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

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Abstract : The reproductive and growth cycles of two common ctenostome bryozoans within a *Fucus serratus* L. community in the Menai Strait, North Wales, are described. *Alcyonidium hirsutum* (Fleming), started to develop embryo sacs in September and larval release occurred between October and January. In *Flustrellidra hispida* (Fabricius), embryo sacs appeared in February or March and larval release occurred between May and November. Fecundity in both bryozoans was linearly related to colony area. Few colonies of either species survived to breed in their second year. After settling in October, *A. hirsutum* grew very slowly throughout winter ; between April and July, growth was exponential, but slowed thereafter. Growth in *F. hispida* started immediately after settlement in July and continued until September ; little or no increase in colony size occurred over winter, but between April and July growth proceeded rapidly. Colony size in both bryozoans was reduced at high population density but no significant size differences occurred anongst colonies attached to the concave or convex surfaces of *F. serratus*. Populations of both species were always heavily skewed towards small colonies.

Résumé : Les cycles de reproduction et de croissance de deux bryozoaires cténostomes communs dans une communauté à *Fucus serratus* L. dans le Menai Strait, Pays de Galles du Nord, ont décrits. Chez *Alcyonidium hirsutum* (Fleming), les sacs embryonnaires commencent à se développer en septembre et les larves sont libérées entre octobre et janvier. Chez *Flustrellidra hispida* (Fabricius), les sacs embryonnaires apparaissent en février ou mars et les larves sont libérées entre mai et novembre. Chez les deux bryozoaires, il existe une relation linéaire entre l'aire des colonies et la fécondité. Peu de colonies des deux espèces survivaient jusqu'à la reproduction pendant leur deuxième année. Après la fixation en octobre, *A. hirsutum* se développe très lentement pendant l'hiver ; entre avril et juillet, la croissance est exponentielle, après quoi elle ralentit. Chez *E. hispida*, la croissance suit immédiatement la fixation en juillet et se continue jusqu'en septembre ; la taille des colonies augmente de très peu ou pas du tout pendant l'hiver, mais entre avril et juillet, la croissance est rapide. Chez les deux bryozoaires, la taille des colonies est réduite quand la densité des peuplements est élevée, mais il n'y a pas de différence de taille significative entre les colonies fixées sur les surfaces concaves ou convexes de *F. serratus*. Dans les populations des deux espèces, les colonies de petite taille sont toujours beaucoup plus fréquentes.

INTRODUCTION

The fronds of many low intertidal and shallow subtidal macroalgae in temperate waters often provide suitable and extensive habitat for a wide range of marine invertebrates. Whilst species from virtually all the major animal phyla are represented, these diverse epialgal communities are typically dominated by sessile suspension feeding taxa such as bryozoans, hydroids, spirorbids, sponges and tunicates (e.g. Stebbing, 1973, Boaden *et al.* 1975, Seed & O'Connor, 1981a ; Fletcher & Day, 1983). Early accounts of these faunas were largely restricted to distributional studies and only within the past decade or so has the emphasis shifted to an understanding of community organisation and dynamics (e.g. O'Connor

et al. 1980, Seed & O'Connor, 1981b ; Seed *et al.* 1983, Cancino, 1986 ; and references therein) as well as of the complex interactions that can exist between these faunas and their algal hosts (e.g. de Burgh & Fankboner, 1979 ; Oswald & Seed, 1986, Williams & Seed, 1991).

In an earlier study Wood and Seed (1980) showed that in the Menai Strait, North Wales, the serrated wrack *Fucus serratus* L. supported twelve relatively comnon sessile invertebrates. Amongst these, the fleshy encrusting bryozoans, *Alcyonidium hirsutum* (Fleming) and *Flustrellidra hispida* (Fabricius), which are often specifically associated with the serrated wrack, were sufficiently abundant throughout the year to merit a more detailed investigation of their life history characteristics. In this paper we have described the reproductive and growth cycles of these dominant epi-algal species, whilst in a subsequent paper we will examine their settlement and mortality and briefly consider how their life history characteristics are closely integrated with those of their algal host.

The study area

The Menai Strait is a narrow tidal channel separating Anglesey from the North Wales mainland. A full description of the study area is provided elsewhere (Wood & Seed, 1980 ; Wood, 1983). Briefly, however, the area is protected from wave action but is scoured by strong tidal currents which can attain 1.2 $m.sec^{-1}$ on an ebbing tide and 0.8 $m.sec^{-1}$ on a flooding tide. Turbidity within the Strait is generally high and there is considerable vertical mixing within the water column. The tidal regime ranges from approximately 7.2 m on extreme spring tides to 3.0 m on extreme neap tides. The substratum varies from open bedrock to boulders and rocks of various sizes, often on a gravelly, sandy or muddy bottom. Four physically contrasting sites were selected for study, two of which (sites 1 and 4) were located near Treborth on the North Wales mainland and two (sites 2 and 3) at Church Island on the Anglesey coast.

Site 1 is situated in the main channel of the Strait and is thus subjected to the full force of the tidal flow. Here a broad *F. serratus* belt extends from just above the *Laminaria digitata* zone (c.1.5 m CD) to a point 4.7 m above Chart Datum where the uppermost plants intermingle with *F. spiralis*. Two shore levels were chosen for study, one at LWST immediately above the kelp zone (site 1 low), the other approximately 1.6 m further upshore (site 1 mid). *Sites 2 and 3* are situated outside the main tidal channel. *Site 2* is located in the outflow channel of a bay created by two small islands. The *F. serratus* zone is approximately 1 m wide, delimited below by *Laminaria hyperborea* and *L. digitata* and above by *F. vesiculosus* and *Ascophyllum nodosum*. *Site 3* is protected by a muddy bank on the flood tide, and water movement, even on the ebbing tide, is quite sluggish. The *F. serratus* belt rises from a mixed *Halidrys*-laminarian zone for about 1 m where it gives way to *A. nodosum*. No reproductive or growth data were collected at this site but we include this brief description simply to avoid the need for further site descriptions in our subsequent paper. *Site 4* is situated in an inlet at the seaward edge of a small boat slipway. Thus, although quite close and similar to site 1, this site is considerably more sheltered from the main tidal current.

Two shore levels were selected, one just above the kelp zone (site 4 low) and one about 1.6 m further upshore (site 4 mid).

MATERIALS AND METHODS

Two main methods have been extensively used for sampling natural populations, one of which involves the routine collection of population subsamples. These subsamples should be sufficiently large to overcome any inherent biological variation but not so large that the population is effectively decimated. Whilst valuable, data generated by this method are sometimes difficult to interpret and a potentially more powerful method, which is especially suitable for sessile species, is to regularly monitor selected individuals (or colonies) within the population over a given time interval. Individuals chosen for study should be representative of the population as a whole, and initially large numbers should be selected in order that sufficient survive to the end of the census period. This method enables the precise fate of each individual to be recorded from the time of its recruitment to its subsequent removal from the population. Both methods have been used in this investigation.

Monitor method : In October 1978 several *F. serratus* plants at site 4 (mid and low) were selected and marked using strips of coloured plastic securely attached to the thickened stipes. Distal fronds were then chosen, tagged with lengths of coloured string and monitored in the field over a period of approximately two years. Every two to four weeks these fronds were supported on a perspex board and overlaid with sheets of clear acetate paper on which frond outline, the exact location of any recently settled *Alcyonidium* and the outlines of individual colonies were recorded using a fine permanent marker pen. The fronds of *F. serratus* have recognisable concave and convex surfaces and each of these was monitored separately. From these data the area of each frond segment and each bryozoan colony could then be calculated. *Alcyonidium hirsutum* and its congener *A. polyoum*, are now thought to comprise several genetically distinct but morphologically indistinguishable species (Thorpe & Ryland, 1979). Although both taxa are known to colonise *F. serratus* in the Menai Strait, *A. polyoum* was only rarely encountered at this particular site. The ancestrulae of these two closely related bryozoans are difficult to distinguish in the field and consequently, therefore, all recently settled *Alcyonidium* were assumed to be *A. hirsutum*. This assumption was subsequently confirmed when colonies had grown to a size at which they could be positively identified and only *A. hirsutum* was found to be present on the monitored fronds.

At site 4 mid approximately 1 000 recently settled *A. hirsutum* were monitored from October 1978 until August 1979 by which time they had all died. The following year almost 1 000 individuals were monitored at site 4 low over a period of approximately six months whilst at site 4 mid just over 2 500 individuals were followed for one year when all surviving colonies (n = 32) were harvested. The final areas of these colonies were measured and the number of embryo sacs and number of embryos within each sac recorded. It was

not possible to monitor *F. hispida* in this way because in the field young colonies of this species were indistinguishable from groups of closely settled ancestrulae. The monitor programme was therefore supplemented with subsamples of *F. serratus* taken from neighbouring plants.

Sampling method : From October 1978 until January 1981 at site 4 mid, and until September 1979 at site 1 mid, populations of *A. hirsutum* and *F. hispida* were sampled at approximately monthly intervals. Samples comprised five to ten distal frond segments about 20-30 cm long, each of which as collected from a different plant. These were stored in 5 % seawater formalin until required. Each frond segment was subsequently reduced to one main apical tip together with one or two lateral branches which were cut off close to the main frond stem. The number of *A. hirsutum* and *F. hispida* on each surface of the segment was recorded, the frond outline traced onto acetate sheets, and the area of each segment and density of bryozoans calculated. Approximately twenty colonies of each *Alcyonidium* and *Flustrellidra* year group on each frond segment, half from the concave surface and half from the convex surface, were then traced onto acetate sheets and their areas estimated. For each breeding colony the number of embryo sacs, the number of embryos within each sac and the number of feeding zooids per unit area of colony surface were also recorded.

Several more limited surveys and monitors were also undertaken. In April and May 1979 at site 1 low and site 2 respectively, samples of breeding colonies of *F. hispida* were collected for comparison with those at site 1 mid and site 4 mid. In March 1980 several plants were collected at site 2 in order to investigate the effects of initial bryozoan density on subsequent growth rates. In the laboratory several distal fronds, with different *Alcyonidium* densities, were selected and the position of each ancestrula marked on acetate sheets. The plants were then returned to the shore on the following low tide and attached to larger "host" plants. After six weeks these fronds were recovered and the size of each colony and the degree of interaction with neighbouring colonies recorded.

RESULTS

Reproduction :

Alcyonidium hirsutum. Colonies of *A. hirsutum* started to develop embryo sacs in September when they were approximately ten months old. Figure 1A illustrates the timing of reproduction in those cohorts which settled in 1978 and 1979. Reproductive development was first detected by the appearance of small white bodies beneath the lophophore. These gradually consolidated into white spherical masses which comprised the developing embryos (larvae). By October, when settlement was first detected on the distal frond segments, several embryos were clearly visible within each sac. Larval release appeared to be highly synchronised in that by November the young distal fronds were peppered with recently attached larvae (ancestrulae) and most colonies had shed all their larvae by January. A large proportion of the *Alcyonidium* colonies at site 4 mid (82 % in 1979 and

95 % in 1980) actually developed embryo sacs ; this compared with 91 % at site 1 (mid) during 1979. Although it was generally the smaller colonies which failed to reproduce (Table I ; see also Fig. 5) there was a large variation in the size of breeding colonies. Thus, whilst colonies < 5 mm^2 sometimes contained embryos, other colonies, up to 130 mm^2, did not.

The initial linear relationship between fecundity and colony size was progressively lost as colonies gradually shed their larvae (Fig. 2A). There appeared to be a systematic maturation of embryo sacs within individual colonies from the oldest central part of the colony to the youngest regions around the growing periphery. Consequently, estimates of colony fecundity were made at the start of the breeding season so as to eliminate any potential errors due to partial larval release ; colonies sampled in September gave higher fecundity estimates than those sampled in October when larval release had started. The regressions for the 1978-79 and 1979-80 generations at site 4 mid (Table I) were in close agreement and indicate that colonies of 50 mm^2 and 100 mm^2 produced an average cf 6.7-8.7 and 17.1-20.4 embryo sacs respectively. Whilst total colony fecundity in *A. hirsutum* is proportional to colony area, relative fecundity (= no. larvae.mm^2 of colony surface) was independent of colony size (r^2 = 0.055 and 0.086 respectively for the 1978-79 and 1979-80 year classes at Site 4 mid ; both at $p > 0.05$) ; thus small colonies produced just as many embryo sacs per unit area as did the larger colonies.

In order to calculate the number of feeding zooids required to support each *Alcyonidium* embryo, we first counted the number of feeding zooids in colonies of different size. These data were then used to generate the following regression :

$$\text{no. feeding zooids} = 0.21 \text{ colony area } (mm^2) + 0.44.$$

Knowing the average number of embryos in each embryo sac (11.4 ± 3.3SD) and the number of sacs per unit area of colony, the number of feeding zooids required to support each embryo could then be estimated. For example, a colony of 100 mm^2 and consisting of 474 zooids would have supported, on average, 176 embryos ; thus an average of 2.7 feeding zooids were required to produce each enbryo. Of the 2 500 ancestrulae that were initially marked in the population monitor only 32 (= 1.3 %) survived to produce breeding colonies. These colonies in turn produced a total of 381 embryo sacs each containing on average 11.4 embryos. Thus, the population subsample produced just over 4 300 larvae. From these data it was estimated that this population of *A. hirsutum* could withstand a loss of up to 42 % of its larvae and yet still be capable of maintaining itself. *Alcyonidium* colonies in this population rarely survived to breed twice ; indeed, less than 2 % actually survived long enough to breed once and only a very small proportion of these could conceivably have survived for a further year to breed for a second time. Even so, a few *A. hirsutum* colonies were observed for two years at site 1 (mid).

Flustrellidra hispida. The timing and duration of the breeding cycle in the 1978 and 1979 generations of *F. hispida* are illustrated in Figure 1B. Whilst a few breeding colonies could be observed when these were only 5-6 months old (Sept-Oct.) most colonies first reproduced when they were about one year old. The 1978 year class at site 4 mid started to

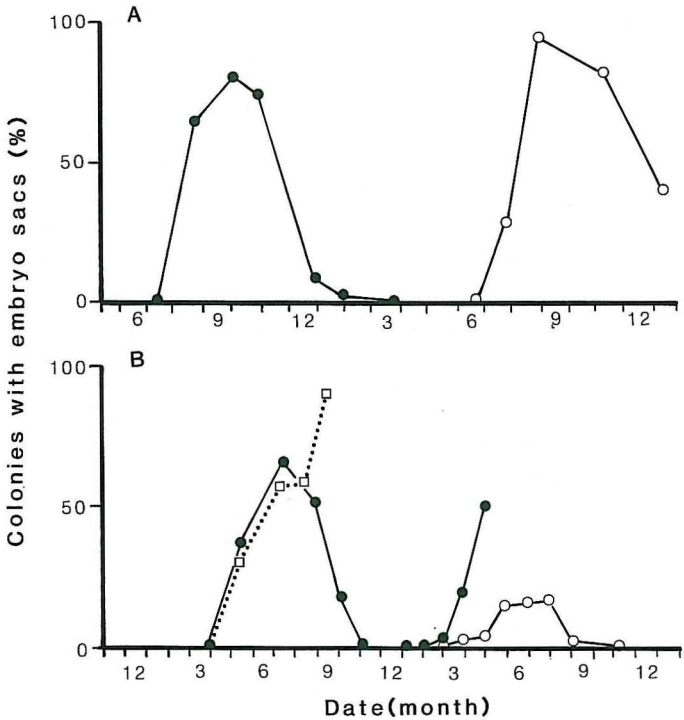

Fig. 1 : Reproductive cycles of A) the 1978-79 (•) and 1979-80 (o) year classes of *A. hirsutum* at site 4 mid and B) the 1978 (•) and 1979 (o) year classes of *F. hispida* at site 4 mid, and the 1978 year class (□) at site 1 mid. Reproduction expressed as % of colonies with embryo sacs.

TABLE I

Differences in fecundity and the mean size (± 1SD, mm²) of breeding and non breeding colonies of *A. hirsutum*. Fecundity expressed as number of embryo sacs (es) per colony. A = colony area. No fecundity data for sample 11.80 as larval release had already started.

Site	Date	Colony size		Fecundity	No.es.col^{-1} A	
		breeding	non breeding		50 mm²	100 mm²
4 Mid	10.79	37.2 (18.8)	8.1 (5.5)	No(es) = 0.18A-0.9	8.1	17.1
	10.80 (monitor)	79.5 (49.1)	13.8 (19.7)	No(es) = 0.18A-0.3	8.7	17.7
	9.80	147.1(143.0)	100.9 (168.0)	No(es) = 0.28A-7.1	6.7	20.4
	11.80	170.4 (182.4)	31.0 (31.2)	-	-	-
1 Mid	9.79	79.8 (67.8)	4.0 (2.5)	No(es) = 0.28A + 4.3*	18.2	32.1

* Embryo sacs at early stage of development and zooids containing developing sperm had probably been mistaken for embryo sacs thus inflating the fecundity estimate.

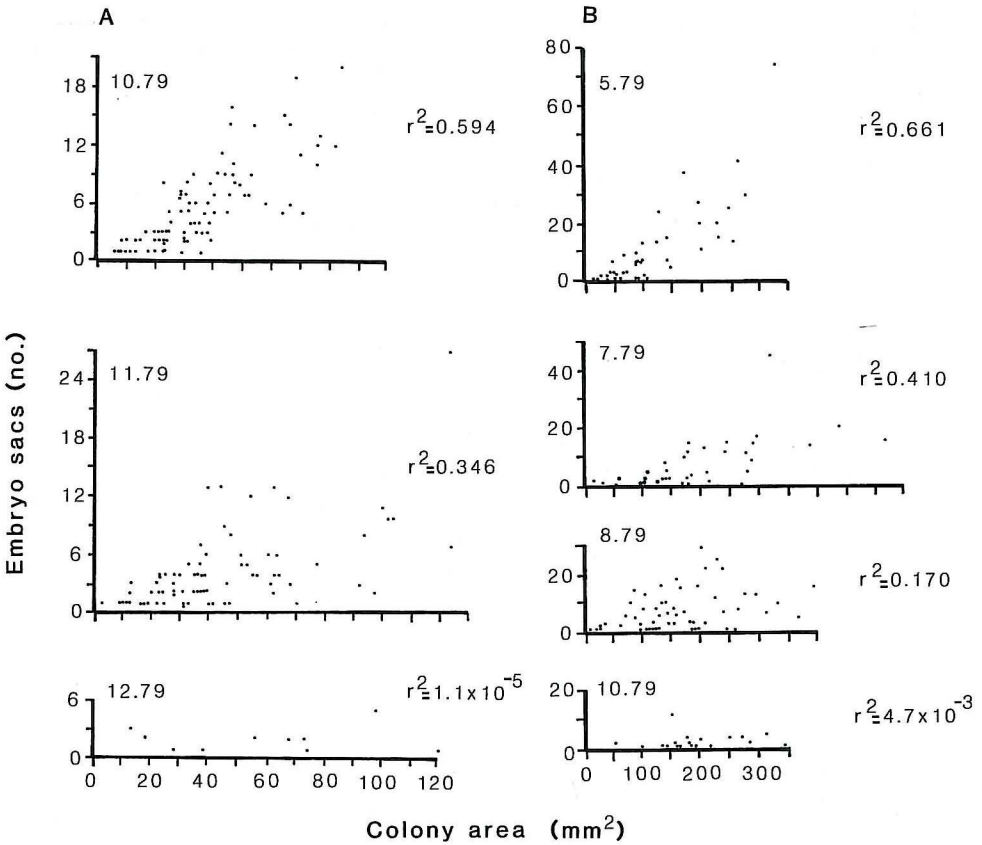

Fig 2 : Relationship between fecundity (no. embryo sacs.colony^{-1}) and colony area in A) the 1978-79 year class of *A. hirsutum* and B) the 1978 year class of *F. hispida* at site 4 mid.

develop enbryo sacs in April 1979. Initially small yellowish spheres appeared beneath the lophophores of several zooids. Gradually as the embryos developed these lophophores degenerated and the frontal membranes were raised as the embryos grew larger and more elongate. More colonies developed embryo sacs as the summer progressed but even at its peak only 66 % of this population was reproductively active. This value then declined through the autumn months until by November only 2 % of the colonies were still in breeding condition. During 1980 the 1978 cohort started to redevelop embryos earlier (i.e. in Feb.) and more extensively than in the previous year (50 % were reproductively active in April 1980 compared with 25 % in April 1979). Nevertheless, the contribution of this cohort to the supply of larvae was probably quite limited since relatively few colonies actually survived for two years. Moreover, many of these ageing colonies showed obvious signs of damage as the fronds on which they occurred were experiencing considerable blade loss. The 1979 cohort started to develop embryo sacs in March 1980 but only a small pro-

portion (<20 %) was reproductively active at any given time (Fig. 1B). The breeding season began earlier than in the previous year and extended from March to September rather than from May-November. Figure 1B also compares the seasonal breeding patterns at the 2 mid shore sites in 1979. At site 4 most of the population was reproducing by July whereas at site 1 the proportion of breeding colonies continued to increase until the last sampling date in September. Table II reveals the marked intersite variation (15-100 %) that existed in the proportion of the *F. hispida* populations in breeding condition ; the relative sizes of breeding and non breeding colonies at each site are also compared. Whilst very small colonies (< 10 mm^2) were capable of breeding, not all did so whilst more occasionally even quite large non-breeding colonies (>200 mm^2) were encountered.

Early in the reproductive season all *Flustrellidra* enbryos were immature but the percentage of mature larvae increased as the season progressed. Even so, at site 4 mid 14 % of all embryos were still immature in October 1979 and as maturation takes between one and two months (in that embryo development began in May and larval settlement was first detected in July) it seems likely that these embryos were newly formed and that individual colonies were thus breeding repeatedly. Figure 2B further suggests that individual colonies did not release all their larvae simultaneously as the correlation between size and fecundity worsened as larval release progressed. Whilst some *Flustrellidra* colonies at the start of the breeding season contained numerous embryo sacs, others contained very few (Fig.3). This could be interpreted as a short, high reproductive effort by the former and a prolonged low effort by the latter.

When the number of larvae per unit colony area in *F. hispida* at the start of each breeding season was related to colony size at the different study sites, the resulting correlations ranged from weakly positive ($r^2 = 0.255$; $p < 0.05$ at site 4 mid) to weakly negative ($r = 0.198$; $p < 0.05$ at site 1 low). Thus, overall, relative fecundity in *F. hispida*, as in *A. hirsutum*, appeared to be virtually independent of colony size. Colonies at site 2 and site 1 mid had rather more embryos per unit area than the other sites. In Table II the minimum number of feeding zooids needed to produce each embryo was estimated using the follo-

TABLE II

Differences in fecundity and the mean size (± 1SD, mm^2) of breeding and non breeding colonies of *F. hispida*. Fecundity expressed as number of embryo sacs(es) per colony. A = colony area. Because of poor correlations of fecundity estimates ($r^2 = 0.213$-0.585) only the most fecund colonies were used to compare intersite reproductive effort (minimum no. of feeding zooids per larva).

Site	Date	% breed. colonies	Colony size		Colony age (months)	Fecundity	Min. no zooids. $larva^{-1}$
			breeding	non bredding			
1 Mid	5.79	26	118.0 (63.6)	38.6 (33.0)	12	No(es) = 0.13 A-3.4	1.3
1 Low	5.79	31	70.4 (38.6)	20.7 (23.5)	12	No(es) = 0.03A+1.9	2.0
2	4.79	100	47.2 (31.6)	-	12	No(es) = 0.05A + 2.4	1.3
4 Mid	5.79	37	122.9 (79.1)	26.6 (23.3)	12	No(es) = 0.15A-6.6	1.9
4 Mid	4.80	49	138.6 (151.4)	24.0 (25.8)	24	No(es) = 0.15A-6.7	2.0
4 Mid	5.80	15	47.8 (36.5)	11.1 (11.5)	12	No(es) = 0.10 A-2.1	2.7

wing regression, which we obtained from counts of the number of feeding zooids present in colonies of different size,

$$\text{no.feeding zooids} = 1.98 \text{ colony area } (mm^2) + 1.3$$

together with the observation that, on average, each *F. hispida* embryo sac contained 5.9 ± 1.7SD embryos. Due to the poor correlation of the fecundity estimates (Table II) only the most fecund colonies at each site were used to compare intersite reproductive effort.

Growth :

Alcyonidium hirsutum. The growth of two cohorts of *A. hirsutum* are illustrated in Figure 4A. Negligible growth occurred from the beginning of settlement until the following April in both these year classes ; colony size averaged 0.2-0.3 mm^2 in October but this had increased to only 0.6-0.9 mm^2 by March. Between March and July growth was exponential. The 1978-79 year class reached a plateau in mean colony size and then oscillated about this value (35-45 mm^2) until the following spring. The 1979-80 cohort achieved its peak size (240 mm^2) in July but thereafter mean colony size declined until January 1981. Log plots (Fig. 4B) clearly reveal the sigmoidal growth pattern of this *Alcyonidium* population. A 5-fold difference existed in the maximum mean size of colonies achieved by the two year classes at site 4 mid (Fig. 4A) ; a corresponding difference in colony density was also noted on the sampled fronds. Thus, whilst in August 1979 there was an average of 1.2 colonies.cm^2 of frond surface, in August 1980 the average density was only 0.25 colonies.cm^2. The dense settlement of *A. hirsutum* in 1978 therefore resulted in numerous small colonies whilst the light, but more variable settlement, in 1979 resulted in fewer larger colonies. This annual variation in colony size may have continued over the following year since settlement of *A. hirsutum* during 1980 was again particularly dense. The timing of growth at site 1 mid (Fig. 4C) was similar to that at site 4 mid (Fig. 4A). However, the maximum mean size of colonies at site 4 mid was only half that achieved by those which settled at site 1 mid in 1978.

By July in both years of the study *A. hirsutum* colonies had formed tight mosaics on the fronds leaving little remaining free space. Nevertheless, a few colonies did continue to grow until October. As *A. hirsutum* colonies increased in size they tended to meet adjacent colonies over an ever- increasing proportion of their growing edge which thus restricted their potential for further growth. Thus, during the summer months (June-July) as growth rate slowed, colonies with more than 75 % of their growing edge surrounded by other colonies were, on average, the smallest whilst those with <25 % of their peripheral growing margin surrounded were the largest (Table III). Colonies which were completely free from interactions with neighbouring colonies were generally found on sparsely colonised fronds and their relatively small average size must reflect their slower than average growth rates, which are presumably related to locally poor environmental conditions. Table IV shows that growth of *A. hirsutum* on high density fronds was much slower than on low density fronds. At high density, virtually all individual colonies were interacting with neighbouring colonies along at least part of their growing edge though the more rapid growth encountered at

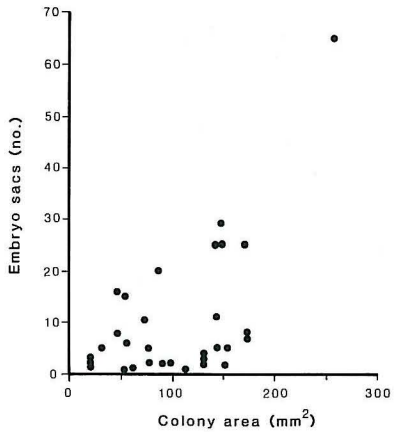

Fig. 3 : Relationship between fecundity (no.embryo sacs.colony^{-1}) and colony area of *F. hispida* at site 1 mid in May 1979 demonstrating the possible existence of two reproductive strategies.

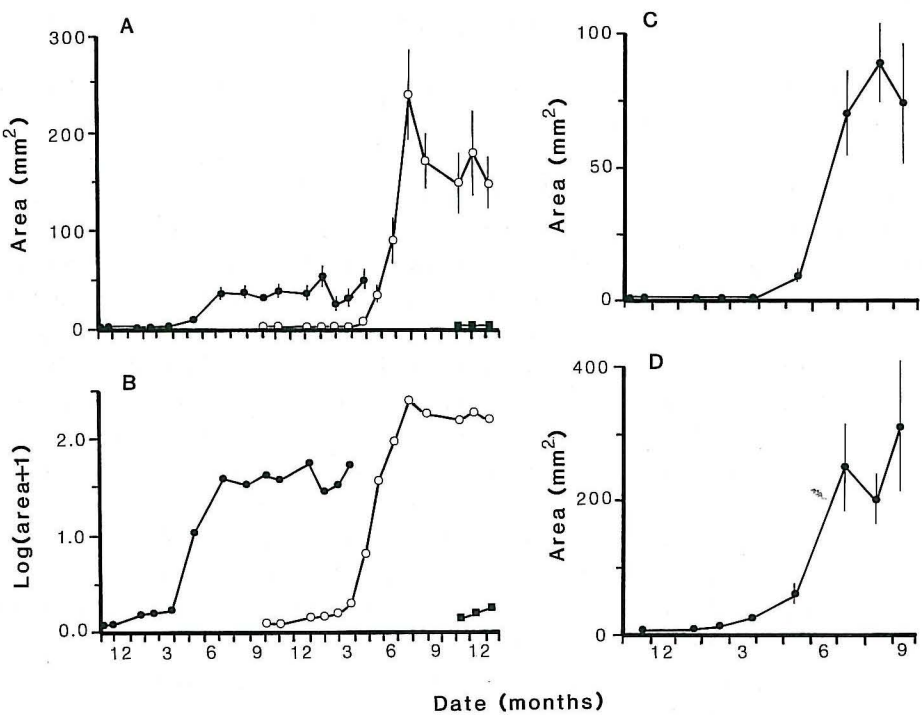

Fig. 4 : A) Growth of the 1978-1979 (•) and 1979-80 (o) year classes of *A. hispida* between Nov.78-Jan.81 at site 4 mid. Each point represents mean area (± CI) of approximately 100 colonies. B) as above but colony area calculated as log (colony area + 1). Growth of C) *A. hirsutum* and D) *F. hispida* at site 1 mid between Nov.78-Sep.79. Each point represents mean area (± CI) of approximately 100 colonies.

TABLE III

Effects of spatial competition on colony size of *A. hirsutum* and *F. hispida* at site 4 mid. Degree of interaction : Values expressed as mean colony area (± 1SD, mm²). 0, <50 %, 50-75 %, >75 % : proportion of colonies with their borders surrounded by other colonies.

Date	*Degree of interaction*				H
	0	<50 %	50 %-75 %	>75 %	
A. hirsutum					
7.79	28.0 (22.6)	46.6 (34.2)	41.0 (26.9)	18.3 (10.9)	11.64*
6.80	59.4 (98.4)	123.8 (160.2)	84.0 (98.7)	17.4 (24.7)	20.17*
F. hispida					
5.79	66.8 (85.4)	70.9 (67.8)	34.4 (33.9)	-	6.14*
6.80	25.4 (33.7)	38.4 (48.0)	30.5 (37.7)	21.2 (22.8)	6.97

H = Kruskal Wallis one way Analysis of Variance.
* $p<0.05$

low population density meant that even here the percentage of intraspecific encounters was quite high. Colony size at the end of the exponential growth phase was not significantly influenced by frond surface (Table V).

Figure 5A illustrates the size-frequency distribution of the 1978-79 *Alcyonidium* year class. From October to March all colonies were <25 mm², and whilst the population mode never shifted from this size class the percentage of colonies within this category declined dramatically between March and June, concurrent with the exponential growth phase. Nevertheless, the population always remained heavily skewed towards smaller colonies. From July until January the distribution remained relatively stable but the proportion of small colonies again increased during February and March. At this time the number of damaged colonies was very high so this influx of small colonies could represent fragmentation of established colonies rather than recent recruitment. New growth started in April. Figure 5B shows that the timing of growth for the 1979-80 cohort was broadly similar to the previous year group though the population spread differed substantially between years. Whilst the population mode by July 1980 had increased to colonies of 100-125mm² the distribution nevertheless remained skewed towards smaller colonies.

Flustrellidra hispida. The growth patterns of three year classes of *F. hispida* are illustrated in Figure 6. Growth started shortly after settlement (May-Sept) and continued until winter. At the end of the first growing season colonies of the 1980 year group were larger than those in either of the two previous year classes. Growth resumed in spring and continued into the second summer, thereafter mean colony size declined throughout the subsequent sampling period. The 1978 generation grew exponentially during March to July 1979, mean colony size then oscillated between 120-160 mm² before finally declining in size during the second winter. Growth of the 1979 cohort over the equivalent period was much more gradual and mean colony size continued to increase until December 1980. Colonies of the

1979 year class, however, were more densely crowded than those of the other generations thus perhaps explaining their rather retarded growth rate. The pattern of growth of *F. hispida* at site 1 mid (Fig. 4D) is similar to that reported for *A. hirsutum* at this site (Fig. 4C) though the mean maximum size of the colonies was much greater ; colonies of *F. hispida* at site 1 also achieved a significantly greater average size than conspecifics at site 4 mid (Fig. 6A). Increased colony interactions tended to reduce *Flustrellidra* growth rate though this trend was not statistically significant for the 1979 generation (Table III). As with *A. hirsutum* colony size in *F. hispida* was apparently unaffected by frond curvature (Table V). The smallest size class was predominant when this population was first sampled in November 1978, until May 1979 (Fig. 7A). A noticeable shift in colony size began in March and ended in July 1979, thereafter only slight changes in population structure occurred until February 1980 when the numbers of small colonies increased, concurrent with the number of damaged colonies. As with *A. hirsutum* the distribution always remained skewed towards small colonies. Changes in the size frequency distribution of the 1979 cohort were broadly similar to those for the 1978 generation (Fig. 7B) though growth out of the smallest size class, which always contained the modal group, was much slower. The presence of a few large colonies was responsible for the larger average size of overwintering colonies of the 1980 generation (Fig. 7C).

DISCUSSION

The breeding cycles of *A. hirsutum* and *F. hispida*, two dominant spatial competitors within the epi-algal community of *Fucus serratus* in the Menai Strait (Wood & Seed, 1980) are temporally separated. Thus, whilst *F. hispida* releases larvae between May and November and settles in abundance during June and July, larval release in *A. hirsutum* occurs from October to January with peak settlement during October and November. Broadly similar results, albeit with slight regional variations, have been obtained for populations of these two bryozoans elsewhere in Britain (e.g. Eggleston, 1972 ; Hayward and Ryland, 1975, Seed *et al.* 1981). In view of this temporal segregation in the main breeding and settlement periods, both inter-and intraspecific competition for space between consecutive generations of each species is substantially reduced, because even though the larvae of both these bryozoans (but more especially *A. hirsutum*) prefer to settle on the younger distal frond segments, plant growth between successive periods of recruitment effectively keeps each generation separate.

Fecundity in those encrusting bryozoans which have been studied is linearly related to colony area and even very small colonies, consisting of only a few zooids, are capable of breeding (e.g. Hayward, 1973 ; Yoshioka, 1977, Hayward & Ryland, 1975 ; Cancino, 1983). This was also found for *A. hirsutum* and *F. hispida* in this study, and even though populations of these species in the Menai Strait are heavily skewed towards small colonies, most colonies are nonetheless capable of reproducing. Indeed, >80 % of the local *A. hirsu-*

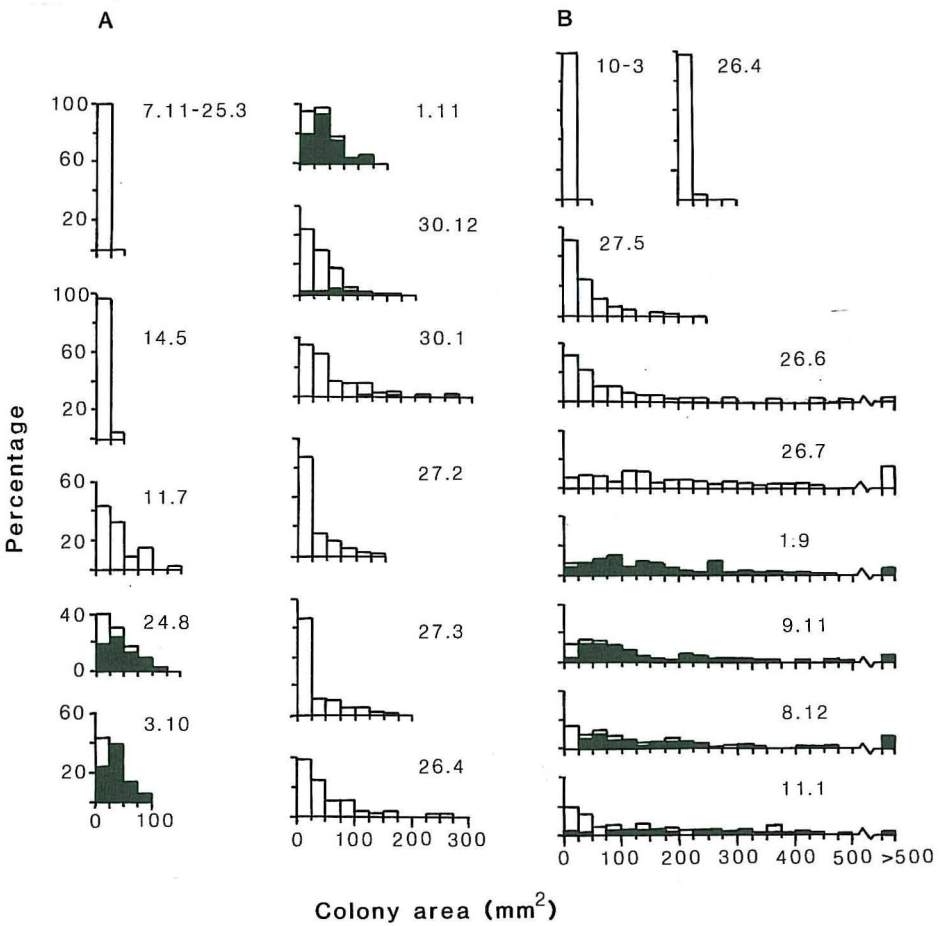

Fig. 5 Size frequency distributions of A) the 1978-79 year class of *A. hirsutum* from Nov.78-Apr.80. B) the 1979-80 year class from Nov.79-Jan.81. Black bars indicate the % of colonies with embryo sacs.

tum population bred in each year of this study. The breeding capacity of *F. hispida*, however, was rather more variable (15-100 %) between sites, presumably reflecting localised differences in habitat suitability.

The patterns of reproduction and life cycles of bryozoans in Manx waters have been examined by Eggleston (1972) who found a whole range of strategies from species such as *Callopora lineata*, which had several generations each year, through annual species like *F. hispida* and *Alcyonidium* spp. to perennial species such as *Flustra foliacea*. Species with short generation times are essentially opportunistic and are generally associated with ephemeral substrata and/or poor competitive ability (e.g. Dudley, 1973 ; Karlson, 1980, Seed and O'Connor, 1981b). Such species start to reproduce shortly after settlement and thereaf-

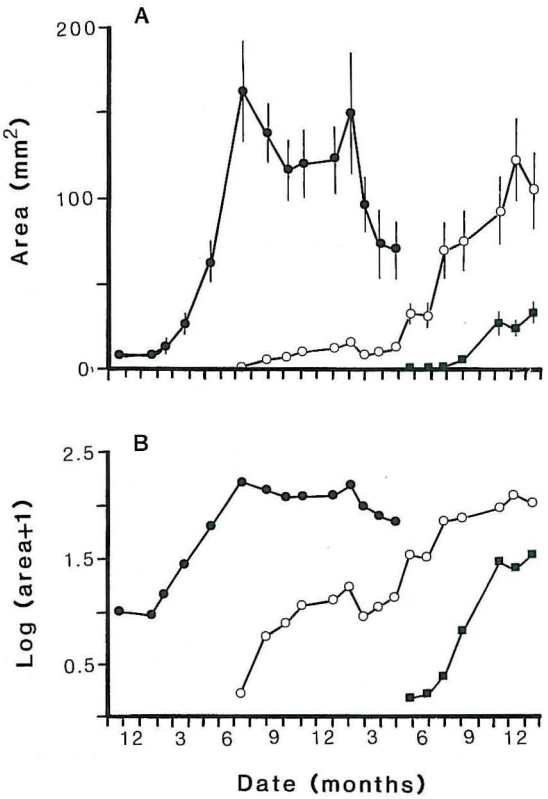

Fig. 6 : A) Growth of three year classes of *F. hispida* at site 4 mid from Nov.78-Jan.81. Each point represents mean area (± CI) of approximately 100 colonies. B) as above but colony area calculated as log (colony area + 1).

TABLE IV

Effect of initial settlement density on the growth of *A. hirsutum* colonies (Mar-May 1980) at site 2.

Initial		*Final*		
no. colonies segment^{-1}	colony density (no. cm^{-2})	colony density (no. cm^{-2})	colony size (± 1SD, mm^2)	no. interactions (%)
16	0.6	0.4	22.5 (19.3	40.3
25	0.8	0.7	18.3 (10.2)	43.6
50	1.4	0.8	22.0 (20.5)	44.2
226	6.3	4.3	6.8 (3.9)	82.5
125	6.4	5.6	10.9 (4.4)	97.3
196	8.2	7.6	6.9 (2.7)	97.8

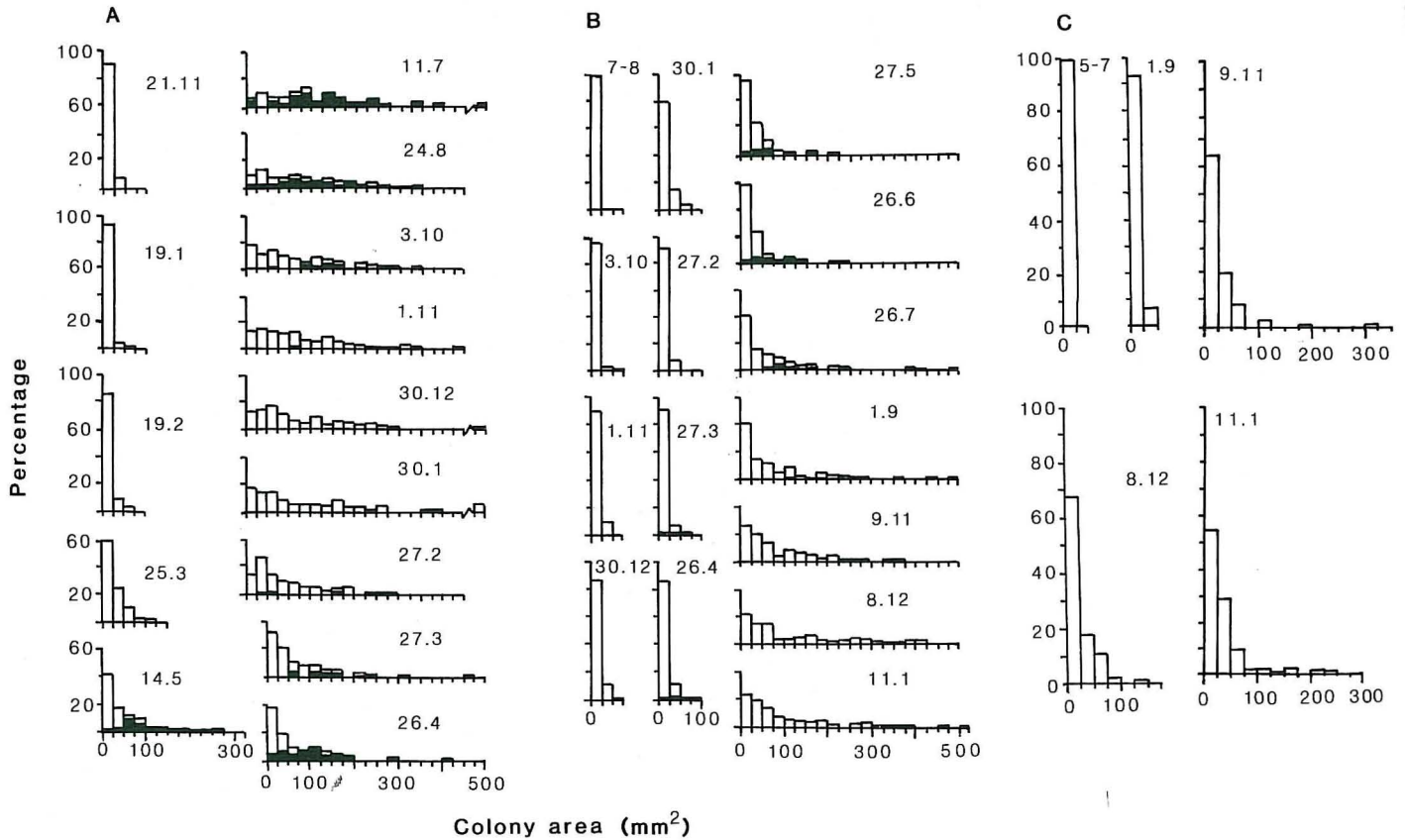

Fig. 7 : Size frequency distributions of A) the 1978 year class of *F. hispida* from Nov.78-Apr.80. B) the 1979 year class from Jul.79-Jan.81 and C) the 1980 year class from May 80-Dec 80. Black bars indicate the % of colonies with embryo sacs

TABLE V

Comparison of mean colony size (± 1SD, mm^2) of *A. hirsutum* and *F. hispida* on concave and convex surfaces of *F. serratus* at site 4 mid.

Date	Species	Colony size		Student's	
		Concave	Convex	t	P
8.79	*A. hirsutum*	39.4 (25.7)	34.5 (28.0)	- 0,96	ns
7.80	*A. hirsutum*	237.9 (264.3)	244.0 (181.5)	-0.13	ns
8.79	*F. hispida*	139.0 (99.1)	134.1 (89.4)	0.25	ns
7.80	*F. hispida*	68.6 (89.5)	70.3 (97.0)	- 0.09	ns

ns = not significant

ter breed and grow concurrently (Bernstein & Jung, 1979 ; Cancino, 1983, 1986). Annual species, by contrast, have a longer pre-reproductive period. Nevertheless, the reproductive strategies of *A. hirsutum* and *F. hispida* differ in respect of their timing and pattern. In our study embryo sac development and larval release were more highly synchronised in *A. hirsutum* than in *F. hispida*, colonies of the latter species containing embryos at various stages of development throughout the breeding season.

Growth of many colonial organisms is exponential when expressed as an increase in the number of units over time ; it is also indeterminate in that there is no genetically fixed adult size and is halted only by certain environmental constraints such as seasonal suitability for growth or competition for space (e.g. Stebbing, 1971, Menon, 1972 ; Dudley, 1973). In temperate waters growth of most sessile marine invertebrates is highly seasonal. Growth of *A. hirsutum* and *F. hispida* is most rapid in spring and early summer but slows appreciably over the summer months as all available frond surface becomes filled in a mosaic of interlocking colonies. Hayward and Harvey (1974) found no differences in the eventual colony size of *Alcyonidium* in predetermined areas of low and high settlement density. However, in our study three factors suggest a degree of density dependent control of growth. Firstly, *Alcyonidium* and *Flustrellidra* colonies which were almost entirely surrounded by other colonies at the end of the exponential growth phase were significantly smaller than those only partially surrounded (Table III). Secondly, growth rates on densely settled frond segments were reduced compared with those on lightly settled fronds (Table IV). Thirdly, the maximun size observed between years for both *Alcyonidium* (see also Hayward & Ryland, 1975) and, to a lesser extent, *Flustrellidra* was inversely related to settlement density. Nevertheless, close examination of monitored colonies showed that growth rates of adjacent colonies were highly variable, a phenomenon previously noted by Vail and Wass (1980) for an unnamed bryozoan in South Australia. Thus, on *Fucus serratus* in the Menai Strait *A. hirsutum* required only a single growing season to fill those frond segments which it colonised whilst *F. hispida* required two growing seasons to achieve the same level of colonisation.

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