Composition and spatio temporal variability of the epiphytic macroalgal assemblage of *Fucus vesiculosus* Linnaeus at Clare Island, Mayo, western Ireland

Fabio Rindi*, Michael D. Guiry

Martin Ryan Institute, National University of Ireland Galway, Galway, Ireland

Abstract

The composition and the patterns of spatial and temporal variability of the epiphytic assemblages of *Fucus vesiculosus* of Clare Island, on the western coast of Ireland, were investigated for an annual cycle. Specimens of *Fucus* were collected on seven sampling dates from three sites of the island (Portlea, Kinnacorra and Portnakilly). Data of cover of the most common epiphytic species were collected and analysed by multivariate and univariate techniques. *Elachista fucicola*, *Polysiphonia lanosa*, *Porphyra umbilicalis*, *Spongonema tomentosum* and *Ulva compressa* were the most common species. Spatial and temporal variation was detected both for the whole assemblage and for the most abundant species. In general, the assemblage was quantitatively more abundant and diverse in spring–summer than in autumn–winter. In spring–summer, there was a clear differentiation among the assemblage of Portnakilly and the assemblages of the other two sites. Individual species were also generally more abundant in spring–summer and their distribution at the three sites was often not consistent in time; *P. lanosa* was the only epiphyte for which a consistent effect of site was found. Spatial variation on a scale of meters to tens of meters was the most striking pattern of distribution of the epiphytic assemblage; significant effects related to this spatial scale were detected both for the whole assemblage and for individual species. Phenological patterns of the epiphytic species determining availability of propagules and limited dispersal, leading to aggregated patterns of distribution, are considered the main factors responsible of such patchiness. The importance of the

* Corresponding author. Tel.: +353-91-524411x3200; fax: +353-91-525005.
E-mail address: fabio.rindi@nuigalway.ie (F. Rindi).

incorporation of small spatial scales in sampling designs analysing the distributional patterns of epiphytic assemblages is discussed.

1. Introduction

Epiphytism is a widespread phenomenon in marine benthic communities; a large number of marine algae can grow epiphytically on other macroalgae or seagrasses. Although most epiphytic algae are essentially facultative and are not specifically associated with a host species (Wahl and Mark, 1999), some are known as specific and obligate epibionts on certain hosts (Harlin, 1980; Pearson and Evans, 1990). Because of the importance of seagrasses as primary producers, most of the literature considering epiphytism in the marine environment has concerned seagrass ecosystems (Harlin, 1980; Borowitzka and Lethbridge, 1989; Jernakoff et al., 1996), focusing in particular on the negative effects of epiphytes on their hosts (Sand-Jensen, 1977; Orth and van Montfrans, 1984; Neckles et al., 1993). Considerably less work has concerned the distribution and effects of epiphytic populations on macroalgal hosts.

Fucus vesiculosus Linnaeus is an intertidal, perennial brown alga widespread in the Northwestern Atlantic (Lüning, 1990). It occurs on most rocky shores, where it often forms an almost monospecific canopy on mid-intertidal rock (Knight and Parke, 1950). Due to its widespread distribution and its structurally important role in intertidal communities, many aspects of the biology of this species have been studied in great detail. In the Baltic Sea in particular, *F. vesiculosus* is the dominant macroalgal species and its well-documented lessening of depth penetration, which took place in the last 40 years (Kautsky et al., 1986), has stimulated numerous studies, concerning primarily its physiology and reproductive ecology (Bäck et al., 1992; Kiirikki and Ruuskanen, 1996; Serrão et al., 1999). It is therefore remarkable that the information available on the epiphytic flora of *F. vesiculosus* is, to date, still relatively scanty. Mention of algae occurring as epiphytes of *F. vesiculosus* is not infrequent (Fletcher, 1987; Johnson and Scheibling, 1987; Russell, 1988; López-Rodríguez et al., 1999), but few studies have reported details on their distribution and effects on the host (Rönnberg and Ruokolahti, 1986; Arrontes, 1990).

Most of the 7000-km-long coastline of Ireland is rocky. The western coast, in particular, represents one of the most habitat-diverse and least impacted shorelines in Europe. Due to extensive taxonomic studies conducted mostly in the last 30 years, the benthic algal flora of western Ireland is generally well known (Guiry, 1978), but virtually no quantitative data on the patterns of spatial and temporal distribution of algal populations are available.

In the present study, we examined the composition and the patterns of spatial and temporal variability of the epiphytic macroalgal assemblage of *F. vesiculosus* of Clare Island, a small island situated at the entrance of Clew Bay, in County Mayo. The natural

history of this locality has been intensively studied, mainly in an extensive survey carried out in 1910–1911 (Guiry, 1997). This work is part of a more general study, that has considered in detail the flora and distribution of the benthic algal assemblages on the island (Rindi et al., 2002; Rindi and Guiry, 2004). Here, we tested the null hypothesis that no significant differences in the composition of the assemblage and in the abundance of the most common epiphytic species will occur among three sites and at different times. The identification of characteristic scales of spatial or temporal variation is a fundamental issue in ecological research; natural assemblages of species are inherently variable and changes in the composition and abundance of organisms occur at several spatial and temporal scales. Analysis of this variability is an essential requirement for understanding ecological processes; detecting at which scales most of variability occurs can focus attention on some processes and exclude others as very unlikely explanation for the observed patterns (Underwood, 1997; Menconi et al., 1999; Benedetti-Cecchi, 2001). The results presented here provide a basis of information on the distributional patterns of this important intertidal community, for which virtually no quantitative data are currently available in the literature. On the basis of the patterns observed, we forward some suggestions about the processes that are most likely to be important in determining such variation. This information will be of great importance for further investigations on benthic intertidal assemblages of the Irish west coast and for comparisons with similar patterns of the same community for other regions of the North Atlantic.

2. Materials and methods

2.1. Study area

Clare Island is situated at the entrance of Clew Bay, County Mayo, on the west coast of Ireland (Fig. 1). Roonagh Point, the nearest part of the Irish mainland, is about 4 km from
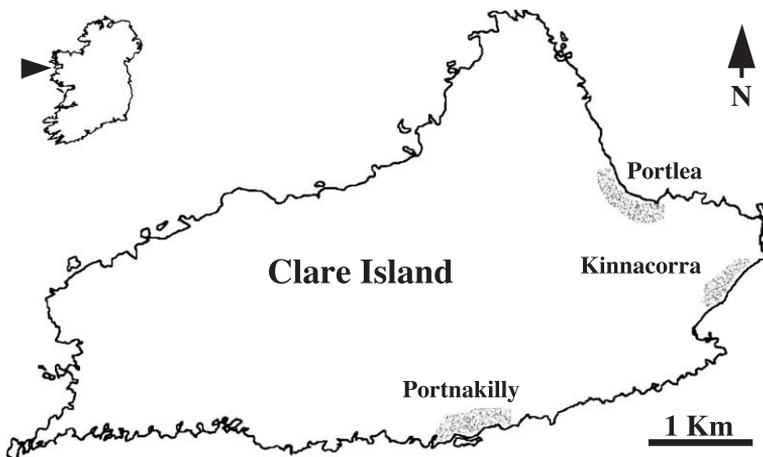
Fig. 1. Map of Clare Island showing the location of the three study sites.

the southeastern shore of Clare Island. With the sole exception of the bay of the harbour, the coastline of the Island is rocky and generally characterised by conditions of strong wave exposure. Three sites, located at 2–5 km from each other, were chosen for this study: Portlea, on the northeastern shore, the shore between Kinnacorra and the harbour, facing SE, and Portnakilly, on the southern shore (Fig. 1). For detailed descriptions of the sites, see Rindi and Guiry (2004). *F. vesiculosus* is generally common on Clare Island, occurring on most of the eastern and southern shores (Rindi et al., 2002). At Portlea, it occurred on large boulders in the mid-upper intertidal and formed a relatively uniform canopy on mid-lower intertidal rock. On the shore between Kinnacorra and the harbour, it was common but showed a quite irregular distribution. Patches of *F. vesiculosus* extended for several meters or tens of meters, alternating with stretches of almost bare rock. At both these sites, *F. vesiculosus* showed the morphology typical of the species: specimens were up to 70 cm tall, with relatively thin stipe and long dichotomies, usually producing a large number of bladders in the upper parts of the fronds. At Portnakilly, *F. vesiculosus* occurred in irregular, more or less isolated patches separated by stretches of rock mostly covered by mussels (*Mytilus* spp.). There, the alga was shorter (<30 cm), with a very robust stipe and short and narrow dichotomies, devoid of bladders; this is the morphotype described by Cotton (1912) as *F. vesiculosus* var. *evesiculosus* Cotton (=*F. vesiculosus* var. *linearis* (Hudson) Kützing). In the course of the study, populations of *F. vesiculosus* on Clare Island were found reproductive from April to July, when many plants bore receptacles.

No sites on the western and northwestern shores could be examined, as they are extremely exposed and mostly bounded by high cliffs, which make access virtually impossible.

2.2. Sampling design and collection of data

Collections of *Fucus* were made on seven dates in an annual cycle (28–29 April 2001; 10–11 June 2001; 20–21 July 2001; 19–20 September 2001; 20–21 October 2001; 4–5 November 2001; 15–16 February 2002). On each sampling date, plants of *Fucus* were collected at each of the three sites selected. Ten plants, at least 10 cm tall, were collected in three areas (stretches of mid-intertidal rock, 5–6 m long) randomly selected at each site. Care was taken not to resample a same area at different times. The plants were transported to the laboratory in large, closed plastic bags, usually 1–2 days after collection, which was sufficient to avoid severe damage to the epiphytic algae. In the laboratory, the material was processed as quickly as possible. For each specimen of epiphytic algae, the parts of the *Fucus* thallus on which it occurred were recorded as follows: stipe, lower dichotomies (dichotomies of first and second order), upper dichotomies (dichotomies of higher order) and tips and receptacles (Fig. 2). The epiphytic algae were then carefully removed and the abundance of each species was estimated by measuring its cover (in cm^2) on a plastic grid. Since to obtain a quick and reliable estimate of the surface area of plants of *Fucus* was not possible, the cover data were not standardised or expressed as percentage of a surface area unit. Non-standardised data, however, provided a correct estimate of algal abundance and were regarded as appropriate for testing the hypotheses considered.
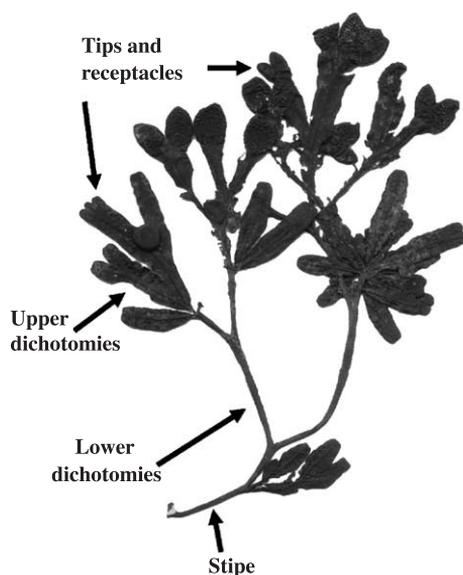
Fig. 2. Parts of the thallus of *F. vesiculosus* on which the distribution of epiphytic algae was examined.

The reproductive condition of the epiphytic red and brown algae was noted. Voucher specimens have been deposited in the Phycological Herbarium, National University of Ireland, Galway (GALW).

2.3. Analysis of data

Cover data were analysed using multivariate and univariate techniques. For the analyses, the cover (in cm^2) of all thalli of an epiphytic species occurring on a plant of *Fucus* (without distinction between thalli occurring on different parts of *Fucus*) was the variable used.

Nonparametric multivariate analyses were carried out for the data obtained for the sampling dates from April to September (1–4). Cover data for the eight most common species of epiphytic algae were used for each sample (i.e., plant of *Fucus*). For the last three sampling dates, the epiphytic vegetation was scanty; many plants of *Fucus* were completely devoid of epiphytes and no multivariate analyses were done. The PRIMER-5 package (Clarke and Gorley, 2001) was used. For each sampling date, a matrix of similarity was obtained among every pair of samples using the Bray-Curtis index of similarity on fourth-root transformed data. Nonmetric multidimensional scaling (nMDS) was used to produce two-dimensional ordinations of the rank orders of similarities of the samples. Two-way nested analysis of similarities (ANOSIM) and multiple pairwise comparisons were used to test for differences in assemblages among sites and areas. When ANOSIM detected a high dissimilarity between sites, analysis of species contributions to similarity (SIMPER) was carried out to detect which species contributed most to the dissimilarity.

A three-factor analysis of variance (ANOVA) was used to test hypotheses concerning spatial and temporal patterns of distribution of the most common epiphytic algae. The factors considered were: site (three levels, random), time (seven levels, random and orthogonal to site) and area (three levels, random and nested in the interaction site × time). Homogeneity of variances was tested by Cochran's C test (Underwood, 1997) and, if necessary, logarithmic transformation was used to reduce heterogeneity of variances. For most analyses, variances were heterogeneous even after transformation. However, for balanced designs with a high number of degrees of freedom, ANOVA is very robust to deviations from the assumption of homogeneity of variances (Under-

Table 1
List of algae recorded as epiphytes of *F. vesiculosus* at Clare Island

Sampling date	1	2	3	4	5	6	7
Chlorophycota							
Cladophora sericea (Hudson) Kützing			Pa				
Cladophora rupestris (Linnaeus) Kützing				Pa			
Ulothrix flacca (Dillwyn) Thuret	Ka, Py						
Ulva compressa Linnaeus		Py	Py	Ka, Py	Py	Py	
Phaeophycota							
Elachista fucicola (Velley) Areschoug	Pa, Ka, Py	Pa, Ka, Py	Pa, Ka, Py	Pa, Ka, Py	Pa, Ka, Py	Pa, Ka, Py	Py
Pylaiella littoralis (Linnaeus) Kjellman	Pa, Py			Ka		Py	
Spongonema tomentosum (Hudson) Kützing	Pa, Py	Pa, Ka, Py	Pa, Ka, Py	Pa, Py			
Rhodophycota							
Ceramium virgatum Roth	Pa			Pa			
Gelidium pusillum (Stackhouse) Le Jolis	Pa						
Lomentaria articulata (Hudson) Lyngbye	Pa, Py		Pa				
Osmundea pinnatifida (Hudson) Stackhouse	Ka	Pa	Ka	Pa, Ka	Ka	Pa	
Palmaria palmata (Linnaeus) Kunze				Pa			
Polysiphonia lanosa (Linnaeus) Tandy	Pa, Ka, Py	Pa, Ka	Pa, Ka	Pa, Ka	Pa, Ka	Pa, Ka	Pa, Ka
Porphyra leucosticta Thuret	Pa, Ka	Pa, Ka					
Porphyra umbilicalis (Linnaeus) Kützing	Py	Py	Py	Py	Py	Py	
Rhodothamniella floridula (Dillwyn) Feldmann						Py	

Pa = Portlea; Ka = shore between the harbour and Kinnacorra; Py = Portnakilly.

wood, 1997) and the results of the analyses were considered reliable. In this case, α was set at 0.01.

3. Results

In the course of the study, 16 species of macroalgae were found as epiphytes of *Fucus*; 4 were Chlorophycota, 3 Phaeophycota and 9 Rhodophycota (Table 1). Relatively few species, however, were common and widespread in space and time. *Elachista fucicola* (Velley) Areschoug and *Polysiphonia lanosa* (Linnaeus) Tandy were the only species collected on each date (Table 1).

The epiphytic community was characterised by a marked variation in time and in space at the scale of tens of meters (related to the factor area), whereas the effect of site varied in time. The assemblage was generally much more diverse and abundant in the period spring–summer (dates 1–4) than in autumn–winter (dates 5–7). *E. fucicola*, *P. lanosa*, *Porphyra umbilicalis* (Linnaeus) Kützing, *Porphyra leucosticta* Thuret, *Spongonema tomentosum* (Hudson) Kützing and *Ulva compressa* Linnaeus were the main contributors to the biomass of the assemblage. The global ANOSIM showed that significant differences between the assemblages of the three sites occurred for some sampling dates but not for other ones; by contrast, significant differences between areas were found for all sampling dates from April to September (Table 2). For April (date 1), the samples of the three sites were scattered throughout the nMDS plot without any separation (Fig. 3); the global and pairwise ANOSIM tests indicated a high similarity among the three sites (Table 2). For June, July and September (dates 2–4), the assemblage of Portnakilly was distinct from those of Portlea and Kinnacorra, that appeared much more similar (Figs. 3 and 4). At these times, *P. umbilicalis* and *U. compressa* were generally abundant at Portnakilly and absent or rare at Portlea and Kinnacorra; the SIMPER analyses showed that *P. umbilicalis* was generally the main contributor to the dissimilarity between Portnakilly and the other two

Table 2
Results of the two-way nested ANOSIM on the effect of area and site

	Global test	Pairwise test	R
Date 1 (April)	Global R (areas): 0.529**	Portlea–Kinnacorra	0.001
	Global R (sites): 0.144	Portlea–Portnakilly	0.185
		Kinnacorra–Portnakilly	0.185
Date 2 (June)	Global R (areas): 0.218**	Portlea–Kinnacorra	0.926
	Global R (sites): 0.860**	Portlea–Portnakilly	1.000
		Kinnacorra–Portnakilly	0.926
Date 3 (July)	Global R (areas): 0.390**	Portlea–Kinnacorra	− 0.074
	Global R (sites): 0.481*	Portlea–Portnakilly	0.778
		Kinnacorra–Portnakilly	0.630
Date 4 (September)	Global R (areas): 0.386**	Portlea–Kinnacorra	0.111
	Global R (sites): 0.514*	Portlea–Portnakilly	0.778
		Kinnacorra–Portnakilly	0.741

$* P < 0.05$.
$** P < 0.005$.
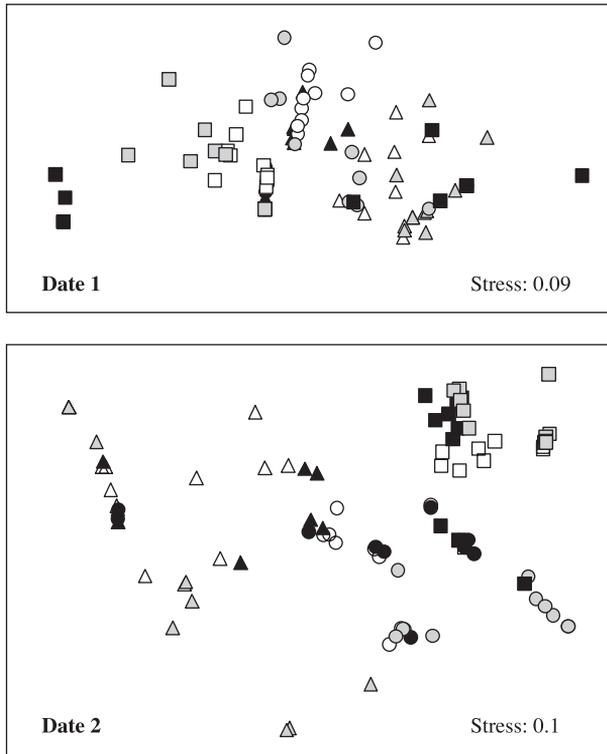
Fig. 3. nMDS ordination plots of the samples for the first and second sampling dates. Different symbols indicate the three sites sampled: triangles = Portlea; circles = Kinnacorra; squares = Portnakilly. For each site, the white, grey and black colours indicate the three areas sampled.

sites (Table 3). At the same time, *P. lanosa* and *P. leucosticta* were common at Portlea and Kinnacorra, but absent at Portnakilly. In the nMDS ordinations, the samples of Portnakilly were clustered in the top right and relatively well separated from the samples of Portlea and Kinnacorra, which were widely spread throughout the plots (Figs. 3 and 4). These patterns are illustrated by the *R* values of the pairwise ANOSIM tests, indicating a high similarity between Portlea and Kinnacorra and a strong dissimilarity of these sites from Portnakilly (Table 2). The only exception was June (date 2), in which a high dissimilarity between Portlea and Kinnacorra was also found. In this case, samples from Portlea were mainly distributed on the left side of the nMDS ordination, whereas samples from Kinnacorra mostly occurred on the right side (Fig. 3). At this time, the epiphytic vegetation at Portlea consisted mostly of *P. lanosa*, which was rare at Kinnacorra, where the dominant epiphyte was *E. fucicola*; these two species were the main contributors to the high dissimilarity, as shown by the SIMPER analysis (Table 3).

Quantitatively, the epiphytic load showed significant variation in space and time. The amount of epiphytes was generally higher in spring and summer (dates 1–4) than in autumn and winter (dates 5–7), but a significant interaction time × site was found; there was also a strongly significant effect of area (Table 4). For most sampling dates,
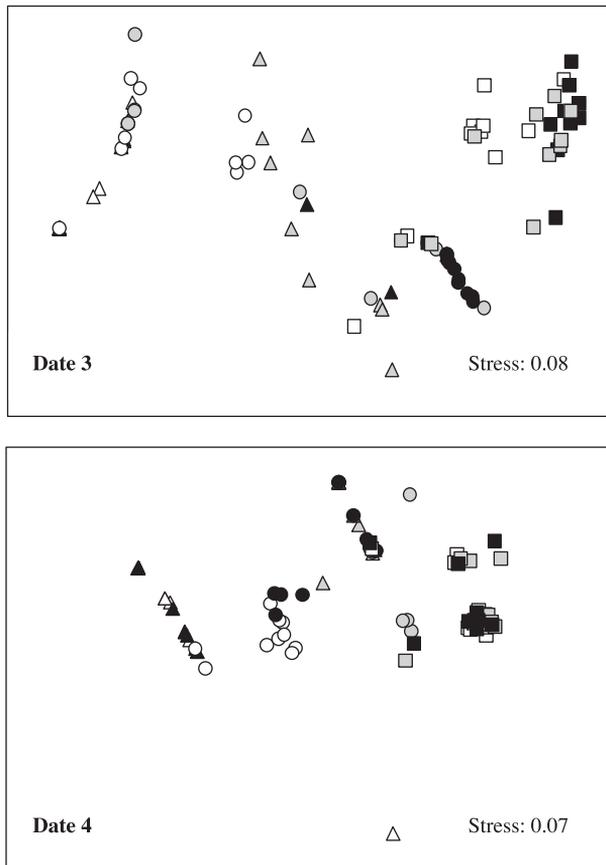
Fig. 4. nMDS ordination plots of the samples for the third and fourth sampling dates. Different symbols indicate the three sites sampled: triangles = Portlea; circles = Kinnacorra; squares = Portnakilly. For each site, the white, grey and black colours indicate the three areas sampled.

the total coverage did not differ significantly between sites. The only exception was September, when the epiphytic coverage was higher at Kinnacorra and Portnakilly than at Portlea.

A marked variability on the scale of tens of meters (indicated by the significant effect of the factor area) was a general feature of the distribution of the most abundant species. Except for this, however, different distributional patterns were observed for different species. ANOVA was performed for five species: *E. fucicola*, *P. lanosa*, *P. umbilicalis*, *S. tomentosum* and *U. compressa*.

E. fucicola was generally the most common epiphyte of *Fucus*. For this species, the ANOVA showed a significant effect of time, due to a higher abundance in the period spring–summer (dates 1–4) than in autumn–winter (dates 5–7) and a significant effect of area (Table 4). This species was widespread on the island and no significant difference between sites was detected. This situation was constant in time, and no significant

Table 3
Results of SIMPER

Species	Percent contribution
Date 2: Portlea vs. Kinnacorra (average dissimilarity = 73.46)	
Polysiphonia lanosa	33.79
Elachista fucicola	29.31
Porphyra leucosticta	19.81
Spongonema tomentosum	17.09
Date 2: Portlea vs. Portnakilly (average dissimilarity = 87.13)	
Porphyra umbilicalis	25.06
Polysiphonia lanosa	24.39
Elachista fucicola	21.55
Spongonema tomentosum	14.75
Date 2: Kinnacorra vs. Portnakilly (average dissimilarity = 58.53)	
Porphyra umbilicalis	35.07
Spongonema tomentosum	21.55
Porphyra leucosticta	17.01
Elachista fucicola	11.25
Date 3: Portlea vs. Portnakilly (average dissimilarity = 84.27)	
Elachista fucicola	25.27
Polysiphonia lanosa	24.89
Porphyra umbilicalis	24.20
Ulva compressa	18.04
Date 3: Kinnacorra vs. Portnakilly (average dissimilarity = 68.21)	
Porphyra umbilicalis	28.96
Polysiphonia lanosa	24.06
Elachista fucicola	21.88
Ulva compressa	21.71
Date 4: Portlea vs. Portnakilly (average dissimilarity = 85.90)	
Porphyra umbilicalis	32.15
Elachista fucicola	26.20
Ulva compressa	20.69
Polysiphonia lanosa	18.75
Date 4: Kinnacorra vs. Portnakilly (average dissimilarity = 59.50)	
Porphyra umbilicalis	38.70
Ulva compressa	24.33
Polysiphonia lanosa	23.18
Elachista fucicola	11.31

Average dissimilarities between sites and percent contributions to the average dissimilarities of individual species are reported.

interaction between time and site occurred (Table 4). *E. fucicola* was most common on the upper parts of *Fucus*; the upper dichotomies were the part on which most specimens were found (Fig. 5). This was also the only species found commonly on tips and receptacles (Fig. 5). Its distribution was mainly associated with portions of the thallus with an

Table 4
Results of the analysis of variance performed on the cover data of the total epiphytic load, *E. fucicola* and *P. lanosa*

	df	Total epiphytic load		Elachista fucicola		Polysiphonia lanosa	
		MS	F	MS	F	MS	F
Time (=T)	6	90.33	5.26*	38.49	5.12*	4.59	0.63
Site (=S)	2	1.71	0.10	38.91	5.17	119.86	16.30***
Area (T × S)	42	5.84	5.38***	5.09	10.78***	9.32	10.18***
Time × site	12	17.18	2.94**	7.52	1.48	7.35	0.79
Residual	567	1.09		0.47		0.91	
Total	629						
Cochran's test		C = 0.0475, P>0.05		C = 0.0839, P<0.01		C = 0.0654, P<0.01	
Transformation		ln(x + 1)		ln(x + 1)		ln(x + 1)	

* $P<0.01$.
** $P<0.005$.
*** $P<0.0005$.

expanded blade and the cover on parts consisting only of the midrib (mainly stipe and lower dichotomies) was very limited. Summer was the time of the year in which *E. fucicola* was best developed. In June, July and September, this alga was most abundant and consisted of large tufts with erect filaments up to 2 cm tall. In the subsequent months, the alga gradually lost most of the erect filaments and specimens collected in November and February (dates 6 and 7) were formed almost only by basal, wart-like cushions. Unilocular sporangia were the only specialised reproductive structures observed. These were observed from April (date 1) to November (date 6), being most common in summer (Table 5).

P. lanosa is the only epiphyte for which a significant and consistent effect of site was found, and for which no significant temporal variation was detectable (Table 4). Even for this species, the ANOVA showed a significant effect of area (Table 4). The distribution of *P. lanosa* did not show a strict association with any particular part of the thallus of *Fucus*. This species most frequently occurred on wounded parts or portions consisting only of the midrib; it was the epiphyte most commonly observed on the stipe and the lower dichotomies (Fig. 5). Usually, specimens of *P. lanosa* were abundant on the upper dichotomies and the tips only in old, battered plants, entirely consisting of the midrib. *P. lanosa* was found reproductive from April to October, dates 1–5 (Table 5). In June (date 2) and July (date 3), most specimens were reproductive; at these times all the types of reproductive structures (tetrasporangia, spermatangia, carposporangia) were abundant. Spermatangia were not found after July. Specimens of *P. lanosa* collected in November and February were not reproductive.

P. umbilicalis was found only at Portnakilly; no specimens of this alga occurred at Portlea and Kinnacorra. However, this species was abundant in late spring and summer (dates 2, 3 and 4) and absent or very rare at other times. This resulted in a significant interaction time × site (Table 6). Even for *P. umbilicalis*, the irregularity in the small-scale spatial distribution was indicated by the significant effect of area. *P. umbilicalis* occurred mostly on the upper dichotomies and lower dichotomies of *Fucus* (Fig. 5); only very rarely it was found on other parts of the thallus.
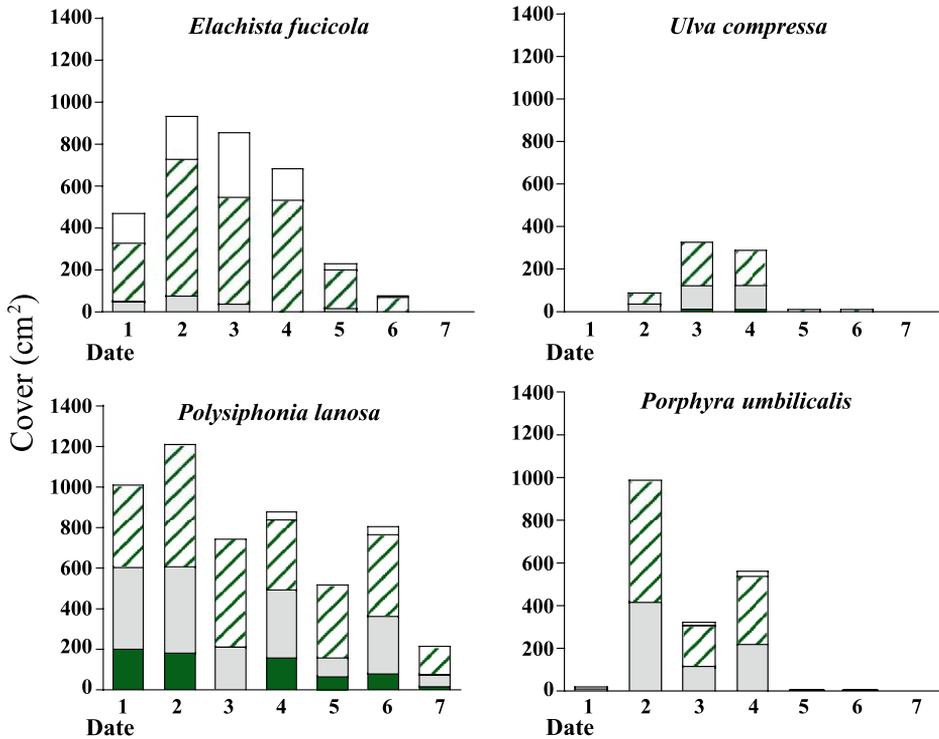
Fig. 5. Relative distribution of the most common epiphytic species on different parts of the thallus of *F. vesiculosus*; white = tips and receptacles; shaded = upper dichotomies; grey = lower dichotomies; black = stipe.

The abundance of *S. tomentosum* showed temporal variability, without any relationship with site. This was indicated by the significant effect of time and the nonsignificant effect of site and interaction time × site (Table 6). This species was recorded from April to September and was most abundant in June (date 2). The ANOVA showed a strongly

Table 5
Reproductive phenology of the most common red and brown epiphytes of *F. vesiculosus*

Sampling date		1	2	3	4	5	6	7
Elachista fucicola	Portlea	Us	Us	Us	Us	Us	–	
	Kinnacorra	Us	Us	Us	Us	Us	–	
	Portnakilly	Us	Us	Us	Us	Us	Us	–
Polysiphonia lanosa	Portlea	C, S, T	C, S, T	C, S, T	C, T	C, T	–	–
	Kinnacorra	C	C, S, T	C, S, T	C, T	–	–	–
	Portnakilly	S						
Spongonema tomentosum	Portlea	–	Ps, Us	Ps	Ps			
	Kinnacorra	–	Ps	–				
	Portnakilly	–	Ps, Us	Ps	–			

C = cystocarps; Ps = plurilocular sporangia; S = spermatangial branches; T = tetrasporangia; Us = unilocular sporangia; – = only unreproductive specimens occurring.

Table 6
Results of the analysis of variance performed on the cover data of *P. umbilicalis*, *S. tomentosum* and *U. compressa*

	df	Porphyra umbilicalis		Spongonema tomentosum		Ulva compressa	
		MS	F	MS	F	MS	F
Time (=T)	6	15.78	1.00	16.72	6.39*	6.99	1.49
Site (=S)	2	86.95	5.51	1.15	0.44	21.42	4.57
Area (T × S)	42	0.91	3.56***	1.56	5.34***	1.14	5.16***
Time × site	12	15.78	17.25***	2.62	1.68	4.68	4.09***
Residual	567	0.26		0.29		0.22	
Total	629						
Cochran's test		C = 0.1471, P < 0.01		C = 0.1687, P < 0.01		C = 0.1294, P < 0.01	
Transformation		ln(X + 1)		ln(X + 1)		ln(X + 1)	

*$P < 0.01$.
***$P < 0.0005$.

significant effect of area also (Table 6). When present, *S. tomentosum* occurred on the tips and upper dichotomies of *Fucus* and was usually found reproductive. Plurilocular sporangia were the most common reproductive structures and were found in June, July and September (Table 5). Unilocular sporangia were infrequent and were recorded only in some specimens collected at Portlea and Portnakilly in June.

U. compressa was generally more abundant in summer. At that time of the year, this species was a common epiphyte of *Fucus* at Portnakilly. In July (date 3) and September (date 4), it was abundant at Portnakilly and rare at Portlea and Kinnacorra; at other times of the year, it was generally rare or absent everywhere, as shown by the significant interaction time × site (Table 6). A significant effect of area was also detected. *U. compressa* was most common on the upper dichotomies and was recorded less frequently on the lower dichotomies and never found on tips or receptacles (Fig. 5).

4. Discussion

The epiphytic community of *F. vesiculosus* of Clare Island consisted of a relatively limited number of species and only a few were relatively well-distributed spatially and temporally. *E. fucicola* is generally reported as the most common epiphyte of *Fucus* (Russell and Veltkamp, 1984; Fletcher, 1987; Johnson and Scheibling, 1987; Russell, 1988; López-Rodríguez et al., 1999). Other brown algae such as *S. tomentosum* (Russell, 1988; López-Rodríguez et al., 1999) and *Pylaiella littoralis* (Linnaeus) Kjellman (Rönnberg and Ruokolahti, 1986; Johnson and Scheibling, 1987; Russell, 1988) have also been frequently recorded. The species of red algae that we found are less frequently reported, particularly *P. lanosa*. This species is a preferential epiphyte of *Ascophyllum nodosum* (Linnaeus) Le Jolis and only rarely occurs on *Fucus* (Lining and Garbary, 1992; Maggs and Hommersand, 1993). It may be common on *Fucus* where *Ascophyllum* is absent (as in Clare Island); when *Ascophyllum* is present, the recruitment of *P. lanosa* to *Fucus* is limited (Lining and Garbary, 1992).

The composition of the epiphytic assemblage and the patterns of distribution of the most common species showed a considerable variation in space and time. Strong temporal differences were evident between the period spring–summer and the period autumn–winter. In late spring and summer (June, July and September, dates 1–3), there was a marked difference between the assemblage of Portnakilly and the other two sites (except for June, when a marked difference among Portlea and Kinnacorra was also detected). *P. lanosa* (which occurred at Portlea and Kinnacorra, but was absent at Portnakilly) and *P. umbilicalis* and *U. compressa* (which were exclusive, or nearly exclusive, of Portnakilly) were mainly responsible for these differences. In autumn and winter (dates 5–7), however, the epiphytic community was quantitatively very reduced and most plants of *Fucus* were devoid of epiphytes; no significant differences among the three sites were detectable. This was an interesting result because, on the basis of preliminary observations, spatial variation at the scale of km (related to the factor site) was initially expected to show a stronger and more consistent effect both on the composition of the community and the distribution of individual species. The location of the three sites selected for this study reflects a gradient of wave exposure, with Portlea moderately sheltered, the shore between the harbour and Kinnacorra moderately exposed and Portnakilly very exposed. We believe that differences among the assemblages of different sites were primarily attributable to this gradient of exposure, but the sampling design used for this study does not provide a rigorous and unconfounded test for this factor. For this, it would have been necessary to sample a number of interspersed sites with different conditions of exposure; but practical constrains and limited accessibility to most parts of the shoreline made this impossible. Wave exposure is considered a major factor influencing the structure of algal assemblages and scales of exposure have been based on the composition of benthic communities (Ballantine, 1961). For the western shore of Ireland, several species of seaweeds are generally known to show a preference for either sheltered (e.g., *A. nodosum*) or exposed conditions (e.g., *Alaria esculenta* (Linnaeus) Greville). For individual species considered in this study, *P. lanosa* is the only one for which a consistent effect of site was found and, consequently, for which a consistent effect of wave exposure can be hypothesised. This species was absent at Portnakilly and generally common at the other two sites. This is in agreement with reports on the distribution of this species in the North Atlantic; although tolerant of moderate exposure, *P. lanosa* does not occur at very exposed sites (Levin and Mathieson, 1991; Maggs and Hommersand, 1993). Further studies will be necessary to quantify rigorously the effect of wave exposure; it should be noted, however, that relatively few studies have incorporated this factor in a balanced experimental design and tested its effect (e.g., Underwood and Jernakoff, 1984), probably because of the technical difficulties to sample areas subjected to different regimes of wave exposure. Sampling designs aimed to test this factor should be designed carefully and keep the direct effect of wave motion separated from other factors that may potentially confound its effect. In the case of the epiphytic assemblage of Clare Island, for example, the morphology of the plants of *Fucus* shows a considerable variation among exposed sites (such as Portnakilly) and relatively sheltered and moderately exposed sites (Portlea and Kinnacorra). The plants of Portlea and Kinnacorra were long, with many bladders, long dichotomies and relatively thin stipe; the plants of Portnakilly were stout, with short and narrow dichotomies and a robust stipe. There is evidence available that morphological

characteristics of the plants of *Fucus* may be important for the settlement and recruitment of some epiphytes. Preferential settlement of zoospores of *E. fucicola* around the mouth of conceptacles has been reported (Russell and Veltkamp, 1984). For *P. lanosa*, recruitment has been reported to occur preferentially in wounded parts of the thallus of *Fucus* (Pearson and Evans, 1990; Lining and Garbary, 1992; Maggs and Hommersand, 1993), and this is in agreement with our observations; at Portlea and Kinnacorra, *P. lanosa* is the only epiphyte that is common on the stipe and the lower dichotomies, and is most abundant in old, battered specimens. Differences in morphology of *Fucus* should theoretically be kept separated from wave motion, although this may be effectively impossible to achieve; the different morphology of *Fucus* is generally considered a direct response to the mechanical effects of wave exposure and at each site only one type of morphology is usually observable.

Other studies on the epiflora of *F. vesiculosus* or other epiphytic assemblages provide limited comparable information in relation to the possible effect of wave exposure. Russell (1988), comparing sites with different exposure, did not mention any evident effect of this factor, whereas Rönnberg and Ruokolahti (1986) reported considerable differences between exposed and sheltered areas in the Baltic Sea. For a seagrass epiphyte community, Kendrick and Burt (1997) found similarly strong differences between exposed and sheltered sites.

However, the most striking characteristic of the spatial distribution of the epiphytic community of Clare Island and of the most common species was a very strong heterogeneity at the scale of meters to tens of meters. This was indicated by the strongly significant effect of area both in the multivariate (Global R for areas in the nested ANOSIM) and univariate analyses (ANOVAs). In fact, area was the only factor that was significant for all the individual species analysed and the total epiphytic load (Tables 4 and 6). Its effect was frequently stronger than the effects of site, time and interaction time × site, even for species that occurred not only as epiphytes, but also on rocky and animal substratum around the plants of *Fucus* (such as *U. compressa* and *P. umbilicalis*). This was not an unexpected result, because small-scale spatial variation is typical of many natural algal populations and other benthic organisms (e.g., Archambault and Bourget, 1996; Underwood and Chapman, 1996; Menconi et al., 1999; Rindi and Cinelli, 2000; Benedetti-Cecchi et al., 2001); however, only few studies of epiphytic assemblages have stressed this aspect (e.g., Vanderklift and Lavery, 2000; Lavery and Vanderklift, 2002). Such a small-scale variation was probably not completely detected by the design used in this study, since we did not incorporate further smaller spatial scales in it (i.e., centimeters or tens of centimeters). We frequently observed, in a same area, plants of *Fucus* with a heavy epiphyte coverage very close to others that appeared almost clean of epiphytes. The sampling design used here did not test directly the effect of any particular process that may be responsible of such patchiness; this study was initiated without any preliminary knowledge and its main objective was in fact to provide a basis of information on the spatial and temporal patterns of the epiphytic vegetation. However, knowledge of spatial patterns is essential to identify at what scales processes need to be invoked in models to explain the observed patterns, and to exclude processes that are unlikely to play an important role (Underwood, 1990, 1997). Among all possible processes operating at this scale, previous studies have considered small-scale inputs of nutrients, grazing pressure,

possible shedding of epidermal layer of *Fucus*, local hydrodynamic flows, restricted dispersal of propagules and influences of biotic and abiotic factors on recruitment.

Inputs of nutrients are spatially and temporally variable and occur in irregular pulses. Such pulses are generated at a number of different spatial scales and several reports have suggested that medium to large-scale eutrophication may have contributed to vigorous epiphytic growth responsible of the decline of *F. vesiculosus* in several areas of the Baltic (Kangas et al., 1982; Rönnberg and Ruokolahti, 1986; Vogt and Schramm, 1991; Rönnberg et al., 1992). Recently, evidence has also been provided that an interaction between nutrient enrichment and grazing can create significant differences in the abundance of epiphytes of *Fucus* at very small spatial scales (Karez et al., 2000; Worm and Sommer, 2000). However, we believe that inputs of nutrients are not a major source of small-scale variability in the epiphytic assemblage of Clare Island. The island is currently inhabited by a limited population ($\sim$ 140 people) and the small sewage discharges, although untreated, are released at a distance of many hundreds of meters to kilometers from the three sites selected. Grazing of fishes and invertebrates at high tide seems also to be of very limited importance, despite of the fact that other studies have mentioned its effect on other north European epiphytic assemblages of *F. vesiculosus* (Karez et al., 2000; Worm and Sommer, 2000). There is evidence that on Clare Island this factor may be important in structuring the populations of other benthic organisms; for Portnakilly, Cussen et al. (2002) provided observational evidence that predation by the ballan wrasse (*Labrus bergylta* Ascanius) may be responsible of the high mortality of mussels (*Mytilus galloprovincialis* (Lamarck) and *Mytilus edulis* Linnaeus) occurring in summer months. However, during the examination of our samples, we never saw any sign of grazing on any of the algal epiphytes found. Shedding of epidermal layers has been documented for several species of fucoids (Filion-Myklebust and Norton, 1981; Moss, 1982; Russell and Veltkamp, 1984) and has been regarded as a mechanism to control heavy epiphytic load; Russell and Veltkamp (1984) suggested that, for *F. vesiculosus*, this mechanism may affect the abundance and distribution of *E. fucicola*. However, the spatial and temporal scales at which this phenomenon operates in the field are unknown and we have never observed any evident sign of shedding in the plants of *Fucus* collected for this study.

We consider that availability and dispersal of propagules are the most important processes responsible of such heterogeneity. The few studies on epiphytic communities that have considered small-scale spatial variation have also stressed the importance of this factor (Vanderklift and Lavery, 2000; Lavery and Vanderklift, 2002). For the most common epiphytes of *Fucus*, the temporal availability of propagules is probably extended to relatively long times during the period late spring–summer. The phenological patterns observed indicate that this is the time of the year at which best development and reproduction occur; this is in agreement with reports for other North Atlantic regions for *E. fucicola* (Hamel, 1935; Fletcher, 1987), *S. tomentosum* (Cardinal, 1964) and *P. lanosa* (Maggs and Hommersand, 1993). Presumably, when released, the propagules tend to settle on the nearest plants of *Fucus*, producing patterns of aggregation at the scale of meters. Features of the habitat that affect local hydrodynamic fluxes, such as orientation of the rocky substratum, presence of local shelters and density of canopy of *Fucus*, will influence the dispersal of propagules and consequently the patterns of distribution of the algal populations. A dense canopy of *Fucus* can also offer protection from desiccation at

low tide for critical life history stages of the epiphytic algae, and consequently enhance recruitment; at the same time, however, a whiplash effect limiting the load of filamentous algae has been noted for Baltic *F. vesiculosus* (Kiirikki, 1996).

Studies incorporating a higher number of spatial scales will be necessary to provide a better resolution of the patterns of spatial variation; further studies will also be necessary to understand if the patterns observed here can be generalised to the whole Irish west coast. In any case, a general conclusion is that patchiness at the scale of meters to tens of meters is typical of epiphytic communities of *F. vesiculosus*. Whatever the causes of such patchiness are, we agree with Vanderklift and Lavery (2000) that it is of critical importance to consider such variation in the design of experimental studies of epiphytic communities, in particular intertidal epiphytic communities. Most studies of intertidal benthic assemblages have focused attention on vertical patterns of distribution (zonation) in response to gradients of emersion and desiccation (Southward, 1958; Lewis, 1964), stressing variation linked to vertical patterns of distribution. However, recent work has documented considerable small-scale heterogeneity within particular levels of the shore, showing that horizontal variation may be as important as vertical variation, or even more important (Benedetti-Cecchi, 2001). We feel that this is most probably true for intertidal epiphytic assemblages also.

Finally, it seems appropriate to conclude with a general qualitative comparison of our results with the observations made by Cotton (1912) during the Survey of Clare Island carried out in 1910–1911. Cotton did not collect quantitative data and both Cotton's survey and our study were carried out on the time span of about a year, which makes it impossible to determine if long-term changes on larger temporal scales took place. However, the description of the epiphytic community that he provided does not show any difference with the present situation; both for exposed shores and relatively sheltered shores, the most abundant species are the same recorded in our study (see Cotton, 1912: 25). This enhances our impression (Rindi and Guiry, 2004) that, in contrast to other regions of northern Europe, the shores of Clare Island, and probably of many other parts of the Irish west coast, are a remarkably well-preserved environment, worthy of vigorous conservation efforts.

References

Archambault, P., Bourget, E., 1996. Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. Mar. Ecol., Prog. Ser. 136, 111–121.

Arrontes, J., 1990. Composition, distribution on host and seasonality of epiphytes on three intertidal algae. Bot. Mar. 33, 205–211.

Bäck, S., Collins, J.C., Russell, G., 1992. Comparative ecophysiology of Baltic and Atlantic *Fucus vesiculosus*. Mar. Ecol., Prog. Ser. 84, 71–82.

Ballantine, W.J., 1961. A biologically defined exposure scale for the comparative description of rocky shores. Field Stud. 1, 1–19.

Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Mar. Ecol., Prog. Ser. 215, 79–92.

Benedetti-Cecchi, L., Rindi, F., Bertocci, I., Bulleri, F., Cinelli, F., 2001. Spatial variation in development of epibenthic assemblages in a coastal lagoon. Estuar. Coast. Shelf Sci. 52, 659–668.

Borowitzka, M.A., Lethbridge, R.C., 1989. Seagrass epiphytes. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), Biology of Seagrasses. Elsevier Science Publishers, Amsterdam, pp. 458–499.

Cardinal, A., 1964. Étude sur les Ectocarpacées de la Manche, Behi. Nova Hedwig. 15, 1–85.

Clarke, K.R., Gorley, R.N., 2001. PRIMER v5: User Manual/Tutorial. PRIMER-E, Plymouth.

Cotton, A.D., 1912. Clare Island Survey: Part 15. Marine Algae. Proc. R. Ir. Acad., B Biol. Geol. Chem. Sci. 31, 1–178.

Cussen, R., Myers, A., McGrath, D., Delany, J., O'Riordan, R., 2002. Turnover in a mussel population on an exposed rocky shore in the West of Ireland. In: Myers, A.A. (Ed.), New Survey of Clare Island. Marine Intertidal Ecology, vol. 3. Royal Irish Academy, Dublin, pp. 121–127.

Filion-Myklebust, C., Norton, T.A., 1981. Epidermis shedding in the brown seaweed *Ascophyllum nodosum* (L.) Le Jolis and its ecological significance. Mar. Biol. Lett. 2, 45–51.

Fletcher, R.L., 1987. Seaweeds of the British Isles. Volume 3. Part 1. Fucophyceae (Phaeophyceae). Natural History Museum, London.

Guiry, M.D., 1978. A Consensus and Bibliography of Irish Seaweeds. J. Cramer, Vaduz.

Guiry, M.D., 1997. No stone unturned: Robert Lloyd Praeger and the major surveys. In: Foster, J.W. (Ed.), Nature in Ireland. A Scientific and Cultural History. Lilliput Press, Dublin, pp. 299–307.

Hamel, G., 1935. Phéophycées de France: 2 Paris.

Harlin, M.M., 1980. Seagrass epiphytes. In: Phillips, R.C., McRoy, C.P. (Eds.), Handbook of Seagrass Biology: An Ecosystem Perspective. Jarland STPM Press, New York, pp. 117–151.

Jernakoff, P., Brearley, A., Nielsen, J., 1996. Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. Oceanogr. Mar. Biol. Annu. Rev. 34, 109–162.

Johnson, S.C., Scheibling, R.E., 1987. Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada. Mar. Ecol., Prog. Ser. 37, 209–227.

Kangas, P., Antio, H., Hallfors, G., Luther, H., Niemi, A., Salemaa, H., 1982. A general model of the decline of *Fucus vesiculosus* at Tvarminne, south coast of Finland in 1977–81. Acta Bot. Fenn. 118, 1–27.

Karez, R., Engelbert, S., Sommer, U., 2000. "Co-consumption" and "protective coating": two new proposed effects of epiphytes on their macroalgal hosts in mesograzer–epiphyte–host interactions. Mar. Ecol., Prog. Ser. 205, 85–93.

Kautsky, N., Kautsky, H., Kautsky, U., Waern, M., 1986. Decreased depth penetration of *Fucus vesiculosus* (L.) since 1940s indicates eutrophication of the Baltic Sea. Mar. Ecol., Prog. Ser. 28, 1–8.

Kendrick, G.A., Burt, J.S., 1997. Seasonal changes in epiphytic macro-algal assemblages between offshore exposed and inshore protected *Posidonia sinuosa* Cambridge and Kuo seagrass meadows, Western Australia. Bot. Mar. 40, 77–85.

Kiirikki, M., 1996. Experimental evidence that *Fucus vesiculosus* (Phaeophyta) controls filamentous algae by means of the whiplash effect. Eur. J. Phycol. 31, 61–66.

Kiirikki, M., Ruuskanen, A., 1996. How does *Fucus vesiculosus* survive ice scraping? Bot. Mar. 39, 133–139.

Knight, M., Parke, M., 1950. A biological study of *Fucus vesiculosus* L. and *Fucus serratus* L. J. Mar. Biol. Assoc. UK 26, 439–514.

Lavery, P.S., Vanderklift, M.A., 2002. A comparison of spatial and temporal patterns in epiphytic macroalgal

assemblages of the seagrasses *Amphibolis griffithii* and *Posidonia coriacea*. Mar. Ecol., Prog. Ser. 236, 99–112.

Levin, P.S., Mathieson, A.C., 1991. Variation in a host-epiphyte relationship along a wave exposure gradient. Mar. Ecol., Prog. Ser. 77, 271–278.

Lewis, J.R., 1964. The Ecology of Rocky Shores. English University Press, London.

Lining, T., Garbary, D.J., 1992. The *Ascophyllum/Polysiphonia/Mycosphaerella* symbiosis: III. Experimental studies on the interactions between *P. lanosa* and *A. nodosum*. Bot. Mar. 35, 341–349.

López-Rodríguez, M.C., Bárbara, I., Pérez-Cirera, J.L., 1999. Effects of pollution on *Fucus vesiculosus* communities on the Northwest Iberian Atlantic coast. Ophelia 51, 129–141.

Lüning, K., 1990. Seaweeds: Their Environment, Biogeography, and Ecophysiology. Wiley, New York.

Maggs, C.A., Hommersand, M.H., 1993. Seaweeds of the British Isles. Rhodophyta: Part 3A. Ceramiales, vol. 1. Natural History Museum, London.

Menconi, M., Benedetti-Cecchi, L., Cinelli, F., 1999. Spatial and temporal variability in the distribution of algae and invertebrates on rocky shores in the northwest Mediterranean. J. Exp. Mar. Biol. Ecol. 233, 1–23.

Moss, B.L., 1982. The control of epiphytes by *Halidrys siliquosa* (L.) Lyngb. (Phaeophyta, Cystoseiraceae). Phycologia 21, 185–188.

Neckles, H.A., Wetzel, R.L., Orth, R.J., 1993. Relative effects of nutrient enrichment and grazing on epiphyte–macrophyte (*Zostera marina* L.) dynamics. Oecologia 93, 285–295.

Orth, R.J., van Montfrans, J., 1984. Epiphyte–seagrass relationships with an emphasis on the role of micrograzing: a review. Aquat. Bot. 18, 43–69.

Pearson, G.A., Evans, L.V., 1990. Settlement and survival of *Polysiphonia lanosa* (Ceramiales) spores on *Ascophyllum nodosum* and *Fucus vesiculosus* (Fucales). J. Phycol. 26, 597–603.

Rindi, F., Cinelli, F., 2000. Phenology and small-scale distribution of some rhodomelacean red algae on a western Mediterranean rocky shore. Eur. J. Phycol. 35, 115–125.

Rindi, F., Guiry, M.D., 2004. A long-term comparison of the benthic algal flora of Clare Island, County Mayo, western Ireland. Biodivers. Conserv. 13, 471–492.

Rindi, F., Guiry, M.D., Maggs, C.A., 2002. Checklist of the benthic marine algae of Clare Island. In: Myers, A.A. (Ed.), New Survey of Clare Island. Marine Intertidal Ecology, vol. 3. Royal Irish Academy, Dublin, pp. 189–205.

Rönnberg, O., Ruokolahti, C., 1986. Seasonal variation of algal epiphytes and phenolic content of *Fucus vesiculosus* in a northern Baltic Archipelago. Ann. Bot. Fenn. 23, 317–323.

Rönnberg, O., Adjers, K., Ruokohlathi, C., Bodestam, M., 1992. Effects of fish farming on growth, epiphytes and nutrient content of *Fucus vesiculosus* L. in the Åland archipelago, northern Baltic Sea. Aquat. Bot. 42, 109–120.

Russell, G., 1988. Distribution and development of some Manx epiphyte populations. Helgol. Meeresunters. 42, 477–492.

Russell, G., Veltkamp, C.J., 1984. Epiphyte survival on skin-shedding macrophytes. Mar. Ecol., Prog. Ser. 18, 149–153.

Sand-Jensen, K., 1977. Effect of epiphytes on eelgrass photosynthesis. Aquat. Bot. 3, 55–63.

Serrão, E.A., Brawley, S.H., Hedman, J., Kautsky, L., Samuelsson, G., 1999. Reproductive success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. J. Phycol. 35, 254–269.

Southward, A.J., 1958. The zonation of plants and animals on rocky sea shores. Biol. Rev. 33, 137–177.

Underwood, A.J., 1990. Experiments in ecology and management: their logics, functions and interpretations. Aust. J. Ecol. 15, 365–389.

Underwood, A.J., 1997. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.

Underwood, A.J., Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107, 212–224.

Underwood, A.J., Jernakoff, P., 1984. The effects of tidal height, wave-exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New South Wales. J. Exp. Mar. Biol. Ecol. 75, 71–96.

Vanderklift, M.A., Lavery, P.S., 2000. Patchiness in assemblages of epiphytic macroalgae on *Posidonia coriacea* at a hierarchy of spatial scales. Mar. Ecol., Prog. Ser. 192, 127–135.

Vogt, H., Schramm, W., 1991. Conspicuous decline of *Fucus* in Kiel Bay (Western Baltic): what are the causes? Mar. Ecol., Prog. Ser. 69, 189–194.

Wahl, M., Mark, O., 1999. The predominantly facultative nature of epibiosis: experimental and observational evidence. Mar. Ecol., Prog. Ser. 187, 59–66.

Worm, B., Sommer, U., 2000. Rapid direct and indirect effects of a single nutrient pulse in a seaweed–epiphyte–grazer system. Mar. Ecol., Prog. Ser. 202, 283–288.