

THE COMPOSITION AND SEASONAL CHANGES
AMONGST THE EPIFAUNA ASSOCIATED WITH
FUCUS SERRATUS L
IN STRANGFORD LOUGH, NORTHERN IRELAND.

by

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Résumé

Les espèces épifaunales dominantes associées au *Fucus serratus* L. ont été étudiées entre décembre 1976 et novembre 1978 en trois sites différant physiquement et biologiquement du Strangford Lough. Les facteurs favorables à rétablissement du *Fucus* favorisent aussi la croissance de plantes individuelles puisque, dans les endroits où ces plantes étaient plus abondantes, elles étaient aussi plus développées et plus ramifiées. Les 50 plantes que nous avons examinées en détail contenaient un total de 42 espèces sédentaires parmi lesquelles 11 étaient des espèces communes, dont 5 Bryozoaires, 4 Serpulides et 2 Hydroïdes. La vase et l'agitation faible semblent, de façon évidente, tolérées par les Serpulides et le Bryozoaire *Alcyonidium polyomm* mais la plupart des autres espèces sont de façon significative plus abondantes sur les plantes soumises à une eau courante rapide et claire. Les espèces n'étaient pas distribuées au hasard le long des frondes individuelles mais occupaient des zones distinctes à l'intérieur des *Fucus*. La plupart des espèces sont, en général, plus prolifiques sur les surfaces concaves des plantes ; les *Flustrellidra* et les *Alcyonidium* s'installent en plus grande abondance sur cette face que sur la face convexe. On observe des changements saisonniers marqués dans l'importance des espèces communes à l'intérieur de la communauté : toutes, excepté les Serpulides, présentant une abondance maximale pendant le printemps et l'été. Le rétablissement de la *Flustrellidra* (printemps, début de l'été) et de l'*Alcyonidium* ssp.) fin de l'automne -hiver) se fait principalement sur les dichotomies les plus jeunes et les plus distales. Le *Spirorbis borealis* s'installe à intervalles réguliers entre mars et septembre. La structure de la population de ce Serpulide montre des variations saisonnières remarquables et la survie individuelle dépasse rarement 15 à 18 mois.

Introduction

Detailed accounts of the epifaunal communities associated with littoral macroalgae are remarkably scarce. This is rather surprising in view of their widespread distribution, the ease with which they can be experimentally manipulated and their obvious potential for studying competitive interactions amongst their predominantly sessile com-

ponent species. Colman (1940) provides one of the earliest accounts of the organisms inhabiting several species of intertidal seaweeds whilst Hagerman (1966) and more recently Stebbing (1973) and Boaden *et al.* (1975) describe the fauna associated more specifically with the serrated wrack *Fucus serratus*. Kitching and Ebling (1967) review several papers dealing with the fauna of marine algae at Lough Ine in S.W. Ireland, an area remarkably similar in its physical characteristics to that which we have investigated.

Little or no data are available, however, concerning the seasonal changes within these intertidal epifaunas though Hagerman (1966) documents the major changes occurring within a subtidal *F. serratus* community. The annual cycles of several species which are frequently well represented within these communities e.g. *Spirorbis spirorbis* (Daly, 1978), *Alcyonidium hirsutum* and other encrusting bryozoans (Eggleston, 1972; Hayward and Ryland, 1975) have also been described as indeed have the seasonal progressions amongst certain sessile fouling communities (e.g. McDougall, 1943; Sutherland and Karlson, 1977; Withers and Thorp, 1977) communities which share many of the characteristics of algal epifaunas.

At the Dorn in Strangford Lough, N. Ireland a sill of bedrock across the narrow entrance to a broad shallow basin prevents the normal pattern of tidal cycling and results in a marine waterfall which fronts a series of partially dammed bays. In a series of earlier papers (Boaden *et al.*, 1975, 1976; O'Connor *et al.*, 1975; O'Connor and Lamont, 1978; O'Connor *et al.*, 1979, 1980; Seed and Boaden, 1977) we have attempted to establish how the fauna associated with *F. serratus* within a relatively restricted body of seawater exposed to different physical and biological conditions is determined. The Dorn has proved ideal for such an investigation since although exceedingly protected from the detrimental effects of wave action, it provides a wide range of environmental conditions within a relatively restricted geographical region.

However, all of our earlier investigations pertain largely to one particular time of the year and it can be argued that gross distribution patterns may be subject to seasonal changes according to variations in recruitment, growth and mortality amongst individual species. The main objective of our present study has therefore been to document some of the major seasonal cycles which occur amongst the principal components of the Dorn *F. serratus* community.

Materials and methods

Three study sites were chosen principally on the basis of their contrasting physical characteristics. Site one was situated immediately above the sill which separates the Dorn from the main body of Strangford Lough. This site is characterised by strong tidal currents, and the fast-flowing turbulent water here carries a relatively low silt load. By contrast there is little or no water movement at site three but the extremely sheltered inner tidal basins, where this particular site is located, receive a supply of highly turbid water from several small streams which discharge into the uppermost reaches of the

Dorn complex. The physical conditions at site two, in the narrow inlet connecting the sill and the inner basins, were more or less intermediate between those prevailing at the other two study sites.

The abundance of *F. serratus* at each site was estimated from twenty 0.5m² quadrats thrown at random at the appropriate shore level. Plants were collected at approximately monthly intervals between December 1976 and November 1978; these were sealed in separate plastic bags and deep frozen until required for subsequent examination. A total of 59 plants were collected and examined in detail during the course of the investigation. After thawing, each plant was weighed to the nearest 10g using a spring balance and its overall length recorded. The ratio of plant weight to plant length provides an index of the amount of branching or business, higher values denoting a proportionately greater degree of branching. This ratio is thus analogous to the volume to length ratio which we have used previously (Boaden *et al.*, 1975). The longest frond of each plant was then removed and subdivided into a number of dichotomies (= Y segments) from the basal Y, to the distal Y_n, the actual number of dichotomies present being related to the size and age of the individual plant. Since fucoid algae grow by means of apical meristems each frond represents an age gradient, basal dichotomies being the oldest regions of the plant, distal dichotomies the youngest. The segment faces of *F. serratus* are often clearly recognisable as either concave or convex; where this was not possible (especially with more basal segments) the faces were designated as concave or convex on a purely random basis.

The common sessile fauna, here defined as those species represented on at least 5 percent of all segment faces examined at one or more of the three study sites, were quantified as follows, (i) Solitary taxa such as spirorbids and the recently settled stages (= ancestrulae) of certain bryozoans were counted. However, since individual *Fucus* dichotomies varied in size, these values were subsequently corrected to a standard unit (10cm²) of frond surface. For *Spirorbis* maximum spire diameter was also measured in randomly selected subsamples and the resulting size-frequency distributions plotted, (ii) For arborescent taxa like *Dynamena* the percentage of the segment face covered by the colony together with the maximum height of the five tallest erect branches were measured, (ii) For encrusting species such as *Alcyonium*, *Electro* and *Flustrellidra* percentage cover alone was recorded. The breeding condition of several of the common species was also noted. Rarer and **vagile** species were simply recorded as either present or absent.

Current readings were obtained at each of the three sites at **approximately** mid ebb tide using a Toho-Dentan current meter. However, in view of the serious practical difficulties which we encountered in obtaining realistic current speed readings amongst dense weed beds, an additional measurement of relative water movement was also attempted using gypsum spheres. These were cast in wax moulds (20mm diameter) and the knotted end of a length of string set into each sphere. After drying to constant weight they were attached at three different levels (viz. basal, mid, distal) to the most bushy *Fucus* plants at each site. After 12 hr exposure they were

collected, dried and reweighed and the percentage weight loss calculated. This **technique** provides a measure of the relative **water** movement/abrasion which **we** shall **hereafter** refer to as "turbulence" in order to maintain consistency with our earlier accounts (Boaden *et al.*, 1976; O'Connor *et al.*, 1979).

Fucus plants at each study site carried a different silt load and a relative measurement of this was made at monthly intervals as follows; plastic bags were carefully placed over the distal 10-15cm of selected plants as these became uncovered by the tide. The fronds **were** then cut and the bags sealed. In the laboratory the severed fronds were shaken in a known volume of seawater (including insings from the bag) and the number of particles in the 3-20 μ m size range in 0.5ml aliquots of the washings **determined** using an industrial model Coulter counter. The area of each cut length of frond was then measured and the particles per unit area of weed calculated. The amount of silt actually suspended in the water at each site was similarly measured from samples of 500ml of seawater collected at low tide. Salinity was measured monthly on the ebb tide whilst the temperature range was recorded using a maximum-minimum thermometer which was left *in situ* on the weed beds and reset after each visit.

RESULTS

: Site and plant characteristics

Table I summarises the main physical conditions which prevailed at the three study sites. Current speed and turbulence were greatest at site one which was situated immediately above the main Sill marking the entrance to the Dorn. Here gypsum spheres attached to large bushy plants routinely lost well over a third of their initial weight after a single tidal immersion. Water flow past individual plants was most severe basally and distally and least severe in the more protected shrubbier mid frond regions. Plant structure clearly

TABLE I
Physical conditions at the three study sites at the Dorn, **Strangford** Lough.

| | Current speed | Turbulence (1) | | | Salinity (2) (p. 1,000) | Silt particles (3) | |
|--------|---------------|----------------|-----------|-----------|----------------------------|---|------------------------|
| | | Basal | Mid | Distal | | Weed (No.ml ⁻¹ cm ⁻²) | (No.ml ⁻¹) |
| Site 1 | Fairly strong | 42.8(1.7) | 19.4(1.1) | 36.6(2.6) | 33.3(29.2-34.3) | 31.6(2.5) | 3357(549) |
| Site 2 | Moderate | 19.3(1.2) | 13.6(1.0) | 14.3(1.1) | 33.6(29.9-34.6) | 83.8(6.3) | 7841(958) |
| Site 3 | Very slight | 5.0(0.5) | 4.2(0.5) | 4.4(0.4) | 31.5(15.1-34.2) | 168.8(18.6) | 16102(3061) |

(1) Measured as **percentage** weight loss in 12h. of **20mm diameter** Gypsum spheres attached at three- plant levels. Values are means (\pm SE) of 15 readings.

(2) Values are means and ranges (in parentheses) for 20 monthly readings.

(3) Number of 3-20 μ particles. Values are means (\pm SE).

has a pronounced influence on localised flow patterns since gypsum balls attached to the mid frond segments of long thin plants at the most turbulent site lost **almost** twice as much weight as those attached to bushy plants (35.1 ± 1.7 SE percent compared with 19.4 ± 1.1 ; $n = 15$) over the same tidal cycle. Site three, situated in the protected inner tidal basins, experienced little or no water movement other than that provided by the rise and fall of the tide, and weight loss of gypsum spheres was here only marginally higher than that of controls placed in still seawater in the laboratory (2-4 percent). The amount of silt, either suspended in the water or deposited on the *Fucus* plants showed an approximately five fold increase between sites one and three but our rather restricted (monthly) sampling programme did not enable us to detect any significant seasonal trends. Plants at site two were intermediate in respect of both the flow regime and the degree of silting to which they were exposed.

Salinity remained constantly high at around 34 permil April and October at all three sites. Thereafter some fluctuations occurred, especially at site three where values as low as 15-16 permil were occasionally recorded during the winter. This latter was due to the local influence of several small streams which open into the Dorn close to this particular site. The average salinity in the main body of Strangford Lough was 34.1 permil (range 33.4-34.5 permil). Air temperature on the actual weed beds throughout the period of investigation ranged between -2.0° (February, 1977) and 23.1° C (July, 1978). Mean weekly surface seawater temperatures taken nearby at Portaferry in Strangford Narrows varied between 6.8° and 13.3° C (Fig. 3e)

P. serratus was considerably more abundant at sites one and two than at site three both in terms of its overall cover of the rock surface and the actual density of established plants (Table II). This presumably reflects the scouring effect of the tide in the narrower channels, and the extensive areas of exposed bedrock, boulders and large stones (especially near the Sill itself) provide numerous suitable surfaces to which the plants can attach. Most of the substratum at site three, on the other hand, is covered by mud and small loose cobbles and *Fucus* is here restricted to localised rocky outcrops, again reflecting the importance of suitable substrata for holdfast attachment.

TABLE II
Sample sizes and characteristics of *F. serratus* at the three sites at the Dorn

| | Plants (1) | Faces (2) | Dichotomies (3) | Plant (4) | | | | |
|--------|------------|-----------|-----------------|-------------|------------|---------------------------------|----------------------|-------------|
| | | | | Length (cm) | Weight (g) | Branching Index (weight:length) | Cover (5) percentage | Density (6) |
| Site 1 | 21 | 310 | 7.3(0.2) | 83.3(3.8) | 501(68) | 5.9(0.7) | 30(8) | 4.4(0.9) |
| Site 2 | 19 | 240 | 6.3(0.2) | 65.9(2.8) | 351(34) | 5.1(0.4) | 30(7) | 3.7(0.8) |
| Site 3 | 19 | 192 | 5.1(0.4) | 52.4(3.5) | 208(37) | 3.5(0.5) | 6(2) | 0.5(0.2) |

(1) Total number of plants examined.

(2) Total number of segment faces examined.

(3) Number of dichotomies along the longest frond. Values are means (\pm SE).

(4) All values are means (\pm SE).

(5) Percentage cover, and (6) Number of plants (>10cm) in twenty 0.5m² quadrats.

TABLE III
Variations in segment dimensions along the longest tronc) of *F. serratus* at the Dorn (1).

| Plant level | Site 1 | | | | Site 2 | | | | Site 3 | | | |
|-------------|--------|-------------|------------|-------------------------|--------|-------------|------------|-------------------------|--------|-------------|------------|-------------------------|
| | n | Length (cm) | Width (cm) | Area (cm ²) | n | Length (cm) | Width (cm) | Area (cm ²) | n | Length (cm) | Width (cm) | Area (cm ²) |
| 1 | 21 | 9.9(0.6) | 1.0(0.1) | 20.7(2.0) | 19 | 8.2(0.3) | 0.9(0.1) | 14.6(1.6) | 19 | 8.2(0.5) | 0.8(0.1) | 13.3(2.8) |
| 2 | 21 | 9.4(0.8) | 1.6(0.3) | 30.0(6.4) | 19 | 7.8(0.3) | 1.3(0.3) | 22.1(5.1) | 19 | 7.9(0.6) | 1.0(0.2) | 18.7(4.6) |
| 3 | 21 | 11.9(0.9) | 2.4(0.3) | 65.3(10.9) | 19 | 10.4(0.7) | 1.9(0.3) | 42.1(8.5) | 19 | 10.7(0.8) | 2.0(0.3) | 42.1(7.5) |
| 4 | 21 | 15.8(1.2) | 3.1(0.3) | 100.4(12.9) | 19 | 12.6(0.7) | 2.8(0.3) | 70.7(7.2) | 16 | 10.0(0.5) | 2.3(0.3) | 45.9(6.0) |
| 5 | 21 | 13.8(0.7) | 3.1(0.2) | 87.4(8.7) | 19 | 11.4(0.5) | 3.2(0.2) | 74.6(5.6) | 10 | 10.2(0.6) | 2.5(0.3) | 47.3(5.8) |
| 6 | 20 | 12.4(0.7) | 3.2(0.2) | 80.7(7.3) | 16 | 9.8(1.0) | 3.0(0.2) | 64.2(9.3) | 7 | 13.4(2.2) | 2.7(0.2) | 72.3(13.2) |
| 7 | 17 | 11.4(1.2) | 3.1(0.2) | 75.9(10.7) | 5 | 12.8(1.7) | 3.5(0.2) | 72.8(11.8) | 5 | 13.2(1.0) | 2.7(0.2) | 71.3(4.4) |
| 8 | 8 | 10.6(1.3) | 3.0(0.3) | 67.0(11.1) | 2 | 10.5(—) | 3.3(—) | 72.0(—) | 1 | 11.7(—) | 2.4(—) | 56.2(—) |
| 9 | 4 | 7.0(0.9) | 2.0(0) | 28.0(3.6) | 1 | 12.0(—) | 3.0(—) | 48.0(—) | 1 | 6.8(—) | 1.7(—) | 9.5(—) |

(1) All values are means (\pm SE).

TABLE IV
Measures of abundance for the eleven most common species in the fauna of *F. serratus* at the three Dorn sites.

| Species | Units (1) | Plants (2) | | | Ubiquity percentage (3) | | | Overall abundance (4) | | | Abundance when present (5) | | | Maximum abundance (6) | | |
|------------------------------|-----------|------------|----|----|-------------------------|----|----|-----------------------|------|------|----------------------------|------|------|-----------------------|-----|-----|
| | | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| <i>Flustrellidra hispida</i> | p.cent | 21 | 10 | 6 | 60 | 11 | 5 | 11.2 | 0.4 | 0.1 | 18.5 | 3.5 | 1.7 | 95 | 20 | 5 |
| <i>Electra pilosa</i> | p.cent | 16 | 8 | 6 | 33 | 13 | 10 | 2.0 | 1.0 | 0.2 | 6.1 | 7.3 | 2.8 | 45 | 80 | 10 |
| <i>Alcyonidium polyomm</i> | p.cent | 10 | 16 | 14 | 12 | 24 | 24 | 0.5 | 2.1 | 2.1 | 4.1 | 8.9 | 8.7 | 25 | 65 | 75 |
| <i>A. hirsutum</i> | p.cent | 11 | 8 | 5 | 22 | 10 | 5 | 2.6 | 0.7 | 0.2 | 12.4 | 7.4 | 2.2 | 70 | 50 | 10 |
| <i>Valkeria uva</i> | — | 5 | 12 | 7 | 3 | 23 | 10 | Not recorded | | | | | | | | |
| <i>Dynamena pumila</i> | p.cent | 21 | 13 | 2 | 69 | 25 | 3 | 17.0 | 1.0 | 0.1 | 24.0 | 4.2 | 2.0 | 100 | 55 | 5 |
| <i>Campanularia flexuosa</i> | — | 12 | 12 | 6 | 24 | 20 | 8 | Not recorded | | | | | | | | |
| <i>Spirorbis borealis</i> | No | 10 | 19 | 19 | 15 | 63 | 77 | 0.4 | 18.5 | 74.7 | 2.3 | 29.5 | 97.5 | 11 | 175 | 170 |
| <i>S. pagenstecheri</i> | No | 1 | 14 | 12 | 1 | 35 | 41 | 0.1 | 4.2 | 15.3 | 0.1 | 12.0 | 40.5 | 1 | 93 | 224 |
| <i>S. spirillum</i> | No | 0 | 3 | 5 | 0 | 3 | 9 | 0 | 0.1 | 1.6 | 0 | 4.3 | 13.1 | 0 | 14 | 70 |
| <i>S. tridentatus</i> | No | 0 | 1 | 5 | 0 | 1 | 5 | 0 | 0.1 | 0.7 | 0 | 0.1 | 11.0 | 0 | 1 | 36 |

(1) Abundance scored either as percentage cover or as number of individuals present.

(2) Number of plants on which the species was recorded at least once (max = 21 for site 1; 19 for sites 2 and 3).

(3) Ubiquity index = 100 (number of faces with species present)/(number of faces examined).

(4) Mean abundance per segment face over all faces examined.

(5) Mean abundance on those segment faces colonised.

(6) Maximum abundance on any single segment face.

Three size measures were recorded for each individual plant—length of the longest frond, total weight and branching index. These data are summarised in Table II and show that site one plants were consistently larger, and site three plants consistently smaller with respect to all three size measures than plants from site two. An analysis of variance showed that these intersite differences were statistically significant ($F = 19.7$ for length, 8.8 for weight and 5.5 for branching index, all at $p < 0.01$).

Table III examines the pattern of segment size along the main fronds of those plants which we examined together with the number of segments at each Y level on which these analyses are based. However, due to variations in plant size it should be noted that somewhat fewer replicates were available for the more distal plant segments. Accordingly, analyses of these dichotomies (especially Y_8 – Y_9) must be treated with some degree of caution. The two most basal segments were consistently smaller than those situated more distally, reflecting the change from the woody rod-like structure of the holdfast stem to the much broader segment faces further out in the main body of the plant. Thus, both the absolute area available for colonisation at successive plant levels, as well as the relative flatness of individual segment faces, increased away from the basal plant dichotomies. Analysis of variance again showed systematic differences between the three sites when the average size of segment faces for each plant i.e. irrespective of their actual position along the plant, are considered ($F = 9.4$ for length, 8.8 for width and 13.0 for area, $P < 0.01$ for all three size measures).

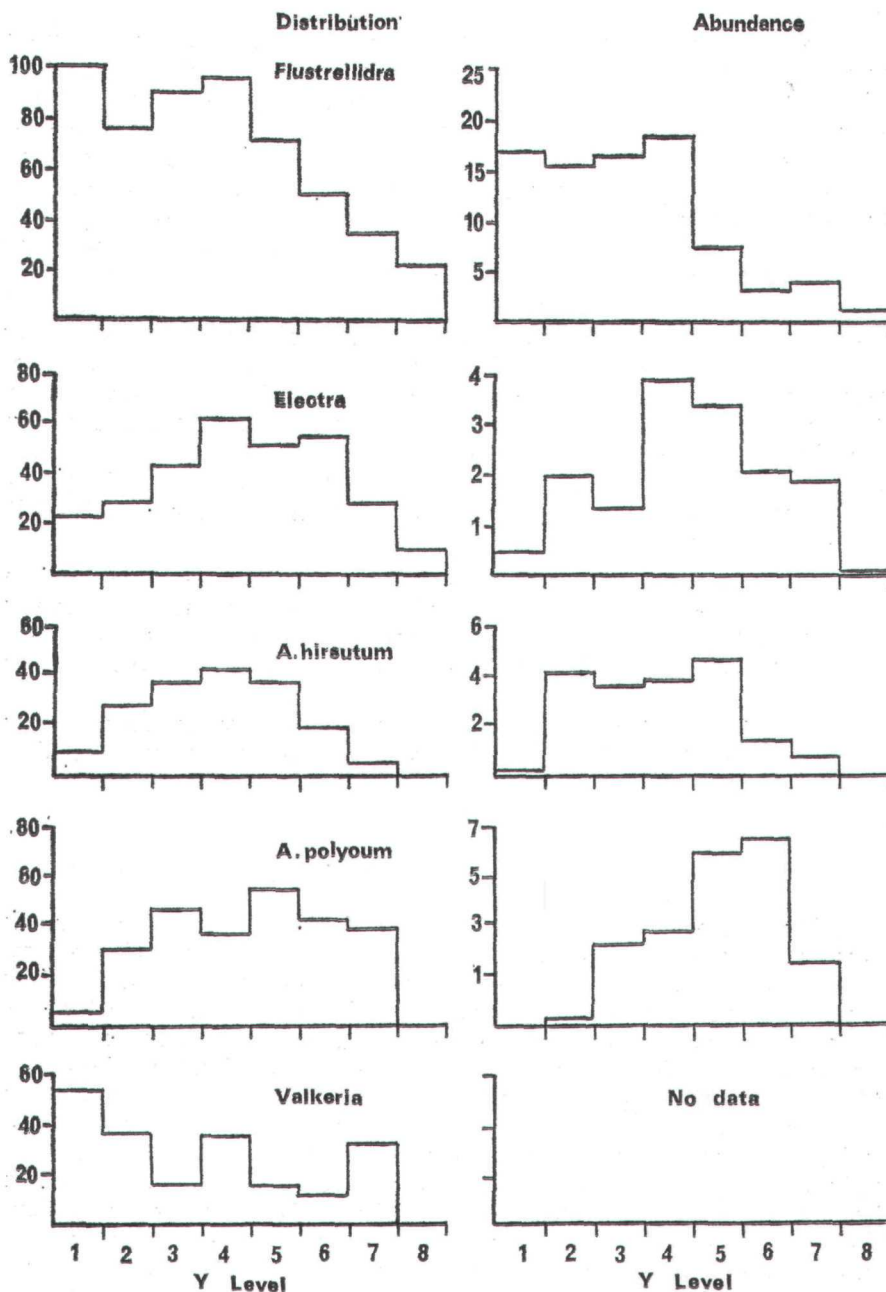
Summarising the above results it appears that those factors which favour the establishment of *F. serratus* at the Dorn also favour the growth of individual plants since where plants were most abundant they were also generally larger and more highly branched. These

results therefore broadly agree with our earlier findings from a more extensive survey of the serrated wrack in this geographical locality (Boaden *et al.* 1975).

The dominant fauna

The fauna associated with the serrated wrack at the Dorn is exceedingly diverse, and although our present survey revealed a total of 40 sessile and numerous vagile taxa, the majority of species were present only in very low numbers. We accordingly selected the eleven commonest taxa for more detailed analysis. These comprised five bryozoans [(*Flustrellidra hispida* (Fabricius), *Electra pilosa* (L.), *Alcyonidium hirsutum* (Fleming), *A. polyoum* Hassel and *Valkais uva* (L.)) four serpulids (*Spirorbis borealis* Daudin, *S. pagenstecheri* Quatrefages, *S. tridentatus* Levinsen and *S. spirillum* (L.)) and two hydroids [*Dynamena pianila* (L.) and *Campanularia* = *Laomedea flexuosa* (Hincks)]. Several measures of abundance of these dominant species are tabulated in Table IV from which it will be seen that quite pronounced differences exist between the fauna at the three sites. Only *Flustrellidra*, *Dynamena* and *Spirorbis borealis* occurred

on all the plants examined at any one site. *Alcyonidium hirsutum*, *Electra*, *Flustrellidra* and *Dynamena* were all much more abundant at the most turbulent site and showed an apparently marked aversion to the quieter, more turbid conditions associated with the inner basins. The erect stems of *Dynamena* were also significantly taller in its more "favoured" habitat (13.1 ± 0.8 SEmm at site one, 7.6 ± 0.4 in site



two, $t = 5.7$, $p < 0.001$). *Alcyonidium polyum* and, more especially, the serpulids, however, were most prolific at sites two and three, the serpulids in particular being exceedingly sparse at the most turbulent site. Of the two remaining taxa, whose numerical abundance we did not quantify, *Valkeria* was most widespread at site two whilst *Campanularia* was more or less equally ubiquitous at sites one and two.

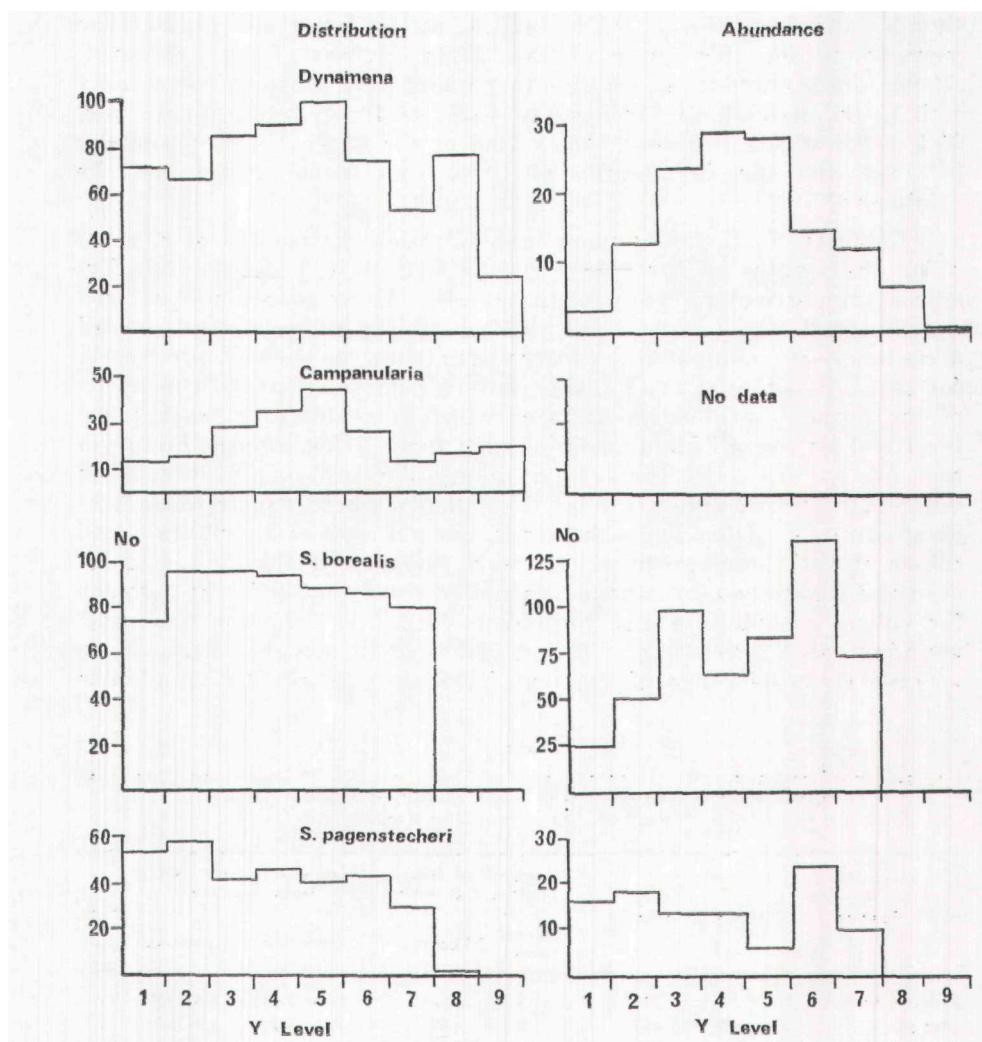


FIG. 1 A, B.

Distribution and intensity of colonisation of *F. serratus* at different plant levels by the common species at sites where each was most abundant: distribution calculated as percentage of available faces colonised, abundance as percentage cover (except for spirorbids which were counted).

It should perhaps be noted that the three somewhat different measures of abundance presented in Table IV are remarkably consistent across each of those species examined.

The relative paucity of *Flustrellidra* at site three appears to be at least partially due to the failure of larvae to colonise plants at this site to any appreciable extent rather than to mortality of established colonies. During the main recruitment period (see later) distal dichotomies from each of fifteen plants at the two most extreme sites were collected and the density (per 10cm²) of *Flustrellidra* ancestrulae noted: settlement at site one (57.0 ± 10.5 SE) was markedly higher than at site three (0.4 ± 0.3). Indeed, at the latter site ancestrulae were found on only three of the thirty segment faces examined. *Alcyonidium* ancestrulae, on the other hand, were more or less equally well distributed at all three study sites (34.4 ± 7.3 SE at site one, 35.5 ± 8.9 at site two and 34.1 ± 26.6 at site three). Unfortunately, however, the specific identity of these ancestrulae could not be established.

Colonies of all the common taxa were not distributed at random along the lengths of the *Fucus* fronds but showed specific "preferences" for particular regions of the plants. These zonal patterns are illustrated in Figure 1 in which both the ubiquity and overall abundance are compared. *Flustrellidra* showed a clear propensity for basal dichotomies (Y₁-Y₄), this pattern being evident both in terms of the proportion of segment faces which it colonised at each plant level and its overall abundance on each face. *Alcyonidium hirsutum* and *Electra* occurred further out along the fronds but were both noticeably less abundant on basal segments where *Flustrellidra* was most common. Once again, however, the patterns of distribution and colony size of these two bryozoans were remarkably similar. *A. polyoum* and *Dynamena*, by contrast, exhibited somewhat different patterns for colony distribution and for colony size. *A. polyoum* was most abundant at Y levels 5 and 6, but although it was distributed over a relatively wide range of segment faces, only rarely did it colonise

TABLE V

Utilisation of concave and convex surfaces of *F. serratus* by the common species at those sites where each was most abundant (1), *P<0.05;

**P<0.01; ns = not significant.

| Species | Site | Faces (2) | Percentage of faces colonised that were | | Mean abundance (\pm SE) on faces that were | | P (3) |
|-------------------------|------|-----------|---|------------|---|------------|-------|
| | | | (a) concave | (b) convex | (a) concave | (b) convex | |
| <i>Flustrellidra</i> | 1 | 186 | 53 | 47 | 11.9(2.3) | 9.9(2.3) | * |
| <i>Electra</i> | 1 | 102 | 55 | 45 | 3.0(1.2) | 1.9(0.7) | * |
| <i>A. polyoum</i> | 2,3 | 105 | 54 | 46 | 2.3(0.8) | 2.9(1.0) | n.s. |
| <i>A. hirsutum</i> | 1 | 68 | 51 | 49 | 5.4(1.9) | 4.5(1.4) | n.s. |
| <i>Valkeria</i> | 2 | 56 | 52 | 48 | — | — | — |
| <i>Dynamena</i> | 1 | 215 | 54 | 46 | 20.0(3.5) | 13.7(3.2) | ** |
| <i>Campanularia</i> | 1,2 | 109 | 60 | 40 | — | — | — |
| <i>S. borealis</i> | 3 | 147 | 56 | 44 | 68.3(16.5) | 62.3(11.7) | n.s. |
| <i>S. pagenstecheri</i> | 3 | 73 | 51 | 49 | 31.7(9.6) | 25.5(5.3) | n.s. |
| <i>S. spirillum</i> | 2,3 | 23 | 48 | 52 | 1.2(0.6) | 4.8(2.7) | * |
| <i>S. tridentatus</i> | 2,3 | 11 | 45 | 55 | 0.9(0.4) | 1.9(0.9) | n.s. |

(1) Only those plants which were colonised by the species were used in these analyses.

(2) Number of faces on which the species was present.

(3) Wilcoxon Matched Pairs Signed Ranks Test.

the most basal segments. *Dynamena* was widespread at most plant levels but attained its maximum abundance in the bushier central regions of the plants (Y_3 - Y_5). Like *Dynamena*, both *Spirorbis paggens-techeri* and *S. borealis* also colonised most plant dichotomies but the latter species tended to be rather more abundant distally.

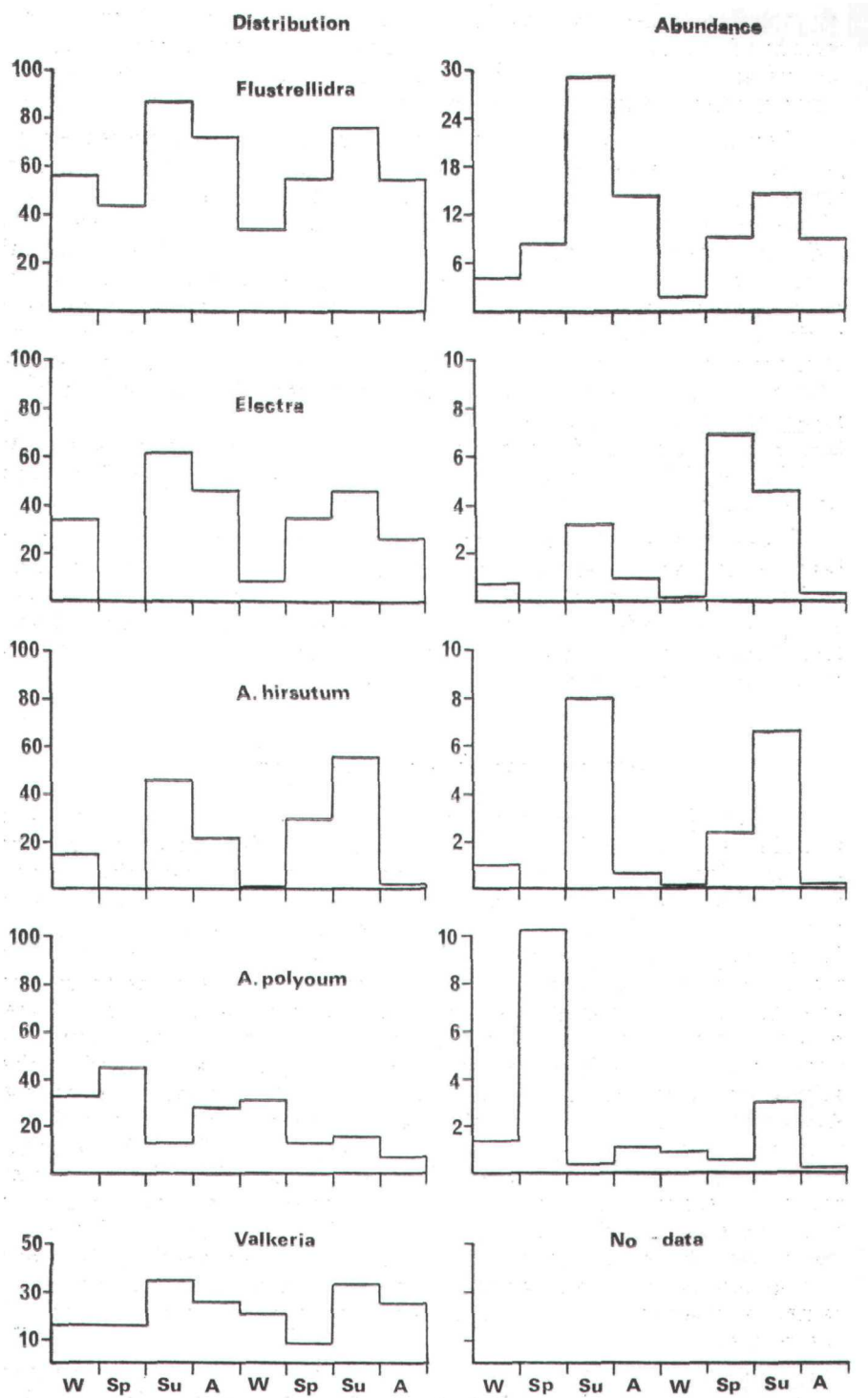
Beyond the most basal segments the fronds of the serrated wrack generally have a recognizable concave face and most of the common species were more widely distributed on this face than on the obverse (Table V). Only in the case of *Campanularia*, however, was this difference statistically significant ($\chi^2 = 4.04$, $P < 0.05$) but when actual abundances on the colonised faces were considered, *Flustrellidra*, *Electra* and *Dynamena* were all found to be more numerous on concave surfaces. *Spirorbis spirillum*, by contrast, was significantly more abundant on convex surfaces, albeit for a much smaller sample (Table V). The erect stems of *Dynamena* were slightly, though consistently, taller on concave (13.2 ± 1.2 SEmm) than on convex (12.1 ± 1.1) surfaces of plants at site one where this species was most prolific ($P < 0.01$, Wilcoxon Matched Pairs Signed Ranks Test) but not at site two (concave 7.7 ± 0.4 , convex 7.3 ± 0.7 , $P = \text{as}$).

Taken overall, the above results indicate that these common sessile taxa, which are potential space competitors within the *P. serratus* epifauna, can probably achieve at least some degree of ecological isolation via their differential use of sites located in different physical and biological environments and by their differential use of the microenvironments provided within single plants.

Seasonal changes within the community

Figure 2 illustrates the seasonal changes in the ubiquity and abundance of nine of the common taxa. Too few data points were available for the two less abundant spirorbids to warrant their inclusion in this analysis. We have grouped our data on a seasonal basis so that most of the columns in this figure are the means for all segment faces (concave and convex) along the longest fronds of three or more plants (very occasionally two). The main point to emerge from this analysis is the striking seasonal changes, especially in abundance, which occur amongst the component species within these communities. Whilst virtually all species were most abundant in either the spring or more especially the summer months, certain species e.g. *Alcyonidium hirsutum*, *Electro* and *Flustrellidra* regressed to such an extent that they were almost totally absent from the community during winter. The pattern for the two spirorbids, however, was rather different from the other major species since these peaked in abundance during the autumn i.e. after the major period of recruitment had occurred. Moreover, unlike the other species, *Spirorbis* was generally minimally abundant during spring after having maintained a relatively buoyant population density throughout much of the winter.

The major settlement periods of several of the most common species are illustrated in Figure 3. *Flustrellidra ancestrulae* (Fig. 3a) first started to appear during the early spring; they were present in



abundance on distal dichotomies during May and June and persisted at somewhat lower densities throughout July and August. The ancestrulae of *Alcyonidium* spp. (Fig. 3b) on the other hand, were most abundant during the autumn and winter. At site one, settlement commenced in October but was heaviest between November and January. The whole cycle at site two was advanced by several weeks

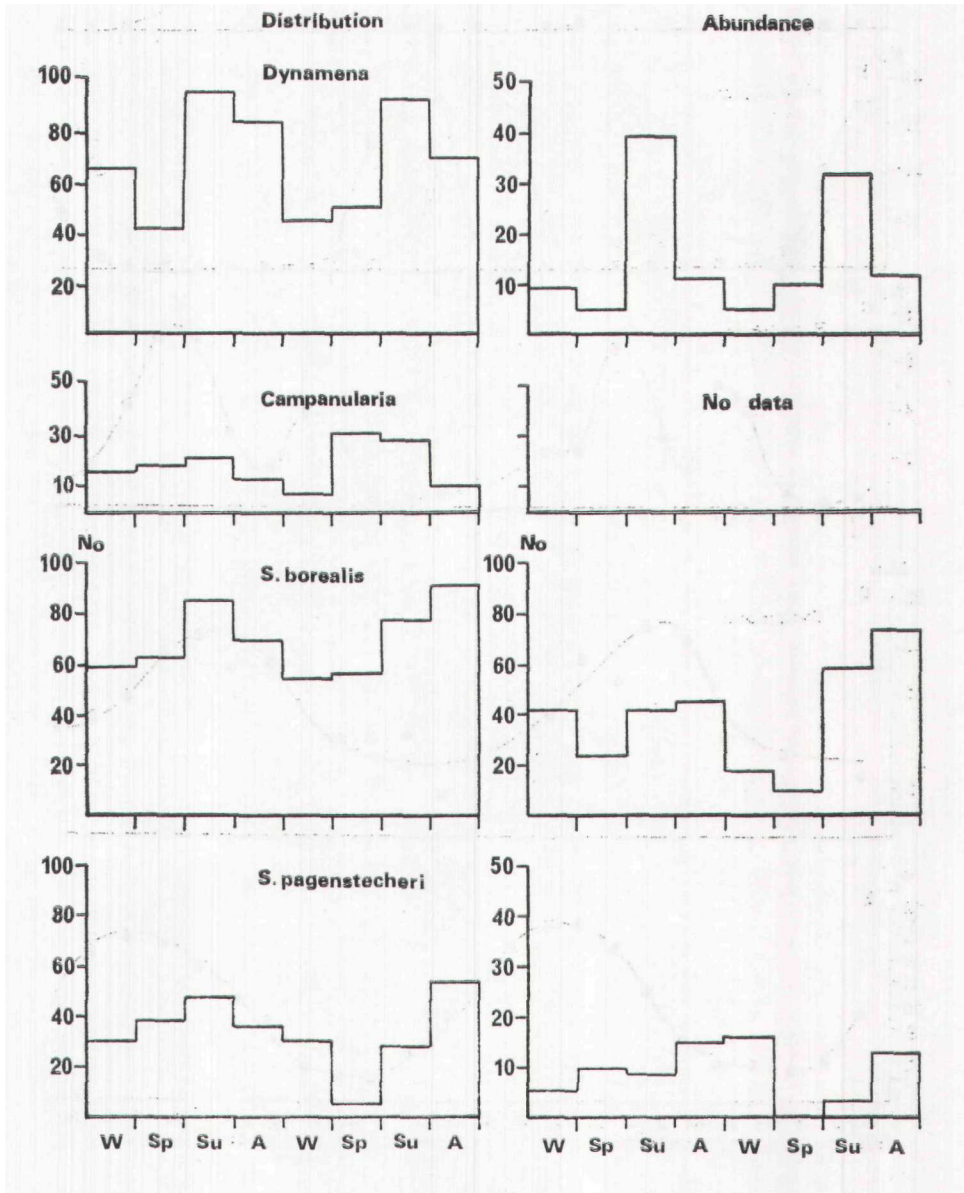


FIG. 2, A, B.

Distribution and abundance in percentage.

Seasonal changes in the distribution and intensity of colonisation of the common species at sites where each was most abundant. Conventions as for Fig. 1. Winter (Dec-Feb), Spring (Mar-May), Summer (Jun-Aug), Autumn (Sep-Xov).

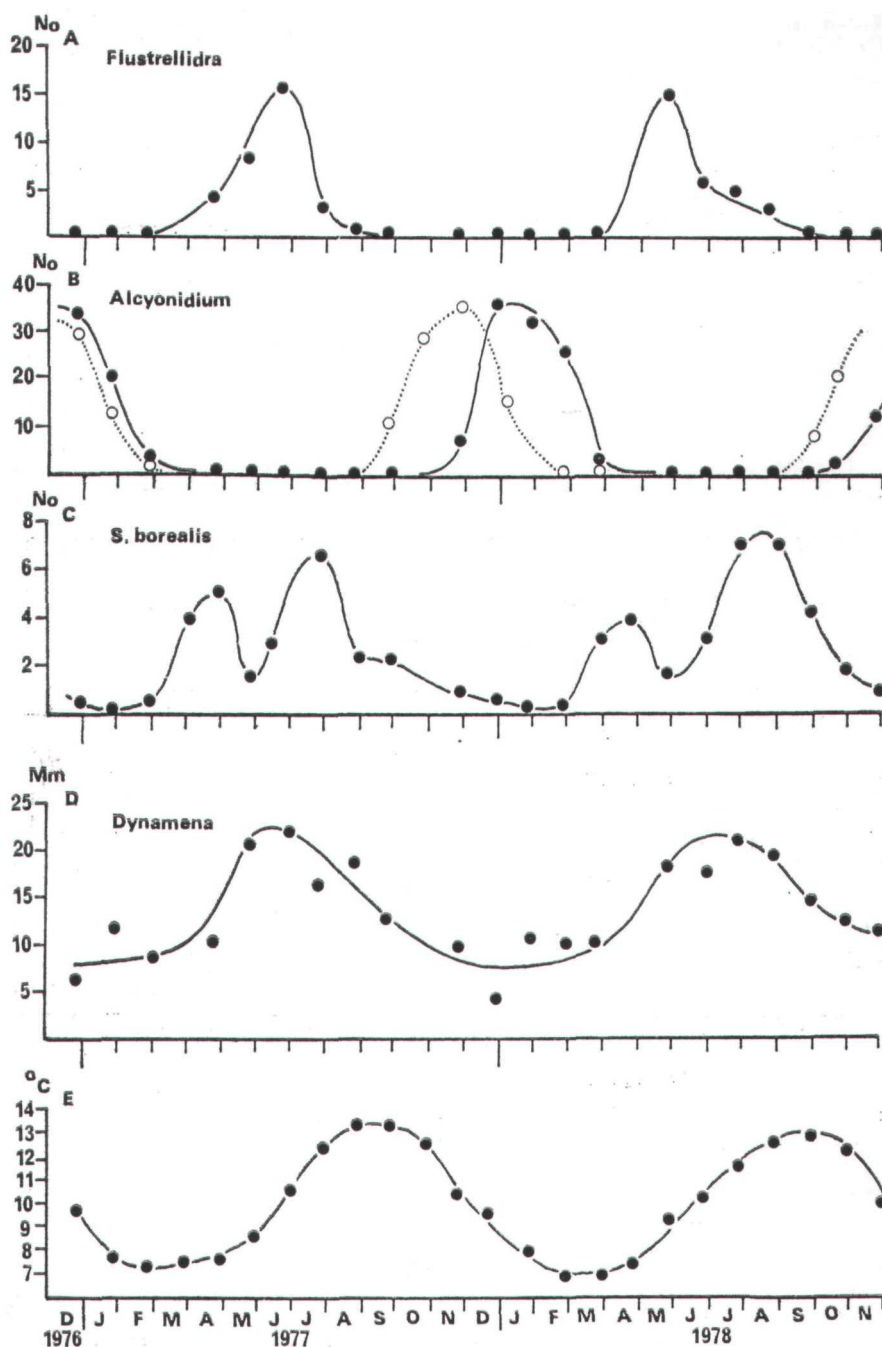


FIG. 3

Distribution and abundance in percentage.

Seasonal variations in (a) the frequency of *Alcyonidium* ancestrinae (site 1 solid line; site 2 broken line) (b) the frequency of *Flustrellidra* ancestrulae (site 1; site 2 broken line) (c) the frequency of recently settled *Spirorbis borealis* (site 3) (d) the height of the five tallest branches of *Dynamena* (site 1) and (e) surface sea water temperature in Strangford Narrows.

in both 1977 and 1978. Since *A. hirsutum* and *A. polyomm* are differentially distributed between these two sites (Table IV) it is tempting to speculate that these differences reflect species-specific patterns in breeding and settlement. It is regrettable, therefore, that we have been unable to satisfactorily separate the ancestrulae of these two closely related bryozoans. Embryo sacs were present in *A. hirsutum* colonies from July through until December with a few residual sacs persisting even into January; in *A. polyomm* they were evident from July until November.

Although settlement of *Spirorbis borealis* occurred predominantly during the spring (March-April) and summer (July-August) months, there was some evidence of a further period of recruitment (at least in 1977) during September (Fig. 3c; see also Fig. 5). *Spirorbis* is hermaphrodite and developing embryo strings could be found in over a quarter of the breeding population (i.e. those over c. 1.9mm diameter) at site three between February and September-October; this figure increased to over 70 percent between May and August.

Dynamena was most luxuriant during the late spring and summer months when its maximum stem height was approximately three times that which obtained during the winter (Fig. 3d). Reproductive zooids (= gonothecae) were present in abundance between May and August but these occurred only on colonies which were above a certain stem height (c. 11-12mm at site one). Once beyond this 'critical' size, however, the density of gonothecae appeared to be an approximately linear function of maximum stem height.

Many bryozoans settle preferentially on the younger, less heavily encrusted, plant dichotomies. However, since not all the plants at any of our sites had precisely the same number of dichotomies this predominantly distal distribution is partially masked when data for several *Fucus* plants, examined simply on the basis of Y levels, are grouped together (Fig. 4a). We therefore reorganised our data as follows: all distal segments (D) were considered together and then, working backwards along the fronds, consecutive segments were numbered D-1, D-2...D_n (Fig. 4b). At the most turbulent site both *Flustrellidra* and *Alcyonidium* ancestrulae were significantly more abundant on concave (80.4 ± 23.7 SE and 38.2 ± 9.0 respectively) than on convex (64.9 ± 17.1 and 20.9 ± 5.4) surfaces ($P < 0.05$ and 0.01 , Wilcoxon Matched Pairs Signed Ranks Test).

Figure 5 examines the seasonal changes in population structure of *Spirorbis borealis* at our innermost site. Recruitment occurred mainly over the spring and summer months but there was evidence of further settlement during September (1977). The high frequencies of juveniles which dominate the population until late summer or early autumn gradually decline, probably through a combination of growth and mortality, until by the winter months (January-February) the population consists mainly of adult worms. The overall picture which emerges for *S. pagenstecheri* is broadly similar to that of its congener but our data for this second most abundant serpulid in this community are not sufficiently complete to justify the inclusion of a similar analysis. From preliminary observations of marked cohorts of *Spirorbis* whose history we have carefully monitored it appears

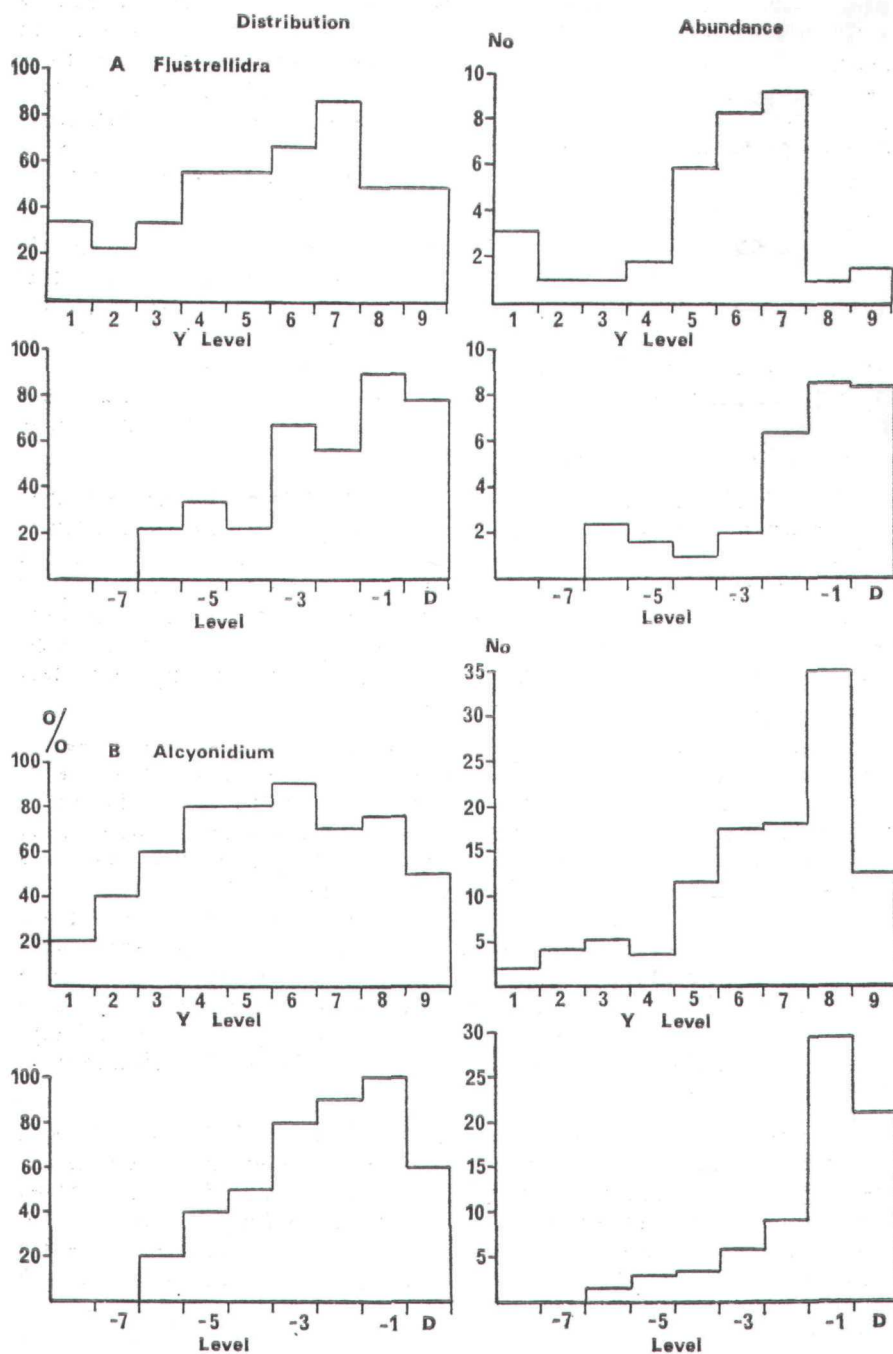


FIG. 4

Distribution and intensity of colonisation of *Fucus* segments at different plant levels by the ancestrulae of (a) *Flustrellidra*, (b) *Alcyonidium*: distribution calculated as percentage of available faces colonised, abundance as *So. ancestrulae*/10cm². D=distal sample. See text (p. 253) for explanation of alternative schemes.

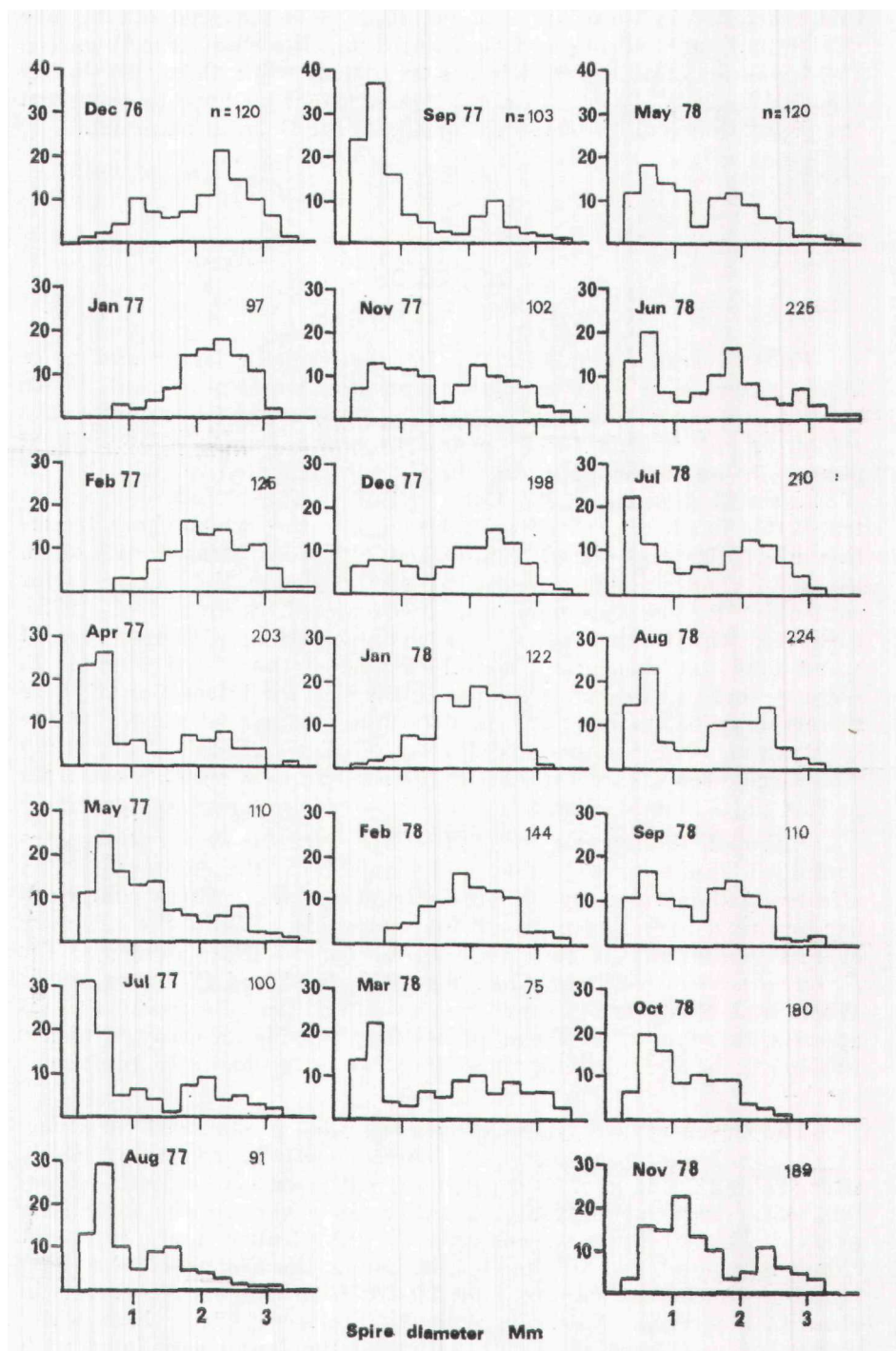


FIG. 5

Distribution in percentage.

Seasonal changes in the size-frequency distribution of *Spirorbis borealis* (site 3t). In percentage.

that mortality in these serpulid populations is maximal during late winter and early spring and that individual life spans rarely exceed 15-18 months, findings which are consistent with those previously reported by Daly (1978). In a subsequent paper we hope to document the population ecology of the spirorbids at the Dorn in more detail.

DISCUSSION

Fucus serratus plants at the Dorn were both larger and more highly branched at the site experiencing most water movement. Here too they were most abundant, suggesting that factors favourable to the establishment of this furoid also favour the growth of individual plants. In an earlier paper in which we documented the distribution of the serrated wrack at the Dorn in rather more detail we demonstrated that in the absence of wave action, a feature which characterises this particularly sheltered land-locked region of Strangford Lough, availability of suitable substratum was probably the major factor controlling the local abundance of this seaweed (Boaden *et al.*, 1975). However, whilst other physical variables such as silt and current speed may not themselves directly influence the distribution of *F. serratus* there still remains the possibility that the interaction of these factors may be instrumental in determining the actual nature of the substratum. The clumped distribution of plants at each of our study sites largely reflects the rather patchy distribution of suitable substrata in this particular locality.

Although the fauna associated with *F. serratus* at our study sites contained numerous sedentary and vagile taxa, the community was effectively dominated by eleven common species. These comprised five bryozoans, two hydroids and four serpulids. Whilst the structure of this community is thus broadly similar to those described for *F. serratus* elsewhere (e.g. Stebbing, 1973; Seed and O'Connor, 1980; Wood and Seed, 1980) some species-differences do exist and it appears, therefore, that *Fucus* plants may provide an array of niches which can be occupied in different areas by ecologically equivalent species.

The eleven most common species exhibited pronounced variations in their abundance at our three environmentally contrasted study sites (Table IV). *Alcyonidium polyomm*, and more especially the serpulids, occurred principally at the siltier sites whereas the remaining taxa were generally most abundant in the cleaner, more turbulent channels around the Sill itself. At Lough Ine Sloane *et al.* (1961) found that whereas *Electra* and *Alcyonidium polyomm* occurred in clear fast currents, *Spirorbis* typically preferred sites where water movement was more sluggish. Although the fauna associated with tidal rapid systems are generally rich in sedentary filter-feeding taxa (Boaden *et al.*, 1975; Kitching and Ebling, 1967; Ryland and Nelson-Smith, 1975) excessive turbulence may sometimes prove determinative to certain species. Relatively few *Spirorbis* for example settled at our

most turbulent site despite their prevalence on plants nearby, and Doyle (1975) has recently demonstrated that turbulence can be a major source of mortality in these serpulids. Slow-moving turbid water, on the other hand, may suffocate many of the more delicate filter-feeding taxa. When five *F. serratus* plants were transferred from a relatively clean fast current area at the Dorn to a quieter more turbid site, the height of *Dynamena* colonies regressed by almost 50 percent in six weeks whilst the control colonies showed little or no change over the same period (Seed and Boaden, 1977). Similar results have also been obtained by Round *et al.* (1961) for the hydroid *Sertularia operculata*. Whilst high turbidity therefore appears to be detrimental to adult hydroid colonies, the virtual absence of *Flustrellidra* at our innermost site seems to be due largely to the failure of larval settlement on plants carrying a relatively high silt load.

Physical factors alone, however, need not always be responsible for intersite differences in species' abundance, biotic factors such as predation and/or competition may frequently be effective in excluding a species from a "preferred" site. *Spirorbis*, for example, is often overgrown by encrusting species (Stebbing, 1973; O'Connor and Lamont, 1978) and whilst some redirection of growth in an attempt to elevate the tube orifice above the competing species is possible, most individuals are ultimately smothered. Such observations thus confirm Jackson's (1977) assertion that colonial species can generally outcompete solitary species. Hydroids such as *Dynamena*, on the other hand, appear to be largely immune from overgrowth by virtue of their arborescent growth habit. We have comparatively little data regarding *Alcyonidium polyoum* but colonies of this smooth-surfaced bryozoan are noticeably thinner than either those of its papillate congener *A. hirsutum* or those of *Flustrellidra* and it is conceivable, therefore, that this species may be outcompeted at sites where these two fleshier bryozoans predominate. It must be emphasised, however, that what we have regarded as two species of *Alcyonidium* (viz. *hirsutum* and *polyoum*) are now thought to include at least ten genetically distinct species (Thorpe and Ryland, 1979). Even more disturbing, especially for population studies, is the existence of sympatric species which are morphologically indistinguishable.

Whilst the distribution of the common species along the *Fucus* fronds are clearly non-random (Fig. 1A, B) any interpretation of these zonation patterns is clearly hindered by our lack of information concerning the actual age of the fronds themselves. *F. serratus* usually lives for about three years though in sheltered conditions it may survive into a fourth or even fifth year (Rees, 1932; Knight and Parke, 1950). Even so, most plants experience varying degrees of annual defoliation, especially during winter, either through basal denudation or the shedding of fertile fronds once these have fruited. The degree of fruiting, and therefore the corresponding loss of foliage, increases with age (Knight and Parke, 1950). Furthermore, branching rates can vary between plants so that well defined zonation patterns of individual species can sometimes be obscured when data from several plants are combined.

Unlike laminarians, fucoid algae grow by apical meristems and their fronds therefore constitute an age gradient in which the older

and frequently most heavily encrusted segments are basal and the younger newly grown segments are distal. We have already seen that recruitment of certain species occurs principally onto the less encrusted distal segment faces (Fig. 4) where competition for space is presumably less severe. If such settlement patterns were typical of all species then zonation patterns along the fronds could simply reflect the differential occurrence of distal segments at each Y-level as a result of a spread in plant age. However, the very fact that distribution patterns varied between species indicate that this cannot be the sole explanation.

Flustrellidra was most successful on more basal segment faces than elsewhere, as indeed it was on plants in the Menai Strait (Wood and Seed, 1980). This could be due to the local relaxation of competition from sponges and tunicates which, when present, are usually most prolific basally (Boaden *et al.*, 1975, 1976). *Alcyonidium hirsutum*, *Electra* and *A. polyomm* peaked in abundance at progressively more distal points along the fronds whereas *Dynamena* and *Spirorbis* had a somewhat more widespread distribution (Fig. 1A, B). Of those species which seem to avoid the most basal dichotomies both *Electra* and *Spirorbis* are known to suffer in competition with certain encrusting bryozoans (Stebbing, 1973; Seed and Boaden, 1977; O'Connor and Lamont, 1978; Wood and Seed, 1980). These species accordingly reduce the effects of competition by their utilisation of sites normally avoided by their major competitors, by being relatively less specific in their choice of algal substrata and by settling on and/or growing towards the younger, less encrusted parts of the plant, "tactics" also used by *Membranipora membranacea* a bryozoan which, like *Electra*, is also susceptible to overgrowth by other species (see also Ryland, 1974, 1979; O'Connor *et al.*, 1979; Ross, 1979). Buss (1979) considers that habitat selection and directional growth are the main mechanisms to have evolved amongst marine invertebrates for the location of spatial refuges or "safe positions". Since individuals within these safe positions will presumably contribute disproportionately more to future generations by virtue of their higher survival, selection might be expected to favour the evolution of mechanisms for exploiting such refugia. Zonation patterns of individual species are also known to vary according to local environmental conditions (O'Connor *et al.*, 1979) and to the position of plants within the intertidal gradient (Wood and Seed, 1980).

Most *F. serratus* fronds are partially folded thereby producing recognisable concave and convex surfaces. Most of the common species in our samples seemed to prefer concave surfaces, this preference being especially pronounced in the case of *Dynamena* (Table V) which was also significantly taller on these surfaces. Whilst this may reflect larval preferences at the time of settlement (*Flustrellidra* and *Alcyonidium* ancestrulae, for example, were both significantly more abundant on concave surfaces) the possibility that mature colonies may also obtain some degree of local protection either from the current or from the abrasive effects of adjacent fronds, cannot be entirely dismissed. It is perhaps significant, therefore, that the taxa which exhibit this effect most markedly i.e. the hydroids and sponges (Boaden *et al.*, 1975, 1976) have erect growth habits. Local eddying

effects, or the development of a specific microflora could also be instrumental in creating a generally more favourable microenvironment on concave surfaces. Wood and Seed (1980) have recently demonstrated that the apparent preference for concave surfaces shown by *Alcyonidium* larvae in the Menai Strait at the time of settlement, increases at higher tidal levels where the problems of desiccation are more acute. Here less time is available for settlement and concave surfaces may retain a surface film of water rather more effectively thereby facilitating attachment and promoting subsequent survival.

Marked seasonal changes occurred in the *F. serratus* epifauna at the Dorn. Most of the common species attained their maximum levels of abundance in the spring and summer months when conditions for rapid growth are presumably optimal but they then regressed to such an extent that many were virtually absent from the community during the winter (Fig. 2, A, B). *Alcyonidium hirsutum*, *Flustrellidra*, *Electro* and *Dynamena* all showed an evidently marked aversion to the silty conditions in the inner tidal basins (Table IV) and the decline in abundance of these species during the winter could reflect the increase in turbidity which is widely reported to occur at this time of the year (Kenchington, 1970; Newton and Gray, 1972). *Spirorbis*, however, was most abundant during the late summer and autumn when settlement was more or less complete.

Spirorbis borcalis (= *S. spirorbis*) is essentially a summer breeder and settlement on *F. serratus* in N.E. England extends from June to October (Daly, 1978). Settlement of *S. pagenstecheri* is evidently rather more extended occurring between April and November (L'Hardy, 1961). Algal extracts are known to stimulate gregarious settlement in spirorbids (Gee, 1965) and whilst this can lead to their mass occurrence the latter is largely a feature associated with unstable environments (Hove, 1979). Knight-Jones *et al.* (1971) and more recently MacKay and Doyle (1978) have found interpopulation differences in substrate preferences in *S. borealis*. Such variations in behaviour between populations can be interpreted in terms of adaptations to different selection pressures known to be acting upon the respective populations.

Crowell (1953) showed that the hydroid *Campanularia flexuosa* was most abundant during the early summer at Wood's Hole, whilst *Pennaria tiarella* and *Eudendrium carneum*, two important fouling species, were most common between July and September at Beaufort, N, Carolina (McDougall, 1943). Many hydroids in fact are known to undergo seasonal regressions during adverse conditions as part of their normal annual cycle (e.g. Tardent, 1963; Hughes, 1977) the following season's growth occurring from a protected system of dormant stolons.

Bryozoans in temperate waters generally breed during the summer and autumn (Ryland, 1970). Gautier (1962) found that Mediterranean bryozoans of northern distribution bred mainly in winter whereas southern species were largely summer breeders. Temperature and daylight, however, may not be the only factors involved and the interaction of numerous variables can effectively modulate reproduction resulting in considerable intraspecific variation from one area to another (Strom, 1977).

Whilst the cyphonautes larvae of *Electra* may be present in the plankton throughout much of the year, Ryland and Hayward (1977) found that most newly settled colonies appeared in late summer and autumn. The larvae of *Alcyonidium hirsutum* are released mainly in February (Eggleston, 1972; Hayward and Ryland, 1975). Growth of young *Alcyonidium* colonies, however, is initially slow but accelerates rapidly during the spring only to slow again by July as space becomes more limiting. *Flustrellidra*, on the other hand, settles between late March and June and grows rapidly from the time of attachment (Eggleston, 1972). In W. Sweden *A. polyoum* on *Fucus serratus* breeds between January and March when sea temperature is at its minimum (Strom, 1977) but maximum fertility in this species was not observed until September at Roscoff (Matricon, 1963).

Alcyonidium and *Flustrellidra*, two of the dominant space competitors in the Dorn community which are known to selectively colonise the serrated wrack (Ryland, 1962) may achieve some degree of ecological isolation by virtue of settling at different times of the year (Fig. 3). Competition, which might normally be expected to result in a cessation of growth (and presumably lower fecundity) is therefore largely averted. Settlement of both species, however, occurs principally onto distal segment faces (Fig. 4) and it seems unlikely therefore that recruitment alone could account for the more basal distribution of adult colonies. The high densities of *Flustrellidra* which are present on basal dichotomies during late spring and summer must therefore presumably come mainly from the development of colonies which have survived the winter in a remarkably regressed form. The formation of hibernaculae in many marine bryozoans seems to be induced by diminishing food resources during autumn (Jebam, 1975).

Acknowledgements

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Summary

The dominant epifaunal taxa associated with *Fucus serratus* L. at three physically and biologically contrasted sites in Strangford Lough were studied between December 1976 and November 1978. Factors which favoured the establishment of *Fucus* also favoured the growth of individual plants since where plants were most abundant they were also larger and more highly branched. The 59 plants which we examined in detail contained a total of 42 sedentary taxa of which eleven were common—these comprised five bryozoans, four serpulids and two hydroids. The serpulids and the bryozoan *Alcyonidium polyoum* were evidently more tolerant of silt and low turbulence but most other species were significantly more abundant on plants exposed to clean, fast-flowing water. Species were not randomly distributed along individual fronds but occupied distinct zones within the *Fucus* plants. Most species were generally more prolific on the concave surfaces of the plants and *Flustrellidra* and *Alcyonidium* settled in greater profusion on this face than on the obverse. There were marked seasonal changes in abundance amongst all the common species within the community; all except the serpulids were maximally abundant during spring and summer. Recruitment of *Flustrellidra* (spring—early summer) and *Alcyonidium* spp. (late autumn—winter) occurred principally on the younger, more distal plant dichotomies. *Spirorbis borealis* settled in pulses between March and September. The population structure of this serpulid exhibited marked seasonal variations and individual survival rarely exceeded 15–18 months.

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