THE SPATIAL NICHE OF *DYNAMENA PUMILA* (L.) AND *GONOTHYRAEA LOVENI* (ALLMAN) (HYDROZOA) WITHIN A *FUCUS SERRATUS* L. COMMUNITY

by

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Résumé

La répartition de *Dynamena pumila* et de *Gonothyraea loveni* sur *Fucus serratus* a été étudiée à Strangford Lough, Irlande du Nord. *Dynamena* montre plus que *Gonothyraea* une préférence sensible pour les courants rapides et les eaux agitées, évitant ainsi les plantes chargées de limon. Les régions préférées de *Dynamena* sont celles où les *Fucus* sont le plus denses, mais le phénomène est vrai pour les deux espèces. On rencontre de façon très significative plus souvent *Dynamena* sur des algues de grande taille mais les zonations des deux espèces sont semblables à l'intérieur de la plante même, quelle que soit sa taille. Il est prouvé que la hauteur des tiges dépend faiblement de leur position le long des frondes.

Les plantes préférentielles de *Dynamena* sont aussi bien colonisées par les Bryozoaires *Alcyonidium hirsutum, Electra pilosa* et *Flustrellidra hispida* mais *Dynamena* et *Alcyonidium* ont une densité locale inversement proportionnelle sur les plantes qu'elles occupent en commun. *Gonothyraea* et *Alcyonidium* sont liés mais les Hydroïdes montrent un rapport inverse avec certains autres membres communs de l'épifaune, en particulier le Serpulide *Spirorbis borealis* et le Bryozoaire *Membranipora membranacea*. Les deux Hydroïdes sont plus abondants sur les plantes riches en Bryozoaires et leur croissance en longueur y est également plus considérable, spécialement là où ces plantes sont en présence d'une nourriture abondante.

Les Bryozoaires et les Hydroïdes sont fréquemment en compétition, les derniers étant recouverts — par ordre de fréquence — par *Flustrellidra, Alcyonidium* et *Electra*. Les densités d'Hydroïdes diminuent lorsqu'ils sont recouverts et il est certain que *Gonothyraea* quitte sa niche des surfaces convexes pour aller vers les surfaces concaves, en présence de *Flustrellidra*. L'ordre de répartition de *Dynamena* dépend de la présence ou de l'absence d'*Alcyonidium*, d'*Electra* et de *Flustrellidra* celui de *Gonothyraea*, de celle d'*Alcyonidium*.

Dynamena et *Gonothyraea* entrent elles-mêmes occasionnellement en compétition mais le résultat dépend de l'environnement. La position des niches varie également avec les actions intraspécifiques, changeant dans toutes les espèces quand la densité de leur propre population augmente. La position générale des deux espèces dans cette communauté est déterminée en partie par leurs différentes réactions à la compétition des Bryozoaires.

Introduction

Epifaunal communities of macroalgae are typically dominated by attached species exhibiting one of three life forms: (1) solitary organisms, (2) colonial erect forms, and (3) encrusting forms.

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Hydroids are the commonest representatives of the second type yet their ecological relationship with other members of their community have hardly been studied. Kato and co-workers demonstrated a hierarchy of competitive relations amongst hydrozoans in which the stolons of one species in overgrowing those of another, stopped the passage of nutrients and thus inhibited growth (e.g. Chiba and Kato, 1966; Kato *et al.*, 1963, 1967). Stebbing (1973) examined the extent to which the ability of hydroid colonies to develop vertically may reduce the impact of overgrowth by adherent forms that do not rise above the substratum whilst Standing (1976) demonstrated that dense canopies of certain hydroids not only supress the recruitment of other species within the community but also effectively reduce local current velocity gradients. Such relationships are of particular interest in view of the work of Jackson (1977) who suggests that colonial species are superior to solitary organisms when there is competition for space. Since some hydroids resemble solitary organisms, in requiring only discrete patches of substratum for attachment, whilst others more nearly resemble encrusting organisms (in their extensive development across the substratum with zooids occurring on vertical stems at discrete points within the stoloniferous attachment) the group provides material of comparative interest when assessing the adaptive significance of epifaunal strategies.

Two hydroid species, *Dynamena pumila* (L.) and *Gonothyraea loveni* (Allman), are especially prominent amongst the rich epifauna found on the serrated wrack, *Fucus serratus,* in Strangford Lough, Northern Ireland (Boaden *et al.*, 1975). Such abundance of these hydroids provides data on their distribution in relation to the occurrence of other dominant members of the *Fucus* epifauna. Nine such taxa have been studied and reports provided for all major groups —sponges and tunicates (Boaden *et al.*, 1976a, b), spirorbids (O'Connor and Lamont, 1978), and bryozoans (O'Connor *et al.*, 1975; O'Connor *et al.*, 1979, 1980). Here we examine the distribution of *Dynamena* and *Gonothyraea* on *F. serratus,* paying particular attention to their relationships with the Bryozoa.

Materials and methods

Data were obtained in 1972 and 1975 as part of a wider study of algal epifaunas at The Dorn in Strangford Lough. This area consists of several partially dammed shallow marine basins which provide several contrasted environments within a comparatively restricted area. A full description of the area is provided by Boaden *et al.* (1975). Briefly, however, the basin complex is normally flooded at each high tide, but as the tide ebbs, water is retained by the «Sill», a ridge of rock across the narrow channel to the main lough, thereby creating a waterfall and a complex of intertidal conditions more typically found only low on the shore. The resulting profusion of macroalgae has created habitat capable of supporting a rich and varied epifauna (Seed and Boaden, 1977).

Our study of the hydroid populations was based on methods fully documented elsewhere (Boaden *et al.*, 1975). Thirteen sites were chosen to provide a stratified sampling of the available environments. At each site we measured current speed, silt load on the fucoids, a «turbulence» or «agitation» index (obtained as the weight loss of gypsum spheres attached to selected plants and weed size (length, weight and volume) and abundance. These data are tabulated in Boaden *et al.* (1976a). Within each site we collected five plants at random from low water level. Each was regarded as consisting of a series of Y-shaped segments whose positions along the plant were specified by «Y-values», from the basal *Yl* to the distal *Yn*. The common fauna on each segment face (concave and convex faces were documented sparately) were recorded quantitatively; encrusting species as percentage cover, arborescent species such as the hydroids as percentage cover and the height of the longest upright branch. The dimensions of each *Fucus* segment were also noted and the approximate area of each calculated.

A second sample consisting of 15 plants from three sites with contrasting environments was collected in 1975. This area-restricted sample was expressly collected for a detailed study of the competitive interactions known to occur amongst the dominant taxa.

Both samples were collected in spring and thus reflect the operation of competition since the settlements of the previous year. Our data thus constitue a cross-sectional sudy of the intra- and interspecific population processes in progress.

TABLE I

Percentage of available plants colonized by hydroids under different environmental conditions

Environmental variable	Range	Plants available	% (no.) of available plants colonized by		Species difference [a]χ^2
			Dynamena	*Gonothyraea*	
Current speed, cm sec^{-1}	$<$ 20	25	52 (13)	24 (6)	
	21- 50	20	85 (17)	45 (9)	
	$>$ 50	20	95 (19)	85 (17)	1.66
Turbulence, [b] percent wt. loss	$<$ 10	20	35 (7)	35 (7)	
	11- 20	25	88 (22)	48 (12)	
	$>$ 20	20	100 (20)	65 (13)	0.90
Silt, [c] particles. ml^{-1}	$<$ 110	25	100 (20)	70 (14)	
	111-320	20	96 (24)	44 (11)	
	$>$ 320	20	25 (5)	35 (7)	2.78
Weed abundance [d]	1	20	30 (6)	50 (10)	
	2	20	100 (20)	50 (10)	
	3	25	92 (23)	48 (12)	4.42

[a] A χ^2 of 5.99 is necessary for significance at the 5 percent level.

[b] Measured as weight loss of 38mm diameter gypsum spheres attached to plant at Y level 3.

[c] Measured as no. of 2-20μm particles. ml^{-1} (x10^3) of weed (distal 25cm of frond).

[d] Abundance categories used were «common» (1), «abundant» (2), and «superabundant» (3).

RESULTS

Site parameters and plant characteristics

Table 1 shows the utilization of plants under various environmental conditions. The percentage of plants colonized by each species increased markedly both with increased current flow and with increased turbulence. *Gonothyraea* was more steeply linked with current flow than was *Dynamena*. Plant silt loads had the reverse effect, with utilization decreasing strongly for both species as silting increased: the main decline occurred at high silt loads in the case of *Dynamena*. Weed abundance had no direct influence on the incidence of *Gonothyraea*, this species occurring on about half the available plants. *Dynamena*, however, was rarer at sites where *Fucus* was merely «common» but was nearly ubiquitous on plants in areas of *Fucus* abundance or superabundance. Table II shows that the abundance (as distinct from incidence) of both species increased with weed density, the effect being more marked in *Dynamena*. Mean height of the longest stems decreased with plant abundance in *Dynamena*, but increased in *Gonothyraea* (Table II).

TABLE II
Relationship of hydroid abundance to *Fucus* abundance.

	Dynamena			*Gonothyraea*		
Fucus [a] abundance	percent cover Mean ± s.e.	Stem height (mm) Mean ± s.e.	N	percent cover Mean ± s.e.	Stem height (mm) Mean ± s.e.	N
1	7.3±.16	13.9±1.4	12	9.3±1.6	9.0±0.8	33
2	11.3±1.7	10.3±0.7	99	11.0±2.0	9.8±1.3	54
3	20.8±2.2	10.0±0.8	145	17.0±2.6	11.9±0.9	53

[a] Abundance categories used were «common» (1), «abundant» (2), and «superabundant» (3).

Plants colonized by *Dynamena* were significantly larger in volume than were those not so colonized (Table III). They also tended to be longer and relatively more branched than non colonized plants albeit without statistical significance. *Gonothyraea* showed no apparent preference for plants of different size or structure (Table III).

Relationships with other species

F. serratus in Strangford Lough is typically encrusted by several non-hydrozoan species, the presence or absence of which on any particular plant may influence the use made of that plant by the two hydroids. Table IV dichotomizes the commonest members of the epifauna on the basis of the presence or absence on the sample plant

TABLE III

Plant parameters in relation to colonization by hydroids. *P<0.05; **P<0.01.

Plant parameter	*Dynamena*				*Gonothyraea*			
	Absent	Present	F	t	Absent	Present	F	t
	Mean ± s.e. (n)	Mean ± s.e. (n)			Mean ± s.e. (n)	Mean ± s.e. (n)		
Length (cm)	72.9± 8.2 (16)	86.7± 3.6 (49)	1.64	1.74	83.6± 5.0 (33)	82.9± 4.9 (32)	1.06	—0.10
Volume (ml)	499 ±108 (16)	876 ±120 (49)	3.74**	2.32*	757 ±114 (33)	810 ±158 (32)	1.89	0.28
Branching ratio (ml.-cm^{-1})	7.3± 1.5 (16)	9.3± 0.9 (49)	1.02	1.13	8.5± 1.0 (33)	9.1± 1.2 (32)	1.45	0.39

TABLE IV

Species abundance on *Fucus serratus* plants colonized and not colonized by each of the two hydroids *P<0.05 **P<0.01; ***P<0.001.

Species	Units	*Dynamena*						*Gonothyraea*					
		Absent		Present		F	t	Absent		Present		F	t
		Mean ± s.e.		Mean ± s.e.				Mean ± s.e.		Mean ± s.e.			
Alcyonidium	%	0.84	0.30	2.40	0.60	12.53***	2.34*	2.34	0.84	1.68	0.37	5.37***	—0.71
Electra	%	0.26	0.23	1.25	0.32	5.67***	2.51*	1.35	0.42	0.66	0.26	2.83**	—1.40
Flustrellidra	%	0.00	—	2.74	1.00	—	2.74**	0.98	0.39	3.19	1.50	14.43***	1.44
Membranipora	%	0.18	0.10	0.26	0.12	4.52**	0.50	0.21	0.13	0.27	0.13	1.04	0.33
Didemnum	%	0.03	0.03	0.28	0.15	94.07***	1.64	0.03	0.02	0.41	0.23	148.11***	1.63
Polyclinum	No.	0.06	0.04	0.14	0.05	6.12***	1.18	0.15	0.06	0.08	0.06	1.27	—0.73
Scypha compressa	No.	0.01	0.01	0.19	0.10	267.76***	1.88	0.02	0.02	0.28	0.15	68.19***	1.71
S. ciliatum	No.	0.01	0.01	0.03	0.01	3.74**	1.14	0.02	0.01	0.03	0.01	1.90	0.96
Spirorbis spp.	No.	15.22	2.73	10.32	1.91	1.49	—1.33	13.72	2.58	9.27	1.82	2.08*	—1.41
Gonothyraea	%	0.97	0.46	1.86	0.39	2.16	1.22	—	—	—	—	—	—
Dynamena	%	—	—	—	—	—	—	5.43	1.59	3.47	1.05	2.34*	—1.03

of *Dynamena* and *Gonothyraea.* The pattern for *Dynamena*-colonized plants is clear-cut: all species except *Spirorbis* were more abundant on plants bearing *Dynamena,* significantly so in the case of the bryozoans *Alcyonidium hirsutum, Electra pilosa* and *Flustrellidra hispida.* The remaining bryozoan, *Membranipora membranacea,* fails to show the same effect in this analysis. However, its distribution on *F. serratus* is already known to be the result of competition from the other bryozoans which force its absence from many plants. Yet even when we consider only those plants bearing at least some *Membranipora,* its abundance on plants colonized by, or free from *Dynamena* still fails to achieve significance ($t = 0.72$, n.s.).

The application of the Binomial Test (Siegel, 1956) to similar subsets of the tunicate and sponge data show significant differences in favour of *Dynamena*-colonized plants in the cases of *Didemnum maculosum* ($P=0.018$), *Scypha compressa* ($P=0.031$) and *S. ciliatum* ($P=0.027$). There was thus significant correlation between these three forms and the presence of *Dynamena* within the subsets of plants suitable for each, possibly the result of their concentration onto those plants most favourable to particle feeders (Boaden *et al.,* 1976a).

Gonothyraea had a very different pattern of relationship with the non-hydroid species of the community (Table IV). None of the differences in mean density were statistically significant. *Didemnum* showed a marked difference between *Gonothyraea*-free and *Gonothyraea*-colonized plants but the increase is not significant, even when only *Didemnum*-colonized plants are considered ($t=1.25$, n.s.). Similarly, *Scypha compressa* showed a pronounced increase with *Gonothyraeas'* presence, though again without significance. *Flustrellidra* also failed to show any association when tested by contingency table. Thus, *Gonothyraea* showed only weak associations with other particle feeders within plants at least minimally suitable for those species.

Table V shows that the abundance of *Dynamena* was most strongly correlated with the abundance of the bryozoans *Electra* and

TABLE V

Correlations between hydroid abundance and other epifaunal species on *Fucus serratus plants.* *$P<0.05$; **$P<0.01$; ***$P<0.001$.

Species	*Dynamena pumila* [a]	*Gonothyraea loveni* [a]
Alcyonidium hirsutum	0.020[b]	0.324*
Electra pilosa	0.594***	0.005
Flustrellidra hispida	0.277*	0.001
Membranipora membranacea	—0.155[b]	—0.035[b]
Didemnum maculosum	0.313*	0.242
Polyclinum aurantium	0.195	0.055
Scypha compressa	0.264*	0.016
Scypha ciliatum	0.248*	0.026
Spirorbis borealis	—0.156	—0.289[b]

[a] Abundance as average percentage cover along the longest frond, for those *Fucus serratus* plants actually colonized by the hydroid.

[b] Non-linear relationships, discussed further in the text.

Flustrellidra, the tunicate *Didemnum* and the sponges *Scypha compressa* and *S. ciliatum*. By contrast, *Gonothyraea* numbers were independent of the abundance of all species except *Alcyonidium*.

Figure 1 details the relationship between the abundance of the hydroids and the density of *Alcyonidium* and *Membranipora*. *Dynamena* shows a marked non-linear pattern with respect to the abundance of both bryozoans, each bryozoan being abundant only on those plants on which *Dynamena* is scarce and vice versa. Similarly, the distribution of *Gonothyraea* is inversely related to that of *Membranipora* but is positively correlated with that of *Alcyonidium*. These relationships broadly reflect congruence in specific environmental preferenda on the part of the hydroids (this study) and of the Bryozoa (Boaden *et al.*, 1975; O'Connor *et al.*, 1979).

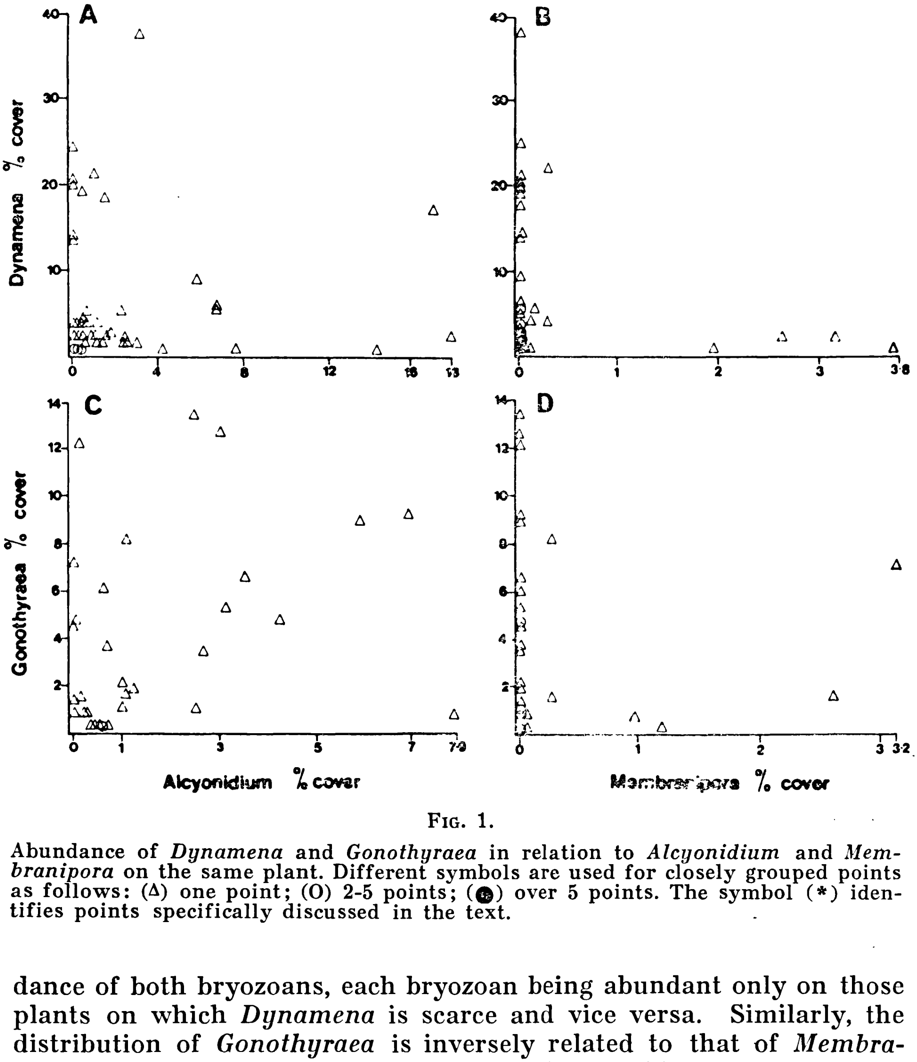

FIG. 1.

Abundance of *Dynamena* and *Gonothyraea* in relation to *Alcyonidium* and *Membranipora* on the same plant. Different symbols are used for closely grouped points as follows: (Δ) one point; (O) 2-5 points; (●) over 5 points. The symbol (*) identifies points specifically discussed in the text.

Figure 2 shows the existence of an inverse relationship between the abundance of *Gonothyraea* and the abundance of *Spirorbis* on the same plant. Both species co-occur either at low densities or with one species particularly numerous but no plant sustained high densities of both. All plants with negligible *Spirorbis* populations came from two highly turbulent, silt-free sites whilst plants with negligible *Gonothyraea* populations were from very silty, quiet waters with below average turbulence. Nearly half the plants, however, came from a variety of sites characterized by turbulence and silt-loads in the lower half of the observed ranges, but with marked differences in current speeds, and yet continued to display the inverse relationship between the two species. It follows, therefore, that the relationship is not environmentally determined (at least within the variables measured here).

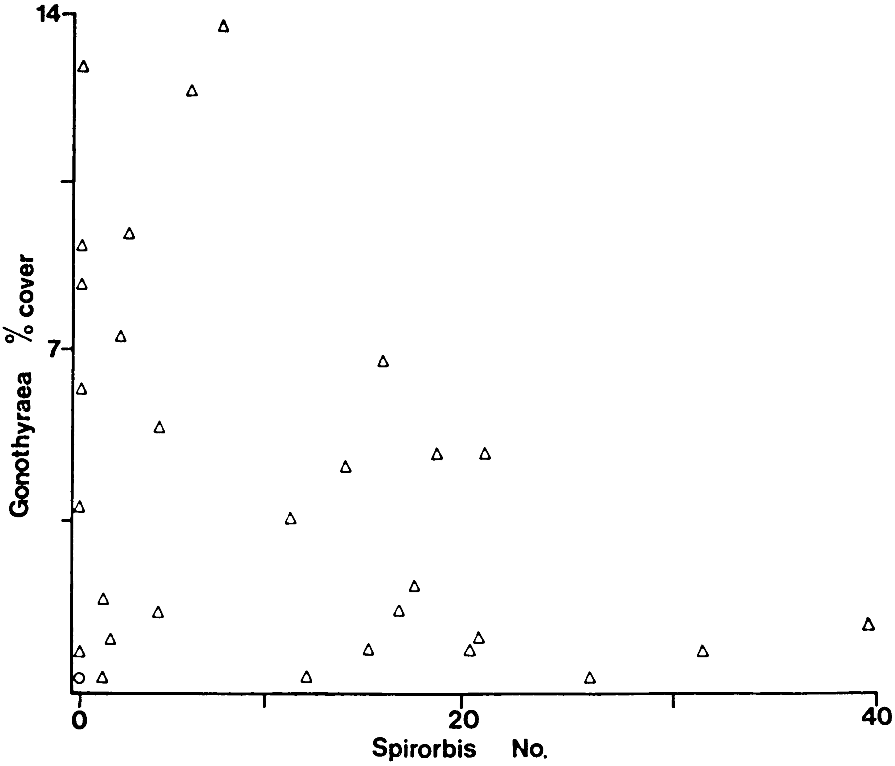

FIG. 2.

Abundance of *Gonothyraea* in relation to *Spirobis* on the same plant. Symbols as for Fig. 1.

The relationships between the hydroids and other species just examined are not independent of each other, since they form recognizable sub-groups within which the abundances of all members are correlated with each other and with some plant or site characteristics (Boaden *et al.*, 1975). We sought to disentangle these relationships by a step-up multiple regression analysis of our data. For *Dynamena* we obtained:

$$D=2.03E+0.75YL+23.11S-7.20 \quad R^2=46.0\%$$

where D, E and S are the abundances of *Dynamena, Electra* and

Scypha ciliatum respectively and YL the average segment length. The variables appear in the equation in order of importance from left to right, with *Electra* alone accounting for 36.4% of the variation in *Dynamena* (against the 46.0% of the complete equation). The result implies that *Dynamena* is more abundant on plants with large populations of *Electra* present, on plants with longer segments, and on plants with *S. ciliatum* present and that these three effects are additive. These results reflect the strong correlations in Table V since *Electra* and *Flustrellidra* are themselves correlated as are the two *Scypha* species (Boaden *et al.*, 1975).

For *Gonothyraea* a similar analysis yielded only a weak relationship with *Didemnum*:

$$G=1.18Di+1.73 \quad R^2=9.6\%.$$

This fits the large increase in *Didemnum* amongst plants colonized by the hydroid (Table IV). The large proportion of plants present in the regression analysis without *Gonothyraea* probably invalidate the regression's use as other than confirmation of that increase. Reference back to Table V indicates that *Gonothyraea* abundance on those plants it actually colonizes was positively correlated only with *Alcyonidium* abundance, and then only weakly so ($R^2=10.5\%$).

In summary of this section, our results show consistent associations between *Dynamena* and several other dominants of the *Fucus* epifauna. *Gonothyraea,* by contrast, showed no strong relationships to any of these species.

Relationships between hydroids

Figure 3 shows the variation in *Dynamena* density relative to that of *Gonothyraea* on the same plant. Ignoring the differences in site environment (coded by using different symbols) an inverse relationship between the higher hydroid densities clearly exists. This could be due (a) to differential environmental tolerances (see Table 1) or (b) to competitive exclusion between the two species. Hypothesis (a) was examined by grouping each site into one of four categories determined by a three-dimensional ordination of the sites on the basis of their current flow, turbulence and silt load characteristics. The four categories are here referred to as *class 1* (sites 2, 3, 4), characterized by high turbulence and low silt loads in conditions of moderate flow; *class 2* (sites 1, 9, 11, 13), characterized by rather lower turbulence and current flow and rather higher (though not excessive) silt loads; *class 3* (sites 5, 6, 10) characterized essentially by very fast currents and moderate (similar to class 2) silt loads, though varying substantially in turbulence; and *class 4* (sites 7, 8, 12), differing from class 2 only by their high silt loads.

Figure 3 illustrates that site class was indeed associated with different hydroid communities, as anticipated from Table 1. Class 4 sites held only very low hydroid populations. Class 3 sites had relatively little *Dynamena* but some plants carried very high *Gonothyraea* populations. Plants in class 2 sites rarely supported *Gonothyraea* but usually bore *Dynamena,* sometimes profusely. Finally, plants in class 1 sites usually bore *Dynamena* and often sustained a *Gonothyraea* population as well. Within each class there is some suggestion of an inverse relationship between the abundance of the two species. These results suggest that the hydroid communities of individual *Fucus* plants are determined in part by environmental factors, but that within a given set of environmental conditions interspecific competition may determine the relative abundance of the two species.

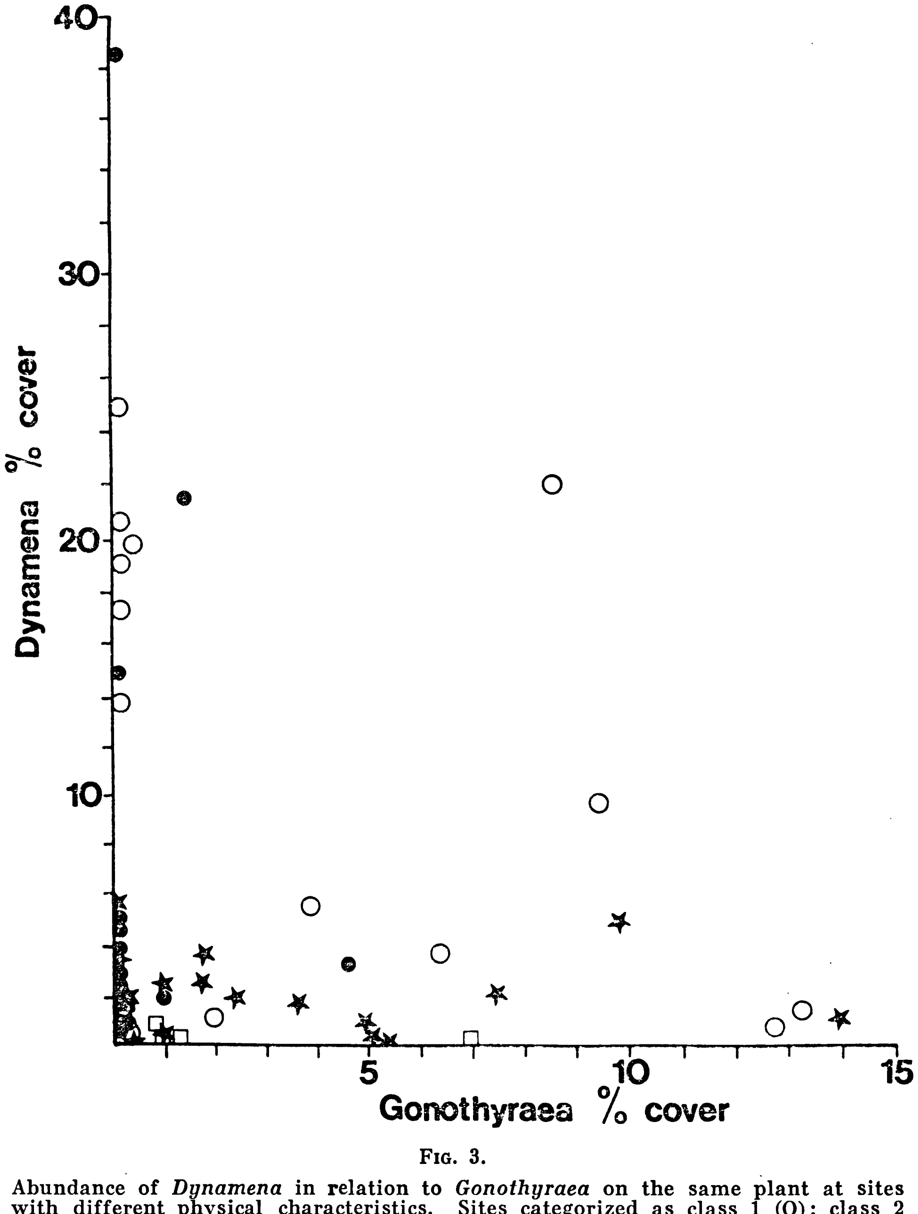

FIG. 3.

Abundance of *Dynamena* in relation to *Gonothyraea* on the same plant at sites with different physical characteristics. Sites categorized as class 1 (O); class 2 (●); class 3 (*); class 4 (□) on the basis of turbulence, current flow and silt content (see text). Thirteen of the 20 class 4 cases fell at the origin and are not plotted.

Within plant distribution

The optimum location of any species within a *Fucus* plant will generally be a compromise between different optima for several constraining factors imposed by either the abiotic or the biotic environment (or both) along the plant. We therefore investigated the relationships between hydroid positions and various plant features known to influence the distribution of other epifaunal species (Boaden *et al.*, 1975, 1976a; O'Connor *et al.*, 1979, 1980).

Frond segments differ substantially in size and must therefore have different turbulence properties in respect of eddying from the segment edges. One might therefore expect hydroid density to vary with segment area. However, hydroid abundances were uncorrelated with segment size for both *Dynamena* ($r=0.004$, n.s.) and *Gonothyraea* ($r=-0.068$, n.s.) *Dynamena* stem heights also failed to display any systematic relationship with segment area. *Gonothyraea* stem heights by contrast, were positively correlated with segment area ($r=0.256$, $P<0.05$) suggesting that colonies on large segments tended to grow taller.

If hydroid distributions within *Fucus* plants were the outcome of environmental factors, one might expect differences in their longitudinal distributions on plants of different size, such as we have demonstrated for other taxa (Boaden *et al.*, 1976a). Longer plants were indeed more frequently colonized by *Dynamena* the additional colonized faces being distal (Table VI). No differences were evident between concave and convex surfaces for either long or short plants ($\chi^2=0.39$ and 0.74 respectively, n.s.). The corresponding data for

TABLE VI

Distribution, abundance and stem heights of *Dynamena* and *Gonothyraea* on segment-faces of *Fucus* plants of different lengths.

	Dynamena						*Gonothyraea*					
	short plants[a]			long plants[a]			short plants			long plants		
Y value	N[b]	percent cover	height (mm)	N	percent cover	height (mm)	N	percent cover	height (mm)	N	percent cover	height (mm)
1	16	2.4	10.5	9	14.4	5.4	8	13.0	6.4	4	9.0	12.0
2	16	13.9	10.6	15	20.1	7.5	11	9.8	10.3	14	23.5	12.6
3	26	15.0	12.6	27	22.1	8.1	19	15.9	10.7	13	16.0	12.4
4	28	9.4	14.3	25	23.6	8.7	16	4.6	8.2	9	5.4	9.6
5	17	10.5	10.1	24	26.1	8.8	13	17.4	13.8	11	13.4	10.1
6	4	2.3	7.5	15	17.5	10.4	5	7.6	8.4	6	10.5	9.5
7	2	7.5	14.5	16	18.8	11.9	4	17.8	4.8	2	15.5	13.0
8	—	—	—	10	20.2	12.6	2	1.0	7.5	2	5.5	13.5
9	—	—	—	3	14.0	12.0	—	—	—	—	—	—
10	—	—	—	3	14.0	9.0	—	—	—	1	1.0	9.0

[a] «Short» and «long» plants are those respectively below and above average plant length for plants actually colonized.

[b] number of faces colonized (concave and convex surfaces combined).

Gonothyraea show that long and short plants were almost equally colonized (Table VI) and although in both size classes colonies on concave faces tended to be more distally located than those on convex faces these differences were again statistically indistinguishable (χ^2= 1.97, n.s. for short plants; χ^2=1.04, n.s. for long plants). *Gonothyraea* was, however, generally more profuse on longer plants, both in terms of its abundance and its vertical development (Table VI). Particularly striking was the greater stem height of this hydroid at the periphery

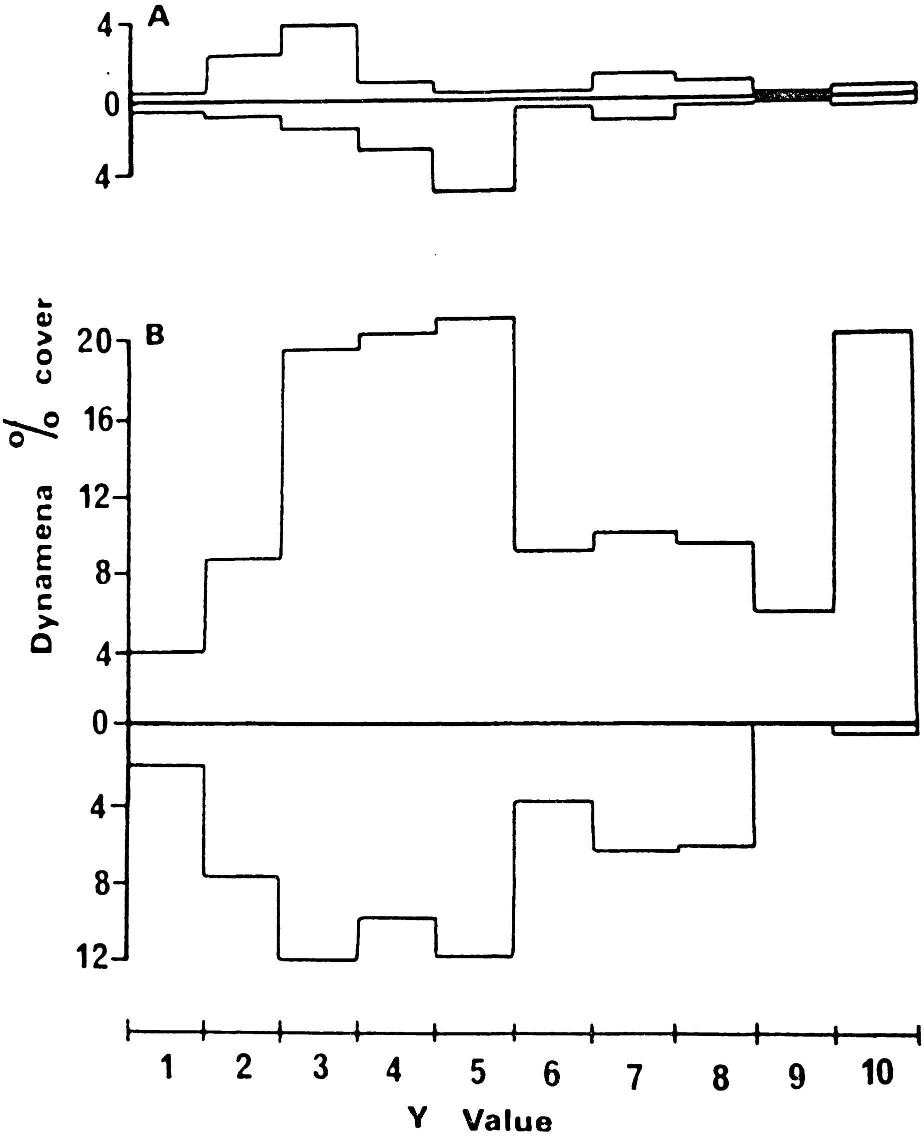

FIG. 4.

Zonation of *Dynamena* on plants with (A) low density (<5percent cover) and (B) high density (>5percent cover). Upper and lower parts of each diagram show the distributions on concave and convex surfaces respectively.

of its distribution on long plants, almost a mirror-image of the pattern on short plants. The abundance of *Dynamena* more or less parallels the distribution of colonies in both plant classes, though perhaps with a slightly more distal bias on long plants (Table VI). Stem height showed no systematic trend on short plants, but on larger plants averaged progressively higher values out to Y9 (Table VI). Thus, on distal segments, the gradual reduction in frequency and abundance of *Dynamena* was offset in part by greater stem growth. Similarly, its greater development on long plants was partly offset by the generally shorter stems grown there (Table VI).

Plant size subsumes a number of environmental variables and the associated hydroid responses because plant length is correlated with certain site conditions, notably water movement and low silt loads (Boaden *et al.,* 1975). An alternative analysis, therefore, is to dichotomize plants on the basis of their hydroid populations and to examine the distribution of each species on plants on which it is present at high and at low densities. For *Dynamena,* median abun-

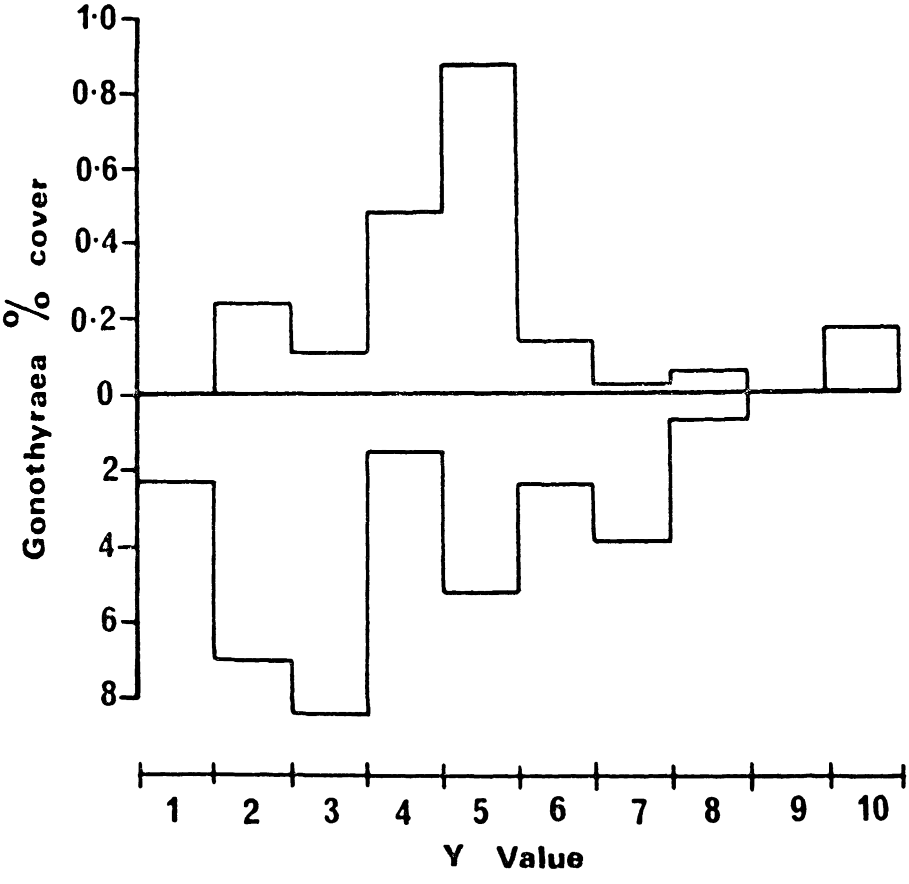

Fig. 5.

Zonation of *Gonothyraea* on plants with (top) below average density and (bottom) above average density. Note tenfold expansion of the scale. Average *Gonothyraea* density was 1.8percent.

dance over the longest fronds was 5% and plants were accordingly sorted on the basis of their carrying greater or lesser densities of *Dynamena*. This procedure largely (but not entirely) segregates dis-

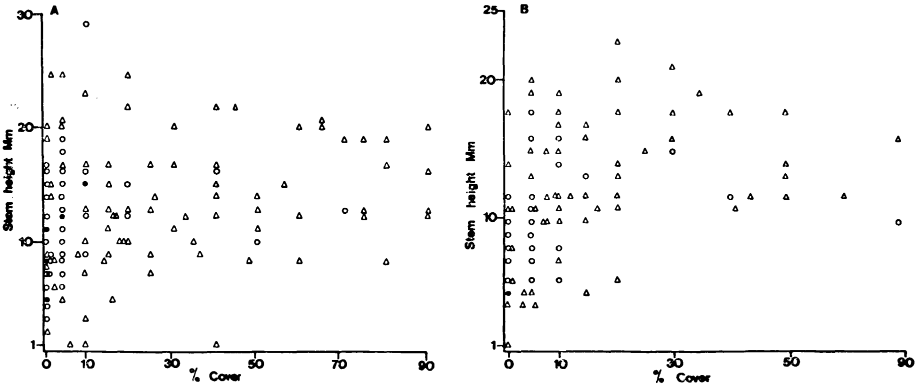

FIG. 6.

Relationship of stem height to abundance for (A) *Dynamena* and (B) *Gonothyraea*. Symbols as for Fig. 1.

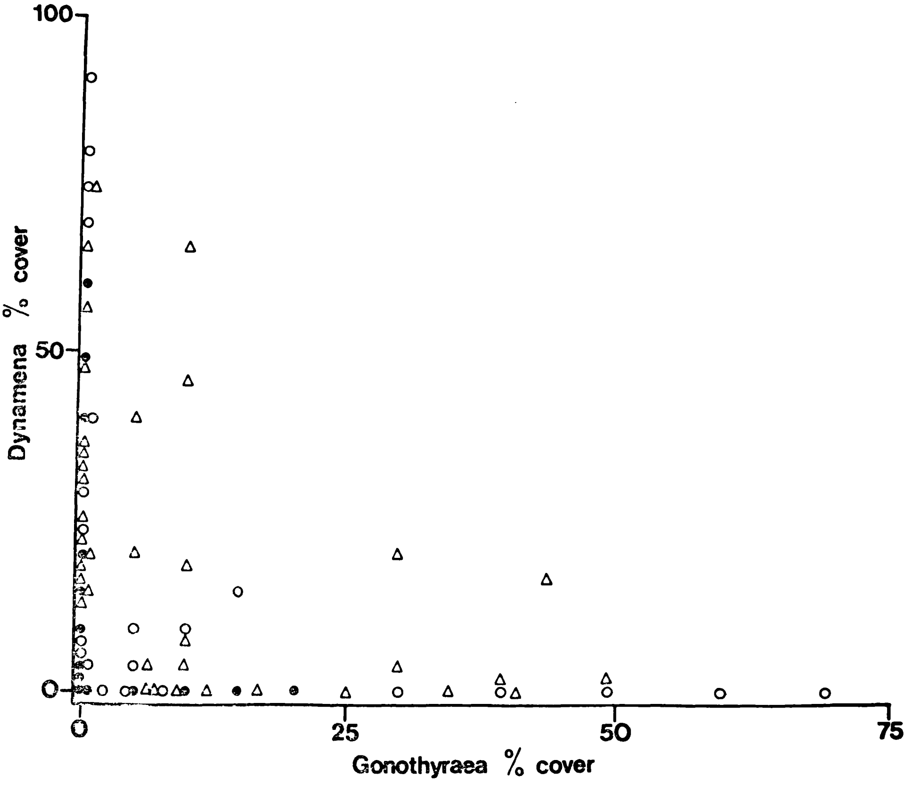

FIG. 7.

Relationship of *Dynamena* abundance to that of *Gonothyraea* on the same segment face. Symbols as for Fig. 1.

tribution on heavily colonized plants in class 1 sites from distributions on all other plants (see Fig. 3)—nine of the 13 plants with more than 5% cover by *Dynamena* were class 1 site plants. Plants with low densities of *Dynamena* had the hydroid concentrated into the Y2-Y3 zone on concave surfaces and into the Y4-Y5 zone on convex surfaces (Fig. 4a). On heavily colonised plants, however, peak cover prevailed in the Y3-Y5 region of both sides, with some suggestion of a more distal bias on the part of the more abundant concave populations (Fig. 4b). These results can be interpreted as showing that the plants in class 1 sites offer an environment favourable to *Dynamena* in a way which reduced the relative advantage of being on a concave rather than on a convex surface.

Figure 5 presents the corresponding analysis for *Gonothyraea* (median abundance 1.8%). Again, the plant split is to some extent correlated with site type (see Fig. 3) though here class 1 and class 3 sites are almost equally dominant. In fact, these sites (primarily sites 6, 5, 3, 2) shared the highest turbulence values, very low silt loads and moderate current flows. They thus formed an environmentally homogenous group in addition to their high *Gonothyraea* levels, features presumably not uncorrelated. *Gonothyraea* was maximally abundant in the Y2-Y3 regions of these plants whilst lower density populations in other sites were centred further out, at the Y5 region (Fig. 5). No differences between the distributions on concave and convex surfaces were demonstrated in either set. We suggest, therefore, that the longitudinal distribution of *Gonothyraea* is essentially a response to the micro-environment at the frond surface, a more distal distribution being adopted on plants in less turbulent waters.

Competition and local density effects

Erect species such as hydroids can largely escape the immediate effects of competition from encrusting species by developing vertically rather than laterally. This was tested for *Dynamena* and *Gonothyraea* in relation to intraspecific competition by plotting stem heights on each segment face against the species' cover of that face (Fig. 6). For both species there was significant correlation (*Dynamena* $r=0.265$, *Gonothyraea* $r=0.403$, both $P<0.001$) but the relationships were clearly not linear. Segments with more than 25% *Dynamena* cover had stems between 10 and 20mm high, whilst on more sparsely covered segments the stems ranged from 1 to 29mm in height. *Gonothyraea* was similarly variable (1 to 23mm) at low densities but above about 25% cover it displayed a steep decrease in stem height. Recency of colonization is an obvious explanation for short stems on sparsely colonized segments but the negative relationship of long stems at low density and short stems at high density requires some other explanation. One such hypothesis would be that the preferred mode of colony growth under optimum conditions is vertical.

Figure 7 shows that one potential competitive relationship, that between the two hydroids, parallels the plant level relationship previously presented (Fig. 3). Note, though, that the two species here show a more marked hyperbolicity, indicating that on plants heavily colonized by both species the two species were respectively most abundant on different plant segments. This implies either that the two species were 'avoiding' each other within the plants they shared or that they tended to prefer slightly different micro-environments prevailing on different parts of the plants. A further analysis suggests that any such specific differences were weak: on 53 faces colonized by both species *Dynamena* stem heights were correlated with those of *Gonothyraea* ($r=0.350$, $P<0.005$), and this over a wide range of stem sizes (1 to 24mm). This suggests that the two species were subject to parallel pressures (or opportunities) for vertical growth. We also compared mean *Gonothyraea* heights on plants colonized by *Dynamena* against those on *Dynamena*-free plants finding the former to be slightly but not significantly taller ($t=1.22$, n.s.), and made the corresponding comparison for *Dynamena* stems with a similar result ($t=1.69$ n.s.). We conclude, therefore, that variation in hydroid stem size was not the result of competition between the two species.

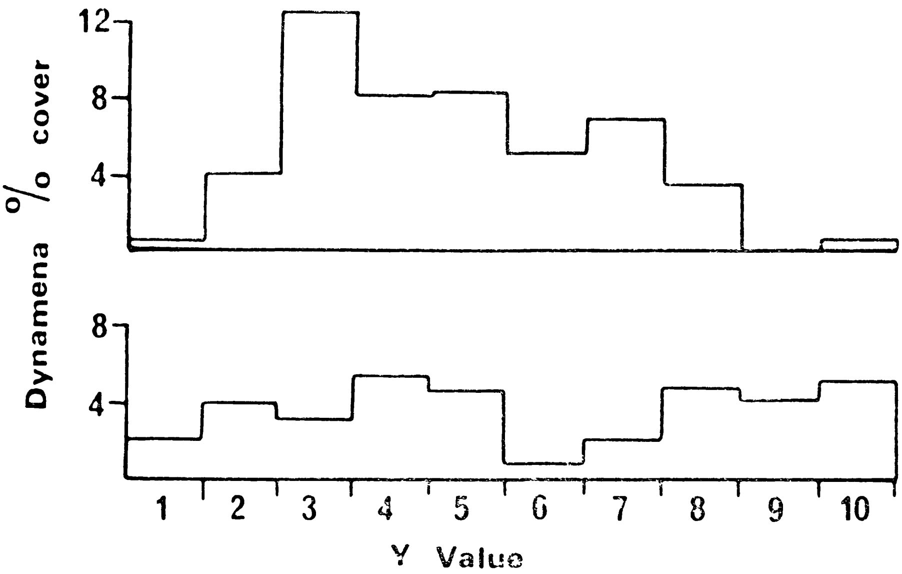

FIG. 8.

Zonation of *Dynamena* on segment faces colonized (bottom) and uncolonized (top) by *Gonothyraea*.

If stolonic and vertical development in hydroids are indeed subject to different selection pressures, as suggested above, there remains the possibility that the abundance of each species over a plant may be adjusted to the presence of the other. Figure 8 shows that such an interaction was in fact present; when *Gonothyraea* was absent from a segment-face *Dynamena* achieved maximum cover on segments distal to and including Y3 whilst when *Gonothyraea* was present *Dynamena* was much more uniformly dispersed. This dichotomization on the basis of presence or absence of *Gonothyraea* (see Fig. 3) was only slightly confounded with environmental differences between the two classes, so the changed distribution of **Dynamena** abundance must be due to the presence of **Gonothyraea.** We showed previously (Boaden *et al.,* 1975) that both species were most frequently found in the Y2-Y5 segments of the plants and inspection of those results (Fig. 7 of that paper) shows *Gonothyraea* to have a distinct bias towards the basal segments of the plants. The results of Figure 8

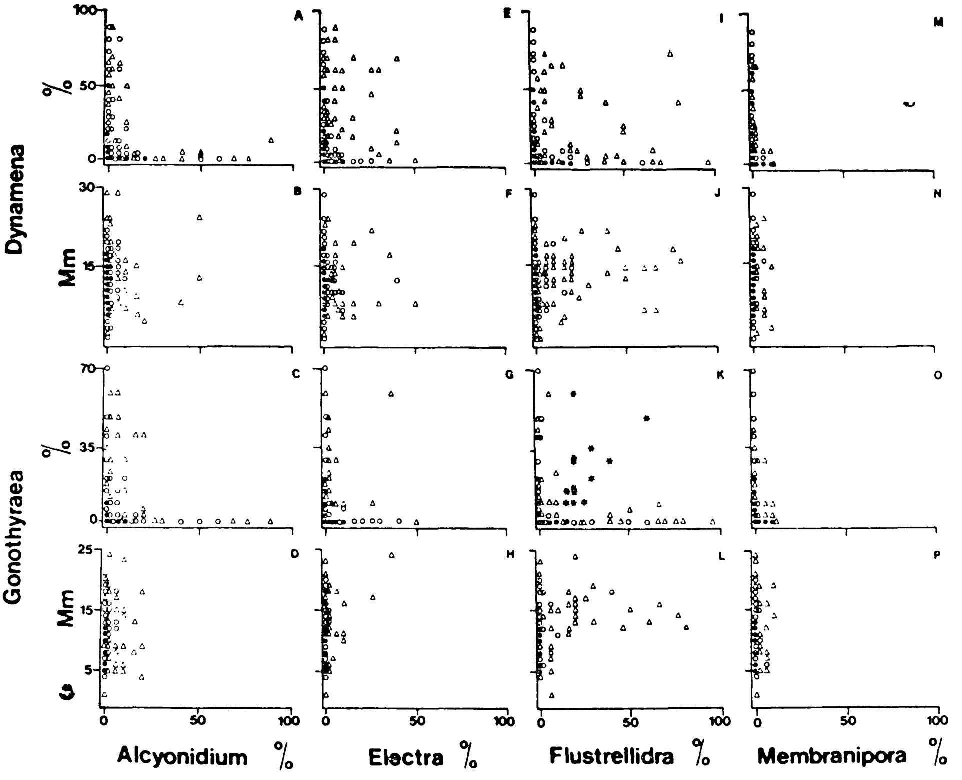

Fig. 9.

Relationships of hydroid abundance and stem height with *Alcyonidium, Electra, Flustrellidra* and *Membranipora.* Symbols as for Fig. 1.

showed no difference in distribution between the concave and convex surfaces of the fronds when this was examined, despite the difference in overall abundance between the two sides. We conclude, therefore, that *Gonothyraea* displaces *Dynamena* from the latter's preferred position on the Y3-Y5 segments when the two species co-occur.

Bryozoans are also potential competitors of hydroids, sharing as they do requirements for attachment space and particulate food. We need therefore to look at the relationships between the hydroids and bryozoans on *Fucus* segments.

Dynamena and *Alcyonidium* were clearly hyperbolically related (Fig. 9a), maximum *Dynamena* cover occurring in the absence of *Alcyonidium.* Note that this relationship could be, to some extent, a statistical artefact: if *Alcyonidium* were responsible for 80% of a segment-face, then *Dynamena* could achieve only a maximum of 20% (unless one species overgrows the other). Inspection of Figure 9a shows that this was not the case here and the data thus support either of the alternative hypotheses, of opposing environmental requirements or of competition. Table VII shows, however, that the incidence of *Dynamena* systematically increased with *Alcyonidium* density, i.e. that *Dynamena* was more frequently encountered on segment-faces bearing all but the highest populations of *Alcyonidium.* The two species are thus unlikely to have opposite environmental optima, so that a competition-based explanation is desirable. *Dynamena* stem heights also declined with increase in *Alcyonidium* abundance (Fig. 9b), further suggesting competitive inhibition of the hydroid's growth.

Gonothyraea showed a less clear-cut relationship with *Alcyonidium,* but a hyperbolic distribution of joint abundances (Fig. 9c) and a shallow decrease in stem height with bryozoan density (Fig. 9d) are both discernible. Since the incidence of the hydroid paralleled that of *Dynamena* (Table VII) our conclusions are that *Gonothyraea* and *Alcyonidium* are similarly in competition.

TABLE VII

Incidence of *Dynamena* and *Gonothyraea* in relation to the local density of *Alcyonidium.*

Density of *Alcyonidium* percent cover	N of cases[a]	*Dynamena* incidence[b] percentage	*Gonothyraea* incidence[b] percentage
0.00	658	25.4	13.5
0.01— 5.00	186	37.6	20.4
5.01— 10.00	19	42.1	36.8
10.01— 15.00	8	50.0	37.5
15.01—100.00	25	28.0	12.0

$\chi^2=0.88$, n.s.

[a] Number of segment-faces carrying the stated density of *Alcyonidium.*

[b] Percentage of faces with the stated *Alcyonidium* density which also bore the hydroid.

Electra resembled *Alcyonidium* in its relationships with *Dynamena* (Fig. 9e, f), with similar conclusions. With *Gonothyraea,* however, the hyperbolicity in abundances was indeed present (Fig. 9g) but stem height steadily increased with bryozoan abundance ($r=0.275$, $P<0.001$). This correlation, however, was largely due to shorter stems on faces not bearing *Electra* (mean stem height with *Electra* absent=10.85 ± 0.43 SE mm, but with *Electra* present=13.48 ± 0.47 mm, $t=2.47$, $P<0.05$). Since *Electra* is an opportunist species, particularly exploiting newly available frond surface (Ryland and Stebbing, 1971) a possible explanation of the patterns reported here is that *Gonothyraea* can persist in the presence of *Electra* only by vertical developments.

The variation in *Dynamena* abundance with *Flustrellidra* (Fig. 9i, j) resembled that just discussed for *Gonothyraea* and *Electra,* except that there was no net change of stem height between faces with or without *Flustrellidra* (12.43±0.54 SE mm and 11.71±0.45mm respectively, t=0.97, n.s.). Our conclusion therefore again favours competition as an explanation. For *Gonothyraea,* however, the data suggest the sample was heterogenous (Fig. 9k); the hydroid was most abundant where *Flustrellidra* was absent (and conversely) in one sub-set, whilst in another sub-set there was a positive correlation between the two species. Variation in *Gonothyraea* stem height (Fig. 9l) again suggested a positive relationship between the two, either because competition induces vertical development or because these species have shared environmental needs. At very high *Flustrellidra* densities, there was a suggestion of a slight decrease in stem height. Those data points showing positive correlation between the two species relate to plants at site 2 of Boaden *et al.* (1976a) i.e. in the main part of the rapids where feeding conditions were particularly favourable. If co-existence were possible anywhere it would be on the large plants and with the rich food supply found here. We therefore again interpret the data as evidence of competition at all sites other than this particularly favourable one.

Dynamena was scarcer and slightly shorter in stem as *Membranipora* increased in abundance (Fig. 9m,n); *Gonothyraea* similarly declined in cover though not in stem height (Fig. 9o,p). Since the relative frequencies of the two hydroids did not increase with *Membranipora* density these results suggest differences in environmental requirements rather than competitive exclusion.

Bryozoa might be responding to the same environmental conditions as attract (or favour) hydroid colonization independently of their specific identity. This is examined in Table VIII. Except for *Dynamena* stem height, all measures increased significantly with number of bryozoan species present, indicating that conditions favourable to the latter also favoured hydroid development. We also calculated bryozoan cover on each segment-face irrespective of species identity and examined its effects on the hydroids. Relations with hydroid cover were badly confounded with environmental effects and were difficult to interpret but stem heights of both species, whilst positively correlated with bryozoan cover at low densities, levelled off or slightly declined at high densities (Fig. 10). The effects are not more pronounced than observed in relation to single species (above) and

TABLE VIII

Hydroid abundance in relation to the number of Bryozoa species present on the same segment face ***P<0.001.

No. species present	*Dynamena* percentage cover	*Dynamena* stem height (mm)	*Gonothyraea* percentage cover	*Gonothyraea* stem height (mm)
	Mean ± s.e. (n)	Mean ± s.e. (n)	Mean ± s.e. (n)	Mean ± s.e. (n)
0	2.6±0.6 (473)	12.2±1.3 (61)	1.3±0.3 (473)	9.6±0.6 (40)
1	5.7±0.9 (301)	11.5±1.0 (82)	2.0±0.4 (301)	11.0±0.6 (55)
2	10.0±1.9 (102)	13.1±0.6 (58)	3.9±1.1 (102)	13.2±0.9 (25)
3	10.0±3.4 (20)	13.9±1.0 (14)	10.6±4.0 (20)	15.3±1.3 (9)
	F=9.93***	F=0.90	F=11.71***	F=6.69***

this appears to be the summed responses to individual species. We conclude therefore that the hydroids share many of their environmental requirements with the bryozoans.

A possible means of reducing over competition between the groups is to partition the available substratum on the basis of concave or convex surface use. Only one possible interaction, however, was detected: *Gonothyraea* showed a *very slight bias* towards the use of convex surfaces in the absence of *Flustrellidra* (52.6%, n=97) but was more likely to be found on concave surfaces when faces carrying both species were considered (65.1%, n=48).

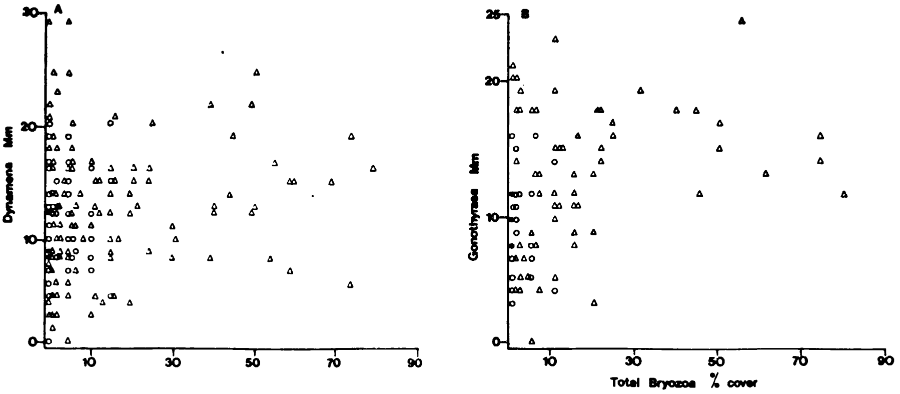

FIG. 10.

Dynamena (A) and *Gonothyraea* (B) stem height in relation to total bryozoan density on the same segment face. Symbols as for Fig. 1.

A logical extension of this analysis is to consider the possibility of adjustment in longitudinal distribution of the hydroid along each frond should a bryozoan competitor (potential or real) be present. We determined the distributions of faces colonized by the hydroid and those colonized by the bryozoan and computed the distribution of joint occurrences of both species which would be expected were these the outcome of their independent assembly from the single species distributions. These computed distributions could then be compared with the observed patterns of joints occurrences to determine the presence of any interactions or other effects associated with the co-occurrences of the two species in the field.

Figure 11a presents the results for *Dynamena* and *Alcyonidium*. Solo occurrences of *Dynamena* were most frequent on Y3 segments and were common over the Y1-Y5 range, whilst solo occurrences of *Alcyonidium* were more frequent at Y6 and common over segments Y2-Y6. The expected distribution for joint occurrences of the two species peaked in the Y3-Y5 region of the fronds but their observed distribution was slightly but significantly more distal than this ($\chi^2=29.1$, $P<0.001$) i.e. the two species were found together on distal segments more frequently, and on basal segments less frequently, than would be expected had they settled (or survived) there independently. Two explanations are possible. In conditions satisfying some common environmental requirement each species might independently need to settle distally, whilst in conditions satisfying either *Dynamena* or *Alcyonidium*, but not the other species, each might best settle basally. Alternatively, the two species might be in competition and able to co-exist in regions of the plant marginal for one or other (or both if differentially so) species. The corresponding analysis for *Dynamena* and *Electra* (Fig. 11b) again shows a bias towards more distal incidence of co-occurrence than would be expected of indepen-

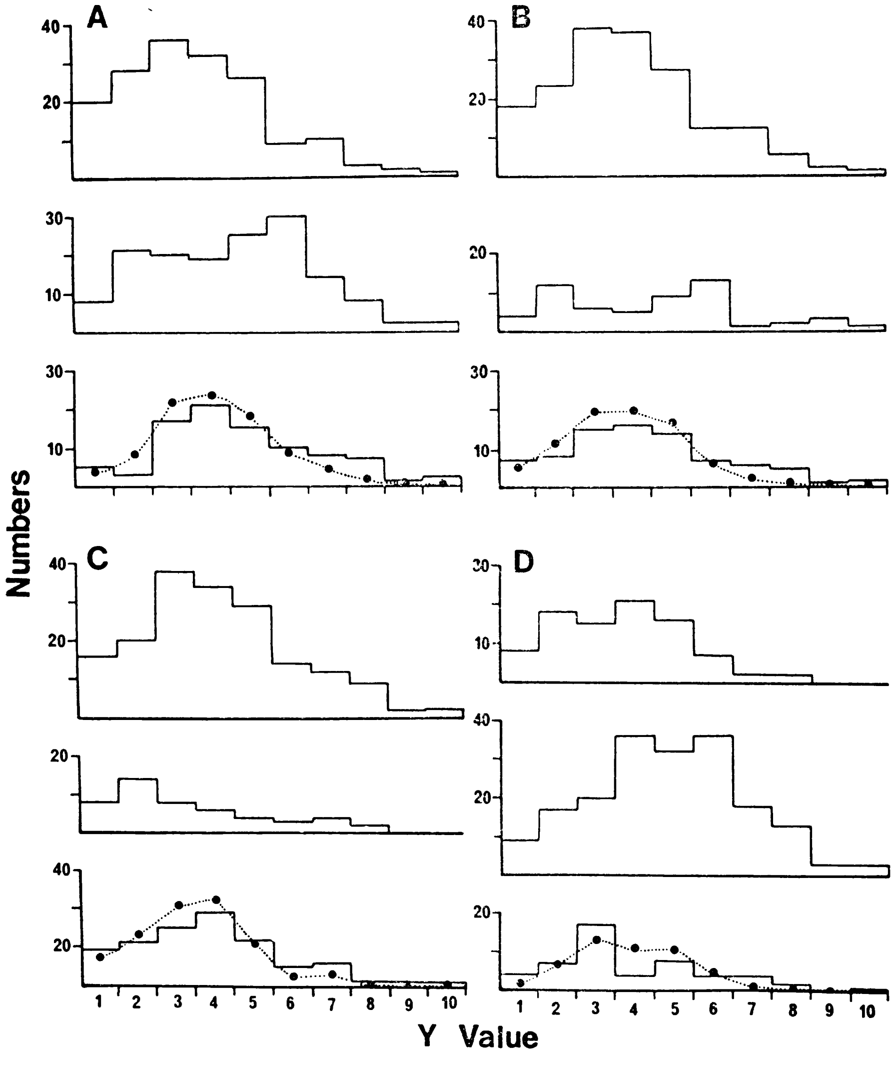

Fig. 11.

Solo and joint distributions of hydroid-bryozoan pairs. In each of the sets A-D, the upper diagram shows the distribution of the hydroid in the absence of the bryozoan, the middle diagram the distribution of the bryozoan in the absence of the hydroid and the lower diagram the distribution on segment faces colonized by both species. Pecked line indicates theoretical distribution of joint occurrences if the two species settled independently (A) *Dynamena-Alcyonidium*, (B) *Dynamena-Electra*, (C) *Dynamena-Flustrellidra*, (D) *Gonothyraea-Flustrellidra* (see text for details).

dent assemblages ($\chi^2=18.83$, $P<0.01$), with similar implications to those noted above. Figure 11c shows the same pattern with *Flustrellidra* ($\chi^2=12.61$, $P<0.01$) but the distribution of joint occurrences of *Membranipora* and *Dynamena* are consistent with independent use of the available segment-faces ($\chi^2=0.62$, n.s.).

None of the corresponding analyses for *Gonothyraea* revealed statistically significant departures from expectation, though that for *Gonothyraea* and *Alcyonidium* came near to doing so ($\chi^2=9.12$, n.s.). The data (Fig. 11d) are rather different from those for *Dynamena*: co-occurrences were less frequent than expected in the Y4-Y6 region where *Alcyonidium* solo occurrences were most frequent, and were more frequent than expected in the two shoulders of the *Alcyonidium* solo distribution, over Y1-Y3 and from Y7 onwards. This suggests that central settlements by *Gonothyraea* were perhaps being eliminated in competition with the high *Alcyonidium* populations there.

Competitive interactions with bryozoans

Details of the interactions between hydroids and bryozoans were studied further in 1975, using a sample of 15 plants drawn from 3 of the 13 sites used in our main study. Hydroid stem densities and stem heights were determined on «clear» parts of the segments—i.e. when not in contact with a bryozoan—and on those parts of the segments where they were «encrusted» by bryozoans. In the latter cases, the erect stems usually emerged from the flat mass of the bryozoan colony, but their areas of attachment were often totally obscured beneath the encrusting zooids. Although *Dynamena* was significantly more abundant in clear areas (0.65 ± 1.75 SD stems/cm^2) than in encrusted areas (0.45 ± 1.02) ($t=2.02$, $P<0.05$), there was little difference in average stem height between the two situations (13.0 ± 3.0mm when clear against 12.7 ± 4.2mm when overgrown, $t=0.66$, n.s.). Since «clear» and «encrusted» colonies were obtained from

TABLE IX

Occurrence of overgrowth of *Dynamena* and *Gonothyraea* by various Bryozoa.

Bryozoan species	*Dynamena*			*Gonothyraea*		
	Joint occurrences[a]	Frequency of overgrowth[b]	Relative frequency of overgrowth, percentage[c]	Joint occurrences[a]	Frequency of overgrowth[b]	Relative frequency of overgrowth, percentage[c]
Alcyonidium	79	29	36.7	34	0	0
Electra	100	29	29.0	71	11	15.5
Flustrellidra	183	110	60.1	95	16	16.8
Membranipora	1	1	0	0	0	0

[a] Number of segment-faces (out of 602 examined) bearing both hydroid and bryozoan.

[b] Number of segment-faces displaying overgrowth of the hydroid by the bryozoan.

[c] Percentages of faces with joint occurrences showing one or more cases of overgrowth.

the same segment-faces the possibilty of an environmental effect is precluded. We conclude that *Dynamena* was indeed being eliminated from areas with high bryozoan densities.

Table IX summarizes the specific origin of this overgrowth. *Flustrellidra* was the species most likely to overgrow *Dynamena,* both because it most frequently occurred on the same segment-face as the hydroid and because it was more given to overgrowth anyway. We have previously demonstrated that *Flustrellidra* is the most dominant of the four bryozoans on *F. serratus* because of its ability to overgrow competing species (O'Connor *et al.,* 1980). *Alcyonidium* was the next most severe competitor for *Dynamena,* followed closely by *Electra. Membranipora* and *Dynamena* only rarely co-occurred. *Gonothyraea* was less prone to overgrowth by *Flustrellidra* and *Electra,* but the small sample of joint occurrences with *Alcyonidium* precluded much further analysis for that species.

Finally, we determined the longitudinal distributions of *Dynamena* overgrowth by the three bryozoans (Fig. 12). The regions of most frequent overgrowth agreed with the regions of maximum deficits in co-occurrences illustrated in Figure 11, bearing in mind that the two analyses are based on different samples. *Gonothyraea* was too sparse to analyse in this way but the modal positions did coincide with peak bryozoan numbers.

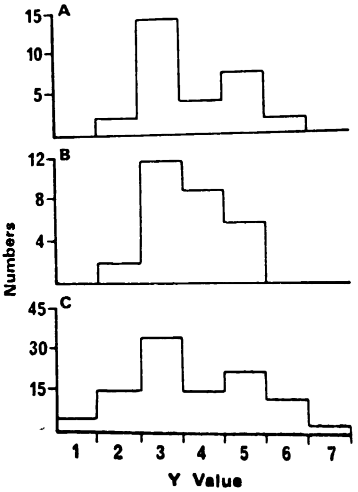

FIG. 12

Frequency distributions of overgrowth of *Dynamena stolons by* (A) *Alcyonidium* (B) *Electra* (C) *Flustrellidra* as a function of position along plants.

DISCUSSION

Environmental requirements

Dynamena and *Gonothyraea* clearly have rather different environmental optima for their establishment and growth on *F. serratus* but share those requirements one might expect to be essential for small-particle feeders. Both species were most abundant at sites with much water movement and low silt loads, a pattern they share with other erect taxa such as the sponges *Scypha compressa* and *S. ciliatum* (Boaden *et al.*, 1976a). *Gonothyraea* was less demanding than *Dynamena* in respect of silt and turbulence but was more sensitive than *Dynamena* to variations in current flow, preferring fast flowing waters (Table I); these differences were reflected in the relative abundance of the two species on the plants they colonized (Fig. 3). Thus, as in our earlier studies of potentially competing species within the *Fucus* epifauna (Boaden *et al.*, 1976a; O'Connor and Lamont, 1978; O'Connor *et al.*, 1979) plants available for colonization and growth are already discriminated on the basis of the gross environment in which they occur.

Within any site environmentally suitable for an epifaunal species, plant size may influence the settlement or subsequent survival and development of the species concerned. Large plant size is known to favour the bryozoans *Flustrellidra* and *Membranipora* (O'Connor *et al.*, 1979) as well as the tunicate *Didemnum* (Boaden *et al.*, 1976a). A similar effect partially segregates the two hydroids studied here, for *Dynamena* was differentially found on plants of large volume (Table III) whilst *Gonothyraea* showed no direct relationship with plant size (Table III). *Dynamena* was also more abundant on plants of above average length whereas *Gonothyraea* showed this effect weakly (Table VI).

Multi-species assemblages such as occur on the segments of *Fucus* fronds may be the outcome of independent responses by each species to its environment, or may be the result of well-defined species interactions (see Simberloff, 1978). Table IV shows that *Dynamena* and the bryozoans, *Alcyonidium, Flustrellidra* and *Electra* tend to co-occur. This could reflect shared environmental requirements and Table I and earlier studies (Boaden *et al.*, 1975) show that these four species have in fact broadly similar responses to their physical environment although *Alcyonidium* is less sensitive to local *Fucus* density than is *Dynamena.*

Dynamena numbers were also correlated with those of the two *Scypha* species and with those of *Didemnum.* These correlations are of particular interest because the erect growth form of the sponges has parallels in the stem development of the hydroid, and because the three species form a closely-interacting sub-community within the *Fucus* epifauna (Boaden *et al.*, 1976a). The pattern shown by both hydroids of slightly shorter stems in basal and distal locations and longer stems more centrally, mirrors that found for *S. compressa* (Boaden *et al.*, 1976b); the greater vertical development is presumably adaptive within the heart of the floating plant where turbulence is known to be lower than on more open distal or basal faces (Seed *et al.*, 1981).

Gonothyraea is known to be significantly associated with (in order of strength of association) *Flustrellidra,* the *Scypha compressa*—*Didemnum*—*S. ciliatum* complex, *Membranipora, Spirorbis borealis, Alcyonidium* and *Dynamena.* Only the last three species (and *Electra*) are less abundant in *Gonothyraea's* presence (Table IV): these patterns may reflect differences in the between plant and within plant relationships of these species with *Gonothyraea.* None of the other species are correlated in abundance with *Gonothyraea* population size on colonized plants, so their associations with the hydroid must be on the basis of common environmental requirements. Similarly, the negative relationships of *Gonothyraea* densities on plants to the populations of *Membranipora* and of *Spirorbis* also present must reflect the greater abundance of these species in silt-laden waters (O'Connor *et al.*, 1979; O'Connor and Lamont, 1978), an environment not favoured by *Gonothyraea.* Finally, the difference in relationships with *Alcyonidium* on the part of *Gonothyraea* and *Dynamena* (Fig. 1) can be attributed to the greater insensitivity of *Gonothyraea* occurrence to *Fucus* densities (Table I), an attribute it shares with *Alcyonidium* occurrence.

Competition with Bryozoa

Since *Dynamena* and *Gonothyraea* share so many environmental requirements with the three most common Bryozoa, they cannot avoid direct competition for space. The better conditions were for Bryozoa on a segment the greater the population of hydroids (Table VII). *Gonothyraea* appeared to be better able to maintain its cover of the fronds at high bryozoan densities than was *Dynamena,* a finding confirmed by the relative incidence of overgrowth of the hydroid by Bryozoa (Table IX). Once overgrown the stolons are presumably hindered in their function of nutrient transport and individual zooids or even complete stems are lost, at least in the case of *Dynamena.*

It is unclear why *Gonothyraea* can withstand high bryozoan densities so much better than *Dynamena.* One striking difference between the two species, however, is the different relationship between stem heights and percentage cover. These were generally well correlated in *Gonothyraea* but were less so in *Dynamena* (Fig. 6, Table VI). We suggest that *Dynamena* normally develops as a stoloniferous network with simultaneous growth in lateral and vertical planes, stem growth allowing the utilization of food in the water currents outside the immediate surface layers. Where conditions are conductive to extensive development there may be less selection for vertical growth because conditions are more favourable at the frond surface. Consequently, we should observe rather shorter stems on those faces with greatest hydroid cover, as in fact found (Fig. 6). Hydroids can be sparse, however, either because they are newly founded or in very poor physical environments (in which cases the stems necessarily will be short) or because they are subjected to bryozoan competition (in which cases the stems may be long, as when differential growth occurs, or short, as when regression following overgrowth occurs). We should therefore observe a greater range of stem heights at low hydroid densities, again as found (Fig. 6). *Gonothyraea,* on the other hand, does not develop an extended stoloniferous network but develops vertically from a relatively discrete holdfast-like attachment to yield a bush-like colony. Extremes of percentage cover will thus be correlated with measurements of maximum stem heights during initial growth, as found (Fig. 6), whilst at higher stem densities intraspecific competition between colonies (each of which constitutes a genetic individual) may occur over food, with consequent starvation and loss of polyps evident as reduced stem heights (Fig. 6). This would be less apparent in *Dynamena* where adjacent stems are likely to belong to the same colony and therefore not in competition with each other.

Dynamena thus appears vulnerable to bryozoan overgrowth as a result of its stoloniferous habit. In support of this, the relative frequency of its overgrowth by different bryozoans (Table IX) was greater in the case of the thick mats of *Flustrellidra* and least in the case of the thin layers of *Electra*. Conversely, *Gonothyraea's* discrete base should afford greater resistance to overgrowth by all three species, as indeed was observed (Table IX). Bryozoa themselves are known to develop peripheral spines to provide effective defense against overgrowth (Stebbing, 1973). Even if overgrown, a hydroid colony may survive if the base continues to function: for *Gonothyraea* this function is as an attachment structure, a function likely to be achieved under all bryozoans, whilst for *Dynamena,* stolon function for food transport is perhaps more likely under the thin layered *Electra* than under the thicker mats of *Alcyonidium* and *Flustrellidra.* This again is consistent with our findings on relative overgrowth and on the incidence of differential stem growth with respect to potential competition (Fig. 10).

Such a differential sensitivity to bryozoan competition between the two hydroids also offers an explanation for their patterns of co-existence (Fig. 11). *Dynamena* was less frequently present on faces bearing *Alcyonidium, Electra* or *Flustrellidra* than expected where such co-occurrences were most likely to occur in the absence of competition or avoidance behaviour, and was more frequently in co-existence with the bryozoans where such co-existence was not anticipated, chiefly on the more distal segments. Since the average cover by these bryozoans declines distally faster than does their probability of being found there (Boaden *et al.*, 1975) what probably happens is that *Dynamena* colonizes the newly grown distal segments and persists there until the segments are colonized and eventually dominated by bryozoans. Hence, *Dynamena* will be less frequent but more abundant distally following colonization of newly-available frond surface. As the plant grows, additional segments develop distal to the one colonized, the chance of colonization of that segment by Bryozoa increases with time and the size of any bryozoan colony present also increases to encrust a larger proportion both of the frond and any *Dynamena* present, following which the hydroid's numbers decline, in some cases to extinction. We thus have an explanation both of the deficit in joint occurrences of *Dynamena* and bryozoans in the zones of greatest expected frequency (Fig. 11a-c) and of the increase in incidence, but not in abundance, of *Dynamena* as one moves down the *Fucus* frond (Boaden *et al., loc. cit.*), an explanation additionally supported by the longitudinal distribution of the observed cases of overgrowth of *Dynamena* by each bryozoan (Fig. 12). *Gonothyraea,* on the other hand, was less susceptible to overgrowth and showed less marked deficits in the distribution of co-occurrences on segment faces, though still with indications of overgrowth effects of the type found for *Dynamena*.

Within hydroid competition

Intraspecific competition in *Dynamena* is suggested only by the existence of a niche shift between low and high populations (Fig. 4) but this effect is probably better ascribed to a correlation of population density with environment. Given that *Dynamena* is strongly associated with high turbulence and current flow we would expect colonies on the convex surface—almost universally the less used by *Fucus* epifauna—to be more distally located in plants in the environmentally poorer sites, since they are thereby exposed to greater turbulence (see Boaden *et al.*, 1976a). In favourable environments, populations are larger and everywhere exposed to rather greater turbulence and so have a broader distribution over the plants (c.f. upper and lower diagrams on Fig. 4). One factor blocking a more basal location under these conditions is the possibility of dehydration at low tide; animals within the main body of the plants are sheltered by the wet fronds under these circumstances but those near the holdfast are at risk. *Spirorbis* populations are differentially distributed between inner and out *Fucus* fronds apparently in response to the same risk (O'Connor and Lamont, 1978).

Although *Dynamena* and *Gonothyraea* differ to some extent in their environmental optima (Fig. 3) they nevertheless overlap sufficiently, both at plant level, and in their use of individual segment faces (Fig. 7) to provide evidence of competitive exclusion. The more uniform distribution of *Dynamena* in *Gonothyraea's* presence (Fig. 8) suggests an ability by the latter to occupy the normal Y3-Y5 location of *Dynamena,* to the latter's exclusion. Since the presence of *Gonothyraea* is coupled with a three-fold increase in the abundance of *Flustrellidra* (Table IV) it is possible than *Dynamena* is actually excluded by the bryozoan, its major competitor. Nevertheless, *Gonothyraea* remains in possession of the niche, probably due to its greater resistance to overgrowth by this species. Part of this ability to co-exist with *Flustrellidra* may depend on the interaction between their concave and convex distributions, the more favourable conditions on concave surfaces perhaps allowing the additional stem growth previously postulated as allowing it escape the effects of overgrowth by *Flustrellidra*. Thus, whilst *Flustrellidra* is particularly abundant on longer than average plants (O'Connor *et al.*, 1979) *Gonothyraea* shows greater stem development on these plants (Table VI), as would be expected on this hypothesis.

These competition based interpretations provide a coherent explanation for our diverse findings but suffer the weakness of being inferred from distributional data. They are, however, considerably strengthened by their consistency with direct behavioural evidence of competitive interactions (Fig. 12; Table IX). Explanations based upon differential settlement (see Crisp, 1974) can be advanced, but such settlement is itself the outcome of evolutionary forces reflecting the ultimate factor of reduced fitness in predatory, competitive or abiotically harsh environments. All of our evidence pertains to the latter two factors. Whilst predation can certainly determine the structure of intertidal communities (e.g. Paine, 1974; Menge, 1976; Peterson, 1979) and some epifaunal communities (Seed, 1976) we have so far found little evidence of significant predation within those *F. serratus* communities which we have studied in the British Isles. A remaining possibility is that both our distributional and behavioural data pertain to a highly seasonal situation with the spatial niche of *Gonothyraea* and *Dynamena* being determined by other factors at other times of the year. Whilst marked seasonal changes certainly do exist (Seed *et al.*, 1981) our preliminary analyses indicate that such changes are consistent with the picture of the hydroid niche developed in the present study.

Summary

The distribution of *Dynamena pumila* (L.) and *Gonothyraea loveni* (Allman) on *Fucus serratus* L. was studied in Strangford Lough, Northern Ireland. *Dynamena* was more sensitive than *Gonothyraea* in preferring fast currents and agitated waters and in avoiding silt laden plants. Areas preferred by *Dynamena* also had higer *Fucus* densities but both species increased their local abundance in dense *Fucus* beds. *Dynamena* was encountered significantly more often on large plants, but both species were rather similar in their within plant zonations irrespective of plant size; evidence was obtained for a weak dependence of stem heights with position along the fronds.

Dynamena - favoured plants were also colonized by the bryozoans *Alcyonidium hirsutum, Electra pilosa* and *Flustrellidra hispida* but *Dynamena* and *Alcyonidium* showed inverse relationships in their local densities on those plants which they shared. *Gonothyraea* and *Alcyonidium* were correlated but the hydroid exhibited an inverse relationship with certain other common members of the epifauna, notably the serpulid *Spirorbis borealis* and the bryozoan *Membranipora membranacea.* Both *Dynamena* and *Gonothyraea* were more abundant on plants where the numbers of bryozoans were high and they also grew taller there, especially where these plants were in particularly favourable feeding areas.

Bryozoans and hydroids came into frequent competition, the latter being overgrown, in order of frequency, by *Flustrellidra, Alcyonidium* and *Electra.* Hydroid densities decreased when overgrown and there was evidence that *Gonothyraea* changed its niche from convex to concave surfaces in the presence of *Flustrellidra.* Distribution patterns for *Dynamena* depended on the presence or absence of *Alcyonidium,* of *Electra* and of *Flustrellidra,* those for *Gonothyraea* on the presence or absence of *Alcyonidium.*

Dynamena and *Gonothyraea* were themselves occasionally in competition but the outcome depended on site environment. Niche position also varied with intraspecific effects, changing in both species as their own population densities increased. The overall position of the two species in this community was determined in part by their different environmental tolerances and in part through their different sensitivity to competition from Bryozoa.

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