THE EFFECTS OF SHORE LEVEL
ON THE EPIFAUNAL COMMUNITIES
ASSOCIATED WITH *FUCUS SERRATUS* (L)
IN THE MENAI STRAIT, NORTH WALES

by

Victoria Wood and **Ray Seed**

Department **of Zoology, The University College of North Wales, Bangor, Gwynedd,** Wales, U.K.

Résumé

Les auteurs étudient l'influence du niveau intertidal sur l'abondance du *Fucus serratus* et de son épifaune, en Galles du Nord, dans le détroit de Menai. Les *Fucus* sont de plus en plus petits et plus rares quand on se rapproche du niveau supérieur, bien que, inversement, l'exposition prolongée aux forts courants de marée réduit aussi la taille et le nombre des algues, au niveau inférieur inter-tidal.

Sur les 19 formes sessiles présentes sur le *Fucus serratus,* seules les cinq espèces les plus abondantes ont été étudiées en détail. Ce sont les Bryozoaires *Flustrellidra hispida, Electro pilosa* et *Alcyonidium hirsutum* et les Hydroïdes *Dynamena puntila* et *Campanularia flexuosa.* Le peuplement et l'abondance de ces espèces épifaunales décroissent de façon remarquable vers les milieux intertidaux supérieurs. Un ou plusieurs des mécanismes suivants favorisent un isolement écologique : le choix de la plante, la répartition des espèces le long des frondes individuelles, la préférence pour les surfaces concaves ou convexes et la crois-sance des colonies qui s'orientent vers les régions distales plus jeunes et moins incrustées de l'algue.

Lorsque les mécanismes ci-dessus échouent, la compétition pour l'espace peut être sévère, particulièrement dans les parties les plus favorables des plantes des niveaux inférieurs. Il est évident qu'une hiérarchie compétitive passe par la séquence *Flustrellidra — Alcyonidium — Electra — Dynamena.* Les larves d'*Alcyo-nidium* s'installent en abondance entre octobre et janvier et montrent une préfé-rence remarquable pour les surfaces concaves des frondes distales à tous les niveaux. La taille de *Dynamena* varie selon le niveau intertidal et selon la position du végétal.

Les présentes recherches indiquent nettement que les principales espèces épifaunales de *F. serratus* sont incapables de profiter de l'espace supplémentaire fourni par la zone étendue de l'algue dans ce lieu géographique particulier. Le fait suggère que les formes sessiles sont incapables de résister à la dessication accrue des niveaux supérieurs intertidaux.

Introduction

Rocky shores sheltered from the direct impact of wave action are generally dominated by large fucoid algae which exhibit a distinct pattern of zonation between high and low water marks (e.g. Lewis, 1964). Many of these macroalgae, particularly the serrated wrack *Fncus serratus,* support rich epifaunal communities the dominant members of which are typically sessile. These include hydroids, serpulids, bryozoans and, more occasion-
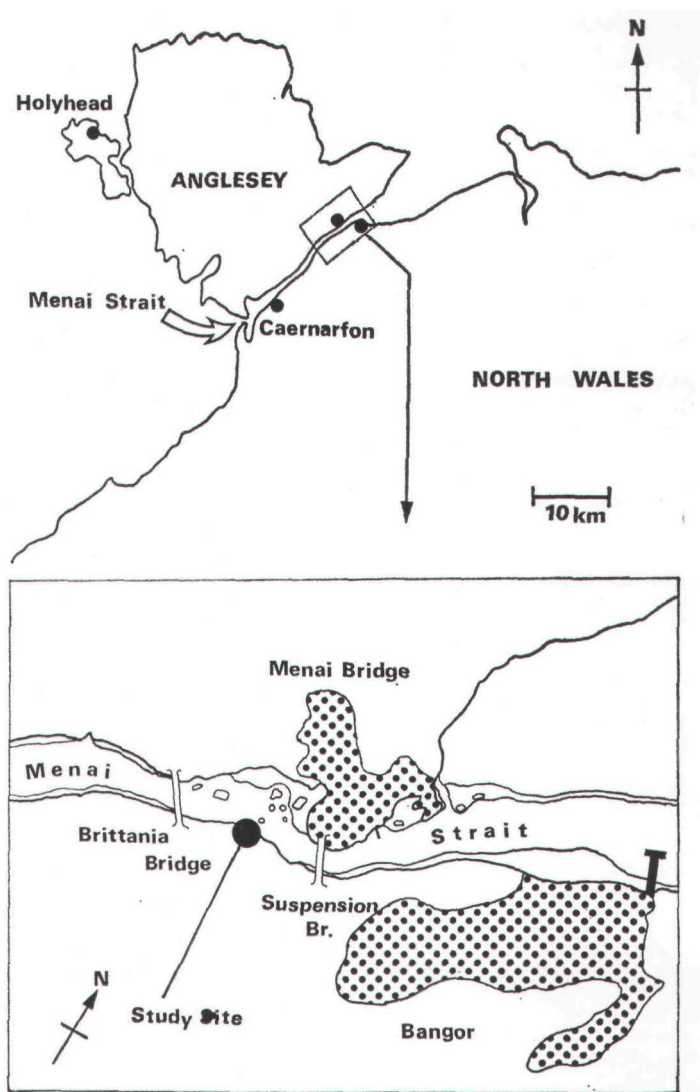
FIG. 1
Map of the area investigated in North Wales.

ally, sponges and tunicates. In view of their sedentary nature, the relative ease with which they can be monitored and experimentally manipulated, these communities are ideal for investigating the dynamic interactions between their major component species. Yet, despite their obvious poten- tial, these epifaunal communities have so far failed to receive the attention that they so clearly deserve. Exceptions include the work of Colman (1940), L'Hardy (1962), Hagerman (1966), Hitching and Ebling (1967) and Stebbing (1973 b). More recently Boaden *et al.* (1975; 1976 a; b) and O'Connor *et al.* (1975) have made a detailed study of an intertidal *F. serratus* community in Strangford Lough, Northern Ireland. However, since *F. serratus* nor- mally occupies a comparatively narrow vertical zone, no studies to our knowledge have so far considered the influence of shore level on the epi- faunal communities of this widespread intertidal alga. In the Menai Strait in North Wales, *F. serratus* largely replaces *Ascophyllum nodosum* the

knotted wrack from much of the mid-low shore and is here present as an exceedingly broad band some 3.5m in vertical extent. This paper therefore examines the effect of intertidal position on the abundance and growth characteristics of *F. serratus* and on the nature of **its** associated epifaunal communities. The investigation was undertaken between October 1977 and April 1978 at a site in the Menai Strait known as the Swellies (Fig. 1).

Materials and methods

Within the broad *F. serratus* zone, five stations were selected for study, the lowest at approximately +1.2m above Chart Datum, the highest 4.9m. At each station the density of *Fucus* plants over 10.0cm in length (i.e. excluding sporelings) was estimated from eight quadrats (30 X 30cm) thrown at random. Five plants were collected from each of the five shore levels for subsequent laboratory examination. Since the degree of encrustation varied quite considerably at each shore level, collection was standardised as far as possible by selecting only the most heavily encrusted
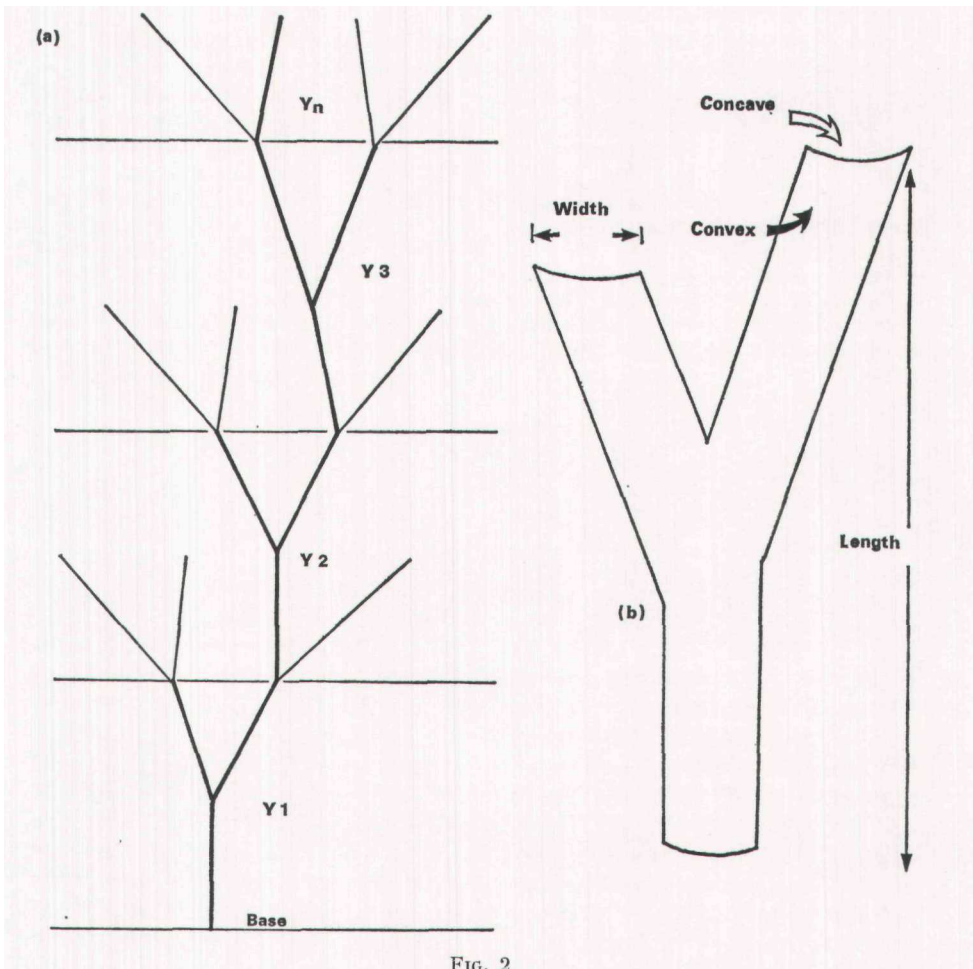

Fig. 2

The structure of a *Fucus serratus* plant.
a: schematic plant showing the course of the longest frond; b: schematic Y segment showing concave and convex surfaces and the dimensions used to calculate its area.

plants. These were deep frozen until required. After thawing, each plant was placed in a bucket of water for five minutes and allowed to drain for one minute. It was then weighed to the nearest 1.0g using a 5.0kg spring balance. Volume was estimated by displacement. Volume to length ratios provided a measure of the relative bushiness of the plants, high ratios denoting bushy plants, low ratios rather more elongate less shrubby plants. The longest frond of each plant was then selected for detailed examination. These were subdivided into segments each consisting of a single Y level or dichotomy (Fig. 2). These Y segments were numbered Y1, Y2 . . . . Yn from the base of the plants upwards. Since fucoid algae grow by means of apical meristems, the frond represents an age gradient, the basal dichotomies being the oldest, the distal dichotomies the youngest regions of the plant. The length and maximum breadth of each segment was also recorded. A close approximation of the area of each dichotomy is given by the equation: A   =   2B.L

where A = area, B = maximum breadth and L = segment length. Each dichotomy was carefully examined under a stereobinocular microscope and all the sessile taxa carefully recorded. Since most *Fucus* fronds have recognisable concave and convex surfaces, separate records were kept for each segment face, as follows.

a) Wherever possible each organism was identified to species.

b) Epiphytes were simply recorded as present or absent.

c) Colonial encrusting species e.g. bryozoans, and arborescent species e.g. hydroids, were recorded as percentage cover. For the latter, the total height of the five longest erect branches on each segment face was also noted.

d) Solitary species e.g. serpulids and recently settled bryozoan larvae (= ancestrulae) were counted.

e) Interactions (e.g. colony overgrowths) between the dominant taxa were recorded, whilst at the lowest shore level the orientation of young colonies of the bryozoans *Flustrellidra hispida* and *Electra pilosa* was also noted (i.e. whether maximum growth was directed towards the base of the plant, towards the tip of the plant or laterally across the fronds).

RESULTS

1) **Physical** conditions and plant characteristics

The Menai Strait at the Swellies is relatively narrow and, consequently, tidal currents are particularly strong. Current speeds of $1.20ms^{-1}$ on an ebbing tide and $0.80m^{-1}$ on a flooding tide have previously been reported at the nearby Brittania rail bridge, (see Kightley, 1977). Maximum current speeds occur immediately after low and high water. Wave action, however, is minimal. The tidal regime at the sampling site ranges from approximately 7.2m (0.5-7.7m above Chart Datum) on extreme spring tides to 3.0m (2.4-5.4m) on extreme neaps. The substratum consists of bedrock overlaid with numerous loose stones and boulders of varying size. Large amounts of silt on the rock surface result in relatively turbid water conditions. The shore is north facing and is almost permanently shaded by a wooded scarp to the rear.

The approximate intertidal heights of the five sampling stations and the amount of time that each was exposed on average spring and
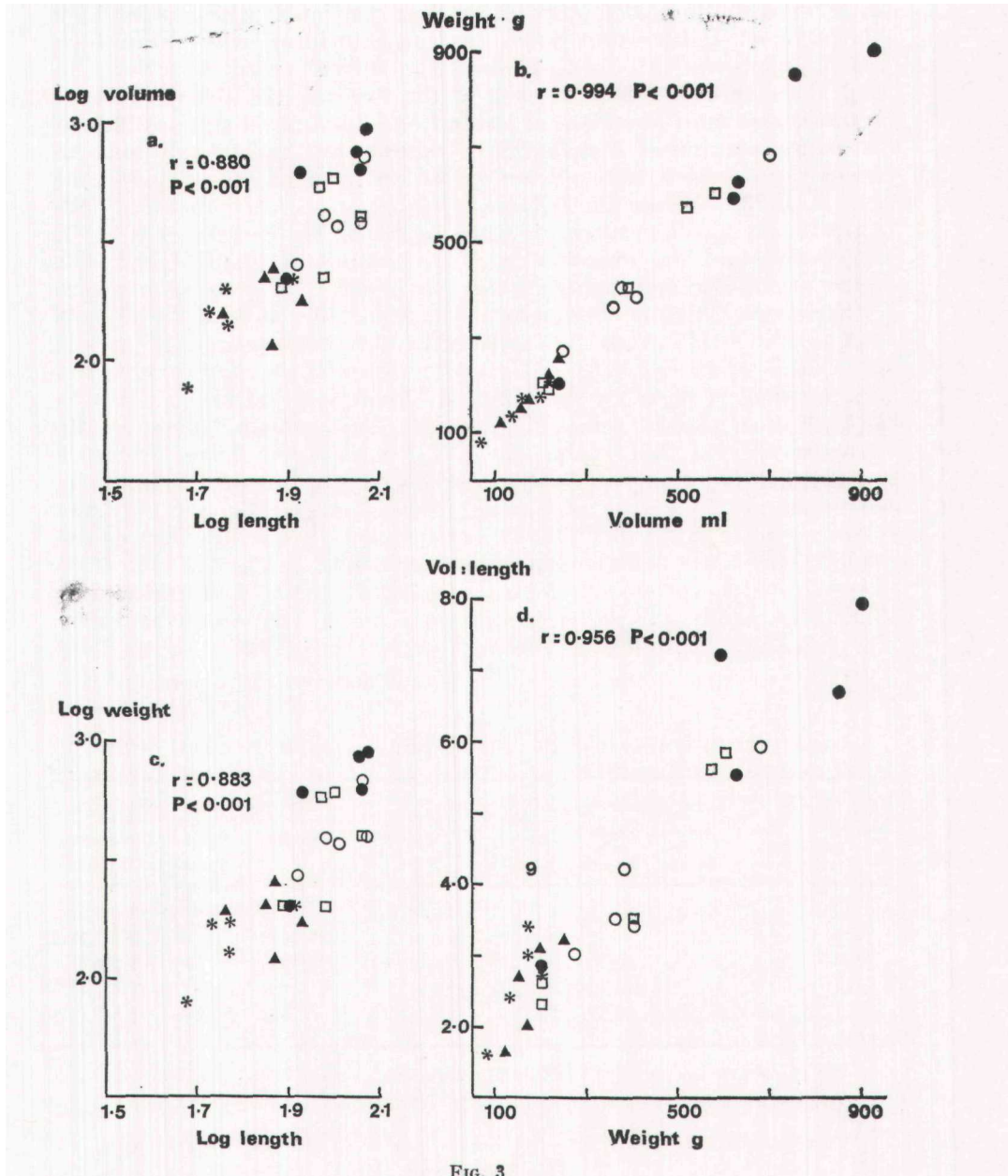
FIG. 3

Correlations between the various size measures of *Fucus* plants from all shore levels.
Black triangle: plants from shore level 1; black circle: shore level 2; white circle: shore level 3; white square: shore level 4; black star: shore level 5.

neap tides are illustrated in Table **1.** Levels **1** and **2** remained un-covered on neap tides whilst the highest levels (Stations **4** and **5)** were exposed for relatively longer periods on neap than on spring tides. The amount of desiccation experienced at any particular shore level thus varies quite significantly according to the tidal cycle. The

uppermost limit of *F. serratus* on this particular shore was 5.5m above Chart Datum thus more or less coinciding with mean high water of neap tides. Table 1 also documents the size characteristics and abundance of *Fucus* at each of the five selected shore levels. *F. serratus* was most abundant at levels 2 and 3 but at all stations had an exceedingly clumped distribution as shown by the high variance to mean ratios which were always significantly in excess of unity (see Elliott, 1973). When plants from all shore levels are considered collectively, all size measures are seen to be highly correlated (Fig. 3) suggesting that the overall size characteristics of plants from each shore level were remarkably similar. In general, however, plants were rather shorter, lighter in weight and less shrubby at both the highest and lowest levels albeit for apparently different reasons. Figure 4 shows that at shore level 5 individual Y dichotomies were consistently smaller than at all other shore levels. Assuming that segment length and/or area affords some measure of plant growth, these results strongly suggest that conditions at the uppermost shore levels are suboptimal for *F. serratus.* In the low shore, however, plants are small simply by virtue of having fewer Y segments and only the youngest most distal dichotomies are significantly smaller than equivalent dichotomies at other shore levels. Conditions in the low shore are thus apparently suitable for plant growth and reduced size is here presumably due either to increased plant attrition or to poorer survival through prolonged exposure to the exceptionally strong tidal currents.

TABLE 1

Plant and site characteristics at the five study areas in the Menai Strait.

Shore level	Height above chart datum m	Time exposed on		Plant				
		spring tide hr min	neap tide hr min	Density N/m²	Length cm	Weight g	Volume / Length	Dichotomies N/plant
1	1.2	02.41	0	1.5(2.1)*	72.5(10.0)	178(50)	2.5(0.7)	7.6(0.5)
2	1.9	03.33	0	4.8(4.6)	101.1(17.5)	633(277)	5.9(1.9)	9.8(1.9)
3	2.8	04.45	02.39	4.8(5.8)	100.9(14.3)	419(154)	4.0(1.2)	9.8(0.8)
4	3.7	05.45	06.32	2.8(4.1)	95.0(12.9)	394(193)	4.0(1.6)	10.4(1.1)
5	4.9	07.14	09.42	2.3(3.6)	60.2(12.5)	150(46)	2.6(0.6)	8.4(1.1)

decreases sharply at this uppermost station and this probably augments the amount of desiccation to which the fauna on these high shore plants will be subjected; small plants dry out more rapidly than larger shrubbier plants and therefore afford substantially less protection to the attached epifauna.

The relative abundance of the six commonest species are documented in more detail in Figure 5. The ubiquity index indicates whether a particular site is suitable for colonisation whereas the overall abundance of a species provides a measure of the relative suitability of that site. Abundance when present, on the other hand, shows how the abundance figure is made up; a species could for example have a generally low abundance or alternatively a relatively more restricted high abundance. The general trend in these three rather different measures was very similar with a general decline in abundance with increasing intertidal height. This decline was more pronounced in some species than in others, presumably reflecting interspecific differences in resistance to desiccation. Some anomalies to this general pattern are, however, evident. *Dynamena* exhibited a marked increase in its abundance when present at shore level 5

TABLE 2

The **distribution of** all sessile taxa on *F. serratus* at the five sampling sites.

	Shore level					Positions on plants (1) Y level
	1	2	3	4	5	
Fauna:						
Laomedea (= *Campanularia*) *flexuosa* Hincks	+	+	+	+	+	**1-8**
Clava spp.	+		+			**3**
Dynamena pumila (L.)	+	+	+	+	+	1-9
Spirorbis borealis Daudin		+	+	+		**2-7**
Elminius modestus	+	+		+	+	1-5
Alcyonidium hirsutum Fleming	+	+	+	+		1-8
Alcyonidium polyoum Hassel	+	+	+			**4-7**
Bowerbankia spp.		+	+	+		1-8
Celleporella hyalina L.	+	+	+	+		**2-8**
Electra pilosa L.	+	+	+	+		1-7
Flustrellidra hispida Fabricius	+	+	+	+		**1-10**
Didemnnm maculosum Milne Edwards	+					1-3
Alcyonidium ancestrulae	+	+	+	+	+	1-12
Flora:						
Ascophyllum nodosum (L.)			+		+	1
Ceramium spp.	+					1
Cladophora spp.	+				+	1
Fucus serratus L.	+	+	+	+		1-3
Rhodymenia palmata L.	+	+	+			1-4
Ulva lactuca L.	+		+	+	+	1-3
Total no. species	**15**	**12**	14	11	**6**	
Total no. **epifaunal** species	**10**	**10**	10	**9**	**3**	

a

Length cm
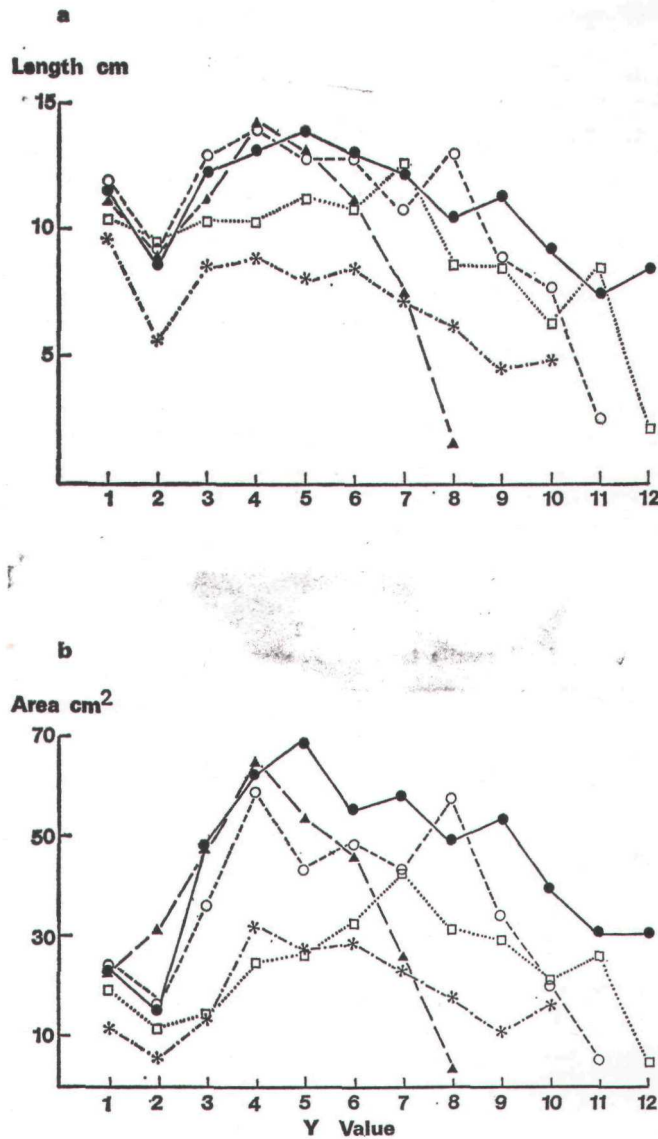

b

Area cm²

FIG. 4

Variations in segment dimensions along the longest fronds of *Fucus serratus.*
Each point is the mean for five plants at each shore level.   Symbols as in Fig. 3.

probably because here it was restricted to a few apparently favour-
able plant segments. *Campanularia* increased in overall abundance
and ubiquity towards the midshore although when present its abun-
dance remained remarkably constant with respect to shore level.
Whilst bryozoan ancestrulae were more ubiquitous in the midshore
the majority of these post larvae occurred in the low shore and settle-
ment decreased markedly with tidal height most especially between
levels 3 and 4.

Zonation **along the fronds.**

Figure **6** shows that the established colonies of all the dominant taxa were considerably more abundant basally (segments **1-5)** than
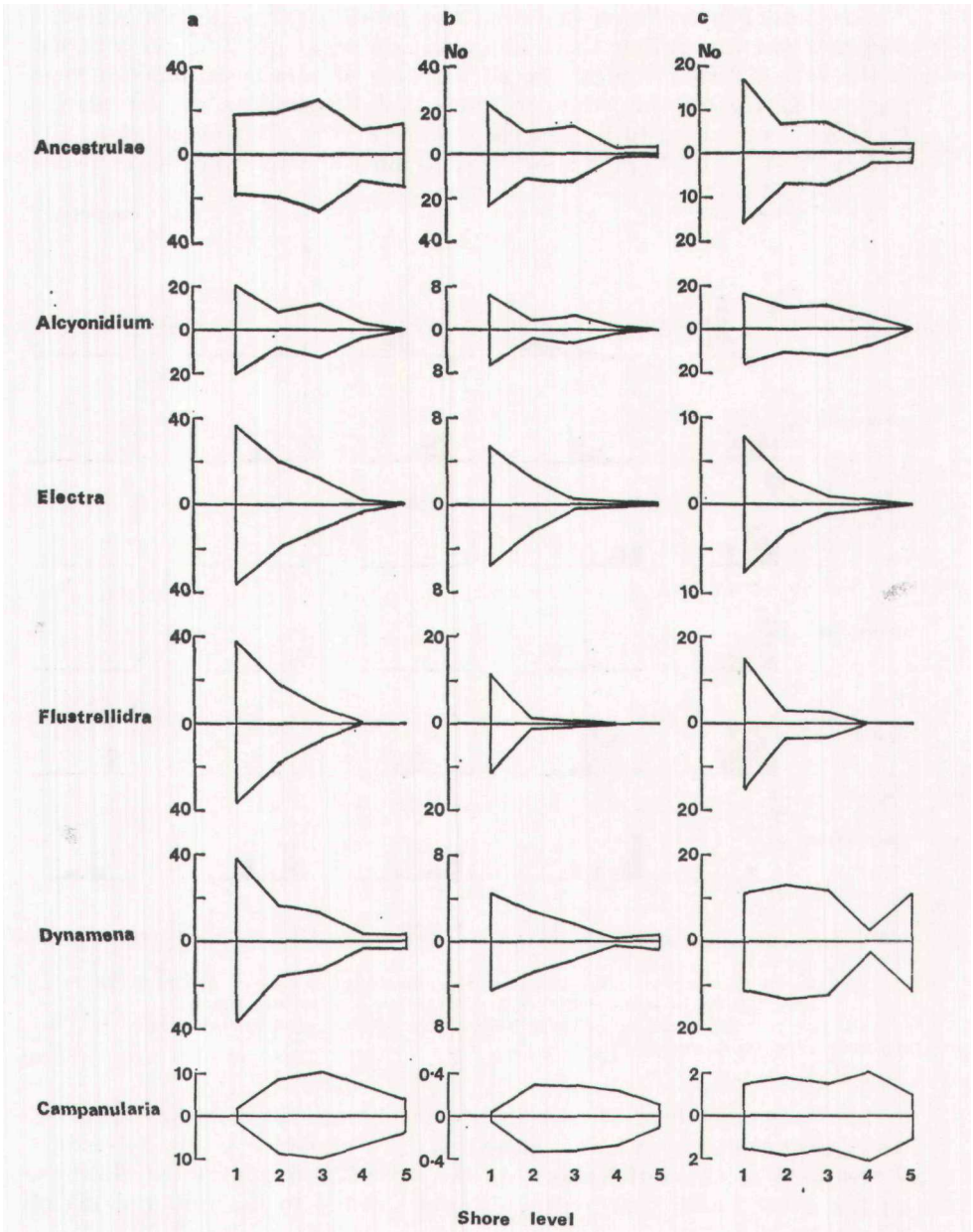

FIG. 5

Distribution of the dominant fauna of *Fucus serratus* at different shore levels. Relative abundance expressed as: a) ubiquity index (percentage); b) overall abundance; c) abundance when present.

Ubiquity index measured as $\dfrac{\text{N. faces with that organism present(n)} \times 100}{\text{No. faces examined at that shore level (Tn)}}$

Abundance as percentage cover (except for ancestralae where the No./segment face were counted.

distally. The marked decrease in the abundance of these taxa at the highest shore level is also clearly evident in this figure. Nevertheless, within the more basal segments of the plant, there is evidence that the different species occupy quite distinct zones. In the low shore, *Electra* and *Flustrellidra* favoured the most basal segments whereas *Alcyonidium* was rather more abundant on segments 2-5. In contrast to the established colonies, the ancestrulae of this bryozoan occurred predominantly on the younger more distal segments of the plants. *Dynamena* appeared to be generally more evenly distributed along the fronds (Y_1-Y_6). At higher shore levels, most species were more proli-
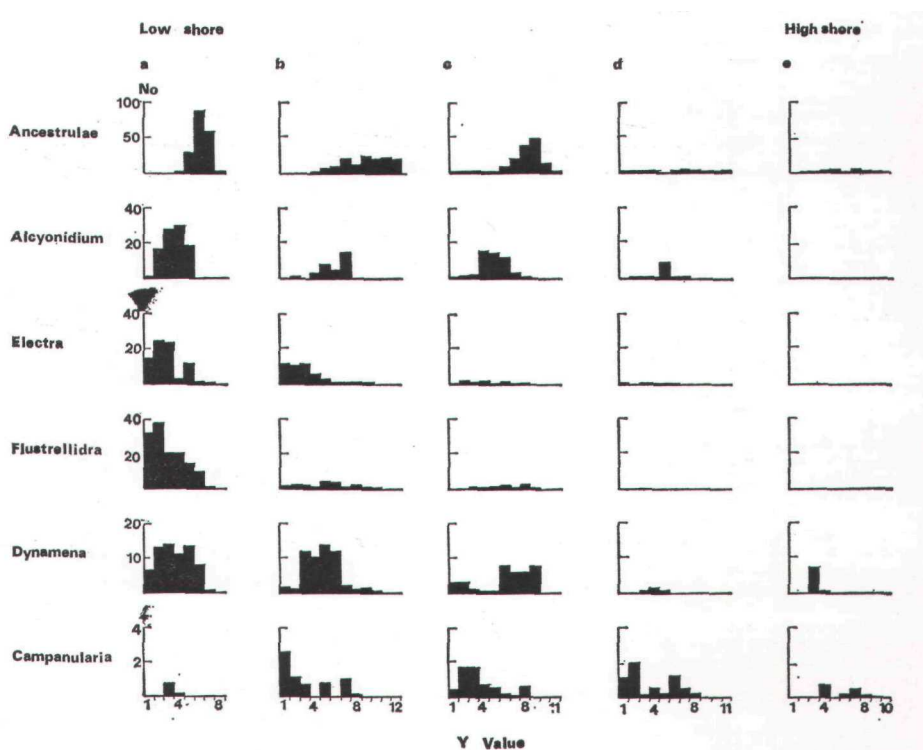

FIG. 6

Changes in the overall abundance of the dominant fauna of *Fucus serratus* along the longest frond with respect to shore level.
Abundance measured as percentage cover (except for ancestrulae where to No./ segment face were counted).

fic in the bushier central regions of the plants. The major exception was *Campanularia* which occurred mainly at shore levels 2-4 where it occupied most plant levels. At the lowest and uppermost stations, on the other hand, this hydroid was restricted to the mid regions of the fronds.

Since individual segments are not of uniform size, the area available for epifaunal colonisation can vary according to position on the plant. Figure 7 therefore examines the change in *absolute* colony area of the five commonest species along *Fucus* plants at the two low shore levels. Comparison of Figures 6 and 7 show that correcting for segment area had little effect on the overall distribution

patterns of these species. Most species (except *Campanularia)* do, however, show a pronounced decline in their absolute abundance between shore levels 1 and 2. Since the areas of equivalent Y segments at these two shore levels are similar, at least up to Y_6 (Fig. 4) and since most species do not occur in appreciable numbers beyond this level, this decline in abundance is not simply due to the same absolute colony area being spread over a greater area of frond. One factor, however, for which we did not control was the increase in the actual number of fronds present at any particular plant level. In the low shore, prolonged exposure to strong tidal currents appears to
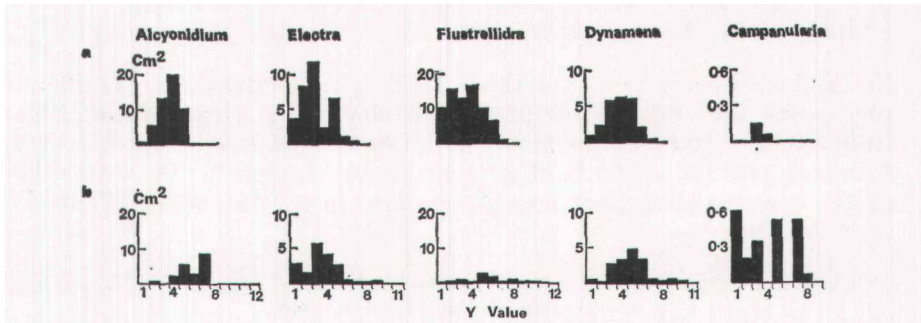

FIG. 7
Changes in the absolute area of the dominant fauna of *Fucus serratus* between: a) shore level 1 and b) shore level 2.

result in considerable loss of plant tissue; consequently, this leaves comparatively fewer dichotomies available for colonisation. Only the ancestrulae of *Alcyonidium* were abundant beyond Y level 6 (Fig. 6). Expressing the density of these recent post-larval stages as numbers per unit area rather than per segment face again had little or no significant effect on the overall pattern of recruitment (Fig. 8).

Preference **for** concave/convex **surfaces.**

Table 3 indicates that the dominant epifaunal species of *F. serratus* exhibit a clear preference for concave surfaces, particularly at

TABLE 3
Preference for concave surfaces of *Fucus* fronds by the dominant epifaunal species at the five study areas (2)

	Shore level				
	1	2	3	4	5
Alcyonidium hirsutum	n.s.(l)	**	n.s.	a	—
Electra pilosa	n.s.	* *	*	a	—
Flustrellidra hispida	n.s.	* *	* *	a	—
Dynamena pumila	* *	* *	* *	a	a
Campanularia flexuosa	a	n.s.	*	* *	a
Alcyonidium ancestrulae	*	* *	* *	* *	* *

   1: n.s.: not significant;   *: p<0.05.;   **: p <0.01 ;   a: too few data;
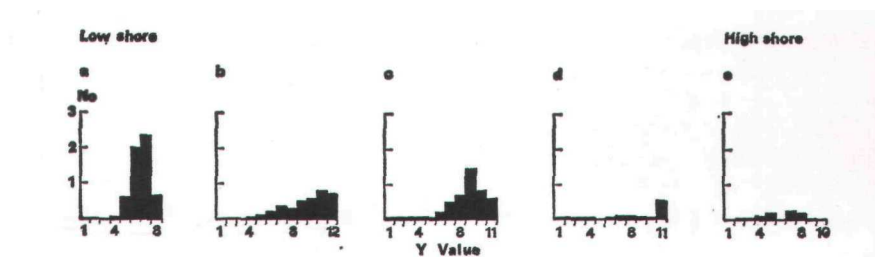— : spp. absent.
   2: Wilcoxon signed Ranks Test.

FIG. 8

Variations in the density of bryozoan ancestrulae (No/cm^2) on each segment along the longest fronds of *Fucus serratus* at different shore levels.

the higher shore levels. At shore level 1, by contrast, no significant preference for concave surfaces were shown by *Alcyonidium, Flustrellidra* or *Electra. Dynamena* and bryozoan ancestrulae, however, favoured concave surfaces at all shore levels though for the latter this preference was somewhat less pronounced in the low shore (Table 4).

TABLE 4

Utilisation of concave and convex surfaces of *Fucus* fronds by *Alcyonidium* ancestrulae at the five study areas

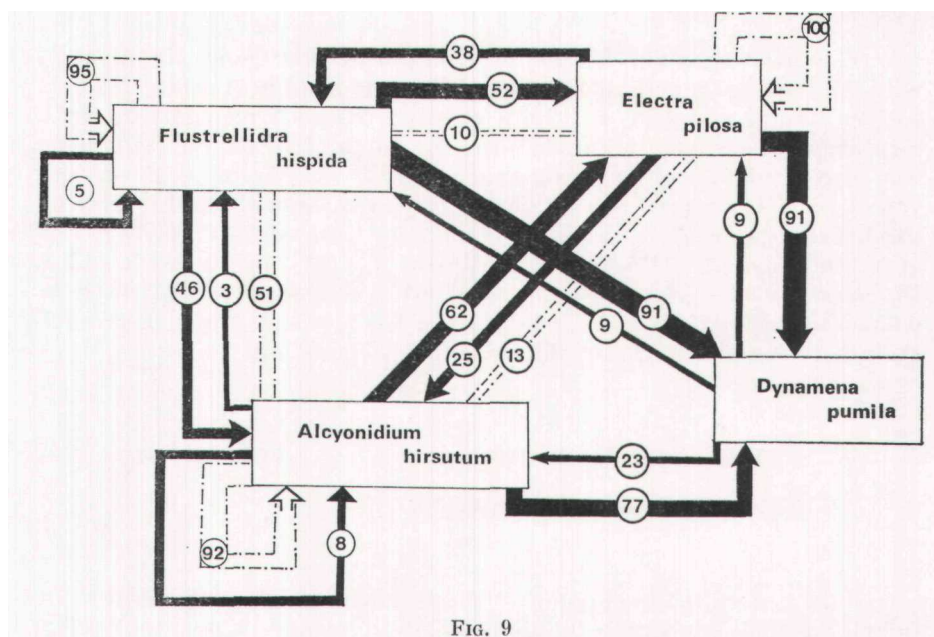| Shore level	Total no. of ancestrulae recorded.	Percentage present on	
		concave surface	convex surface
1	1765	63	37
2	1005	80	20
3	1526	80	20
4	136	94	6
5	184	91	9

Orientation of small colonies.

Where growth was evidently not impeded by interaction with other colonies or by the edge of the frond, young colonies of *Electra* (N = 27) and *Flustrellidra* (N = 55) were predominantly orientated towards the distal regions of the fronds (78 and 46 per cent respectively). Only a very small proportion of these colonies were growing towards the older more basal regions of the plants *(Electra* 0 per cent; *Flustrellidra* 6 per cent); the remaining colonies were orientated more or less laterally across the fronds.

Intercolony interactions.

Colony interactions were studied only in the four most abundant species—*Flustrellidra, Alcyonidium, Electra* and *Dynamena*.   The number of interactions, as one might perhaps predict, was strongly correlated with the relative abundance of these species as measured by their percentage cover of individual segment faces (r_s = 0.550; P<0.05). Thus significantly more interactions occurred in the low shore than for equivalent Y levels elsewhere. Moreover, at any one shore level, more interactions were found in the basal regions of the

plant than on younger less heavily encrusted distal segments. Inter-
actions were, however, still evident even where the abundance of a
particular species was comparatively low suggesting that colonies tend
to aggregate in the more favourable regions of each segment. Figure 9
summarises the dominant trends in inter- and intraspecific competi-
tion between the four major components of the epifaunal community
at the low shore site. Where colonies meet several types of interactions
are possible. One colony may overgrow that of another or may itself
be overgrown. Alternatively growth may simply be redirected away
from the edges along which the colonies meet without any actual over-

FIG. 9

Dominant trends in inter- and intraspecific competition among the dominant
fauna of *Fucus serratus* at shore level 1.

Each value represents the percentage of the total number of interactions involving
the species connected by the lines. Dotted strokes: colonies met with no over-
growth; thick strokes: overgrowth occurred in the direction indicated.

growth occurring. This latter reaction is most commonly encountered
where colonies of the same species meet i.e. intraspecific overgrowth
rarely occurs. On fronds which are particularly heavily encrusted,
Alcyonidium may occasionally form gelatinous finger-like projections
from the surface of the fronds. *Flustrellidra* appears to be the best
competitor for space in this system overgrowing *Alcyonidium* on 46
per cent of those occasions that these two species met. The latter
species on the other hand, overgrew *Flustrellidra* on only 3 per cent
of these occasions. Both *Flustrellidra* and *Alcyonidium* readily over-
grew *Electra,* the other major bryozoan in this community. Although
Electra did manage to overgrow both of its major competitors to a
limited extent, these overgrowths tended to consist of small, rather
scattered colonies or short chains of individuals. *Dynamena* was
extensively overgrown by all three bryozoans. The nature of several

of the above interactions varied slightly, though not significantly, with respect to position along the plant.

At shore levels 2 and 3 colony overgrowths were considerably reduced and between them these two stations had only 25-30 per cent of the number of interactions found at the low shore site. *Dynamena* again showed a high degree of overgrowth by the bryozoans and although *Flustrellidra* and *Alcyonidium* also frequently overgrew *Electra,* these two dominant bryozoans themselves showed no evidence of overgrowing each other at these higher shore levels.

Dynamena stem height.

The average stem height of *Dynamena* decreased significantly with increasing intertidal height e.g. 7.54 ± 2.0mm at shore level 1; 6.01 ± 1.4mm and 4.71 ± 1.2mm at levels 2 and 3 respectively (both significant at $P<0.05$, Mann Whitney). In the low shore, *Dynamena* was also significantly larger on concave (6.30 ± 1.35mm) than on convex (5.10 ± 1.00mm) faces ($P<0.05$, Wilcoxon Signed Ranks) and on the basal segments of the plants (8.49 ± 1.31mm at Y_1-Y_3, 6.40 ± 1.43 at Y_4 and beyond; $P<0.05$, Mann Whitney). At shore levels 2 and 3, *Dynamena* was significantly larger where it was most abundant (r. = 0.653 and 0.650; both at $P<0.05$) but at the low shore site, the correlation between size and abundance was not significant.

DISCUSSION

It is generally accepted that from low to high watermarks the intertidal zone represents a gradient of increasing stress to marine organisms and results in the vertical zonation patterns characteristic of most rocky shores (Southward, 1958; Lewis, 1964; Stephenson and Stephenson, 1972). In the Menai Strait, the major factor determing this gradient is the tidal regime since wave action is here minimal. Several factors, however, mitigate the amount of desiccation experienced at this particular site. These include the time of low water of spring tides (around 0630 and 1830 hrs.) the north facing scarp which shades the shore, and the local topography and heterogenous nature of the substratum itself. Two other factors likely to influence epifaunal viability in the Swellies are the strong tidal currents, via their affects on larval recruitment, and high turbidity, which may adversely affect the efficiency of many of the filter feeding taxa. These factors may also have a further indirect effect by their influence on plant growth and survival.

The highest occurring *F. serratus* plants at the collecting site more or less coincide with MHWN suggesting that this weed may be unable to withstand emersions of more than one tidal cycle. The critical upper limit of *F. serratus* distribution is probably determined by the suitability of conditions for settlement and subsequent sporeling survival since these early stages are apparently somewhat less

tolerant of desiccation than established plants (Baker, 1910). Baker (1909) also found that growth of *Fucus* and *Ascophyllum* varied according to the amount of time they were exposed. Intertidal algae require water for respiration and photosynthesis (Zaneveld, 1969) and decrease in plant size at higher tidal levels presumably reflects the rather limited amount of time available for these essential processes. Neither inadequate illumination (due to high turbidity) nor competition for space with laminarians seem to be important in limiting the size or abundance of *F. serratus* in the low shore. Although *Fucus* plants here were indeed smaller, their growth rate was not markedly different from plants at higher levels suggesting that they were probably not physiologically limited at this shore level. Their smaller size and reduced abundance at station 1 appear to be attributable to their prolonged exposure to strong tidal currents. These currents probably result in increased attrition amongst established plants and create poorer conditions for the settlement and subsequent survival of young plants.

Knight and Parke (1950) and Boaden *et al.* (1975) found that the establishment and growth of *F. serratus* varied between shore sites. The latter authors, working at several sites experiencing a wide range of environmental conditions within a very sheltered area, found that plant abundance and size were not related to current speed or local silt conditions. "Abrasion", however, did appear to retard growth. Nevertheless, factors favouring the establishment of plants also seemed to favour their subsequent growth. In the present investigation, plant abundance and size progressively decreased at higher shore levels although enhanced "abrasion" at the lowest site did appear to have a rather detrimental effect on abundance though not on growth.

The number of sessile epifaunal species decreased with intertidal height, probably due to the gradient of desiccation across the shore. At higher levels, the time available for feeding will also be significantly curtailed. Just as the total number of species present declined with increasing intertidal height, so too did the overall abundance of each species. No species seemed unaffected by, or increased in abundance with increasing shore level unlike the oligochaetes or the small bivalve *Lasaea rubra* respectively in Wieser's (1952) study. However, many of the common epifaunal species found during this investigation (e.g. *Flustrellidra* and *Alcyonidium)* are known to exhibit a specific preference for *F. serratus* (Ryland, 1959, 1962) and this alga is normally restricted to a relatively narrow vertical band just above the laminarian zone. Thus many of the attached epifaunal species which we have recorded are adapted to life near low water mark and may not therefore be able to profit by this unusually extended vertical range of *F. serratus* in this locality. Jackson (1977) suggests that colonial organisms may have relatively limited success intertidally compared with their competitive superiority in more amenable subtidal regions. The rapid expansion of these colonial forms does not permit thick calcareous walls to be produced and consequently many of these species are not especially well adapted to withstand excessive desiccation.

The total number of sedentary species recorded during this investigation is much lower than that found by Boaden *et al.* (1975).

Sponges and tunicates, for example, are largely absent on *F. serratus* in the Menai Strait. Nevertheless, those species that were present generally had a greater overall abundance than on plants from Strangford Lough. Strong water movement (though not wave action) is generally beneficial to filter feeding taxa. However, Moore (1973) suggests that turbidity may reduce species diversity and this is probably an important factor in the Menai Strait.

Boaden *et al.* (1975) and O'Connor *et al.* (1979 a) report that epifaunal species do not colonise plants randomly but occur in quite distinct zones. Our observations that *Alcyonidium hirsutum* generally occurred on more distal segments than *Flustrellidra* broadly agree with those of the above workers. However, *Flustrellidra* on plants from the Swellies were rather more basal than on plants from Strangford Lough possibly due to the relaxation of competition from sponges and tunicates. *Electro's* distribution on plants from these two geographical areas also differed. In Strangford Lough it has a generally low abundance whereas in the Menai Strait it appeared to show a marked preference for more basal segments.

O'Connor *et al.* (1979a) found that the zonation patterns of Bryozoa were influenced by differing environmental conditions. In our study these also changed with intertidal height. For example, in the low shore, *Alcyonidium* favoured segments Y_2—Y_5 whilst at shore levels 2 and 3 it was more abundant on segments Y_4—Y_7. This probably reflects the gradient of stress from desiccation which exists along the plants. The lowest Y segments soon dry out once they are exposed whilst fronds in the shrubbier parts of the plant retain water and provide a more humid environment throughout the period of emersion. Slightly enhanced protection against desiccation on the concave surfaces of a few tightly folded fronds may explain the locally high abundance of *Dynamena* at the highest shore level. The decline in the number of established colonies and the smaller stem height of *Dynamena* on the distal fronds at any given shore level is probably related to the form of plant growth i.e. by apical meristems.

Some epifaunal species achieve a certain degree of ecological isolation by their choice of weed. Although this will be documented in more detail in a subsequent paper, we can note that although *Electra* and *Dynamena* were equally abundant on both *F. serratus* and *Ascophyllum* at the same shore level in the Menai Strait, the congeners *Alcyonidium hirsutum* and *A. polyoum,* which are probably more alike in their ecological requirements and competitive ability, were most abundant on different species of weed; the former on *F. serratus,* the latter on *Ascophyllum.* Both these species are, however, found in abundance on *F. serratus* elsewhere (Ryland, 1962; Stebbing, 1973 b). Although *Spirorbis* was **relatively** abundant on *Fucus,* it was locally absent on *Ascophyllum,* whilst the bryozoan *Bowerbankia* was far more abundant on *Ascophyllum.*

Competition for space can sometimes be exceedingly severe along the fronds of *F. serratus* (Stebbing, 1971; O'Connor *et al,* 1979 b). Zonation of the dominant species will clearly result in some ecological isolation and will therefore reduce the amount of competitive interaction. Growth orientated towards the younger, less heavily encrusted

parts of the plants will have a similar effect (see also Ryland and Stebbing, 1971). Larval preferences at the time of settlement will obviously dictate the environment of future adult colonies. *Alcyonidium* settled in abundance between October and January with most ancestrulae being found on the distal segments of low shore plants. The presence of ancestrulae and the relative absence of adult colonies at higher shore levels suggests that post larval mortality is here quite severe. Further detailed observations on the settlement, growth and mortality of Bryozoa at different shore levels are therefore required if the dynamics of these dominant epifaunal species are to be properly understood.

Bryozoan larvae at all shore levels seemed to settle preferentially on the concave surfaces of the most distal Y segments. This has previously been noted both experimentally (Ryland, 1959) and in field populations (Hayward, 1973; Hayward and Harvey, 1974 a). It appears therefore, that even if these bryozoan larvae are unable to determine their dispersal to any great extent, they do, nonetheless, possess mechanisms which allow them to settle on selected areas of the fronds which are presumably best suited for adult survival (see also Hayward and Harvey, 1974 b; Ryland, 1976). The apparent preference for concave surfaces increased at higher shore levels. Here less time is available for settlement and concave surfaces may possibly retain a surface film of water rather more effectively thereby facilitating settlement and enhancing subsequent larval survival. In the low shore, however, where the weed is submerged for proportionately longer periods of time, this effect may be negligible though even here local eddies could conceivably carry more larvae onto the more protected concave surfaces. The preference for grooves (e.g. along the midrib of the frond) and concavities was particularly noticable where *Dynamena* was present when many of the ancestrulae settled in rows along the stolons of this hydroid.

Established colonies of most of the dominant species were also more abundant on concave surfaces above shore level 1. Whilst this could merely reflect improved conditions for settlement, it might also indicate that conditions for growth are also better on these surfaces. Hayward and Ryland (1975) however, could find no size differences between the colonies of *Alcyonidium hirsutum* from high and low density settlement areas on individual plants at the end of the growing season. The approximately equal distribution of adult colonies on concave and convex faces in low shore plants may be due to the relatively restricted amount of free space which is here available for growth; at high population densities, individual colonies grow around the edges of the frond and colonise the less optimal convex surface. Hayward (1973) noted that *Alcyonidium* larvae along the midrib groove did not appear to space themselves out at settlement. This might lead one to suggest, therefore, that more interactions should occur at low levels of encrustation than might be expected on a purely random basis.

Dynamena branch height as well as colony size was also greater on concave surfaces of the plants. Boaden *et al.* (1975) also found that their eleven most common species, except *Electra,* tended to be more abundant on concave surfaces, but this was not statistically

significant. However, they later found (Boaden *et al.,* 1976 a, b) that this preference was in fact significant for the sponges *Sycon* and *Grantia* and that the latter also achieved a greater size on concave surfaces. This strongly indicates that concave surfaces are more favourable, possibly due to the reduced amount of abrasion experienced here, and also to the local eddies which produce improved feeding conditions.

At the low shore level, most young *FAectra* colonies were growing distally along the fronds. This agrees with the observations of Ryland and Stebbing (1971) who showed that this bryozoan grows towards the youngest parts of the plant. Young *Flustrellidra* colonies were not so obviously orientated though it was noticeable that only 6 per cent of these colonies grew towards the base of the plants. Orientated growth towards the younger distal segments is clearly adaptive since these regions will generally be less heavily encrusted. Furthermore, a considerable amount of frond attrition occurs from the older basal regions of *Fucus* plants.

The number of interactions between individual colonies was well correlated with their overall abundance. Stebbing (1973, a, b) examined the competitive interactions between the epifauna of *Fucus serratus* at Wembury whilst Seed and Boaden (1977) report data for this weed in Strangford Lough. The outcome of intercolony competition in our investigation is much the same as in previous investigations. We found little evidence for intraspecific overgrowths whilst inter-subspecific competitive ability declined through the sequence—*Flustrellidra, Alcyonidium, Electra* and *Dynamena.*

The major difference between the above studies is the actual degree of interspecific overgrowth. Hayward (1973) found that *Alcyonidium* grew most rapidly in early summer until all available space was occupied by a mosaic of interlocking colonies. This may go some way to explaining the higher incidence of overgrowths recorded in our investigation. Seed and Boaden (1977) and Stebbing (1973 a, b) sampled their plants in February—March and June—July respectively whilst most of the plants in our study were collected in November i.e. at the end of the growing season. The character of certain interactions changed slightly with position on the plant. For example, *Flustrellidra's* competitive ability over *Alcyonidium* declined with Y level (see also O'Connor *et al.,* 1979 b). This may reflect differential growth rates of the individual bryozoan species at different levels of the plant. Although *Flustrellidra* emerges as the superior competitor on *F. serratus* in the Menai Strait, it should be remembered that interactions between bryozoa and tunicates or sponges nearly always result in the bryozoans' death (Ryland, 1976).

It will be seen from the above account that the change in environmental conditions with intertidal height appears to have a pronounced effect on the abundance and size of *F. serratus* and. on its attached epifauna. At low shore levels where *Fucus* plants are rather small, competition between the dominant epifaunal species is quite severe resulting in numerous intercolony overgrowths. At higher shore levels, however, reduced colonisation and slower growth rates result in considerable free space even on the most favourable fronds; inter-

actions are here consequently much reduced. The dominant epifaunal organisms appear therefore to be unable to take full advantage of the extra space available to them by virtue of the extended vertical distribution of *F. serratus* in this particular locality.

Summary

The influence of shore level on the size and abundance of *Fucus serratus* and its associated epifauna in the Menai Strait, North Wales, has been examined. *Fucus* plants became progressively smaller and less abundant with increasing intertidal height although prolonged exposure to strong tidal currents adversely affected plants at the lowest shore levels.

Of the 19 sessile taxa present on *F. serratus* only the five most abundant species were considered in detail. These were the bryozoans *Flnstrellidra hispida, Electra pilosa* and *Alcyonidium hirsutum* and the hydroids *Dynamena pumila* and *Campanularia flexuosa*. The establishment and abundance of these epifaunal species decreased markedly at the higher shore levels. One or more of the following mechanisms promote ecological isolation—choice of plant, zonation of species along individual fronds, preference for concave or convex surfaces and colony growth orientated towards the younger, less encrusted distal regions of the plants. Where these mechanism fail, competition for space can be severe, particularly in the most favourable parts of low shore plants. A competitive hierarchy through the sequence *Flustrellidra—Alcyonidium—Electra—Dynamena* was clearly evident. The larvae of *Alcyonidium* settled in abundance between October and January and exhibited a clear preference for concave surfaces of distal fronds at all shore levels. The stem height of *Dynamena* varied with respect to shore level and position along the plant.

This investigation strongly suggests that the major epifaunal species of *F. serratus* are unable to take full advantage of the additional space provided by the unusually extended zone of this alga in this particular geographical locality. This probably reflects a general inability of these sessile taxa to resist the increased desiccation experienced at higher tidal levels.

REFERENCES

BAKER, S.M., 1909. — On the causes of the zoning of brown seaweeds on the seashore. I. *New Phytol.,* 8, *pp.* 196-202.

BAKER, S.M., 1910. — On the causes of the zoning of brown seaweeds on the seashore. II. *New Phytol.,* 9, *pp.* 54-67.

BOADEN, P.J.S., O'CONNOR, R.J. and SEED, R., 1975. — The composition and zonation of a *Fucus serratus* community in Strangford Lough, Co. Down. *J. exp. mar. biol. Ecol.,* 17, *pp.* 111-136.

BOADEN, P.J.S., O'CONNOR, R.J. and SEED, R., 1976 a. — The fauna of a *Fucus serratus* community: ecological isolation in sponges and tunicates. *J. exp. mar. Biol. Ecol.,* 21, *pp.* 249-267.

BOADEN, P.J.S., O'CONNON, R.J. and SEED, R., 1976 b. — Some observations on the size of the sponges *Granfia compressa* (Fabr.) and *Sycon ciliatum* (Fabr.) in Strangford Lough, Co. Down. *Proc. Roy. Irish. Acad.* 76 B, *pp.* 535-542.

COLMAN, J., 1940. — On the fauna inhabiting intertidal seaweeds. *J. mar. biol. Ass. U.K.,* 24, pp. 129-183.

ELLIOT, J.M., 1973. — *Some methods for the Statistical Analysis of samples of Benthic Invertebrates.* Freshwater Biological Association Pub. 25.

HAGERMAN, L., 1966. — The macro- and microfauna associated with *Fucus serratus* L., with some ecological remarks. *Ophelia* 3, *pp.* 1-43.

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, *pp.* 107-113.

HAYWARD, P.J. and HARVEY, P.H., 1974 a. — The distribution of settled larvae of the bryozoans *Alcyonidium hirsutum* (Fleming) and *Alcyonidium polyoum* (Hassall) on *Fucus serratus L. J. mar. biol. Ass. U.K.,* 54, *pp.* 665-676.

HAYWARD, P.J. and HARVEY, P.H., 1974 b. — Growth and mortality of the bryozoan *Alcyonidium hirsutum* (F.) on *Fucus serratus* (L.). *J. mar. biol. Ass, U.K.,* 54, *pp.* 677-684.

HAYWARD, P.J. and RYLAND, J.S., 1975. — Growth, reproduction and larval dispersal in *Alcyonidium hirsutum* (Fleming) and some other Bryozoa. *Pubbl. Staz. Zool. Napoli,* 39, Suppl. 1, *pp.* 226-241.

JACKSON, J.B.C., 1977. — Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *Am. Nat.* 111, pp. 743-767.

KIGHTLEY, P.J., 1977. — A review of literature concerning the Menai Strait. Unpublished MSc. Thesis U.C.N.W. Bangor. 31 *pp.*

HITCHING, J.A. and EBLING, F.J., 1967. — Ecological studies at Lough Ine. *Adv. ecol. Res.,* 11, *pp.* 197-291.

KNIGHT, M. and PARKE, M., 1950. — A biological study of *Fucus vesiculosus* (L.) and *Fucus serratus* (L.). *J. mar. biol. Ass. U.K.,* 29, *pp.* 439-514.

L'HAUDY, J.P., 1962. — Observations sur le peuplement épiphyte des lames de *Laminaria saccharina* (Linné) Lamoureux en Baie de Morlaix (Finistère). *Cah. Biol. Mar.,* 3, *pp.* 115-127.

LEWIS, J.R., 1964. — *The Ecologa of Rocky Shores. E.U.P.,* 323 *pp.*

MOORE, P.G., 1973. — Bryozoa as a community component on the North East coast of Britain. *In: Living and Fossil Bryozoa,* ed. G.P. Larwood, Academic Press, New York, *pp.* 21-36.

O'CONNOR, R.J., BOADEN, P.J.S. and SEED, R., 1975. — Niche breadth in Bryozoa as a test of competition theory. *Nature* London, 256, *pp.* 307-309.

O'CONNOR, R.J., SEED, R. and BOADEN, P.J.S., 1979 a. — Effects of environment and plant characteristics on the distribution of Bryozoa in a *Fucus serratus* L. community, *J. exp. mar. Biol. Ecol.,* 38, *pp.* 151-178.

O'CONNOR, R.J., SEED, R. and MADEN, P.J.S., 1979 b. — Resource space partitioning by the Bryozoa of a *Fucus serratus* L. community. *J. exp. mar. Biol. Ecol., in press.*

RYLAND, J.S., 1959. — Experiments on the selection of algal substrates by polyzoan larvae. *J. exp. Biol.,* 36, *pp.* 613-631.

RYLAND, J.s., 1962. — The association between Polyzoa and algal substrata. *J. Anim. Ecol.,* 31, *pp.* 331-338.

RYLAND, J.S., 1976. — Physiology and Ecology of Marine Bryozoa. *Adv. mar. Biol.,* 14, pp. 285-443.

RYLAND, J.S. and STEBBING, A.R.D., 1971. — Settlement and orientated growth in epiphytic and epizoic bryozoans. *In: IV th European Marine biological Symposium,* ed. D.J. Crisp. C.U.P. Cambridge, *pp.* 105-123.

SEED, R. and BOADEN, P.J.S., 1977. — Epifaunal ecology of intertidal algae. *In: Biology of Benthic Organisms,* eds. B.F. Keegan, P.O. Ceidigh and P.J.S. Boaden. Pergamon Press, New York, *pp.* 541-548.

SOUTHWARD, A.J., 1958. — Zonation on rocky shores. *Biol. Rev.,* 33, *pp.* 137-177.

STEBBING, A.R.D., 1971. — The epizoic fauna of *Flustra foliacea* (Bryozoa). *J. mar. biol. Ass. U.K.,* 51, *pp.* 283-300.

STEBBING, A.n.D., 1973 a. — Observations on colony overgrowth and spatial competition. *In: Living and Fossil Bryozoa.* ed. G.P. Larwood. Academic Press, New York, *pp.* 173-183.

STEBBING, A.R.D., 1973 b. — Competition for space between the epiphvtes of *Fucus serratus* (L.). *J. mar. biol. Ass. U.K.,* 53, *pp.* 247-281.

STEPHENSON, T.A. and STEPHENSON, A., 1972. — *Life between the Tide Marks on Rocky Shores.* Freeman. 425 *pp.*

WIESER, W., 1952. — Investigations on the microfauna inhabiting seaweeds on rocky coasts. *J. mar. biol. Ass. U.K.,* 31, pp. 145-174.

ZANEVELD, J., 1969. — Factors controlling the delimitations of littoral benthic marine algal zonation. *Am. Zool.,* 9, *pp.* 367-391.