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Variation in a host-epiphyte relationship along a wave exposure gradient*

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ABSTRACT: The red alga *Polysiphonia lanosa* (L.) Tandy is an obligate epiphyte that primarily occurs on the fucoid brown algal basiphyte *Ascophyllum nodosum* (L.) Le Jolis. In the present study we examine how epiphytic interactions between *P. lanosa* and *A. nodosum* vary along a wave exposure gradient within the southern Gulf of Maine, USA. *P. lanosa* was most dense on protected shores; however, because the stature of *P. lanosa* was greater on exposed than on sheltered shores, greater biomass occurred in exposed habitats. Epiphytic *P. lanosa* primarily attached to injured vegetative tissue at exposed sites, while its occurrence was primarily receptacular at sheltered sites. A significantly stronger correlation was found between host receptacle abundance and epiphyte abundance at a protected low than an exposed site. As a result, the distribution of epiphytes along the host's stipe varies at different sites. We suggest that changes in the distribution and abundance of *P. lanosa* across this wave exposure gradient are highly influenced by variations in the distribution and persistence of suitable attachment sites on the host plant. Because both the quantity and quality of attachment sites varies with exposure, we hypothesize that different processes limit or determine *P. lanosa* populations in different locations. In protected sites *P. lanosa* may be limited by the presence of adequate substrata (injured tissue and lateral pits) where successful recruitment may occur. By contrast, at exposed sites the supply of *P. lanosa* sporelings, rather than quantity of appropriate substrata, may limit population size.

INTRODUCTION

The processes that limit or modify abundances of individuals in populations on rocky shores have received considerable attention. Most of this work has focused on sessile invertebrates, while considerably fewer studies have examined the population ecology of intertidal seaweeds, particularly algal epiphytes.

Epiphytes are ubiquitous and important components of marine communities (Orth & Montfrans 1984, Arrontes 1990), especially when primary substratum is limiting (Hay 1981a, b). The presence of epiphytes on marine macrophytes may result in a variety of complex interactions between hosts and epiphytes; as a result, the ecology of epiphytes is fundamentally different from that of algae attached to primary substratum (Hayward 1980, Orth & Montfrans 1984). Such interactions may begin with non-random patterns of settle-

ment and recruitment (Gonzales & Goff 1989, Pearson & Evans 1989, 1990). Host specificity by several epiphytic algal species is a dramatic example of non-random settlement and recruitment (Ducker & Knox 1984). Additionally, post-recruitment survivorship of epiphytes may be related to the host, as epiphytes may experience reduced herbivore pressure when associated with a chemically defended host (Hay 1986).

Basiphytes or epiphyte hosts (*sensu* Ducker & Knox 1984) exhibit a variety of defensive strategies to reduce epiphytism. Such strategies include the abscission or sloughing of outer cell walls ('skin') in fucoid and coralline algae (Filion-Myklebust & Norton 1981, Johansen 1981, Moss 1982, Steneck 1982, Russell & Velcamp 1984). Additionally, the release of phenolic compounds (Zapata & McMillan 1979, Moss 1982, Harlin 1987) and ephemeral life histories (den Hartog 1972) have been suggested as defenses from epiphytism.

Numerous investigators have studied patterns of species richness within epibiotic assemblages (Markham 1969, Ballantine 1979, Whittick 1983, Grahame & Hanna 1989, Arrontes 1990, Rodriguez & Stoner 1990). The composition of these assemblages varies both seasonally

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and spatially on macrophyte host tissues (Markham 1969, Whittick 1983, Arrontes 1990). Epiphytism is often greatest on old or injured sections of basiphytes (Ballantine 1979, Lobban & Baxter 1983, Ducker & Knox 1984, Pearson & Evans 1989, 1990, Arrontes 1990). Physical factors, particularly desiccation and wave action, may also determine the species composition of epiphyte guilds (Hayward 1980, Grahame & Hanna 1989).

Despite substantial work on marine epiphytes, their population ecology has received little attention (Harlin 1987). Of the numerous selective forces affecting epiphyte growth, the distribution and stability of suitable substrata is critically important (Benzing 1987). Although it is well known that the density, stature, longevity and dispersion of potential basiphytes varies with wave exposure (Lewis 1964, Lubchenco 1980, Cousens 1985, Mathieson & Hehre 1986), the effects of such demographic patterns on epiphyte ecology have rarely been investigated (Harlin 1987).

The red alga *Polysiphonia lanosa* is an obligate epiphyte (Taylor 1957, Turner & Evans 1977) that primarily occurs on the fucoid brown alga *Ascophyllum nodosum*. The rhizoids of *P. lanosa* penetrate the host and obtain some nutrition from *A. nodosum* (Rawlence & Taylor 1970, Turner & Evans 1977). However, the quantity of carbon obtained by *P. lanosa* is minimal (Harlin & Craigie 1975) and *P. lanosa* is pigmented and capable of photosynthesis (Bidwell 1958, Fralick & Mathieson 1975).

In the present study we examine the spatial variation of epiphytic interactions between *Polysiphonia lanosa* and *Ascophyllum nodosum* at several rocky intertidal habitats in the Northwest Atlantic. Field observations suggest that the distribution and abundance of *P. lanosa* are highly dependent upon the occurrence of injured host tissue and/or number of lateral shoots (Lobban & Baxter 1983, Burke 1986, Pearson & Evans 1989, 1990). Both of these morphological features of *A. nodosum* appear to be maximal in locales exposed to moderate wave action (Cousens 1985). In this paper we seek to extend previous studies on the population ecology of epiphytes by attempting to answer the following 3 questions: (1) Does the abundance and/or biomass of *P. lanosa* vary with wave exposure? (2) Does *P. lanosa* exhibit site-specific attachment to *A. nodosum* under varying wave exposure? (3) Is there any relationship between epiphyte abundance and the reproductive capacity of *A. nodosum*? If so, does this relationship change with varying wave exposure?

METHODS

The study was conducted at 3 sites: the sheltered (northwestern) and semi-exposed (eastern) shorelines of Jaffrey Point, Newcastle, New Hampshire and the

exposed easternmost shoreline of Smuttynose Island, Maine, USA. The eastern shoreline of Jaffrey Point consists of large granitic outcrops on a semi-exposed shore, while the northwestern shoreline is protected from direct wave action from all directions (Mathieson et al. 1981). Smuttynose Island is the easternmost island of the Isles of Shoals archipelago, with the eastern shoreline being exposed to extreme wave action, particularly during storms (Sideman & Mathieson 1983, Mathieson & Penniman 1986). The 3 sites were selected to represent a gradient in wave exposure, with Smuttynose Island being the most exposed, the northwestern shoreline of Newcastle Island being the most protected, and the easternmost shoreline of Jaffrey Point being intermediate. Previous work has characterized this exposure gradient, and detailed descriptions of these sites have been published elsewhere (Mathieson et al. 1981, Mathieson & Hehre 1986, Mathieson & Penniman 1986).

During February and March 1989, 50 *Ascophyllum nodosum* fronds were haphazardly collected at the upper and lowermost boundaries of the mid-intertidal zone of each site. The lower mid-intertidal zone was sampled because it is the location of highest *Polysiphonia lanosa* density (Burke 1986), while the upper mid-intertidal boundary was used for comparative evaluations. After being collected the samples were brought to the laboratory for an assessment of the number, weight and vertical stratification patterns of *P. lanosa* on host plants, as well as the occurrence of *A. nodosum* receptacles. Initially each *A. nodosum* frond was weighed (damp-dried) and measured (length from holdfast to apical tip). After the epiphytes were removed, the fronds were reweighed. An individual *P. lanosa* plant was designated as an individual sporeling or a clump having a discrete (single) attachment point. Ultimately the number and weight of *P. lanosa* plants per *A. nodosum* frond were enumerated for each site. To assess vertical stratification patterns of *P. lanosa* on *A. nodosum* fronds, the numbers of *P. lanosa* within 10 cm intervals along the frond were enumerated. The occurrence of injury sites on *A. nodosum* was also enumerated while quantifying the presence of *P. lanosa*. A variety of injury sites were apparent, including the loss of apical meristematic tissue, as well as various lesions, cuts and breakages on the intercalary surfaces and edges of *A. nodosum*.

Differences among sites for the various parameters evaluated were assessed using analysis of variance (ANOVA). An analysis of covariance was also used to test for differences of regression line slopes (Zar 1984). Prior to the analyses, data were tested for heteroscedasticity, using Cochran's test (Underwood 1981). If variances were heterogeneous (< 0.05 for Cochran's test), analyses were performed on transformed data. Counts

were changed to $\log(x \pm 1)$ values and proportions were arcsine transformed (Underwood 1981).

RESULTS

Conspicuous differences in the abundance of *Polysiphonia lanosa* on vegetative tissue were evident among the study sites (Figs. 1 & 2; $F_{5,144} = 4.29$, $p = 0.001$). The mean number of *P. lanosa* clumps per *Ascophyllum nodosum* frond on vegetative tissues at the protected low site was 38.2, which was ca 2 times greater than at any other site. Such differences were statistically significant (Tukey's HSD, $p < 0.01$). As the stature of epiphytes from the protected low site was much smaller than at the exposed sites, conspicuous



Fig. 1. *Ascophyllum nodosum*. Silhouettes of attached plants from 3 study sites, 2 at Jaffery Point, New Hampshire (A & B = sheltered, C = semi-exposed) and one from the exposed site of Smuttynose Island, Maine (D to H). Note the elongated, reproductive fronds of *A. nodosum* without (A & B) and with (C) visible epiphytic *Polysiphonia lanosa*. A reduction in stature of *A. nodosum* and increased biomass of epiphytes are evident at Smuttynose Island versus Jaffery Point (D to H)

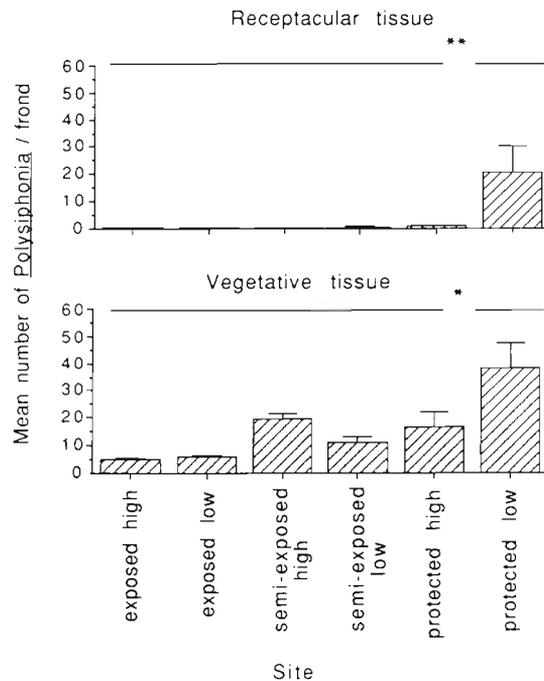


Fig. 2. *Polysiphonia lanosa*. Mean number on vegetative and receptacular tissues of *Ascophyllum nodosum* at 6 study sites. Horizontal bars join means which were not significantly different ($p > 0.05$) by Tukey's HSD tests. * Significant at $p < 0.05$; ** significant at $p < 0.01$. Error bars are 1 SE

differences of *P. lanosa* biomass on vegetative tissue were evident ($F_{5,144} = 5.06$, $p < 0.001$). Thus, the mean biomass at the exposed high and low sites were at least an order of magnitude greater than at any of the other sites (Fig. 3). Such patterns were still evident even when the data were standardized by dividing *P. lanosa* biomass by *A. nodosum* biomass.

Significant differences in the mean number of *Polysiphonia lanosa* clumps on receptacular tissue were also evident (Fig. 2, $F_{5,144} = 4.26$, $p = 0.001$). For example, at the protected low site the number of receptacular epiphytes was at least 18 times greater than at the other 5 sites. As *Ascophyllum nodosum* sheds its receptacles precipitously each spring (Mathieson 1989), all of the receptacular epiphytes must be from the same cohort. When we accounted for differences in frond size among sites by dividing *P. lanosa* biomass by *A. nodosum* biomass, no differences in mean biomass of receptacular attached *P. lanosa*/*A. nodosum* were evident among any sites ($F_{5,144} = 1.47$, $p = 0.20$).

Conspicuous differences in the location of *Polysiphonia lanosa* clumps on *Ascophyllum nodosum* fronds were found among exposed and protected sites (Fig. 4). The mean proportion of receptacular epiphytes varied significantly among sites ($F_{3,116} = 18.12$, $p < 0.001$), with the protected low site having the highest value (Tukey's HSD, $p < 0.01$). Furthermore the pro-

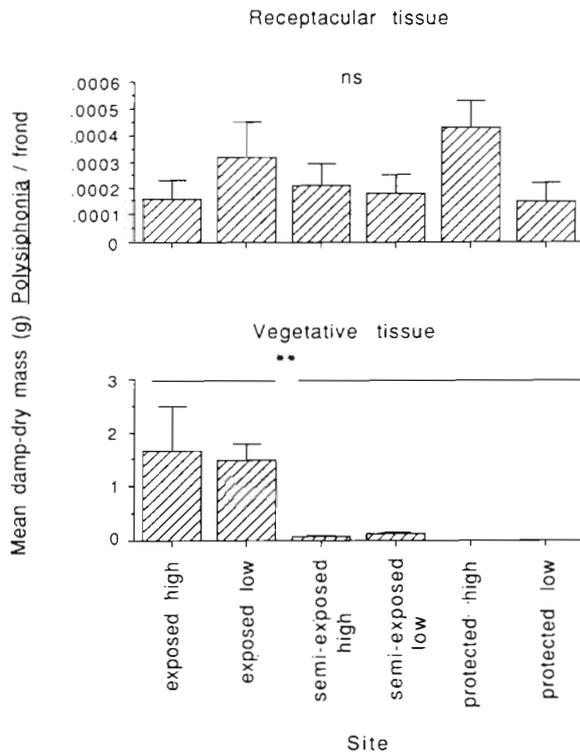


Fig. 3. *Polysiphonia lanosa*. Mean damp-dried weight of plants on receptacular and vegetative tissues of *Ascophyllum nodosum* at 6 study sites. Horizontal bars join means which were not significantly different ($p > 0.05$) by Tukey's HSD tests. ** Significant at $p < 0.01$. Error bars are 1 SE

tected high site had a significantly higher proportion of receptacular epiphytes than the exposed high site (Tukey's HSD, $p < 0.05$).

Injured *Ascophyllum nodosum* tissue had significantly higher numbers of *Polysiphonia lanosa* clumps than uninjured material (Fig. 4; $F_{3,116} = 11.59$, $p < 0.001$). Plants from exposed sites had a significantly higher proportion of epiphytes attached to injured tissue than those from protected sites (Tukey's HSD, $p < 0.01$). The mean proportions of epiphytes attached to injured tissue at the exposed high and low sites were 0.58 and 0.57, respectively, while at the protected high and low sites the mean values were 0.19 and 0.019, respectively.

The proportion of *Polysiphonia lanosa* attached to uninjured vegetative tissues was not significantly different among sites (Fig. 4; $F_{3,116} = 2.15$, $p = 0.1$). However, the mean proportion of uninjured attachment locations was more than twice that of injured tissues at the protected sites and nearly half the value of injured tissues at the exposed sites. Such results suggest that uninjured vegetative tissues are relatively more important attachment points at protected sites than at the exposed sites.

An analysis of covariance revealed significant differences among sites in the relationship between numbers of *Polysiphonia lanosa* clumps and numbers of *Ascophyllum nodosum* receptacles (Table 1). The slope of the regression line at the protected low site was significantly greater than at all other sites (Tukey's HSD, $p < 0.001$; Fig. 5), indicating that a stronger relationship existed between receptacular number and the abundance of *P. lanosa* at this site than at the other 5 sites. In addition, the amount of variance in *P. lanosa* abundance explained by receptacular abundance varied among sites (Fig. 5). While 84.1% of the variation in epiphyte abundance was explained by receptacular abundance at the protected low site, less than 37% was explained at the other 5 sites.

The distribution of clumps of *Polysiphonia lanosa* was not uniform along *Ascophyllum nodosum* fronds

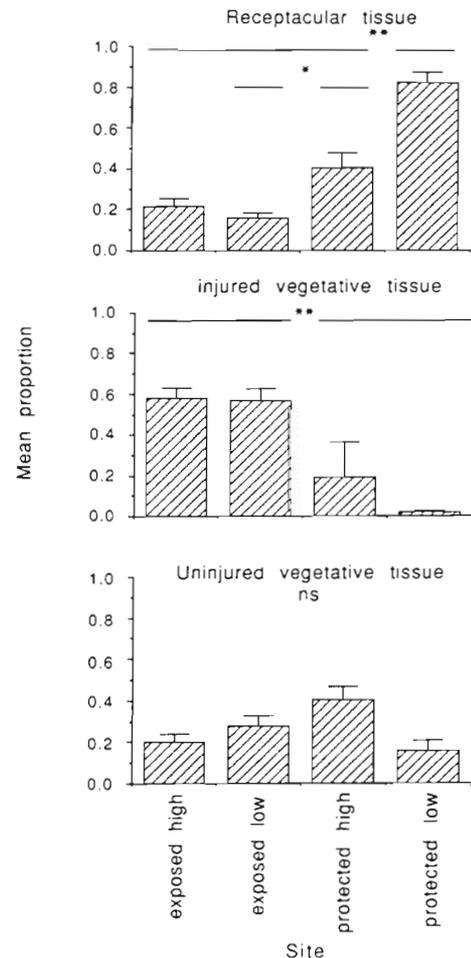


Fig. 4. *Polysiphonia lanosa*. Mean proportion of plants attached to receptacular and vegetative tissues (injured and healthy) at 4 study sites. Horizontal bars join means which were not significantly different ($p > 0.05$) by Tukey's HSD tests. * Significant at $p < 0.05$; ** significant at $p < 0.01$. Error bars are 1 SE

Table 1. *Polysiphonia lanosa*. Results of an analysis of covariance on the effects of site and receptacle number on abundance. The significant interaction term indicates that the relationship of *P. lanosa* and receptacle abundance varies among sites

Source of variation	Sum of squares	df	Mean square	F	p
Site	32.21	5	6.64	11.24	<0.001
Receptacle number	87.66	1	87.66	148.35	<0.001
Site × Receptacle number	32.457	5	6.491	10.99	<0.001
Error	170.167	288	0.591		

(Kolmogorov-Smirnov 1-sample test, $p < 0.001$; e.g. Fig. 6). At the protected low site, the non-uniform distribution of epiphytes may result from the strong relationship between the abundances of receptacles and epiphytes which could produce a high correlation between the distribution of epiphytes and receptacles. However, this high correlation should not exist at the other 5 sites. Fig. 6 presents an initial assessment of these predictions using the protected low and exposed low sites. These 2 sites represent extremes along the wave exposure gradient we examined and provide an excellent contrast to test our hypothesis. Epiphyte distribution appears to be correlated with receptacular distribution at the protected low site, with maximal numbers near the frond's mid-length. In contrast, at the exposed site most *P. lanosa* was found near *A. nodosum*'s holdfast, while its receptacles were most abundant at the mid-frond length.

DISCUSSION

Epiphyte populations are highly dependent upon the distribution and abundance of suitable substrata (Benzing 1987). *Polysiphonia lanosa* generally requires injured host tissues or lateral pits (i.e. sites of actual or potential branching) in order to successfully recruit onto host plants (Lobban & Baxter 1983, Burke 1986, Pearson & Evans 1989, 1990). In controlled laboratory experiments, Pearson & Evans (1990) found that higher numbers of spores settled on the thallus and lateral pits of *Ascophyllum nodosum* fronds than onto vesicles. On the other hand, survivorship of in situ sporelings was highest in lateral pits and wound sites. Cousens (1985, 1986) demonstrated that these morphological features of *A. nodosum* fronds vary with wave exposure. In very sheltered coastal habitats, the number of injury sites (i.e. wounded tissue) on *A. nodosum* fronds is low. Addition-

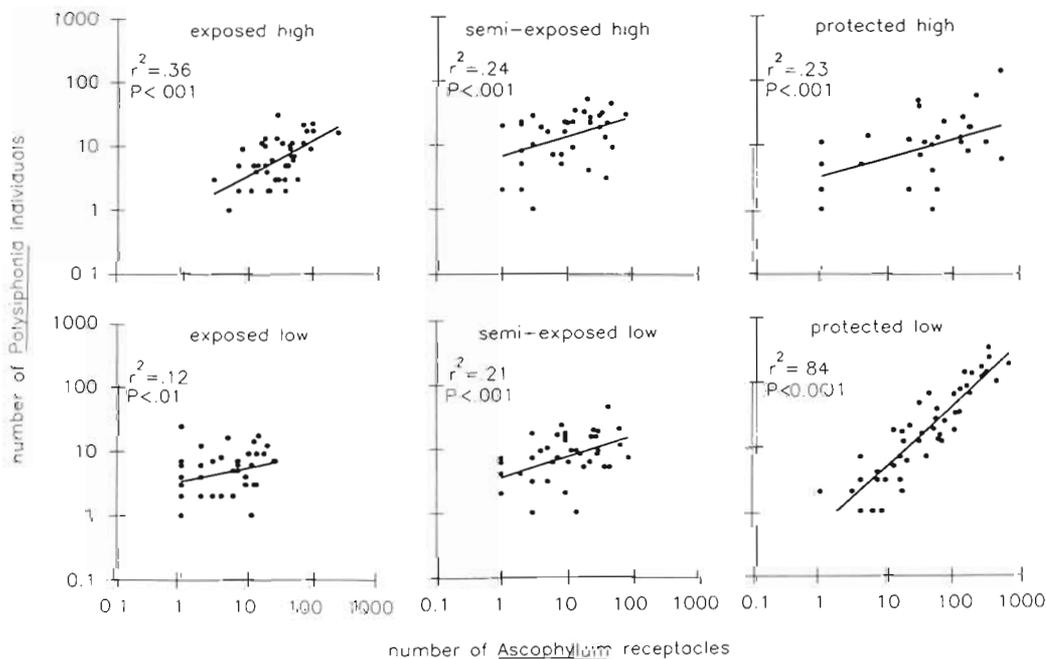


Fig. 5. Relationship between *Polysiphonia lanosa* and receptacular abundance at 6 study sites. The slopes of these regression lines are not equal (see Table 1), with the protected low site having a significantly greater slope than the other 5 sites

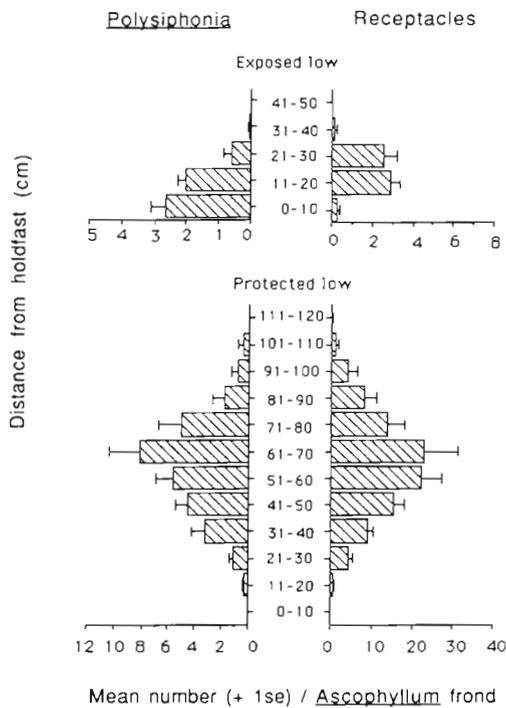


Fig. 6. An initial assessment of the hypothesis that *Polysiphonia lanosa* distribution is correlated with receptacular distribution at a protected site, but not at an exposed site. Error bars represent 1 SE

ally, the numbers of vegetative and reproductive laterals are reduced, and a truncation of the primary apex results in higher initiation of laterals than in sheltered locales (Cousens 1985). *A. nodosum* also exhibits its highest reproductive effort (i.e. receptacle mass/net annual production) in more exposed habitats (Cousens 1986).

The above-described changes in the morphology of *Ascophyllum nodosum* influence both the distribution and abundance of its epiphytes. Thus, we found much greater numbers of small *Polysiphonia lanosa* at the protected low site than at the other more exposed locations; however, these sporelings were primarily attached to receptacles. The lack of wounded tissue and vegetative laterals at such a protected low site suggests that reproductive laterals become the primary attachment point for settling germlings. During April and May when *A. nodosum* dehisces its receptacles (Mathieson et al. 1976, Mathieson 1989) most of the biomass of *P. lanosa* biomass would be lost at this site. By contrast, at exposed sites epiphytes are primarily attached to injured vegetative tissues. Thus, the spring dehiscence of *A. nodosum* receptacles in exposed sites would not result in as significant a loss of epiphyte biomass as at protected sites.

The factors that limit or induce change in marine populations have been a matter of much debate (see reviews by Underwood & Denley 1984 and Doherty &

Williams 1988). While we did not directly investigate the regulation or limitation of *Polysiphonia lanosa* populations our data suggest that this host-epiphyte system may be ideal for experimental manipulations investigating factors important to the structure of marine populations. Because the morphology of *Ascophyllum nodosum* changes dramatically between different habitats, different processes may limit or induce spatial variation in *P. lanosa* population size in different sites. Thus, we propose the following hypothesis. In sheltered coastal sites, populations of *P. lanosa* are limited by the number of locations where successful recruitment may occur (i.e. wounded tissue and lateral pits). Such a hypothesis suggests that sporelings are plentiful and that intraspecific competition for wound sites or lateral pits results in density-dependent rates of recruitment to mature populations. Therefore, in the absence of disturbance, *P. lanosa* (or other similar epiphytes) would saturate the available permanent habitats. Excess sporelings would be forced to colonize receptacles and would subsequently be lost before entering the adult population.

In exposed locations, *Ascophyllum nodosum* fronds may be undersaturated with sporelings relative to the number of available wound sites and lateral pits. Such patterns would indicate that populations of *Polysiphonia lanosa* are recruitment limited (sensu Doherty 1981, Victor 1983) or recruitment determined (sensu Forrester 1990). If populations of *P. lanosa* are recruitment limited then the abundance of sporelings would set the upper boundary of population size. Similarly, if these populations are recruitment determined then differential availability of sporelings in space and time would be reflected in subsequent spatial and temporal variations of adult populations. In either case it is the supply of sporelings, not the amount of suitable substrata, which would be the critical factor to the dynamics of the epiphyte population.

Some brown algal epiphytes (e.g. *Elachista fucicola*) also exhibit differential abundances on fucoid receptacular tissue depending on habitat. Russell (1988), for example, found that *E. fucicola* occurred on receptacles of *Fucus vesiculosus* more frequently on protected versus exposed shores. In exposed sites *E. fucicola* was more common on stipes than on receptacles. As in the host-epiphyte association we described, the annual shedding of receptacles will result in a substantial loss of epiphytes in protected sites, but less so at exposed sites (Russell 1988). Consequently, the hypothesis that different processes limit *P. lanosa* populations in varying habitats may be generalizable to other epiphyte populations.

Other biotic factors may also contribute to these complex patterns of epiphyte distribution and abundance. Mesograzers (small herbivorous invertebrates) are important members of intertidal communities (Lub-

chenco 1978, 1980, Lubchenco & Gaines 1981, Mathieson et al. 1991). Mesograzers may directly consume epiphytes, and they may indirectly influence epiphyte distribution by creating patterns of injury. Several studies have recently implicated amphipods as important mesograzers in host-epiphyte relationships (Zimmerman et al. 1979, Brawley & Adey 1981, Norton & Benson 1983, D'Antonio 1985, Buschmann & Santelices 1987, Duffy 1990). One of the most abundant algal-dwelling amphipods in the Northwest Atlantic is *Hyale nilssonii*, which readily consumes both *Polysiphonia lanosa* and *Ascophyllum nodosum* (McBane & Croker 1983). Hence, it may play a role in this host-epiphyte relationship by directly consuming *P. lanosa* or by injuring *A. nodosum*.

The most abundant and important mesograzers on New England rocky shores is the gastropod *Littorina littorea* (Lubchenco 1978). *Polysiphonia lanosa* is consumed by *L. littorea* (Lubchenco 1978), and we have often observed this gastropod, as well as *Littorina obtusata*, grazing on *P. lanosa* at Jaffery Point. Additionally, grazing by *L. littorea* or *L. obtusata* on *Ascophyllum nodosum* or its epibiota may result in tissue injury, influencing the number and/or location of attachment sites available to *P. lanosa* spores.

All populations of *Ascophyllum nodosum* investigated to date harbor the ascomycete fungus *Mycosphaerella ascophylli* (Kohlmeyer & Kohlmeyer 1972). Garbary & Gautam (1989) found a strong correlation between the biomass of *Polysiphonia lanosa* and perithecial density of *M. ascophylli*. Their study also showed that receptacles of *A. nodosum* had the highest density of fungal hyphae. One might speculate that the presence of the fungus could provide a cue for the attachment of *P. lanosa* sporelings (but cf. Pearson & Evans 1990). Future work enumerating how *M. ascophylli* perithecial density changes with wave exposure as well as experimental manipulations of fungal densities would be of interest.

Most earlier studies of host-epiphyte interactions have been conducted primarily at single sites (e.g. Markham 1969, Lobban & Baxter 1983, Garbary & Gautam 1989, Grahame & Hanna 1989, Pearson & Evans 1990). The present study demonstrates that the nature of host-epiphyte interactions changes with wave exposure. We believe that comparative investigations among sites or habitats are necessary to illuminate the complex nature of these interrelationships.

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