

SETTLEMENT AND SURVIVAL OF POLYSIPHONIA LANOSA (CERAMIALES) SPORES ON ASCOPHYLLUM NODOSUM AND FUCUS VESICULOSUS (FUCALES)¹

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ABSTRACT

The settlement patterns of spores of *Polysiphonia lanosa* (L.) Tandy on *Ascophyllum nodosum* (L.) Le Jolis and *Fucus vesiculosus* L. were studied using a flow tank. Settlement sites were defined as 'sheltered' or 'exposed.' Surface area calculations revealed non-random settlement on *A. nodosum*, with higher than expected spore frequencies on the thallus and lateral pits and lower than expected frequencies on the vesicles. Settlement on *F. vesiculosus* was random and significantly lower than on *A. nodosum*.

On the shore, survival of sporelings from September (post-sporulation) to May (pre-sporulation) was highly non-random on both basiphytes. On *A. nodosum*, lateral pits ('sheltered') showed the highest survival frequency. Here the proportion of surviving sporelings increased over the study period, whereas the proportion on open thallus area ('exposed') decreased. On *F. vesiculosus* also, preferential survival occurred on 'sheltered' sites such as vesicle/thallus interfaces and wounds. Between September and May, all *P. lanosa* sporelings were lost from 'exposed' areas (thallus surface and vesicles). Overall, frequencies of surviving sporelings were much greater on *A. nodosum* than on *F. vesiculosus*. These results are discussed with reference to basiphyte morphology, epiphyte removal mechanisms and the survival strategy of *P. lanosa*.

Key index words: *Ascophyllum nodosum*; basiphyte; epiphyte; *Fucus vesiculosus*; *Polysiphonia lanosa*; spore settlement; sporeling survival.

The red alga *Polysiphonia lanosa* (L.) Tandy is an epiphyte found almost exclusively on the fucoid *Ascophyllum nodosum* (L.) Le Jolis. Attachment of the mature epiphyte is by means of penetrating unicellular rhizoids (Rawlence and Taylor 1970, 1972). Initial attachment is a surface phenomenon involving spore (and host) mucilage (Boney 1975) and the release of adhesive vesicles (Chamberlain and Evans 1973). However, penetration of the basiphyte by the primary rhizoid of a spore may take up to two months (Rawlence and Taylor 1970).

During this period, the sporelings are prone to dislodgement by wave action, grazing and epidermal skin-shedding (Filion-Myklebust and Norton 1981, Moss 1982). The latter has been observed by the authors as the loss of thickened mucopolysaccharide caps from the surfaces of epidermal cells. This has

not been observed around the branch axils and axil slits. These, together with wound sites, are where mature epiphyte plants are most commonly found (Lobban and Baxter 1983).

P. lanosa has been observed growing on rock (Rat-tray 1885) and on other fucoids growing within the same tidal range as *A. nodosum*. For example, mature plants were found growing on *Fucus vesiculosus* L. by Cotten (1912) as well as in the present study, thereby casting doubt on possible biochemical epiphyte/basiphyte specificity. The relative infrequency of colonization of this basiphyte, however, raises questions about its suitability as a substrate.

The first part of our study deals with spore-settlement in laboratory flow tanks. The second part follows the survival of sporelings in the field over one growing season, from the end of spore release in late September to the period prior to the next release in May. The two basiphytes studied were *A. nodosum* and *F. vesiculosus* since these share a similar vertical distribution and co-exist at the study site selected. Such an approach should lead to a better understanding of the influence of the basiphyte on the settlement pattern of *P. lanosa* spores and on the subsequent fate of settled sporelings, especially on *F. vesiculosus*, where few survive to maturity.

MATERIALS AND METHODS

Plants were collected from Rhosneigr on the south-west coast of Anglesey, N. Wales, U.K. The study area was a sheltered rock outcrop, lying upshore of further outcrops, at the southern end of the beach and in the middle of the vertical range of *A. nodosum*. For the spore-settlement experiments, *A. nodosum* plants heavily epiphytized by tetrasporic *P. lanosa* were taken, as well as undamaged *A. nodosum* and *F. vesiculosus* plants without epiphytes. Collection of these plants took place in late August. After transportation back to Leeds on ice, algae were kept aerated in large tanks of 'Instant Ocean' artificial seawater at 12°C under artificial illumination (16:8 h LD cycle).

Material for each seasonal sample was taken from the same area. Fronds of *A. nodosum* and whole plants of *F. vesiculosus* were taken randomly using a 0.5 m² quadrat, subdivided into 0.1 m². Material was taken by point sampling the intersections of the squares. Algae were brought back to Leeds in plastic bags on ice and stored frozen at -20°C prior to use.

Spore-settlement experiments and analysis. The flow tank used was of the 'race track' design mentioned in Denny (1988:301) and consisted of a horizontal oval track, over which 'Instant Ocean' artificial seawater at a depth of 15 cm was moved by a paddle wheel powered by a constantly-variable speed electric motor (Fig. 1). One small piece (15-20 cm long) each of undamaged *A. nodosum* and *F. vesiculosus* was used for each experiment to allow direct pairwise comparison of spore density/basiphyte area. Basiphyte pieces were checked with a dissecting microscope, and ep-

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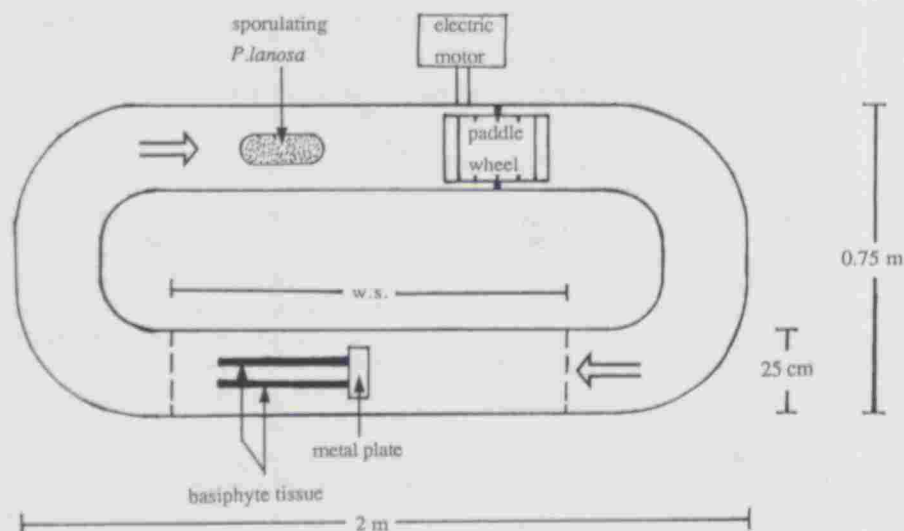


FIG. 1. Diagram showing flow tank design (not to scale). Open arrows show direction of flow with rate $0.2 \text{ m} \cdot \text{s}^{-1}$; w.s. = working section.

epiphytes were removed. The basiphyte tissue was then placed in position (Fig. 1), held on the bottom by a thin metal plate, and the flow was started. The flow rate was $0.2 \text{ m} \cdot \text{s}^{-1}$, determined over a 1 m part of the working section from multiple timed runs with a water-filled (table-tennis) ball of neutral density. Small blocks of *A. nodosum* with tetrasporic *P. lanosa* plants (6–8 g dry wt) were tied together with cotton thread and after emersion for 12 h at 12°C , introduced into the flow tank. After 1 h to allow spore release, the epiphytic tissue was removed for dry weight determination. Each experiment was run for a total of 24 h. For analysis, basiphyte tissue was lightly pinned to a sheet of paper and accurately traced to give a tissue map. The material was then examined under a dissecting microscope, and the position of each spore was recorded on the map. The map was then overlaid with a transparent sheet of dots, 1 mm in diameter and regularly arranged at 2 mm intervals. Tissue regions were then scored by counting the number of dots overlying them. In the case of *F. vesiculosus* the regions were defined as thallus, vesicles and vesicle/thallus interfaces and for *A. nodosum* as thallus, vesicles and lateral pits (including branch axils) as shown in Figure 2. The plant area was then cut out, weighed and converted (to allow for vesicles and the elliptical cross-section of *A. nodosum*) to give total area. Individual areas for sites were approximated from the corresponding dot counts. This technique is a modification of that used in electron microscope autoradiograph analysis (Evans and Callow 1978).

Chi-square analysis was then performed to compare dot distribution and spore distribution, with the null hypothesis that spore settlement is random on both basiphytes.

Seasonal samples: analysis of *A. nodosum*. Individual fronds of *A. nodosum* were point sampled from the site described (one frond per plant) and only those fronds with an intact apical meristem were used for analysis. Fronds were aged by the method of Lobban and Baxter (1983) and divided into year classes from the apices (0+) down to the older parts. Mature *P. lanosa* and remaining basiphyte tissues were separated and their fresh weights determined after blotting dry.

Using a dissecting microscope the numbers of sporelings at 'exposed' sites (thallus tissue, including vesicles) and at 'sheltered' sites (lateral pits, including axils, and wound sites) were scored. A lateral pit is the site of a potential meristem and was termed a lateral axil if branching growth had taken place. A wound site was defined as the loss of an apical meristem (where more than one was present) or a lateral meristem. Superficial grazing marks

were not considered as wounds. Analysis of *A. nodosum* by surface area measurements worked well for the relatively small pieces of tissue used in the flow tank experiments, but it was not considered practicable for seasonal samples due to the large size, complex shape and 3-dimensional nature of the fronds.

Seasonal samples: analysis of *F. vesiculosus*. After removal of visible epiphytes the fresh weight of the basiphyte was recorded. Determining the relative age of *F. vesiculosus* is more problematic than for *A. nodosum*. However, since the two-dimensional nature of the thallus lends itself to surface area calculations the method

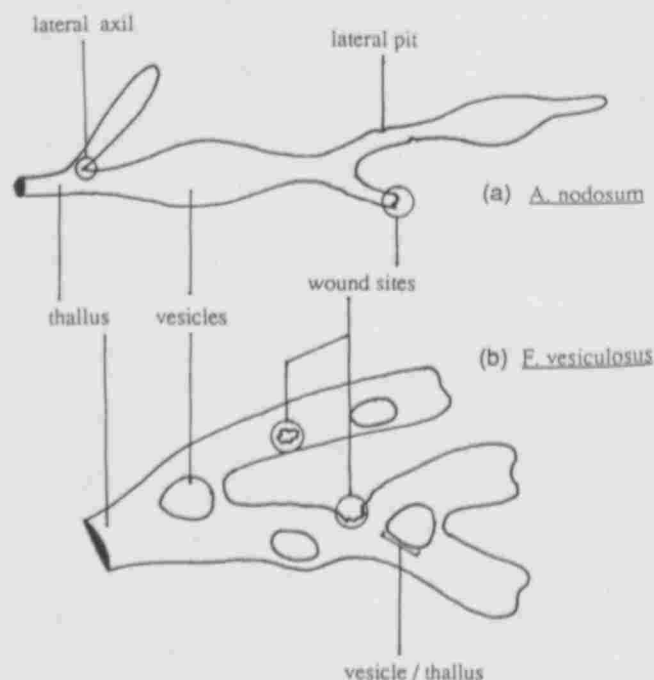


FIG. 2a, b. Diagram showing the areas of the frond defined as 'sheltered' and 'exposed' for *A. nodosum* (a) and *F. vesiculosus* (b). Wound areas are relevant only for the sporeling survival study as undamaged tissue was used for the spore settlement experiments.

TABLE 1. Numbers of settled spores of *P. lanosa* (with expected frequencies in parentheses) on *F. vesiculosus* and *A. nodosum* after 24 h in a flow tank. The data for each basiphyte are pooled from five experiments, following heterogeneity chi-square analysis. *thsp* = sporelings on thallus, *vsp* = sporelings on vesicles, *shsp* = sporelings on sheltered sites, *df* = degrees of freedom.

Basiphyte	thsp	vsp	shsp	Total	χ^2	df
<i>A. nodosum</i>	3846 (3033.24)	719 (1661.60)	176 (46.16)	4741	1117.719	2
<i>F. vesiculosus</i>	1129 (1157.16)	373 (354.74)	91 (81.11)	1633	2.830	2

of analysis described for spore-settlement experiments was used. Sporelings at 'exposed' sites were defined as those found on the thallus (including the midrib) or the vesicles. Sporelings at 'sheltered' sites were defined as those found at the interface between vesicles and thallus or on wound sites (areas of lost or damaged tissue, not including superficial grazing marks). The sheets of dots were regularly arranged at 4 mm intervals.

Following analysis, we found that the expected frequencies for sporelings on some sites were smaller than unity. When this situation arises, the chi-square statistic is not a reliable method of analysis. The preferred method is the log-likelihood ratio (Wilks 1935) and the calculation of the *G*-statistic. *G* approximates the chi-square distribution and Williams (1976) recommends its use whenever $|f_i - \hat{f}_i| < \hat{f}_i$ (see Zar 1984:52–53).

RESULTS

Spore-settlement experiments. The data from five replicate experiments based on *A. nodosum* as the basiphyte and five replicates based on *F. vesiculosus* were each analyzed using chi-square. These data were then pooled following heterogeneity chi-square analysis ($P > 0.25$, *A. nodosum*; $P > 0.75$, *F. vesiculosus*) (Zar 1984:49–52). Spore settlement patterns vary greatly (Table 1). On *A. nodosum* settlement was highly non-random ($P < 0.001$), with higher than expected numbers of spores on the thallus and lateral pit regions and much lower than expected numbers on vesicles. Settlement on *F. vesiculosus*, on the other hand, was random ($P > 0.10$). Paired sample *t*-tests showed that while there was no difference between the areas of the two basiphytes used ($P > 0.5$), significantly more spores settled on *A. nodosum* (4.262 ± 1.408 spores \cdot cm $^{-2}$) than on *F. vesiculosus* (1.501 ± 0.519 spores \cdot cm $^{-2}$) ($P < 0.05$). The mean dry wt of tetrasporic *P. lanosa* used for each experiment was 6.871 ± 0.7 g.

Seasonal samples: *A. nodosum*. In September, sporelings were found either as uniseriate filaments or, more commonly, as small unbranched plantlets. In the latter case, penetration of the basiphyte by the primary rhizoid had been initiated. Spores were not found, and observations suggested that although both tetrasporic and carposporic tissue remained until well into October, release did not generally occur. Such reproductive tissues were frequently necrotic. By the end of the study in May, epiphytic plants were branched, easily visible to the naked eye and could be distinguished by the lack of secondary rhizoids. In all seasonal samples, numbers of mature *P. lanosa* plants were low on the undamaged fronds

and were present on a negligible number of the sites available.

Sporeling numbers on lateral pits are shown in Figure 3 ($f: X \rightarrow \log_{10}[X+1]$ transformations were used where logarithms are shown in the results). Both the maximum number of sporelings for each year class and the maximum within year class variation occurred in September ($n = 5$). Variances between monthly samples were not homogeneous, when tested by the method of Bartlett (1937) ($P < 0.001$), therefore a two factor extension of the Kruskal-Wallis non-parametric analysis of variance was used to test for the effects of month and year class of basiphyte tissue on sporeling survival per lateral pit (see Zar 1984:219–222). This revealed significant differences due to month ($P < 0.001$), year class ($P < 0.05$), and month \times year class interaction ($P < 0.001$). Growth of *A. nodosum* in the winter/spring results in the 0+ year class from September and January becoming the 1+ year class in May. The analysis showed a significant difference ($P < 0.001$) between all monthly samples based on Tukey-type multiple comparisons using rank sums instead of means (Zar 1984:199–201). Significant differences due to year class occurred between 1+ and 4+ (2+ and 5+ in May). None of the interactive effects occurred within monthly samples, and all occurred between September and May except September 0+, 1+, 2+ which were greater than January 4+ ($P < 0.01$, $P < 0.025$, $P < 0.025$, respectively). The other significant differences were September 0+ > May 1+, 4+, 5+ ($P < 0.005$, $P < 0.01$, $P < 0.01$, respectively); September 1+ > May 1+, 4+ ($P < 0.01$, $P < 0.025$, respectively); September 2+ > May 1+, 4+, 5+ ($P < 0.01$, $P < 0.025$, $P < 0.025$, respectively). There were no interactive effects between January and May, indicating that the greatest rate of decline in sporelings per lateral pit occurred between September and January.

Sporelings found on the thallus ('exposed' site) expressed as \log_{10} numbers \cdot g $^{-1}$ fresh wt basiphyte are shown in Figure 4. Both the maximum number of sporelings and the maximum within year class variation again occurred in September ($n = 5$). The variances between samples are not homogeneous (Bartlett's test; $P < 0.001$), so the data were analyzed with a two factor non-parametric ANOVA. Differences were found due to month ($P < 0.001$), year class ($P < 0.025$) and month \times year class interaction

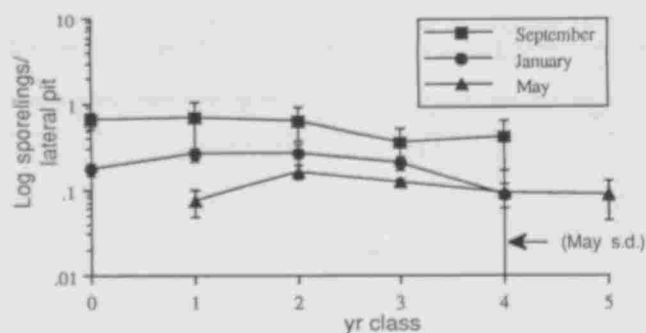


FIG. 3. Numbers of *P. lanosa* sporelings surviving on lateral pit sites of *A. nodosum* on the shore in September, January and May for each year class of basiphyte tissue.

($P < 0.005$). Tukey-type multiple comparison tests showed differences between all monthly samples (September > January, $P < 0.05$; January > May, $P < 0.01$; September > May, $P < 0.001$). In addition, differences were found between year classes 0+ and 4+ (1+ and 5+ in May) and 1+ and 4+ (2+ and 5+ in May) ($P < 0.025$ in both cases). None of the interactive effects occurred within monthly samples, and all occurred between September and May except September 0+, 1+ > January 4+ ($P < 0.05$ in both cases). The other significant differences are: September 0+ > May 3+, 5+ ($P < 0.025$ in both cases); September 1+ > May 2+, 3+, 4+, 5+ ($P < 0.05$, $P < 0.01$, $P < 0.05$, $P < 0.01$, respectively); September 2+ > May 3+, 5+ ($P < 0.05$ in both cases). As in the instance of sporelings/lateral pit, there are no interactive effects between January and May, indicating that the greatest rate of decline of sporelings on this site took place between September and January.

The numbers of wound sites and sporelings/wound site for each frond ($n = 5$ for each monthly sample) were analyzed by Kruskal-Wallis tests (Zar 1984:176–178). Although the numbers of wounds did not differ between samples, there were differences in sporelings/wound site ($P < 0.001$). This was due to the counts for September being greater than those for May ($P < 0.01$).

While the absolute numbers of sporelings found on 'exposed' (thallus) and 'sheltered' (lateral pit and wound) sites decreased markedly from September to May, the relative frequencies of sporelings on these sites also changed. The frequency of combined 'sheltered' site sporelings (lateral pit plus wound) increased from between 73.2–88.7% in September (3+ and 4+ year classes), rising to 91.5–98.3% in January (1+ and 4+) and reaching 97.2–100% in May (1+ and 3+). This increase was accompanied by a concurrent decrease in sporeling frequency on thallus sites.

Seasonal samples: *F. vesiculosus*. Although sporelings found on *F. vesiculosus* in September were at a similar stage of development to those found on *A. nodosum* (uniserial filaments or unbranched plant-

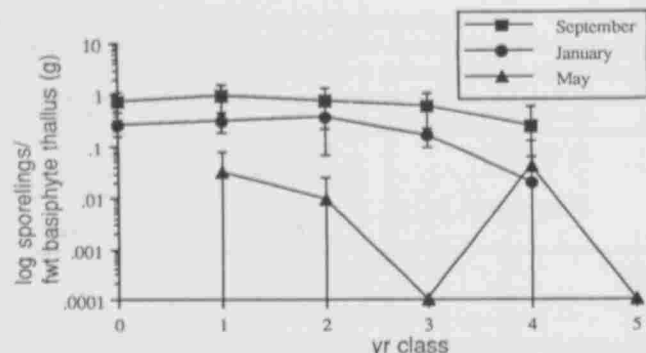


FIG. 4. Numbers of *P. lanosa* sporelings surviving on thallus sites of *A. nodosum* on the shore in September, January and May for each year class of basiphyte.

lets), growth of the epiphyte in the January and especially the May samples was noticeably more stunted. Branching was less common, and the plants were generally smaller.

The results of the log-likelihood analysis for each seasonal sample ($n = 4$ plants) are given in Table 2. Heterogeneity analyses (Zar 1984:49–52) revealed that the data for each monthly sample may not be pooled ($P < 0.001$). The pattern of sporeling survival was non-random, and the significant values occurred because 'sheltered' sites (vesicle/thallus, wounds) had more sporelings than predicted. The converse was the case for 'exposed' sites (thallus, vesicles). This pattern was evident in each sample. As noted for *A. nodosum*, survival was quite variable in September, plant 2 in Table 2 having a particularly low number of sporelings on the thallus and close to the expected number on vesicles. Sporeling numbers per area of site available were expressed as \log_{10} sporelings cm^{-2} (Fig. 5). Since variances were not homogeneous between samples (Bartlett's test; $P < 0.001$), the data were analyzed by two factor non-parametric ANOVA. The differences which arose were due to month ($P < 0.01$) and site ($P < 0.001$). No significant effects were found due to interaction of month and site ($P > 0.10$). Tukey-type multiple comparison tests were performed to locate significant differences. The numbers of sporelings surviving in September were greater than in January ($P < 0.025$) and May ($P < 0.005$), but the numbers present in January and May were not significantly different. The number of sporelings on wound sites was greater than on vesicles ($P < 0.001$) and thallus ($P < 0.001$). Similarly, the number of sporelings on vesicle/thallus sites was greater than on either of the 'exposed' sites ($P < 0.005$ in both cases).

The relative frequency of sporelings on each site changed between the end of one sporulation period and the beginning of the next. Only one sporeling on vesicles was found in January, supporting the hypothesis that the vesicles are the most exposed sites. Those on the thallus declined from an initial 26.4% to 6.8% in January, with none observed in

TABLE 2. Numbers of surviving sporelings of *P. lanosa* (with expected frequencies in parentheses) on *F. vesiculosus* on the shore. Analysis by the Log-likelihood method. thsp = sporelings on thallus, vsp = sporelings on vesicles, vthsp = sporelings at vesicle/thallus interface, wsp = sporelings at wound sites. df = degrees of freedom, G = G-statistic; n = 4.

Plant	thsp	vsp	vthsp	wsp	df	G	P
September							
1	36 (72.94)	1 (11.94)	14 (3.90)	39 (1.22)	3	250.23	<0.001
2	3 (34.85)	2 (1.62)	18 (0.24)	15 (1.29)	3	215.23	<0.001
3	37 (173.77)	0 (10.31)	18 (4.08)	141 (7.84)	3	163.69	<0.001
4	174 (389.04)	19 (46.14)	132 (9.01)	123 (3.81)	3	1249.71	<0.001
January							
1	1 (9.24)	0 (1.39)	2 (0.32)	9 (1.13)	3	40.23	<0.001
2	12 (54.23)	0 (4.30)	3 (1.06)	49 (4.40)	3	206.24	<0.001
3	0 (24.84)	0 (7.46)	16 (1.60)	24 (2.10)	3	190.62	<0.001
4	0 (18.12)	1 (5.13)	3 (0.96)	21 (0.74)	3	141.71	<0.001
May							
1	0 (1.79)	0 (0.94)	1 (0.13)	2 (0.13)	3	14.98	<0.005
2	0 (7.71)	0 (2.14)	3 (0.36)	8 (0.78)	3	49.94	<0.001
3	0 (3.69)	0 (1.57)	1 (0.26)	5 (0.48)	3	26.22	<0.001
4	0 (36.92)	0 (6.58)	7 (0.90)	41 (3.60)	3	228.24	<0.001

May. The relative frequency of sporelings surviving at the vesicle/thallus interface remained fairly constant at 18.3–25.4%. Wound sites showed the greatest survival frequency throughout the year, increasing from 45.5% (September) to 73.9% (January), and reaching 77% of all sporelings in May.

Survival of *P. lanosa* sporelings g^{-1} fresh wt of each basiphyte in September on *A. nodosum* was approximately $3 \times$ higher than on *F. vesiculosus* and remained much higher throughout the study period, with sporeling losses from *F. vesiculosus* between September and January occurring at a greater rate than from *A. nodosum* (Fig. 6). The surface of *A. nodosum* (especially the lateral pits) provided an environment which allowed a greater frequency of sporeling survival.

DISCUSSION

The conditions under which the flow experiments were conducted can at best only partially mimic the processes occurring on the shore. Flow was unidirectional, rather than undulatory, with a narrow cross-section resulting in concentrated spore densities compared with those expected in the field. In addition, the basiphytes were not subjected to the brief, intense pressures generated by breaking waves, together with the complexity of flow and eddy pat-

terns which occur on rocky shores (Vogel 1981:98–99). The advantage with these experiments, however, is that they allow comparisons of numbers and patterns of spore settlement under controlled, low flow rate conditions similar to those occurring in deeper water (i.e. at high tide) when conditions for settlement seem to be optimum. The high spore densities also allow patterns of settlement to be more easily elucidated. The results clearly showed a higher frequency of settlement on *A. nodosum* compared with *F. vesiculosus*. This cannot be explained in terms of more 'sheltered' sites on *A. nodosum*, since the lateral pits and axils account for only a very small number ($3.75 \pm 0.97\%$) of the settling spores. The frond as a whole is a more effective substrate for settlement.

The non-random pattern of settlement on *A. nodosum* was in contrast to the random pattern found on *F. vesiculosus*. The lower than expected number of spores found on the vesicles of *A. nodosum* may be partly accounted for by their streamlined shape and presumably lower drag coefficient and turbulence. If turbulence is lower downstream from the vesicles, then higher spore settlement may be expected on the thallus (Vogel 1981:135–137, 161) compared to *F. vesiculosus*, with its more hemispherical vesicles. This must remain as conjecture, how-

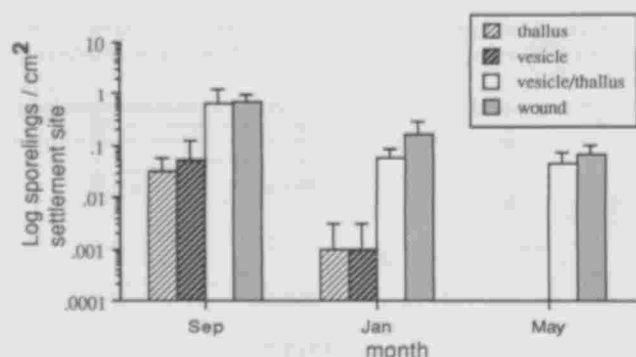


FIG. 5. Numbers of *P. lanosa* sporelings on 'sheltered' and 'exposed' sites on *F. vesiculosus* on the shore at different months. (Error bars = SD, $n = 4$).

ever, until detailed hydrodynamic measurements are attempted on the basiphytes. The most interesting result, in terms of the ecology of sporeling development, is the higher than expected frequency of settlement on lateral pit and axil sites, as this is where the majority of surviving young sporelings are found in the field. The pattern of water flow over the surface of *A. nodosum* resulted in spores being deposited in protective niches advantageous to their penetration, growth and development. These sites are natural discontinuities in the thallus analogous to the cryptostomata of *Himanthalia*, where spores of *Elachista scutulata* have been observed to settle preferentially (Russell and Velkamp 1984). If they settle in lateral pits and axils, *P. lanosa* spores bypass antifouling mechanisms such as skin-shedding (Filion-Myklebust and Norton 1981). This passive process may itself largely explain the success of *P. lanosa* as an epiphyte on *A. nodosum*. Interestingly, settlement in association with the cryptostomata of *F. vesiculosus* was not observed, either experimentally or in the field; this is probably due to the large size of *P. lanosa* spores, which have a mean diameter of $\sim 85 \mu\text{m}$.

Numerical variation in sporeling survival was large between fronds (*A. nodosum*) or plants (*F. vesiculosus*) in September. This initial variation became lower later in the year as the effects of factors such as wave action, mechanical abrasion between fronds and grazing overcame the initial variability in survival, which was due to the position of basiphyte plants in relation to spore-bearing currents and consequently initial numbers of settled spores.

Survival patterns were highly non-random on both basiphytes. Sporeling frequency on lateral pits (including axils) of *A. nodosum* was greater than on other sites in September and became progressively higher in January and May. This is despite the very low surface area of lateral pit sites compared to the thallus area as a whole. Lobban and Baxter (1983) found damaged fronds to be the most heavily colonized by mature *P. lanosa* and suggested that the

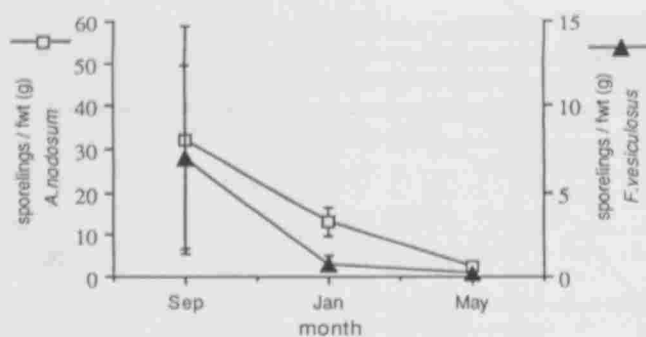


FIG. 6. Survival of *P. lanosa* sporelings on *A. nodosum* and *F. vesiculosus* on the shore from post-sporulation (September) to pre-sporulation (May).

reason might be the increased number of lateral axils following the loss of the apical meristem. The steady decline in the relative frequency of sporelings on 'exposed' sites throughout the study period reinforces the view that the occurrence of sufficiently sheltered sites on the basiphyte is necessary for successful colonization by *P. lanosa*.

On *F. vesiculosus*, wound sites are the major surface discontinuity, and by far the highest frequency of sporeling survival occurs on wounds. Penetration by the primary rhizoid may be more rapid where the epidermis is broken and skin-shedding cannot occur. This may be further aided if exuded chemical factors from the basiphyte are required by *P. lanosa* for germination as suggested by Harlin and Craigie (1975). It is apparent that *P. lanosa* spores are capable of settling on and penetrating *F. vesiculosus*, and mature plants have been observed on this basiphyte. However, the exposed nature of the thallus and paucity of natural breaks and irregularities make it unsuitable for colonization to any great degree.

The reason for the more stunted growth of sporelings and young plantlets on *F. vesiculosus* is unclear. Brown algae produce a variety of allelopathic compounds, notably polyphenols, but fatty acids (Kakisawa et al. 1988) and diterpenes (Kurata et al. 1988) have also been reported. *F. vesiculosus* exudate was found to suppress the growth of microalgae (McLachlan and Craigie 1964). Allelochemical effects from *A. nodosum* have also been observed (Walker and Smith 1948). Perhaps *P. lanosa* is adapted to overcome the allelochemicals from *A. nodosum* but is susceptible to certain of those from *F. vesiculosus*. This is unlikely, since both basiphytes produce polyphenols, and *P. lanosa* is capable of reaching maturity on either. The stress of greater exposure may simply be the reason for stunted growth on *F. vesiculosus*.

Although the *P. lanosa*-*A. nodosum* relationship is complex and may involve nutritional (Turner and Evans 1977) as well as other, more subtle chemical interactions, *P. lanosa* is not a species-specific epiphyte. Early settlement patterns and basiphyte mor-

phology, i.e. the availability of sheltered sites for further development, seem to be of prime importance in determining the extent of colonization.

This study was carried out by G. A. Pearson during the course of a Natural Environment Research Council studentship.

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EFFECT OF NITROGEN AND PHOSPHORUS SUPPLY ON GROWTH AND TISSUE COMPOSITION OF *ULVA FENESTRATA* AND *ENTEROMORPHA INTESTINALIS* (ULVALES, CHLOROPHYTA)¹

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ABSTRACT

The chlorophyte macroalgae *Ulva fenestrata* (Postels and Ruprecht) and *Enteromorpha intestinalis* (Linnaeus) Link. were grown under various nutrient regimes in indoor semi-continuous and batch cultures. Tissue nitrogen contents ranged from 1.3–5.4% N (dry wt), whereas tissue P ranged from 0.21–0.56% P (dry wt). Growth in low nitrogen medium resulted in N:P ratios of 5–8, whereas growth in high nitrogen medium resulted in N:P

ratios of 21–44. For *U. fenestrata*, tissue N:P < 16 was indicative of N-limitation. Tissue N:P 16–24 was optimal for growth and tissue N:P > 24 was indicative of P-limitation. Growth of *U. fenestrata* was hyperbolically related to tissue N but linearly related to tissue P. Phosphorus-limited *U. fenestrata* maintained high levels of tissue N, but N-limited algae became depleted of P. For *E. intestinalis*, tissue N remained at maximum levels during P-limitation whereas tissue P decreased to about 85% of maximal levels during N-limitation. Growth rates for *U. fenestrata* decreased faster during P-limitation than during N-limitation. Simultaneously, tissue P was depleted faster than tissue N. Our results suggest that comparing tissue N and P of macroalgae grown in batch cultures is useful for monitoring the nutritional status of macroalgae.

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