regression analyses revealed positive relationships between this species and slope, and negative relationships with silt and *S. polyschides* (Fig. 3, Table 4). Multiple regression analysis indicated the main effects of the 3 variables were of the same relative magnitude; their standardized regression coefficients were not significantly different (Table 4).

High slopes and reduced sediment loading might favour *Gelidium sesquipedale* development. This species is more abundant than the kelp *Saccorhiza polyschides* in such zones. On the other hand, *S. polyschides* is more abundant than *G. sesquipedale* on low slope surfaces with high siltation. *S. polyschides* may tolerate siltation better than *G. sesquipedale*; in culture studies, Norton (1978) found that spores of this kelp would germinate even when covered with a silt layer.

Within the depth range studied (0 to 18 m), *Saccorhiza polyschides* density is the only variable correlated with depth (Fig. 3). The density of this kelp drops at depths greater than 10 m (Fig. 4). This agrees with other reports of *S. polyschides* vertical distribution, which found this species confined to the upper zones of the subtidal (John 1971, Lüning 1990). In contrast to Cape Espichel, where *G. sesquipedale* is not correlated with depth, Gorostiaga (1990) reported that along the NE coast of Spain both biomass and cover decrease with depth. He suggested that this is an effect of siltation which increases with depth. In this area, the depth limit of *G. sesquipedale* is 9 m.

The density of *Laminaria ochroleuca* populations is relatively uniform through the study area, overlapping the distribution of *Saccorhiza polyschides* (Figs. 2 & 4).

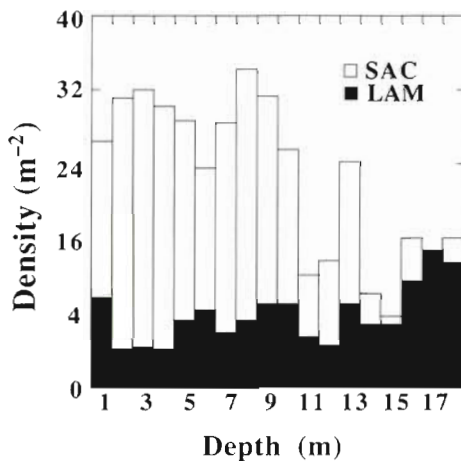


Fig. 4. *Saccorhiza polyschides* (SAC) and *Laminaria ochroleuca* (LAM). Vertical distribution of densities (m⁻²)

This pattern has not been observed by other authors. John (1971) found distinct, non-overlapping zones of vertical distribution of these species in exposed sites off NW Spain and Lüning (1990) reports that through its geographical distribution *L. ochroleuca* occupies a deeper zone (down to 25 to 30 m) than *S. polyschides*.

The interactions of abiotic and biotic factors affecting subtidal algal stands have seldom been studied (Schiel & Foster 1986). The only interaction significantly related with *Gelidium sesquipedale* cover variation was Lam × Depth. Although *Laminaria ochroleuca* by itself does not contribute significant variation, this interaction suggests that at higher depths *L. ochroleuca* dominates *G. sesquipedale*. This is supported by analysis of the correlations between these species in shallow versus deeper zones (Table 5). *L. ochroleuca* and *G. sesquipedale* are negatively correlated in deeper zones, which contrasts with their positive correlation in shallow zones. On the other hand, *Saccorhiza polyschides* abundance has a negative correlation with *G. sesquipedale*, of the same magnitude at all depths.

Table 5. Pearson correlation matrices of the 3 species in shallow (≤ 9 m) and deeper (≥ 13 m) zones. Values in bold text are significant at $p < 0.05$ (Bonferroni-corrected probability)

	Gel	Lam	Sac
Depth ≤ 9 m (n = 390)			
Gel	1.000		
Lam	0.155	1.000	
Sac	-0.372	-0.225	1.000
Depth ≥ 13 m (n = 58)			
Gel	1.000		
Lam	-0.491	1.000	
Sac	-0.315	-0.089	1.000

Abiotic factors

Austin (1980), searching for a model of the determinants of plant distribution, recognized 3 types of environmental factors: indirect factors, which have no direct physiological influence; direct factors, with direct physiological influence; and factors that are an essential resource for plants. Of the environmental gradients considered in this study, sediment is a direct environmental factor. The direct effects of siltation on *Gelidium sesquipedale* are more likely to influence spore settlement and development, and growth of new vegetative shoots from creeping axes, than adult plants. Devanny & Volse (1978) found that even small amounts of sediment would greatly reduce the settlement and development of *Macrocystis pyrifera* spores. Only in extreme conditions of sand movement may seaweeds be broken by abrasion or killed by prolonged burial (Dahl 1971, Daly & Mathieson 1977). In contrast, the topographic shape of rocky bottom, or slope, may not have a direct influence on *G. sesquipedale* but rather an indirect one, by affecting the type of water flow. The fluid dynamics resulting from wave-induced water movement and its interactions with the topographic features of the bottom, the presence and shape of plants, and depth are very complex (Vogel 1981, Denny 1988). Water movement has both positive and negative direct effects on seaweed development: negative, since the mechanical stress on the plants may increase mortality or breakage (Koehl 1986); positive, through increasing nutrient availability and spore dispersal (Lobban et al. 1985, Lüning 1990).

A distinct difference in *Gelidium sesquipedale* density and frond morphology between horizontal and inclined surfaces is evident in the study site. Frond density on inclined surfaces decreases with increasing depth (unpubl. data). As well, fronds are shorter and bushier on horizontal surfaces than on inclined surfaces where they are longer. The positive relationship between slope and *G. sesquipedale* cover reflects this. Higher densities on horizontal substrata may be a population response to physical disturbance. Turbulent patterns of water flow are enhanced by the presence of obstacles (Denny 1988), which are more common on horizontal surfaces. The turbulent flow increases the availability of nutrients as well as the availability of light by increasing frond breakage. This may result in an increase of vegetative growth of new fronds from creeping axes.

Depth (through decreasing light) may also be an important indirect factor influencing the morphology of *Gelidium sesquipedale* fronds. Macler & West (1987), in culture studies of *Gelidium coulteri*, showed that plants grown under low light levels were stoloniferous with little branching. When irradiance was

increased, plants developed branches. Nevertheless, effects of depth on *G. sesquipedale* cover were not detected, even as an interaction with slope.

Biotic factors

Competition between kelp and understory species has been described as being for space and for light. Understory species seem adept at monopolizing the substrate, whereas kelps may shade rivals (see review by Kain & Norton 1990). Many manipulative field experiments have shown that canopy species may reduce the settlement and growth of understory species (e.g. Reed & Foster 1984, Dean et al. 1989, Kennelly 1989).

Ojeda & Santelices (1984) performed the only competition experiments involving *Gelidium* species, between *Gelidium chilense* and the kelp *Lessonia nigrescens*. If kelp was removed in summer, *G. chilense* monopolized the substratum and the next year kelp settlement did not occur. By contrast, if kelp was removed in winter, kelp settlement occurred the following year, though *G. chilense* did extend into the low intertidal levels previously occupied by the kelp. *Saccorhiza polyschides* is an annual species which loses all its fronds during the fall season. If this species does compete with *Gelidium sesquipedale* their competitive relationship may follow a similar process.

The processes that regulate local patterns in the abundance of *Gelidium sesquipedale* can only be completely understood when mechanistic causes are revealed. Associations among variables do not imply causation (Hastings 1987). Three types of information are required to support causality: consistency, responsiveness and a mechanism (Mosteller & Tukey 1977). There is not sufficient information to assess whether the relationships shown at Cape Espichel occur elsewhere, in other populations or at other times. Palminha et al. (1982), off the south coast of Portugal, and Gorostiaga (1990), off the NE coast of Spain, subjectively observed negative relationships between *G. sesquipedale* abundance and the amount of sediment. Gorostiaga (1990) also points out the lack of relationship between *G. sesquipedale* cover and substratum slope, but the range of slopes observed is very low (0 to 40°).

To assess the responsiveness of *Gelidium sesquipedale* to changes in abiotic and biotic factors, experimental studies must follow this study, manipulating the variables and measuring their effects on demographic rates *in situ*. The mechanism behind the causal relationships can only be revealed through understanding the behavior of the vital rates that regulate population dynamics, when subjected to changes of the background abiotic and biotic factors.

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