

## Recruitment and mortality of *Alcyonidium hirsutum* (Fleming) and *Flustrellidra hispida* (Fabricius) (Bryozoa : Ctenostomata) within a *Fucus serratus* L. community

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**Abstract :** The recruitment and mortality of two common ctenostome bryozoans within a *Fucus serratus* L. community in the Menai Strait, North Wales are described. Larvae of *Alcyonidium hirsutum* (Fleming) settled between August and February, whereas those of *Flustrellidra hispida* (Fabricius) settled from April to November ; maximum recruitment of these bryozoans occurred during early November and July respectively. Colonisation intensity of both species varied between sites and between years. At each site variations in recruitment occurred between plants and within individual plants, though concave surfaces of younger more distally located frond segments were generally preferred, particularly by *A. hirsutum*. Our data suggest that at settlement the larvae of *Alcyonidium* may be capable of detecting the presence of conspecifics and potential competitors already present on the plant fronds. Both bryozoans experienced high levels of post-settlement mortality. Less than 1.5 % of the monitored *Alcyonidium* colonies survived long enough to breed successfully and release larvae. Mortality rates were higher on densely colonised fronds but it was generally from these plant regions that colonies survived to reproduce. Only a relatively small proportion of the total mortality of *A. hirsutum* (< 30 %) was attributable to frond loss. Habitat selection by *A. hirsutum* and *F. hispida*, and the relationship between the life cycles of these two spatially dominant bryozoans and that of their main host species, *F. serratus*, are briefly discussed.

**Résumé :** Le recrutement et la mortalité de deux Bryozoaires Ctenostomes largement répandus dans une communauté à *Fucus serratus* du nord du Pays de Galles sont décrits. Les larves d'*Alcyonidium hirsutum* se fixent d'août à février, tandis que celles de *Flustrellidra hispida* se fixent d'avril à novembre. Leurs phases maximales de recrutement sont respectivement début novembre et juillet. L'intensité de colonisation de ces deux espèces varie selon les localités et les années. A chaque station, des différences dans le recrutement apparaissent sur les thalles de différents individus de *Fucus serratus*, ainsi que sur les thalles d'un même individu ; cependant les parties concaves des régions les plus jeunes du thalle, situées plus près du sommet, sont en général préférées, en particulier par *A. hirsutum*. Nos données suggèrent que les larves d'*Alcyonidium* pourraient être capables de détecter la présence d'individus de leur espèce et celle de compétiteurs potentiels déjà présents sur les thalles. Les deux Bryozoaires subissent d'importantes pertes après fixation. Moins de 1,5 % des colonies d'*Alcyonidium* étudiées *in situ* survivent assez longtemps pour se reproduire avec succès et libérer leurs larves. Les taux de mortalité sont plus élevés sur les thalles densément colonisés, mais c'est en général dans ces régions que les colonies survivent pour se reproduire. Seule une relativement faible proportion (inférieure à 30 %) de la mortalité totale d'*Alcyonidium* est due à la perte de thalle. Le choix du substrat par *A. hirsutum* et *F. hispida* et la relation entre les cycles biologiques de ces deux Bryozoaires dominants et celui de leur hôte principal, *Fucus serratus*, sont brièvement discutés.

### INTRODUCTION

Rocky shores in north temperate waters, particularly those sheltered from direct wave impact, are typically dominated by a wide variety of macroalgae which exhibit distinct patterns of zonation across the physical exposure gradient that exists between high and low water marks. These macroalgae, which also extend subtidally to depths that are largely dictated by the availability of light for photosynthesis, provide an array of resources for exploi-

tation by a wide range of organisms from virtually all the main animal phyla (e.g. Seed & O'Connor, 1981 ; Williams & Seed, 1992). Algae situated in the more desiccating conditions of the upper intertidal zone are usually colonised only by mobile taxa that can easily migrate into the humid recesses of the weed bed during periods of aerial exposure (e.g. Dunstone *et al.*, 1979). Epialgal communities associated with lower shore and subtidal algae, by contrast, are more typically dominated by sessile suspension feeding taxa (e.g. Boaden *et al.*, 1975 ; Cancino, 1986). Moreover, complex interactions often exist between many of these sessile faunas and their algal hosts (e.g. Oswald & Seed, 1986 ; Williams & Seed, 1992).

In the Menai Strait in North Wales the serrated wrack, *Fucus serratus* L., is routinely colonised by around twelve relatively common invertebrate taxa amongst which the two encrusting bryozoans, *Alcyonidium hirsutum* (Fleming) and *Flustrellidra hispida* (Fabricius) are especially abundant (Wood & Seed, 1980). In an earlier paper (Wood & Seed, 1992), we documented the growth and reproductive cycles of these two spatially dominant bryozoans ; here we describe the recruitment patterns and mortality rates of these epialgal bryozoans, and briefly consider how their life history characteristics relate to those of their algal host.

#### The study area

A full description of the study area is provided elsewhere (Wood, 1983 ; Wood & Seed, 1992). Briefly, however, the Menai Strait is a tidal channel which although largely protected from wave action is scoured by a strong tidal flow. Four physically contrasted sites were chosen for study. Site 1 is situated within the main tidal channel and is thus subjected to extremely strong and turbulent water flow ; plants at this site were sampled at two shore levels, one at LWST (site 1 low), the other (site 1 mid) approximately 1.6 m further upshore. Sites 2 and 3 are located outside the main channel, site 2 in the outflow of a bay created by two small islands, site 3 on the leeward side of an extensive muddy bank ; at both these sites, therefore, tidal flow is substantially reduced and *F. serratus* occurs only at and around LWST. Site 4 is situated in an inlet at the seaward edge of a small boat slipway and although close to site 1, it is more sheltered from the main tidal currents ; as at site 1, two shore levels (site 4 low and site 4 mid) were selected for study.

#### MATERIALS AND METHODS

Two main methods were used for sampling these epialgal bryozoan populations. *Monitor method* - In October 1978 several *F. serratus* plants at site 4 mid were selected and marked using strips of plastic securely attached around the plant stipes. Distal frond segments were then chosen, tagged with lengths of coloured string, and monitored in the field over a period of approximately two years. Every two to four weeks these fronds were overlaid with sheets of clear acetate paper onto which the frond outline, position of the midrib,

and exact location of any recently recruited ancestrulae of *A. hirsutum*, were recorded using a fine permanent marker pen. *F. serratus* fronds have recognisable concave and convex surfaces and these were monitored separately. From these data the precise fate of each recruit from the time of its first appearance on the frond to the subsequent death of the resulting colony could be established. The actual cause of mortality was recorded whenever this could be linked with loss of substratum, whether this be of the entire *Fucus* plant or the whole or part of the monitored frond. Frond growth and tissue loss were calculated from the changes in frond outlines on successive sampling dates. Plants at site 4 low were similarly monitored between October 1979 and October 1980.

Commencing in October 1978 approximately 1000 recently settled *A. hirsutum* at site 4 mid were monitored until August 1979 by which time all the resulting colonies had died. The following year almost 1000 individuals were monitored at site 4 low over a period of about six months, whilst at site 4 mid just over 2500 individuals were followed for one year when all the surviving colonies ( $n = 32$ ) were harvested. Unfortunately this monitor method could not be easily applied to *F. hispida* because in the field young colonies of this bryozoan were often indistinguishable from groups of closely settled ancestrulae. The monitor method was therefore supplemented with subsamples of *F. serratus* taken from plants immediately adjacent to those used in the population monitor programme.

*Sampling method* - From October 1978 populations of *A. hirsutum* and *F. hispida* were sampled at approximately monthly intervals until either September 1979 (site 1 mid) or January 1981 (site 4 mid). Each sample comprised five to ten distal frond segments about 20-30 cm long, each collected from a different plant. On many of the plant fronds it was usually possible to distinguish a seasonal sequence of settlement; consequently it was these fronds that were selected so as to minimize the risk of mixing successive year classes of the two bryozoan species. Each frond segment was reduced to one main apical tip together with one or two lateral branches (Fig. 1A) which were subsequently cut close to the main frond stem except when bryozoan density was exceptionally low. The outlines of these fronds were then traced onto acetate paper and the area of each internode calculated. The population density of *Flustrellidra* and *Alcyonidium* on each internode could then be established.

The seasonal settlement of *F. hispida* and *A. hirsutum* was also recorded using previously uncolonised (= "clean") *F. serratus* plants. Every four to six weeks for a period of one year, starting in March 1979, twelve "clean" plants were collected from the uppermost intertidal limit of *F. serratus* and securely tied onto four large marked host plants at each of three of the low shore sites. On the same low tide the twelve plants which had been set out on the previous date were collected, returned to the laboratory, and the following samples taken from each plant: (i) two or three distal fronds each consisting of 3-4 internodes, (ii) the basal three or four internodes and (iii) two areas of old frondage each comprising two internodes, from the main frond. The number of recently settled *Flustrellidra* and *Alcyonidium* on these samples was recorded separately for each surface of each frond segment and the area of the segments calculated. The number of recently settled individuals could then be expressed as numbers.cm<sup>-2</sup>.28d<sup>-1</sup>.

Other more limited surveys were also undertaken throughout this investigation. In November 1978 five plants were collected at site 1 mid and several distal segments, approximately four internodes in length, taken from the longest fast-growing fronds, and from the slower-growing fronds in the bushier central region of each plant. The area of each segment and the density of newly recruited *Alcyonidium* were recorded thus allowing the distribution of ancestrulae on the youngest segments within individual plants to be analysed. In December 1980, several young *F. serratus* plants (4-12 cm long) were collected at site 4 low in order to examine the distribution of recently settled *Alcyonidium* and young *Flustrellidra* colonies along the entire length of each plant. The outline of each plant was traced onto acetate paper and divided into 1.0 cm segments starting at the holdfast; the number of ancestrulae or small colonies on each segment face was then recorded. In March 1980 several *F. serratus* plants were collected from site 2 in order to investigate the dispersion pattern of newly settled *Alcyonidium* ancestrulae.

*A. hirsutum* and its congener *A. gelatinosum sensu* Thorpe & Winston (= *A. polyomm*) are now thought to comprise several genetically distinct but morphologically indistinguishable species (Thorpe & Ryland, 1979). Moreover, it has recently been shown that these cryptic species may also differ in their reproductive biology (d'Hondt & Goyffon, 1992). Although both *A. hirsutum* and *A. gelatinosum* colonise *F. serratus* in the Menai Strait, the latter species was rarely encountered at the study area. The ancestrulae of these two bryozoans are indistinguishable in the field and consequently, therefore, all recently settled *Alcyonidium* were assumed to be *A. hirsutum*. This assumption was subsequently confirmed when colonies had grown to a size at which they could be positively identified and only *A. hirsutum* was found to be present on the monitored plants.

## RESULTS

### Recruitment

Figure 1A illustrates the seasonal recruitment of *Alcyonidium* and *Flustrellidra* on previously uncolonised *Fucus* plants at site 1 low between March 1979 and March 1980. *F. hispida* breeds mainly during the summer months and whilst there was some larval settlement between April and November, most recruitment occurred during July. Recruitment of *A. hirsutum*, by contrast, started in August, peaked in October, and ended in early February. Thus, *Alcyonidium* larvae arrived on *F. serratus* plants only when the recruitment of *Flustrellidra* was all but complete. A total of 4806 *A. hirsutum* and 3555 *F. hispida* ancestrulae recruited onto the sample fronds during this period. Figure 1A also reveals that the recruitment of *Alcyonidium* was more variable than, and greatly exceeded that of, *Flustrellidra*.

The timing and intensity of recruitment of *A. hirsutum* and *F. hispida* on monitored plants at the three contrasting low shore sites are illustrated in Figure 1B; results are presented separately for whole plants and for distal concave fronds where maximum recruit-

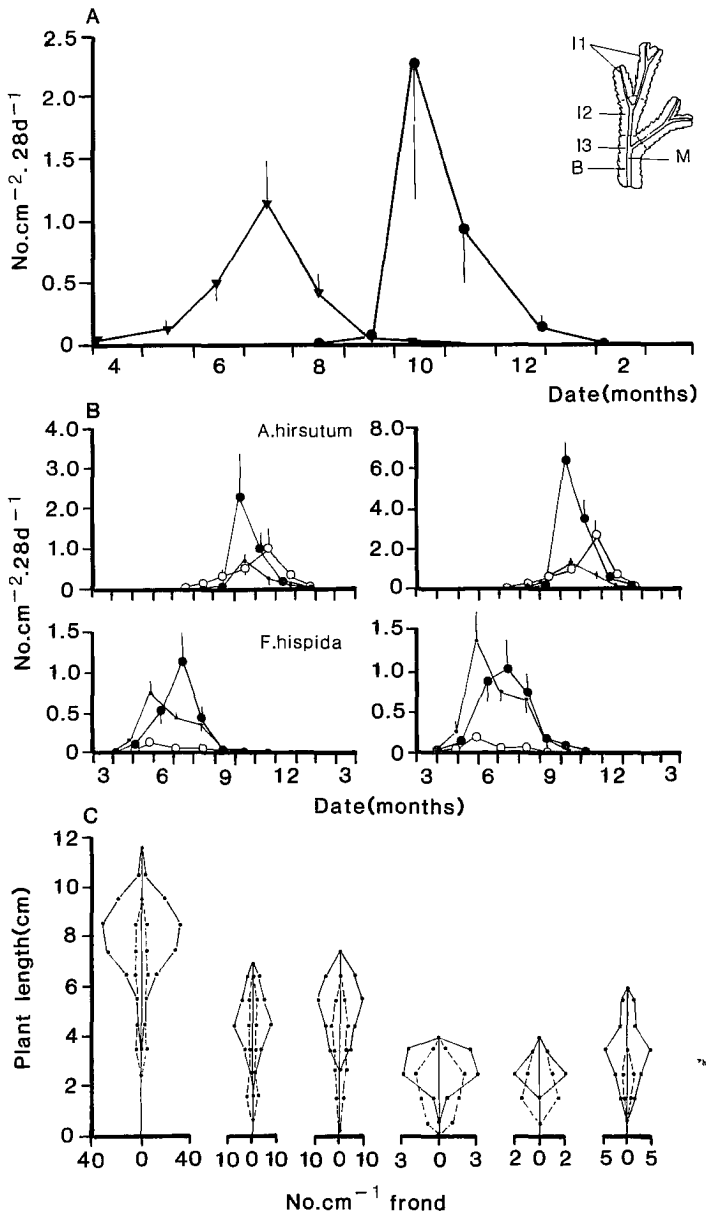


Fig. 1 : (A) Seasonal recruitment of *A. hirsutum* (●) and *F. hispida* (▼) on previously uncolonised *F. serratus* at site 1 low, Mar. 1979 - Mar. 1980, each mid sample point is the mean number of ancestrulae ( $\pm$  CI) recruited onto distal, mid and basal fronds, inset : terminology of distal segment ; I1, internode ; M, midrib ; B, blade. (B) Recruitment of *A. hirsutum* and *F. hispida* on low shore plants at sites 1 (●), 2 (●) and 3 (○), Mar. 1979 - Mar. 1980 ; each point is the mean number of ancestrulae ( $\pm$  CI) for whole plants (left) and distal concave fronds only (right). (C) Distribution of *A. hirsutum* (●—●) and *F. hispida* (●- -●) ancestrulae along small *F. serratus* at site 4 low ; concave and convex surfaces are considered together.

ment occurred. Recruitment intensity of both bryozoans was greatest at the most turbulent location (site 1). Nevertheless, *Flustrellidra* recruitment at the intermediate location (site 2) was similar to, and on distal concave fronds actually exceeded, that at site 1 whilst recruitment at the most protected location (site 3) was negligible by comparison. Recruitment of *Alcyonidium* was lowest at site 2. Intersite variability also occurred in the actual timing of recruitment. Thus, whereas recruitment of *F. hispida* peaked later at site 1 than at sites 2 and 3 in *A. hirsutum* it started earlier and peaked later at site 3 than at sites 1 or 2. Table I shows the relative recruitment levels of these bryozoans onto different regions of previously uncolonised *F. serratus* plants at three of the low shore sites. Recruitment intensity of both species onto concave frond surfaces decreases from the younger distal plant tissues towards the basal holdfast, whilst recruitment onto distal concave surfaces was always greater than onto distal convex surfaces. However, this tendency was considerably reduced on the older fronds taken from the bushier central regions of the plants, even though frond curvature was here usually more pronounced. The relative colonisation levels of these different regions of the frond varied between species and was also influenced by environment. Colonisation of distal convex surfaces by both species was inversely related to site turbulence. *A. hirsutum* appeared to be the more selective species, occurring much more frequently on distal frond segments; thus 91 % of all *A. hirsutum* ancestrulae were located on distal fronds at site 1, 78 % at site 2 and 84 % at site 3. *Flustrellidra* larvae, however, settled over a much broader region of the plant with only  $\leq 54$  % of ancestrulae occurring on distal fronds (Table I). When the number of prospecting larvae of these species was low, as at the beginning and end of the respective settlement seasons, those areas of frond which were least attractive at the height of the settlement season were generally avoided.

TABLE I

Distribution of *A. hirsutum* and *F. hispida* ancestrulae along *F. serratus* at three low shore sites during the period of maximum settlement of each species. Recruitment to each frond region expressed as a percentage of that on distal concave fronds (actual mean number of ancestrulae.cm<sup>-2</sup>.28d<sup>-1</sup>).

| Species            | Site | Frond region |        |         |        |       | % distal <sup>1</sup> |
|--------------------|------|--------------|--------|---------|--------|-------|-----------------------|
|                    |      | distal       |        | mid     |        | basal |                       |
|                    |      | concave      | convex | concave | convex | stipe |                       |
| <i>A. hirsutum</i> | 1    | 100 (62.7)   | 41     | 9       | 5      | 0     | 91                    |
|                    | 2    | 100 (12.1)   | 61     | 22      | 22     | 2     | 78                    |
|                    | 3    | 100 (25.7)   | 88     | 17      | 18     | 2     | 84                    |
| <i>F. hispida</i>  | 1    | 100 (10.2)   | 27     | 111     | 71     | 100   | 31                    |
|                    | 2    | 100 (13.7)   | 51     | 39      | 33     | 57    | 54                    |
|                    | 3    | 100 (1.9)    | 62     | 51      | 69     | 39    | 50                    |

<sup>1</sup> Percentage of total recruitment on distal frond segments, concave and convex surfaces combined.

Figure 1C shows that recruitment of both *A. hirsutum* and *F. hispida* extended from the basal segments to the distal apices of small plants. Maximum recruitment of *Alcyonidium* on these plants in December 1979 was distal to that of *Flustrellidra*, and occurred on areas of new plant growth which had been added after the recruitment of *Flustrellidra* (summer) had ended. The density of ancestrulae on these plants was comparable to that on distal fronds of nearby monitor plants at site 4 (Table II).

In Table III recruitment densities of *A. hirsutum* on fast-growing and slower-growing fronds from the same plants are compared. Thus the slower-growing fronds of plant 3 were more heavily colonised than the faster-growing fronds whereas the converse was true for plant 4 ; no significant differences could be detected for the other three plants. Consequently, when the data for all plants are combined, no consistent difference between recruitment densities onto the two frond types is apparent ( $Z = 1.24$ ,  $P > 0.05$  ; Mann Whitney Test). Significant interplant variation in colonisation levels occurred on both the slow- and fast-growing fronds ( $H = 14.51$ ,  $P < 0.05$  and  $H = 19.23$ ,  $P < 0.05$  respectively ; Kruskal Wallis Anova). Recruitment intensity was therefore extremely variable even on similarly located fronds within and between plants at a single site.

TABLE II

Recruitment intensity of *A. hirsutum* and *F. hispida* on small *F. serratus* and on the distal frond segments of larger plants ; all values expressed as mean number of ancestrulae.  $\text{cm}^{-2}$  ( $\pm 1$  SD).

| Species            | Large plants |            | Small plants | F <sup>1</sup> |
|--------------------|--------------|------------|--------------|----------------|
|                    | site 4 mid   | site 4 low | site 4 low   |                |
| <i>F. hispida</i>  | 0.5 (0.3)    | 1.2 (0.7)  | 0.8 (0.6)    | 4.59*          |
| <i>A. hirsutum</i> | 1.3 (0.9)    | 2.2 (1.0)  | 2.2 (1.3)    | 5.46*          |

<sup>1</sup> Anova, \*  $P < 0.05$  ; recruitment of each species is significantly lower at site 4 mid whilst recruitment rates on small and large plants at site 4 low are similar (Newman Keuls Multiple Range Test).

The disparity between recruitment intensity on concave and convex surfaces of distal fronds became less pronounced as site turbulence decreased (Table I). Table IV indicates that significant differences in recruitment intensity between the two plant surfaces occurred for both species, even at the most sheltered site, and that settlement onto the two surfaces was usually independent. Nonetheless, recruitment intensity of *F. hispida* onto concave and convex surfaces at site 2 was positively correlated, as was the recruitment of *A. hirsutum* on the monitored fronds at site 4.

Table V shows the distribution of ancestrulae on distal fronds when these are subdivided into internodes (see Fig. 1A). Recruitment of *A. hirsutum* onto convex surfaces at site 4 low showed no systematic trend, but declined between internodes 1 and 3 on concave surfaces at site 4 low and on both surfaces at site 4 mid. Newman Keuls Multiple Range tests on

TABLE III

Inter- and intra-plant variability in recruitment intensity of *A. hirsutum* on distal segments of fast-growing and slow-growing fronds of *F. serratus* at side 1 mid ; all values expressed as mean numbers of ancestrulae.cm<sup>-2</sup> ( $\pm$  1 SD).

| Plant No       | Slow-growing fronds |        |   | Fast-growing fronds |        |   | U <sup>1</sup> |
|----------------|---------------------|--------|---|---------------------|--------|---|----------------|
|                | $\bar{X}$           | (SD)   | n | $\bar{X}$           | (SD)   | n |                |
| 1              | 0.19                | (0.18) | 4 | 0.13                | (0.17) | 8 | 22             |
| 2              | 2.99                | (1.42) | 4 | 1.78                | (1.19) | 8 | 25             |
| 3              | 4.78                | (3.23) | 8 | 1.48                | (0.91) | 8 | 93*            |
| 4              | 0.66                | (0.64) | 4 | 3.50                | (1.87) | 6 | 23*            |
| 5              | 2.80                | (3.30) | 6 | 1.59                | (1.50) | 8 | 31             |
| H <sup>2</sup> | 14.51*              |        |   | 19.23*              |        |   |                |

<sup>1</sup> Mann Whitney 'U' Statistic ; <sup>2</sup> Kruskal Wallis 'H' Statistic ; \* P < 0.05

TABLE IV

Recruitment intensity of *A. hirsutum* and *F. hispida* onto distal concave and convex frond surfaces of *F. serratus* ; all values expressed as the mean number of ancestrulae.cm<sup>-2</sup> ( $\pm$  1 SD).

| Species                         | Site               | Plant surface |             | T <sup>1</sup> | r <sup>2</sup> |
|---------------------------------|--------------------|---------------|-------------|----------------|----------------|
|                                 |                    | concave       | convex      |                |                |
| <i>F. hispida</i>               | 1 low              | 0.95 (0.32)   | 0.19 (0.08) | 0*             | 0.172          |
|                                 | 2 low              | 1.32 (0.43)   | 0.67 (0.25) | 0*             | 0.690*         |
|                                 | 3 low              | 0.18 (0.07)   | 0.11 (0.05) | 3*             | 0.364          |
| <i>A. hirsutum</i>              | 1 low              | 6.27 (1.40)   | 2.59 (8.00) | 0*             | 0.375          |
|                                 | 2 low              | 1.76 (0.41)   | 1.08 (0.35) | 1*             | - 0.380        |
|                                 | 3 low              | 2.84 (1.45)   | 1.61 (0.73) | 11*            | - 0.015        |
| <i>A. hirsutum</i> <sup>3</sup> | 4 mid <sup>4</sup> | 1.85 (1.73)   | 1.13 (1.38) | 11*            | 0.952*         |
|                                 | 4 mid <sup>5</sup> | 1.86 (1.31)   | 1.02 (0.58) | 15*            | 0.560*         |
|                                 | 4 low <sup>5</sup> | 2.64 (1.20)   | 1.81 (0.97) | 0*             | 0.827*         |

<sup>1</sup> Wilcoxon Matched Pairs Signed Ranks Test ; <sup>2</sup> Correlation coefficient ; <sup>3</sup> Monitored plants ; <sup>4</sup> 1978 ; <sup>5</sup> 1979 ; \* P < 0.05.

these data indicate that recruitment to the two younger more distal internodes significantly exceeded that on internode 3. Recruitment of *Flustrellidra* onto concave surfaces increased significantly from internode 1 to internode 3 whilst that onto convex surfaces was more



TABLE V

Recruitment intensity of *A. hirsutum* and *F. hispida* on the first three internodes of distal frond segments of *F. serratus*; all values expressed as the mean number of ancestrulae.cm<sup>-2</sup> ( $\pm$  1 SD).

| Species            | Site  | Frond surface | Internode      |        |      |        |      |        | H <sup>1</sup> | Newman Keuls |
|--------------------|-------|---------------|----------------|--------|------|--------|------|--------|----------------|--------------|
|                    |       |               | 1 <sup>2</sup> |        | 2    |        | 3    |        |                |              |
| <i>A. hirsutum</i> | 4 low | concave       | 4.06           | (1.51) | 2.64 | (1.38) | 1.20 | (0.64) | 11.46*         | (1=2) ≠ 3    |
|                    |       | convex        | 1.66           | (0.75) | 2.13 | (1.53) | 0.85 | (0.68) | 4.99           |              |
|                    | 4 mid | concave       | 2.42           | (1.78) | 1.63 | (1.34) | 0.60 | (0.71) | 13.50*         | (1=2) ≠ 3    |
|                    |       | convex        | 1.38           | (0.90) | 0.87 | (0.61) | 0.45 | (0.38) | 8.61*          |              |
| <i>F. hispida</i>  | 4 mid | concave       | 0.1            | (0.2)  | 1.4  | (1.3)  | 3.8  | (3.7)  | 14.36*         | 1=2=3        |
|                    |       | convex        | 0.1            | (0.1)  | 0.4  | (0.6)  | 0.4  | (0.4)  | 4.90           |              |

<sup>1</sup> Kruskal Wallis 'H' Statistic ; <sup>2</sup> the youngest most distal internode ; \* P < 0.05.

TABLE VI

Recruitment intensity of *A. hirsutum* and *F. hispida* on the midrib and blade regions of distal *F. serratus* fronds ; all values expressed as mean number of ancestrulae.cm<sup>-2</sup> ( $\pm$  1SD).

| Species            | Site  | Frond surface | Midrib      | Blade       | T <sup>1</sup> |
|--------------------|-------|---------------|-------------|-------------|----------------|
| <i>A. hirsutum</i> | 4 low | concave       | 8.30 (3.69) | 1.34 (0.50) | 0*             |
|                    |       | convex        | 3.84 (2.61) | 1.33 (0.67) | 0*             |
|                    | 4 mid | concave       | 5.54 (3.73) | 0.74 (0.61) | 0*             |
|                    |       | convex        | 2.52 (1.30) | 0.58 (0.40) | 0*             |
| <i>F. hispida</i>  | 4 mid | concave       | 6.8 (4.2)   | 0.5 (0.4)   | 0*             |
|                    |       | convex        | 0.8 (1.1)   | 0.2 (0.3)   | 5 <sup>2</sup> |

<sup>1</sup> Wilcoxon Matched Pairs Signed Ranks Test ; <sup>2</sup> becomes significant when one spurious value is excluded ; \* P < 0.05.

uniformly distributed. In Table VI the distribution of ancestrulae is shown when midrib and blade areas of distal fronds are considered separately. Both bryozoans recruited more profusely along the midrib groove on concave surfaces and along the midrib keel on convex surfaces.

The recruitment of *A. hirsutum* was also monitored on distal fronds which varied in terms of the density of other epialgal organisms which they already supported (viz. the bryozoans *F. hispida* and *Electra pilosa*, and the spirorbid worm *Spirorbis spirorbis*).

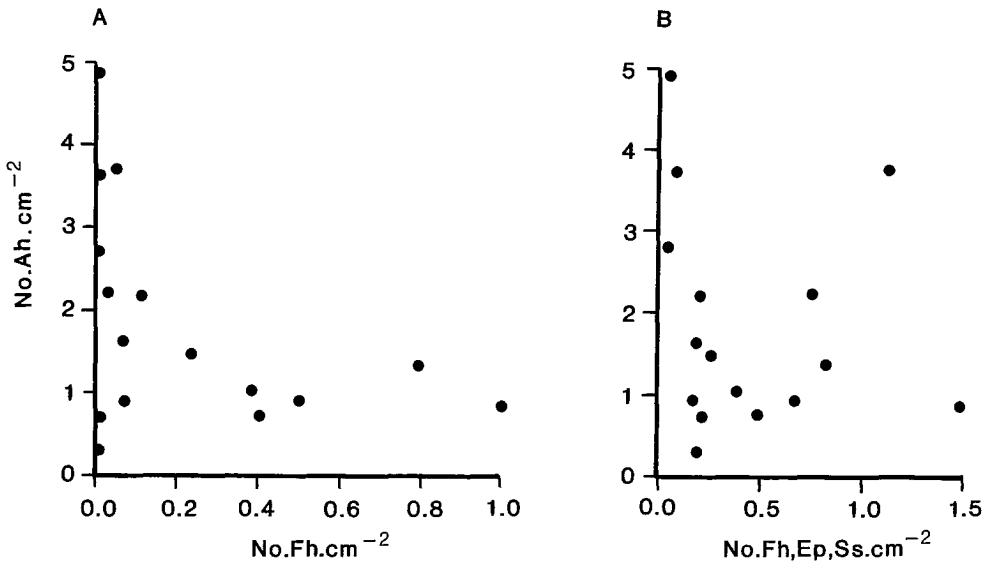


Fig. 2 : Relationship between recruitment intensity of *A. hirsutum* (Ah) on distal fronds of *F. serratus* at site 4 mid and (A) the density of recently established *Flustrellidra* (Fh) colonies, (B) the combined densities of recently established populations of *Flustrellidra* (Fh), *Electra* (Ep) and *Spirorbis* (Ss).

Figure 2A reveals a considerable degree of variability in the density of *A. hirsutum* ancestrulae on those fronds that were uncolonised by *F. hispida*, but substantially reduced variability, and lower levels of recruitment, on those fronds occupied by small *Flustrellidra* colonies at densities  $> 0.3$  colonies. cm<sup>-2</sup> of frond surface. This trend is less pronounced when other epialgal species are included in the analysis (Fig. 2B). Figure 3 illustrates the relationship between the presence of recently recruited *Alcyonidium* ancestrulae and the subsequent settlement of this bryozoan on the same frond segments. At site 4 mid during 1978-79 (Fig. 3A), and at site 4 low during 1979-80 (Fig. 3C) significant positive correlations were recorded, suggesting either the presence of a gregarious response, or that certain fronds were generally more attractive to the prospecting larvae. At site 4 mid 1979-80, however, recruitment of *A. hirsutum* appeared to be unaffected by the presence of already established ancestrulae (Fig. 3B). The dispersion patterns of recently settled *Alcyonidium* on distal segments of *F. serratus* at site 2 ranged from random to clumped, in that in a nearest neighbour analysis of ancestrulae on twenty five fronds, values of *R* ranged from 0.53-0.95 (where *R* = 0 for maximum aggregation and *R* = 1 for random dispersion).

In summary, therefore, our results clearly indicate that the settlement of *Alcyonidium* and *Flustrellidra* larvae on *F. serratus* is highly selective. Moreover, our data also suggest that the prospecting larvae of *A. hirsutum* may be capable of detecting and responding to the presence of potential competitors and/or conspecifics already present on the fronds ; our results concerning this particular aspect of recruitment, however, are rather equivocal and further studies are required in order to test this hypothesis more rigorously.

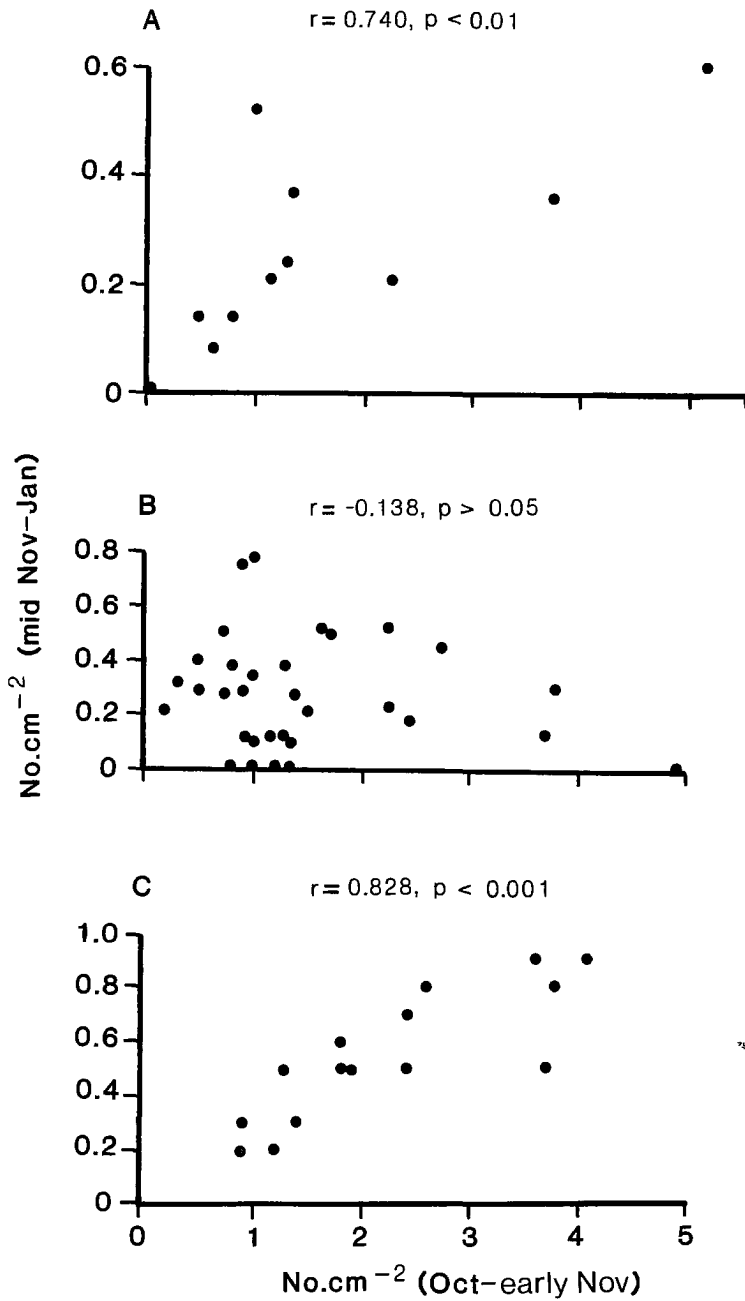


Fig. 3 : Relationship between the presence of *A. hirsutum* ancestrulae (settled Oct. - early Nov.) and the subsequent recruitment of this species (mid Nov. - Jan.) at (A) site 4 mid, 1978-79, (B) site 4 mid, 1979-80, (C) site 4 low, 1979-80.

## Mortality

Figure 4 illustrates the mortality rates of three successive year classes of *A. hirsutum* and *F. hispida* estimated from changes in colony density on plants sampled at monthly intervals at site 4 mid. The large confidence intervals reveal the high degree of variability within these data. The density of *Alcyonidium* increased during the period of recruitment from October to December in 1979 and 1980 (Fig. 4A). After settlement was complete, the density of the 1979-80 cohort declined sharply until May but thereafter stabilised at around 0.2-0.4 colonies.cm<sup>2</sup>. The 1978-79 cohort, which was only monitored from May 1979, showed a similar decline, although actual colony density was significantly higher at comparable times of the year than in 1980. Thus, by the time these cohorts were ready to release their larvae (when c. one year old) there were approximately 0.9 colonies.cm<sup>-2</sup> during October 1979 but only 0.4 colonies.cm<sup>-2</sup> in October 1980. Following larval release the population density of the 1978-79 cohort continued to decline slowly.

The data for *F. hispida* (Fig. 4B) are less easily interpreted as the larvae of this species, unlike those of *A. hirsutum*, tended to settle amongst previously established colonies as well as on the recently grown distal fronds. Thus, as the newly-recruited ancestrulae started to grow during the summer months it became increasingly difficult to distinguish between these colonies and the established colonies of the previous year class. Nevertheless, Figure 4B does reveal the periods of recruitment between July and November in 1979 and between May and November in 1980. The density of the 1979 cohort declined from c. 1.2 to 0.4 colonies.cm<sup>-2</sup> between November 1979 and May 1980 but any further mortality trends for either the 1978 or the 1979 year classes were largely confounded by recruitment. However, more colonies in the 1979 cohort were present on the fronds at equivalent stages in the life cycle than in either of the 1978 or 1980 cohorts.

The decline in density of those *Alcyonidium* colonies which were monitored at monthly intervals is illustrated in Figure 5A; values obtained for the 1979-80 cohort accord reasonably well with those obtained from the population sample (Fig. 4A). However, the higher densities obtained for the 1978-79 cohort on the sampled fronds (Fig. 4A) were not reflected in the population monitor for that particular year class, because the entire monitored population had died by August 1979 (Fig 5A). The population density on monitored fronds at site 4 low fell from an average of  $2.3 \pm 1.1$  SD.cm<sup>-2</sup> in November 1979 to an average of  $0.6 \pm 0.3$  SD.cm<sup>-2</sup> by February 1980. Thus, although the initial population density of *A. hirsutum* at site 4 low was higher than that at site 4 mid, by the end of the settlement period population densities were broadly similar.

Figure 5B shows that the mortality rate of *A. hirsutum* varies throughout the year. During the period between December when settlement of this species was virtually complete and the onset of the rapid growth phase in April (Wood & Seed, 1992), mortality rate was essentially linear ( $F_L = -0.515$  and  $1.46$  for the 1978-79 and 1979-80 year classes respectively, both at  $P > 0.05$ ; test for linearity Zar, 1974). After April there was a marked decline in the mortality rate strongly suggesting that the ancestrula is the most vulnerable post-settlement stage in the life cycle of these bryozoans. The percentage mortality of monitored

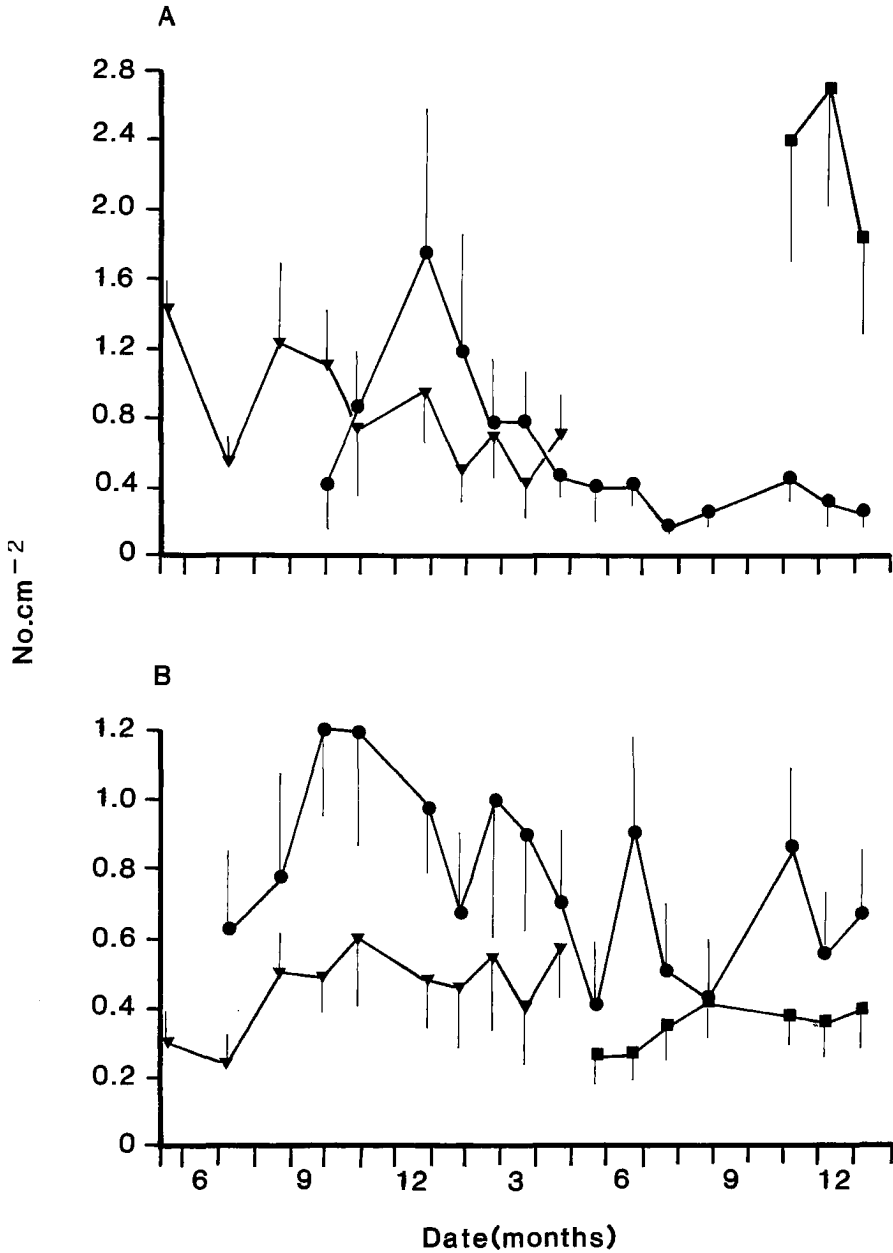


Fig. 4: Changes in population density of three successive year classes of (A) *A. hirsutum*, (B) *F. hispida* on *F. serratus* sampled at monthly intervals at site 4 mid, May 1979 - Jan. 1981; each point represents the mean number of colonies ( $\pm$ CI).

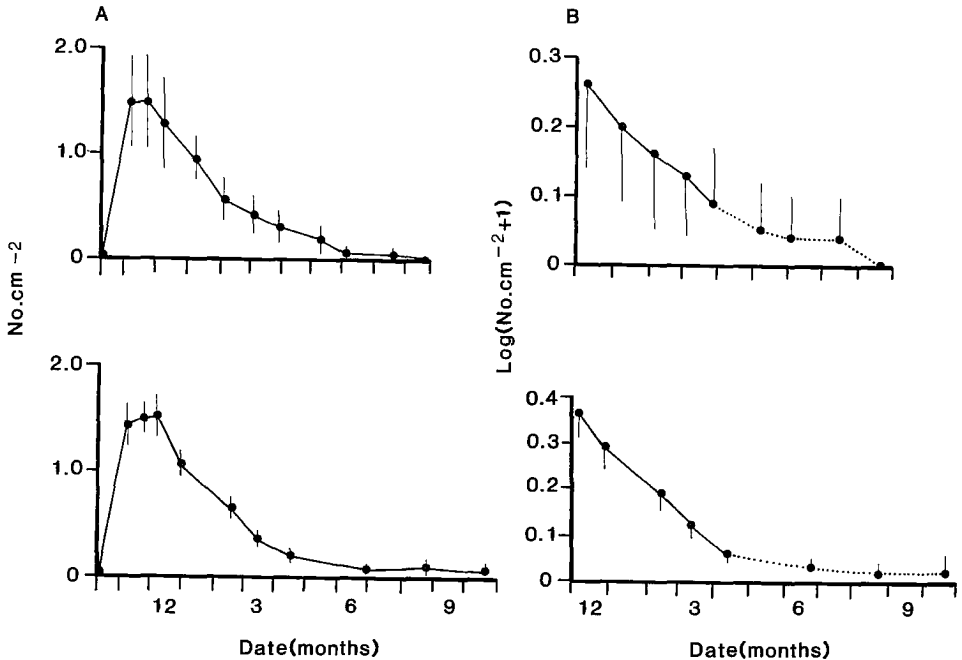


Fig. 5 : (A) Changes in population density of the 1978-79 (upper) and 1979-80 (lower) year classes of *A. hirsutum* on monitored *F. serratus* at site 4 mid ; each point represents the mean number of colonies ( $\pm$  SE). (B) Mortality of the 1978-79 (upper) and 1979-80 (lower) year classes of *A. hirsutum* from Dec. when recruitment was virtually complete until either all colonies had died, or until Oct. when the surviving colonies started to release larvae ; each point is the mean log (no. colonies.cm<sup>-2</sup>. + 1)  $\pm$  CI. Mortality rates over the solid line sections are linear.

*Alcyonidium* colonies is illustrated in Figure 6A. Approximately 50 % of these colonies had died by the end of the settlement period at site 4 mid ; at site 4 low, the comparable value was 85 %. Survival to sexual maturity was extremely low with none of the 1978-79 year class, and only 1.3 % of the 1979-80 year class at the midshore site surviving long enough to release larvae. Figure 6A further indicates that some of this high mortality could be attributed to the loss of substratum. Thus approximately 30 % of the mortality in the 1978-79 cohort and 13 % of the mortality of the 1979-80 cohort at site 4 mid was due to frond loss ; at site 4 low 10 % of the total mortality of the 1979-80 generation of *Alcyonidium* could also be attributed to this cause by February 1980. Since potential bryozoan predators were rarely observed on the *Fucus* plants at the study sites, most of the recorded mortality of *A. hirsutum* throughout this investigation had to be ascribed to unknown causes.

Only 20 % of the monitored fronds which had survived to July 1979 were still colonised by *A. hirsutum* (Fig. 6B). Some fronds lost all of their *Alcyonidium* colonies whereas others did not, and consequently the population tended to become progressively concentrated onto fewer fronds. This trend was less discernible in the 1979-80 generation (Fig. 6B) because

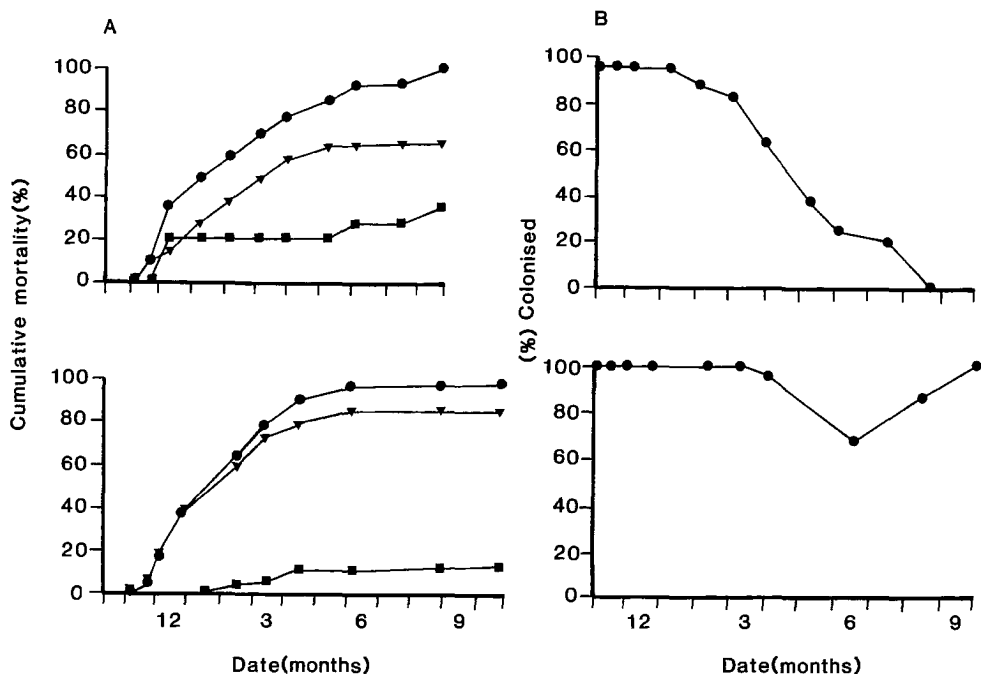


Fig. 6 : (A) Cumulative mortality (% of colonies lost) of the 1978-79 (upper) and 1979-80 (lower) year classes of *A. hirsutum* on monitored *F. serratus* at site 4 mid, (●) total loss, (■) mortality due to loss of substratum, (▼) causes of mortality unknown. (B) Changes in the proportion of monitored *F. serratus* fronds colonised by *A. hirsutum* during 1978-79 (upper) and 1979-80 (lower) ; note how plant mortality tends to concentrate the bryozoan population onto progressively fewer fronds.

frond loss, even amongst those on which all the ancestrulae or colonies had disappeared, was so high ; by October only four of the monitored frond surfaces actually carried *Alcyonidium* colonies.

In Figure 7 the mortality of recently settled *A. hirsutum* in different areas of the fronds is compared. Mortality rates were significantly higher on distal fronds which carried an initially high population density of *Alcyonidium* ancestrulae than on those which were less heavily colonised (Fig. 7A,  $t = -3.45$ ,  $P < 0.05$ ). Nevertheless, only those individuals on initially densely settled fronds survived long enough to breed. Similar contrasts can also be made between the initially high settlement densities on concave rather than convex surfaces (Fig. 7B,  $t = -2.62$ ,  $P < 0.05$ ), midrib rather than blade areas (Fig. 7C,  $t = 6.195$ ,  $P < 0.05$ ) and younger rather than older internodes of distal fronds (Fig. 7D,  $F = 5.90$ ,  $P < 0.05$ , Newman Keuls Test indicates that  $(1=2) \neq 3$ ).

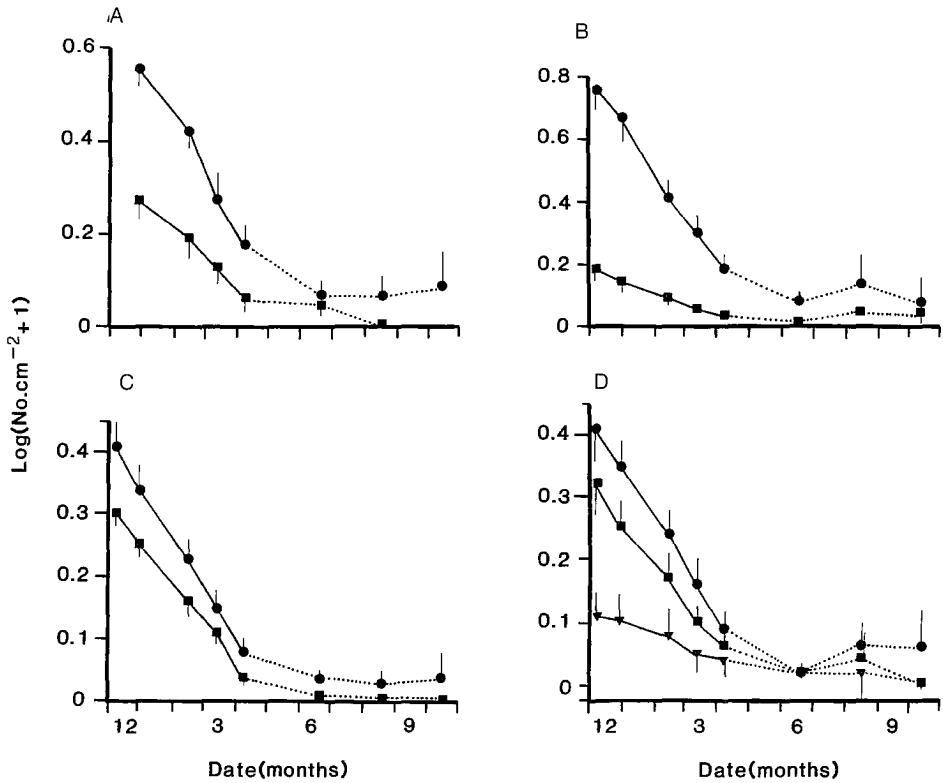


Fig. 7: Mortality of *A. hirsutum* on selected high and low density regions of *F. serratus* fronds at site 4 between the end of recruitment in Dec. 1979 and when the surviving colonies began to release larvae in Oct. 1980, each point is the mean  $\log(\text{no. colonies} + 1) \pm \text{SE}$ . (A) high (●) and low (■) density distal fronds, (B) concave (●) and convex (■) surfaces, (C) midrib (●) and blade (■), (D) internodes 1 (●), 2 (■) and 3 (▼). Mortality rates are linear over the solid line sections (values of  $F_L$  range from - 0.906 to 0.468, all at  $P > 0.05$ ; test for linearity).

## DISCUSSION

Like many epialgal taxa *F. hispida* and *A. hirsutum* exhibit a suite of larval behaviour patterns and settlement preferences which effectively ensure that they settle in the most favourable habitats. Both of these spatially dominant bryozoans settle preferentially on intertidal or shallow subtidal *Fucus serratus* (Ryland, 1959; Wood & Seed, 1980; Oswald & Seed, 1986). Such settlement preferences appear to have a chemical basis since inert surfaces filmed with algal extract can be rendered more attractive to the prospecting larvae (e.g. Crisp & Williams, 1960). Epialgal taxa also display habitat selection on a much finer scale often settling preferentially on the younger parts of the growing fronds (Stebbing, 1972; Oswald & Seed, 1986), in surface concavities and grooves (Ryland, 1959; Hayward & Harvey, 1974a) or even avoiding certain parts of the algal substratum altogether



(Hayward & Harvey, 1974a ; Ryland, 1974a). Maximum recruitment of *Alcyonidium* occurs on the youngest most distal frond segments of *F. serratus* (Table I). *Flustrellidra*, by contrast, settles more extensively over the entire length of the plant, and although the highest densities of ancestrulae were recorded on the concave surfaces of distal fronds (Table I), the youngest plant internodes were often avoided (Table V). Both bryozoans settle in greater abundance along the midrib grooves of *Fucus* fronds (Hayward, 1973 ; Hayward & Harvey, 1974a ; Table VI) and recruitment is greater on the concave rather than on the convex frond surfaces (Table IV). The larvae of these bryozoans are therefore either channelled onto concave surfaces by microenvironmental currents, or else they are capable of detecting slight differences in the microtopography of the actual frond surface.

Such habitat selection, which frequently results in aggregated settlement, seems designed to prevent recruitment in areas where growth and reproduction would be sub-optimal and to minimize the effects of inter- and intraspecific competition. Both Ryland & Stebbing (1971) and Stebbing (1972) noted that bryozoan settlement on, or the subsequent oriented growth of colonies towards, the youngest regions of both ephemeral substrata such as kelp blades and perennial substrata such as *Fucus* fronds, effectively reduced competition with established adult populations. Moreover on ephemeral substrata such responses also maximize the potential residence time of the colonising species. *F. serratus* plants lose tissue via defoliation of basal and reproductive frondage and it is these areas that are generally avoided by the prospecting larvae of many species including *F. hispida* and *A. hirsutum* (Ryland, 1959 ; Hayward & Harvey, 1974a ; Table I). However, the settlement patterns of some epialgal species appear to be related to the distribution of antibacterial activity along the fronds. Sieburth & Conover (1965) and Ryland (1974b) for example, found that the branch tips of *Sargassum natans* were free of epialgal species, whilst tannins, which inhibit the growth of surface microflora and are toxic to certain epialgal species, are concentrated in these areas. A species may have different settlement patterns in different parts of its geographical range (e.g. Ryland, 1974a ; Doyle, 1975) presumably reflecting differing selective pressures such as the local availability of suitable substrata. In the present study recruitment intensity of *Alcyonidium* and *Flustrellidra* varied between sites (Fig. 1B) whilst on a finer scale *Alcyonidium* recruitment was highly variable even between comparable fronds on different plants at a single site (Table III). Similar results have also been obtained by Ryland (1972) regarding the settlement of the bryozoans *Electra pilosa* and *Celleporella hyalina* on *Fucus* and *Laminaria* fronds respectively. Differences in recruitment intensity between individual *F. serratus* plants, and even between neighbouring fronds within the same plant, could be due largely to extremely localised variations in the small scale patterns of water flow over the frond surfaces at the precise time that the planktonic larvae acquire their competence to settle and metamorphose.

Seed *et al.* (1981) noted that water turbulence varies along the length of individual *F. serratus* plants as well as with plant structure. Changes in photosynthetic rate have also been recorded along the fronds of several algal species including *F. serratus* (King & Schramm, 1976 ; Oswald *et al.*, 1984). Such variations may lead to differences in the che-

mistry of the frond surface, which in turn could result in localised changes in the microbial community. Cundell *et al.* (1977) showed that the microbial community associated with *Ascophyllum nodosum* varied along the age gradient of individual fronds. Prospecting larvae could therefore be responding to changes in any or all of these microenvironmental gradients. It is interesting to note, therefore, that the recruitment intensity of *A. hirsutum* and *F. hispida* onto young *F. serratus* plants is comparable to that on the younger distal fronds of larger, older plants (Table II).

The prospecting larvae of many non-colonial marine invertebrates are highly gregarious, a response which can play a major role in the development of aggregated distributions. Investigations of gregariousness in colonial taxa such as bryozoans, by contrast, are relatively scarce (but see Ryland, 1974a ; Harvey *et al.*, 1976), though experiments have demonstrated that the larvae of *F. hispida* and *A. hispida*, like those of many other species of encrusting bryozoans, do not exhibit a gregarious response at the time of their metamorphosis. Similarly we could find no conclusive evidence of gregariousness in *A. hirsutum* during the present investigation (Fig. 3). However, *Alcyonidium* recruitment was substantially reduced on fronds which carried recently established *Flustrellidra* colonies (Fig. 2) and it is now known that the larvae of some marine invertebrates can detect the presence of competitively dominant species and avoid settling near them (e.g. Grosberg, 1981). The main biological advantage of aggregation, however induced, is that the population is effectively concentrated into those regions where survival, growth and reproduction are likely to be optimal ; for some species it may also facilitate cross-fertilization. A major disadvantage, however, is locally increased levels of competition although many gregarious organisms alleviate the effects of overcrowding by spacing themselves apart at settlement. Bryozoans, on the other hand, which form aggregations largely without the aid of a gregarious response, do not generally space themselves at settlement (Ryland, 1976). Spacing is not necessary for these encrusting organisms (see Stebbing, 1973 ; Harvey *et al.*, 1976 for discussion) in view of the lability in the direction of subsequent colony growth which enables all available space to be colonised, and the very small size at which bryozoan colonies can breed (Wood & Seed, 1992).

The life history parameters of a species are the result of evolutionary pressures exerted by its physical and biotic environment. *F. serratus* generally lives for around three to five years (Wood, 1983), although there are three sources of defoliation (i) that associated with secondary thickening, which begins at the holdfast and proceeds in an acropetal fashion throughout the life of the plant, (ii) that associated with reproduction which affects distal frondage and is of minor significance in young plants but may be extensive in older plants, and (iii) that associated with water movement which can be highly variable. Thus, the most stable habitat for sessile epialgal species is located at mid-plant levels (Hayward & Harvey, 1974a) which is precisely where the highest population densities and species diversities on *F. serratus* are found (O'Connor *et al.*, 1979 ; Wood & Seed, 1980 ; Wood, 1983). The availability of space for further colonisation by the larvae of epialgal taxa is largely predictable and depends on variables such as plant growth and the seasonal de-population of older fronds.

dage (both of which create free space), plant defoliation and the seasonal growth of established epialgal colonies (both of which eliminate free space). By far the greatest source of free space on algal fronds is that generated by plant growth (Seed & O'Connor, 1981) which in fucoids occurs via apical meristems. Both *F. hispida* and *A. hirsutum* have essentially annual life cycles with well developed seasons of reproduction and growth (Seed *et al.*, 1981 ; Wood & Seed, 1992) and as *F. serratus* lives for several years, close synchronisation of the life cycles of these bryozoans with that of the host, is not essential. Synchronisation, however, becomes increasingly important on more ephemeral substrata such as kelp blades where the life cycles of both the colonising species and the host are effectively annual (e.g. Bernstein & Jung, 1979 ; Cancino, 1986). Because of their different breeding seasons the major recruitment periods of *A. hirsutum* and *F. hispida* are temporally separated. Maximum settlement of *Flustrellidra* generally occurs during June-July (Ryland, 1959 ; Eggleston, 1972 ; Seed *et al.*, 1981 ; this study) whilst that of *Alcyonidium* varies between October-November in the Menai Strait and Northern Ireland (this study ; Seed *et al.*, 1981) and February in Manx waters and South Wales (Eggleston, 1972 ; Hayward, 1973). Inter- and intraspecific competition for space between successive generations is therefore effectively reduced because even though the larvae of both species (though more especially *A. hirsutum*) settle in greater abundance on younger, distal frond segments, seasonal plant growth between successive periods of recruitment keeps each generation largely separate.

There have been surprisingly few studies of mortality in bryozoans. Hayward & Harvey (1974b) estimated the mortality rate of *A. hirsutum* on *F. serratus* from monthly samples. This technique was also used in the present study in order to follow populations of *Alcyonidium* and *Flustrellidra*, but unlike the population monitor this sampling method fails to identify the extremely high levels of mortality that actually occur. Thus, in one of the monitored *Alcyonidium* year classes none of the marked individuals survived long enough to release larvae, whilst in a second year class only 1.3 % of the colonies survived to reach breeding condition ; the population monitor therefore reveals sources of mortality which otherwise go undetected when using the sampling method. Several fronds which initially received *Alcyonidium* settlement eventually lost their entire complement of colonies, thus effectively concentrating the remaining population onto fewer fronds as the season progressed. From April-May onwards most of the subsequent mortality of *A. hirsutum* was attributable to frond loss. Hayward & Harvey (1974b) speculated that the two major causes of mortality in *A. hirsutum* were predation and loss of substratum. Predation was an unlikely source of mortality at our study site as potential predators such as opisthobranch molluscs were only occasionally recorded on *F. serratus* throughout the entire course of this investigation. Moreover, only a relatively small proportion (< 30 %) of the total mortality of *A. hirsutum* could be attributed to loss of substratum, though the impact of such mortality on the population may be more serious than this figure actually suggests because this tends to affect those established colonies which have already survived a whole range of mortality sources acting earlier in the life of these colonies ; approximately 50 % of the mortality of

*A. hirsutum* occurs before March when colonies consist of little more than the primary zooid. Bushnell (1966) showed that mortality of *Plumatella repens*, a freshwater species with quite different life history characteristics to *Alcyonidium*, varied considerably between sites but was especially high amongst colonies near submerged vegetation which harboured numerous potential predators.

Partial destruction as a result of predation or physical disturbance has been noted for many colonial organisms including bryozoans (e.g. Jackson & Palumbi, 1979 ; Ayling, 1981). Similarly, the capacity for regeneration of damaged tissues is well documented (e.g. Ryland, 1979 ; Palumbi & Jackson, 1982). Colonies of *A. hirsutum* and *F. hispida* sustain damage during the year until by the autumn most of the population is affected to some extent. The causes of such damage remain unknown, though abrasion against adjacent fronds or the underlying barnacle encrusted rock surface is a likely factor. Some damage, particularly to *Flustrellidra* colonies in view of their predominantly proximal location on *F. serratus* (Boaden *et al.*, 1975 ; Oswald & Seed, 1986) is due to necrosis of the frond blade which occurs during the process of secondary thickening. The incidence of damaged colonies decreases during spring thus reflecting either a capacity for regeneration, or the loss of such colonies from the population.

The life-span of many sessile organisms which colonise living substrata is frequently determined by the longevity of the host (e.g. Gili *et al.*, 1993 ; Cancino, 1986). *Fucus serratus* typically lives up to approximately five years and this must therefore represent the maximum life expectancy of any epialgal species colonising this particular fucoid. However, high mortality rates of both the alga and the epialgal fauna ensure that very few colonies of *Alcyonidium* or *Flustrellidra*, if indeed any at all, actually realise this potential. *A. hirsutum* and *F. hispida* should perhaps therefore be considered as "indeterminate annuals" in that although they normally live for only around one year they can, given the opportunity, live much longer.

## REFERENCES

- AYLING, A.M., 1981. The role of biological disturbance in temperate subtidal encrusting communities. *Ecology*, 62 : 830-847.
- BERNSTEIN, B.B. & N. JUNG, 1979. Selective pressures and coevolution in a kelp canopy community in Southern California. *Ecol. Monogr.*, 49 : 335-355.
- BOADEN, P.J.S., R.J. O'CONNOR & R. SEED, 1975. The composition and zonation of a *Fucus serratus* community in Strangford Lough, County Down. *J. Exp. Mar. Biol. Ecol.*, 17 : 111-136.
- BUSHNELL, J.H., 1966. Environmental relations of Michigan Ectoprocta, and dynamics of natural populations of *Plumatella repens*. *Ecol. Monogr.*, 36 : 95-123.
- CANCINO, J.M., 1986. Marine macroalgae as a substratum for sessile invertebrates : a study of *Celleporella hyalina* (Bryozoa) on fronds of *Laminaria saccharina* (Phaeophyta). In : *Simposio Internacional. Usos y funciones ecológicas de las algas marinas bentónicas*, ed. B. Santelices. *Monogr. Biol.*, 4 : 255-277.
- CRISP, D.J. & G.B. WILLIAMS, 1960. Effect of extracts from fucoids in promoting settlement of epiphytic Polyzoa. *Nature*, London, 188 : 1206-1207.
- CUNDELL, A.M., T.D. SLEETER & R. MITCHELL, 1977. Microbial populations associated with the surface of the brown alga *Ascophyllum nodosum*. *Microb. Ecol.*, 4 : 81-91.

- DOYLE, R.W., 1975. Settlement of planktonic larvae : a theory of habitat selection in varying environments. *Am. Nat.*, 109 : 113-126.
- DUNSTONE, M.A., R.J. O'CONNOR & R. SEED, 1979. The epifaunal communities of *Pelvetia canaliculata* and *Fucus spiralis*. *Holarctic Ecol.*, 2 : 6-11.
- EGGLESTON, D., 1972. Patterns of reproduction in marine Ectoprocta of the Isle of Man. *J. Nat. Hist.*, 6 : 31-38.
- GILL, J.M., P. ABELLO & R. VILLANEUVA, 1993. Epibionts and intermoult duration in the crab *Bathynectes piperitus*. *Mar. Ecol. Prog. Ser.*, 98 : 107-113.
- GROSBERG, R.K., 1981. Competitive ability, influences on habitat choice in marine invertebrates. *Nature*, London, 290 : 700-702.
- HARVEY, P.H., J.S. RYLAND & P.J. HAYWARD, 1976. Pattern analysis in bryozoan and spirorbid communities. II. Distance sampling methods. *J. Exp. Mar. Biol. Ecol.*, 21 : 99-108.
- HAYWARD, P.J., 1973. Preliminary observations on settlement and growth in populations of *Alcyonidium hirsutum* (Fleming). In : *Living and Fossil Bryozoa*, ed. G.P. Larwood, Academic Press, New York.
- HAYWARD, P.J. & P.H. HARVEY, 1974a. The distribution of settled larvae of the bryozoans *Alcyonidium hirsutum* (Fleming) and *Alcyonidium polyoum* (Hassall) on *Fucus serratus* (L.). *J. Mar. Biol. Ass. UK.*, 54 : 665-676.
- HAYWARD, P.J. & P.H. HARVEY, 1974b. Growth and mortality of the bryozoan *Alcyonidium hirsutum* (Fleming) on *Fucus serratus* (L.). *J. Mar. Biol. Ass. U.K.*, 54 : 677-684.
- HONDT, J.-L. d' & M. GOYFFON, 1992. Le complexe d'espèces "*Alcyonidium hirsutum* (Fleming, 1828)" ; comparaison avec *Flustrellidra hispida* (Fabricius, 1780) (Bryozoaires, Cténostomes). *Bull. Soc. Zool. Fr.*, 117 : 45-64.
- JACKSON, J.B.C. & S.R. PALUMBI, 1979. Regeneration and partial predation in cryptic reef environments. Preliminary experiments on sponges and ectoprocts. In : C. Levi & N. Boury-Esnault, (eds.) *Biologie des Spongiaires*, éditions du CNRS 1 : Paris.
- KING, R.J. & W. SCHRAMM, 1976. Determination of photosynthetic rates for the marine algae *Fucus vesiculosus* and *Laminaria digitata*. *Mar. Biol.*, 37 : 209-213.
- O'CONNOR, R.J., R. SEED & P.J.S. BOADEN, 1979. Effects of environment and plant characteristics on the distribution of Bryozoa in a *Fucus serratus* L. community. *J. Exp. Mar. Biol. Ecol.*, 38 : 151-178.
- OSWALD, R.C. & R. SEED, 1986. Organisation and seasonal progression within the epifaunal communities of coastal macroalgae. *Cah. Biol. Mar.*, 27 : 29-40.
- OSWALD, R.C., N. TELFORD, R. SEED & C.M. HAPPEY-WOOD, 1984. The effect of encrusting bryozoans on the photosynthetic activity of *Fucus serratus* (L.). *Estuarine Coastal Mar. Sci.*, 19 : 697-702.
- PALUMBI, S.R. & J.B.C. JACKSON, 1982. Ecology of cryptic coral reef communities. II. Recovery from small scale disturbance events by encrusting Bryozoa : the influence of "host" species and lesion size. *J. Mar. Biol. Ecol.*, 64 : 103-115.
- RYLAND, J.S., 1959. Experiments on the selection of algal substrates by polyzoan larvae. *J. Exp. Biol.*, 36 : 613-631.
- RYLAND, J.S., 1972. The analysis of pattern in communities of Bryozoa. I. Discrete sampling methods. *J. Exp. Mar. Biol. Ecol.*, 8 : 277-297.
- RYLAND, J.S., 1974a. Behaviour, settlement and metamorphosis of bryozoan larvae. A review. *Thalass. Jugoslav.*, 10 : 239-264.
- RYLAND, J.S., 1974b. Observations on some epibionts of gulfweed, *Sargassum natans* (L.) Meyen. *J. Exp. Mar. Biol. Ecol.*, 14 : 17-25.
- RYLAND, J.S., 1976. Physiology and ecology of marine bryozoans. *Adv. Mar. Biol.*, 14 : 285-443.
- RYLAND, J.S., 1979. Taxes and tropisms of bryozoans. In : R.M. Woollacott & R.L. Zimmer, (eds.), *Biology of Bryozoans*, Academic Press, New York.
- RYLAND, J.S. & A.R.D. STEBBING, 1971. Settlement and orientated growth in epiphytic and epizoid bryozoans. In : *Proc. Fourth Europ. Mar. Biol. Symp.*, ed. D.J. Crisp, Cambridge University Press, Cambridge.
- SEED, R., M.N. ELLIOTT, P.J.S. BOADEN & R.J. O'CONNOR, 1981. The composition and seasonal changes amongst the epifauna associated with *Fucus serratus* L. in Strangford Lough, Northern Ireland. *Cah. Biol. Mar.*, 22 : 243-266.
- SEED, R. & R.J. O'CONNOR, 1981. Community organisation in marine algal epifaunas. *Ann. Rev. Ecol. Syst.*, 12 : 49-74.
- SIEBURTH, J.M. & J.T. CONOVER, 1965. *Sargassum* tannin, an antibiotic which retards fouling. *Nature*, London, 208 : 52-53.
- STEBBING, A.R.D., 1972. Preferential settlement of a bryozoan and serpulid larvae on the younger parts of *Laminaria* fronds. *J. Mar. Biol. Ass. UK.*, 52 : 765-772.
- STEBBING, A.R.D., 1973. Competition for space between the epiphytes of *Fucus serratus* L. *J. Mar. Biol. Ass. U.K.*, 53 : 247-261.
- THORPE, J.P. & J.S. RYLAND, 1979. Cryptic speciation detected by biochemical genetics in three ecologically important intertidal bryozoans. *Estuarine Coastal Mar. Sci.*, 8 : 395-398.

- WILLIAMS, G.A. & R. SEED, 1992. Interactions between macrofaunal epiphytes and their host algae. In : Systematics Association Special Volume, 46, Plant-Animal Interactions in the Marine Benthos, D.M. John, S.J. Hawkins & J.R. Price, (eds.) Clarendon Press, Oxford.
- WOOD, V., 1983. *A Population Study of the Major Sedentary Faunal Associates of Fucus serratus L.* Unpubl. Ph. D. Thesis, University of Wales, 238 pp.
- WOOD, V. & R. SEED, 1980. The effects of shore level on the epifaunal communities associated with *Fucus serratus* L. in the Menai Strait, North Wales. *Cah. Biol. Mar.*, 21 : 135-154.
- WOOD, V. & R. SEED, 1992. Reproduction and growth of *Alcyonidium hirsutum* (Fleming) and *Flustrellidra hispida* (Fabricius) (Bryozoa : Ctenostomata) within a *Fucus serratus* L. community. *Cah. Biol. Mar.*, 33 : 347-363.