ORGANISATION AND SEASONAL PROGRESSION WITHIN THE EPIFAUNAL COMMUNITIES OF COASTAL MACROALGAE

by

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Résumé

Les macroalgues côtières fournissent un éventail de ressources à exploiter pour une grande variété d'invertébrés. Leurs frondes supportent fréquemment de denses assemblages épifaunaux parmi lesquels des organismes filtreurs sessiles tels que les Bryozoaires, les Serpulides, les Hydroïdes, les Spongiaires et les Tuniciers sont largement représentés. La disponibilité d'espace bi-dimensionnel pour l'attachement étant souvent restreinte dans de tels habitats, la compétition pour cette ressource est potentiellement énorme. Nous considérons comment cette ressource, limitée bien que renouvelable (grâce à la croissance de la plante), est répartie parmi les espèces dominantes, et nous examinons quelques-uns des facteurs qui déterminent la capacité compétitive. Les fluctuations saisonnières dans le recrutement larvaire, l'abondance des espèces, le pouvoir d'entrer en compétition, et les interrelations complexes qui se sont développées entre les épifaunes et leurs hôtes algaires sont aussi examinés. Les principaux éléments déterminants d'une organisation communautaire dans les épifaunes algaires sont comparés aux facteurs établis précédemment comme importants pour déterminer l'organisation de communautés benthiques marines.

Introduction

Fronds of coastal macroalgae provide a suitable habitat for a wide variety of invertebrates. Early work on these associations was largely restricted to distributional studies; more recently emphasis has shifted towards understanding community organization and dynamics. Benthic community structure depends largely upon a) choice of suitable substratum by prospecting larvae and b) successful establishment and subsequent competition for limiting resources, mainly space and food, which in the case of filter feeders are probably synonymous. Mechanims for the determination of community structure have been suggested in which common species interact as hierarchies or networks, space is generated by physical and/or biological disturbance, and more or less importance is attached to seasonal, stochastic, and other factors.

Our research has focussed on *Fucus serratus* L. which supports a diverse epifaunal community in which bryozoans, ascidians, hydroids, sponges, and spirorbids predominate. At our main study site in the Menai Strait, North Wales, the most abundant species are the encrusting bryozoans *Flustrellidra hispida* (Fabricius), *Alcyonidium polyoum* Hassal, *A. hirsutum* (Fleming), *Electra pilosa* (L.), and *Cel-*

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leporella hyalina (L.), the stoloniferous hydroid *Dynamena pumila* (L.) and the polychaete *Spirorbis spirorbis* L.

In this paper we will examine the major determinants of ecological pattern within the epifaunal community, then consider seasonal progression. Attention will be given to isolating mechanisms and the importance of structural complexity in reducing competition, and to some of the factors which determine competitive ability when these isolating mechanisms fail. Finally we will compare the processes determining epifaunal community structure with paradigms from other benthic communities.

ECOLOGICAL PATTERN

Various physical and temporal mechanisms effectively isolate the major components of the *F. serratus* epifauna. Species distributions result from larval selectivity and the differential survival and growth of recruits and established colonies. The major physical factors determining epifaunal distribution are tidal range (ca. 10 m in the Menai Strait), water flow, turbulence and silt loading. Most species are significantly more abundant in sites of fast-flowing, turbulent water, whereas others, especially the calcified members of the community *(Electra, Celleporella, Spirorbis)* are maximally abundant in more turbid, slo"-moving water. Transference of plants between sites differing in physical characteristics results in marked changes in community composition. (Seed, 1985).

TABLE 1

Choice of algal substrate[#] by larvae of *Alcyonidium hirsutum* (Bryozoa)

Experimental condition	Total no. settled larvae	No. replicates	Ratio	p[*]
1 *Fucus serratus : Laminaria digitata*	76	10	18.0:1	< 0.05
2 *Fucus serratus : F. vesiculosus*	86	10	5.1:1	< 0.05
3 *Fucus serratus*				
a) concave : convex faces	171	20	5.3:1	< 0.05[+]
b) apical : basal segments	81	18	7.1:1	< 0.05
c) low shore : high shore plants	68	8	1.1:1	ns
mid shore : high shore plants	69	12	0.9:1	ns
mid shore : low shore plants	58	10	2.6:1	ns
d) encrusted : non encrusted plants	78	20	0.6:1	ns

[#] <Clean> unencrusted fronds used for all choice experiments.

* Mann Whitney 'U' test

\+ Wilcoxon matched pairs test

Macroalgal species vary in their attractiveness to prospecting larvae, precise levels of specificity varying with species and locality (Ryland, 1976). Table 1 summarises the results of a series of laboratory based choice experiments using the larvae of *A. hirsutum,* one of the competitively dominant members of the community, to illustrate larval selectivity in the local *F. serratus* epiphyte community. *F. ser-*

ratus, the normal «host» of this bryozoan, was significantly more attractive than cither *Laminaria digitata* (Huds.) Lamour, or *F. vesiculosas* L. which occur respectively below and above it on the shore. *Alcyonidium* larvae are not only selective with respect to different algal species, but also discriminate between different regions within individual plants, and between the recognisable concave and convex surfaces of *F. serratas* fronds; similar results have been obtained by Ryland (1959). Plants from different positions along the intertidal gradient, however, do not differ in their attractiveness, nor do «clean» segments of frond from heavily encrusted and unencrusted plants (Table 1).

The ability of larvae to distinguish between different algal species and different regions within plants introduces the question of interactions and adaptation. When organisms are associated over evolutionary time, especially where the « host» is growing vigorously and producing a variety of exudales, it would be surprising if some degree of adaptation had not occurred. The competitively dominant species within this community, *Flustrellidra* and *A. hirsutum* (and to a lesser extent *A. pohjoum)* occur almost exclusively on *F. serratas.* The competitively inferior opportunists *Electra* and *Celleporella,* on the other hand, are eurylopic.

Fig. 1 shows that photosynthesis rises steadilly from the base to the lip of F. *serratas.* Such a gradient could provide appropriate chemical cues for prospecting larvae and may also account for the orientated growth patterns noted among some *F. serratas* epifauna (Ryland, 1979; Wood and Seed, 1980) Crisp and Williams (1960) showed that bryozoan larvae are attracted to fucoid extracts, and this combined with the abiliLy of some larvae to discriminate between basal and apical frondage (Table 1) indicates a sophistication of larval sensitivity to exudales.

To assess the possible effect of encrustation on algal desiccation when emersed, encrusted and unencrusted frond segments were placed in a constant humidity environment at 30 °C for three hours and weighed half hourly. Desiccation rales are constant for any given species, and in Table 2a, comparison of log/normal regressions reveals significant differences between all three bryozoans. The two competilively dominant species provide the greatest protection against frond desiccation. Although F. *serratas* and other fucoids can become air-dry and still rehydrate, recovery of photosynthelic ability is severely impaired when volatile water loss exceeds a critical value (approximately 60 p. 100 for *F. serratas* (Dring and Brown, 1982)) and there may also be resultant tissue necrosis.

By protecting plants from water loss, encrusting bryozoans must benefit the host plant and in so doing promote their own fitness. Increased substratum longevity is presumably of greater importance to the longer-lived, seasonally reproducing, community components *Flustrellidra* and *A.. hirsatum* than to the shorter-lived *Electra* with its extended fecundity.

Brown algae produce various exudales of potential importance to community dynamics. Larval response to fucoid extract films has already been mentioned, and algal polyphenols and tannins have a deleterious effect on bacteria (Hornsey and Hide, 1976) and on some invertebrates (Conover and Sieburth, 1966; Geiselman and McConnell, 1981). Dissolved Organic Carbon (DOC) is an important energy source in marine systems, and release by macroalgae may supply a large proportion of this: DOC exuded by the kelp *Nereocytis luetkeana* (Poslels and Ruprecht) was taken up by the bryozoan *Membranipora membranacea* (L.) (De Burgh and Fankboner, 1979). Other evidence suggesting, that DOC uptake may be widespread in bryozoans, as indeed it is in other marine invertebrates, is provided by ultrastructural studies of two species regularly present in the *F. serratas* community. Both *Electro* and *A. hirsutum* have been demonstrated to have a microvillous epithelium characteristic of absorptive tissue (Maricon, 1973; Lutaud, 1973). To assess whether DOC uptake occurs in the local

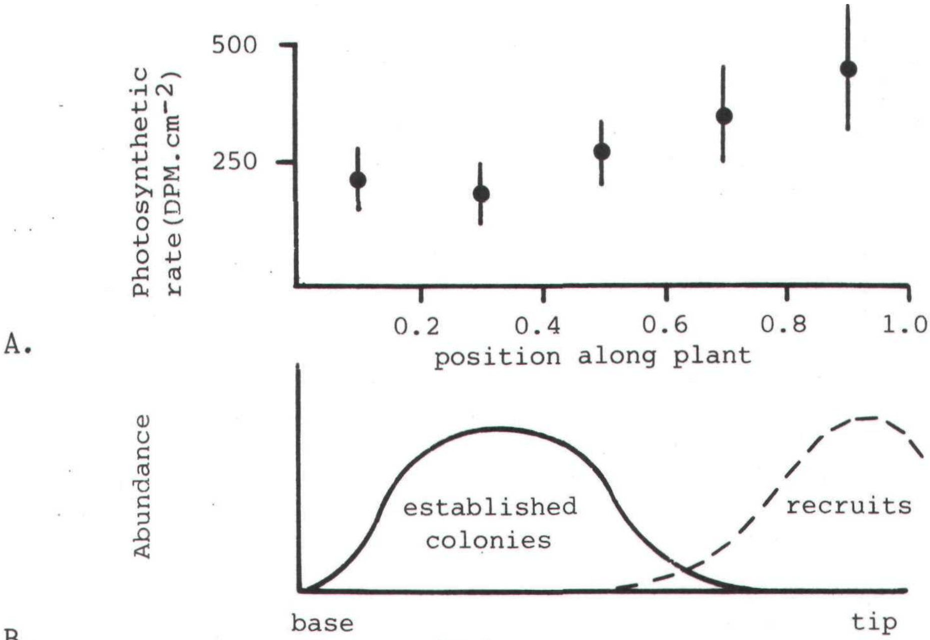

FIG. 1

A. Photosynthetic rate along plant length expressed as uptake of radioisotope per unit area of frond.

B. Diagrammatic representation of the distribution of recruits and established colonies of *A. hirsutum* along the plant.

F. serratas community plant segments encrusted by the common bryozoan species were placed in perspex clamps designed to restrict possible sources of DOC to the localised area of frond colonised. These segments where then incubated in seawater labelled with NaH [^{14}C) O_3 (for general method see Oswald *et al.,* 1984). Net DOC uptake occurred for all five species incubated, but differed between species (Table 2b); *Fhistrllidra,* the overall community dominant, showed a substantially higher value (29,3 Disintegrations per minute (DPM).mg^{-1}) than any other species, followed by *Electra* (7.6 DPM.mg^{-1}).

Sheets of opaque encrusting bryozoans frequently cover large areas of frond. To assess whether such encrustations affect algal photosynthesis, encrusted and unencrusted frond segments were incu-

TABLE 2

Outline results of investigation into interactions between *F. serratus* and common bryozoan epifauna

	Flustreillidra	**A. *hirsutum***	***Electro***	**Unencrusted *F serratus***
a) Desiccation rateµ	0.20 (0.01)**	0.24 (0.02) *	0.27 (0.03)**	0.80 (0.27)
b) Net DOC uptakc#	29.3 (13.1)***	4.7 (1.9)	7.6 (3.3) - -	
c) Photosynthetic activity#	25 (12)** *	107 (60)	350 (147) ns	653 (242)

Values are mean (standard deviation). Probability of differences between adjacent values being due to chance : *at 0.05; ** at 0.01; ***at 0.001.
µexpressed as slope of log/normal regression of volatile water loss/time.
(DPM.mg^{-1}).

bated in seawater labelled with NaH [^{14}C] O_3, allowed to photosynthesis and the uptake of radioisotope was measured (Oswald *et al.,* 1984). Table 2c shows that photosynthesis is significantly reduced on encrusted fronds, with *Flustrellidra* and *A. hirsutum* having the most marked effect (96 p. 100 and 70 p. 100 respectively). It might have been anticipated that those bryozoans most regularly associated with and possibly best adapted to *F. serratus* would impose the lowest cost on their host plant. However, because space generation in these communities is primarily mediated through plant growth (Seed and O'Connor, 1981), the marked reduction in photosynthesis, and presumably therefore plant growth, may permit competitively superior species such as *Flustrellidra* to dominate the substratum more effectively. Stunting of algae by fouling bryozoans has been found elsewhere (Woollacott and North, 1971) whilst O'Connor *et al.* (1979) showed that the bryozoans of *F. serratus* could be segregated on the basis of host plant form.

In encrusting communities competition is mediated by allelochemicals (Jackson and Buss, 1975), by overgrowth (Jackson, 1979) or by more efficient exploitation of food and other resources (Jackson and Winston, 1982).

Allelochemicals are frequently used by sponges and ascidians but although these taxa are known to occur on *F. serratus* elsewhere they are rarely found at our study site in the Menai Strait. Competition among encrusting bryozoans is normally through overgrowth with one colony elevating or thickening its growing edge and smothering its competitor. A frequent outcome of competitive encounters is a «stand-off» where growth ceases at the encounter edge, although encounters between the competitively inferior *Electra* and the more dominant species do frequently result in overgrowth. Our results are therefore broadly similar to those obtained by Stebbing (1973). Wood and Seed (1980) demonstrated an essentially hierarchical structure for a subset of species in the Menai Strait *F. serratus* community, where *Flustrellidra* > *A. hirsutum* > *Electra.* Reversals in competitive ability, however,, were not uncommon.

Differential competitive ability between members of epifaunal communities is difficult to explain: *Electra,* which exhibits rapid vegetative growth, produces spines near encounter areas, and can rapidly alter its growth orientation in order to colonise vacant space, might be expected to be a superior competitor. *Electra* occurs, however, on a wide variety of substrata, both organic and inorganic, and is probably not especially well adapted to any one particular type. *Flustrellidra* and *A. hirsutum,* by contrast, are largely confined to *F. serratus,* and consequently may have become adapted to exploit their algal host. They protect frond tissue from desiccation, utilise exudates, and by affecting photosynthesis, may alter plant structure. The combination of these adaptive features together with isolating mechanisms which effectively reduce competition has produced a spatially heterogeneous environment. Seasonal variation further increases this complexity by adding a dimension of temporal heterogeneity to the system.

SEASONAL PROGRESSION

Larvae of opportunistic species such as *Electra* are relatively long-lived (several weeks) and settle throughout much of the year. *Flustrellidra* and *Alcyonidium* have short-lived (several hours) lecithotrophic larvae which are produced seasonally. These latter species show no appreciable growth in the winter, whereas many larvae of the opportunists settle and have become established colonies by the time *Flustrellidra* and *Alcyonidium* resume their growth in the spring.

Settlement and seasonal changes in surface cover by the three common bryozoans are shown in Fig. 2. Settlement peaks during May to June for *Flustrellidra,* and in December to January for *Alcyonidium.* *Electra* by contrast shows a fairly constant level of settlement throughout the year, with a slight increase during the summer. Maximal growth rates for all species occur during the summer, but of these three species only *Electra* grows appreciably during winter. *Flustrellidra* colonies frequently survive the winter and grow and breed during their second year, despite damage and fragmentation caused by frosts and abrasion. Consequently late spring and summer see a rapid increase in surface cover; on the basal levels of plants this is due largely to regrowth of surviving colonies, on the mid plant levels to growth of newly settled colonies. *A. hirsutum* is essentially an annual and after the winter the population is at a very low level. Surface cover increases rapidly during spring and summer, but is mainly confined to the mid levels of the plant, with little recruitment to the basal levels. *A. hirsutum* settles principally on distal plant segments during late autumn and early winter but no appreciable growth occurs until the following spring. Rapid growth over the spring and summer frequently produces fleshy protuberances which place an excessive load on fronds by the late summer. This often results in extensive frond loss and sloughing off of colonies, leading to high *A. hirsutum* mortality during the autumn equinoctial gales. By autumn *Electra* is largely smothered by *Flustrellidra,* but a resurgence of growth occurs in the winter. Differences in larval selectivity and timing of settlement by *A. hirsutum* and *Flustrellidra* combined with the biennal survival of the latter ultimately lead to the partition of plants into a *Flustrellidra* dominated basal zone and an *A. hirsutum* dominated mid region (Fig. 3).

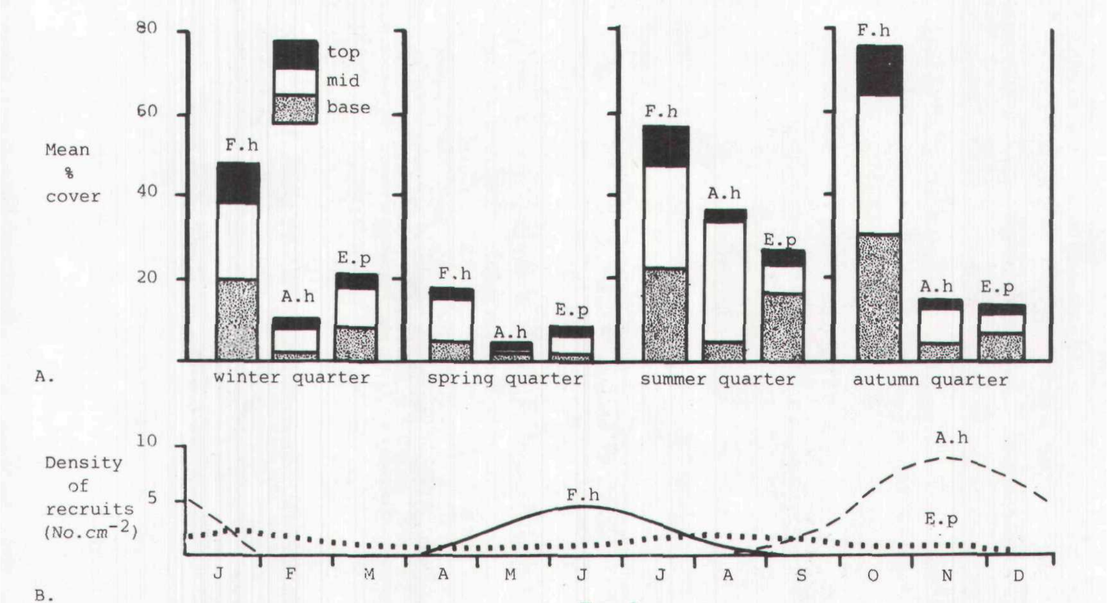

FIG. 2

A. Mean percentage cover at different plant levels for the three commonest bryozoan species, Sampled quarterly. Combined data 1981-82.

B. Annual settlement patterns for the three commonest bryozoans. F.h = *Flustrellidra,* A.h = *A. hirsutum,* E.p = *Electra.*

Relative competitive ability also varies with season, as shown in Fig. 4. The competitive differential between *Electra* and *Flustrellidra* significantly reduced in spring and summer, when the latter is devoting considerable resources to reproduction and the former is **growing** vigorously. Similarly in the autumn when *A. hirsutum* is reproductively active, *Electra* approaches it in competitive ability. Despite the greatly increased number of encounters between *Flustrellidra* and *A. hirsutum* in the summer, when both are growing actively, little effort is expended on overgrowth, and standoffs are common. Such changes in competitive ability facilitate the persistence of opportunist species such as *Electra* within the community.

Seasonal catastrophes (e.g. storms, frosts) may be important in producing changes in community composition and often provide access for fugitive species. Alternatively by removing predators they may enable competitively superior species effectively to monopolise resources. However, such catastrophes appear to have little effect on the local *F. serratus* community. A series of especially cold frosts during the winter of 1981-1982 led to exceptionally high mortality of all overwintering species, but despite this, summer growth of the surviving colonies rapidly returned the community to normal. Vegetative growth facilitates this rapid recovery and Wood (1983) has demonstrated that where the density of *A. hirsutum* ancestrulae is lower, eventual average colony size is greater. This density-dependence of colony growth must serve to reduce unnecessary intraspecific competition, and instances of intraspecific overgrowth are rare (Wood and Seed, 1980). No significant increase in the populations of fugitive species followed the hard winter, although there was a slight rise in the surface cover of *Electra*.

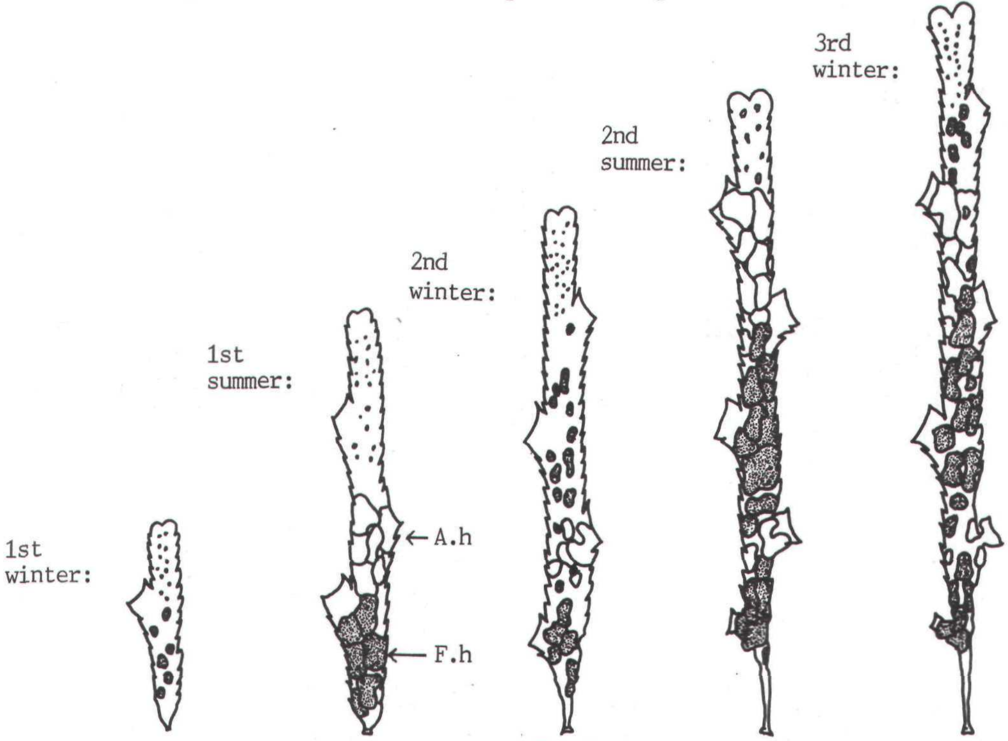

Fig. 3

Partition of *F. serratus* plants into *Flustrellidra* (F.h) dominated basal and *A. hirsutum* (A.h) dominated apical regions. (Modified from Wood, 1983).

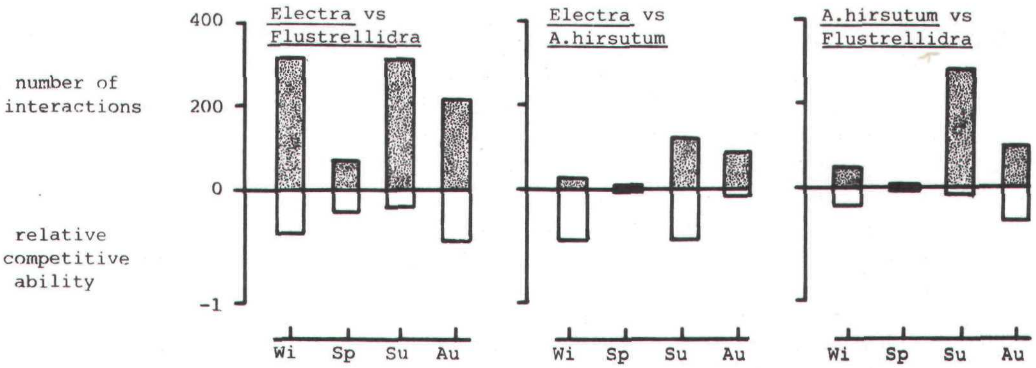

Fig. 4

Interactions and differential competitive ability between bryozoan species, on ten plant samples per season over two years (1981-82). Longest frond sampled from each plant. Competitive ability obtained by valuing defeats = —1, victories = +1, then summing and expressing as proportion of number of interactions. The first named of each species pair is the inferior competitor.

COMMUNITY ORGANISATION

On rocky shores there is a tendency for a small number of competitively superior species to dominate the community. However, disturbance, either physical (e.g. log or wave damage) or biological (i.e. predation) serves to reduce monopolisation by dominant competitors by constantly renewing space, the primary limiting resource (Dayton, 1971). Fugitive species can occupy the space thus provided, and their survival is also enhanced wherever the environment is sufficiently heterogeneous to provide spatial refuges. The competitive relationships between species on rocky shores are generally hierarchical, and within any given community the presence or absence of «keystone» species may have a disproportionate influence on community composition (Paine, 1969).

Cryptic coral reef faunas live in relatively undisturbed environments, but although competition is intense, complete monopolisation of the substratum seldom occurs. Inferior competitors may have some advantage over species apparently higher up the competitive hierarchy (e.g. by producing allelochemicals), thus introducing an element of intransitivity. Such relationships have been termed «competitive networks» by Buss and Jackson (1979).

Fauna of subtidal boulders may have essentially similar community dynamics to cryptic reef faunas, if because of size or reduced water movement they lie undisturbed. Where rolling over occurs, however, space is constantly regenerated. Sousa (1979) found there is an optimal boulder size where diversity is maximal. Small boulders suffered great disturbance and supported impoverished communities, whereas large and undisturbed boulders in the absence of spatial refuges tend to be dominated by a few species. Where rolling over of boulders creates space, competition and predation are relatively unimportant in shaping the community.

In soft sediment communities depth introduces a third dimension which, with seasonal changes, varying levels of disturbance and different sediment types produce a highly complex system. The Petersen-Thorson system (see Gray, 1981) describes species assemblages which are dominated by characteristic species, in environments which can be consistently defined in physical terms (depth, saliniy, sediment type, exposure). Because of inconsistencies which arose when attempts were made to apply it in the field, this system has been largely abandoned in favour of a continuum concept. The continuum concept does, however, still define communities in terms of environmental characteristics. Holland *et al.* (1980) considered that the physical environment is the major factor determining community structure and species abundance. They found that exclusion of predators led to an increase of infaunal abundance, but with no corresponding change in species diversity. Similarly competition did not appear to be important for the control of infaunal density. Woodin (1974, 1978), however, concluded that biological factors are important to community composition, and that communities may be viewed as compilations of species successfully exploiting refuges in space or time.

Unlike those communities so far discussed, algal epifaunas occur on a rapidly growing substratum, with its own inherent seasonal characteristics (Wood, 1983). In addition the plant often produces allelochemicals which discourage bacteria and some invertebrates, and DOC which may act as a nutritive source. Metabolic gradients along the fronds provide potential cues to settling larvae and for the orientation of colony growth. Sophisticated isolating mechanisms have evolved which effectively result in the partial segregation of species along the plant, thereby reducing competitive interactions. Other interactive features including the whole area of cost and benefit between host and epifauna are also important in structuring these communities.

In any given locality, tidal range and timing of low spring tides, combined with other important physical factors such as water movement and silt loading, will determine which species will occur. KarLson and Buss (1984) argue that competitive intransitivity is of less importance in affecting community composition in highly disturbed environments. In the *F. serratas* community the analogue of disturbance is space generation through frond growth. This, combined with the other elements of complexity in the system, could explain why fugitive species can persist, and why little effort is apparently expended on competitive interactions.

In attempting an empirical investigation of the *F. serratus* community, we view the inherent physical and temporal features of the environment as a template upon which the biological interactions of those community components capable of surviving in this particular environment are superimposed. For any community, this environmental template, and its degree of heterogeneity, will dictate the characteristics of the community, for instance whether competition will be severe, whether refuges will be present, which strategies will be optimal, and so forth. Given spatial heterogeneity (providing refuges from predators) and a benign physical environment, networks rather than hierarchies are likely to be produced within the highly competitive community which results (e.g. cryptic reef faunas). In a spatially homogeneous environment with similarly benign conditions there will be a tendency for superior competitors to monopolise the available space, but such conditions may also be ideal for predators, and these will effectively reduce this monopolisation (e.g. mussel beds on sheltered shores).

In algal epifaunas the living substratum adds extra dimensions to heterogeneity, reducing the importance of predation and competition as community shapers. Adaptation to the substratum is likely to occur because of the predictability of the heterogeneous features of the environment (e.g. seasonal plant growth, production of exudates) and to be important in determining competitive ability. This combination of stability and heterogeneity has produced a community in which there appears to be an inbuilt homeostasis. Competitively superior species are generally restricted to specific regions of the plant, but despite their adaptations they are unable to dominate the substrattini completely because of space generation by plant growth. Finally, catastrophes have little effect on these communities because vegetative growth means that minimal survival is necessary for rapid recovery. Sponges and ascidians are primarily subtidal organisms; the stressful nature of the physical environment generally prevents these potentially superior competitors from becoming dominant within intertidal algal epifaunas. Fugitive species within these communities occur on a variety of substrata, and thus lack the finely tuned characteristics of those species specifically associated with *F. serratus.*

Summary

Coastal macroalgae provide an array of resources for exploitation by a wide variety of invertebrates. Their fronds frequently support dense epifaunal assemblages within which sedentary filter feeders such as bryozoans, serpulids, hydroids, sponges and tunicatcs are well represented. Since the availability of two dimensional space for attachment is often restricted in such habitats, competition for this resource is potentially severe. This paper considers how this limited, though renewable (through plant growth) resource is effectively partitioned amongst the dominant species and examines some of the factors determining competitive ability. Seasonal fluctuations in larval recruitment, species abundance, competitive ability and the complex interrelationships which have evolved between epifaunas and tbe'r algae hosts are examined. Th principal determinants of community organisation in algal epifaunas are compared with those factors previously established as being important in determining the organisation of other benthic marine communities.

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