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The influence of neighbors on the feeding of an epifaunal bryozoan

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Abstract: In North Wales the encrusting bryozoans *Electra pilosa* (Linnaeus), *Alcyonidium hirsutum* (Fleming), and *Flustrellidra hispida* (Fabricius) are epifaunal on the fucoid alga *Fucus serratus* (Linnaeus). Colonies occur in close proximity and overgrowth frequently results. This study experimentally demonstrates how suspension-feeding of *Electra* is affected by degree of association with neighboring colonies and by ambient flow velocity. In slow flow, feeding of *Electra* colonies was reduced when *Alcyonidium* colonies were present upstream. An even greater reduction in feeding occurred when *Alcyonidium* colonies surrounded *Electra*. However, evidence suggests that such reduction in feeding should be only a transient phenomenon in natural habitats because of the very short duration of low-flow velocities during the tidal cycle. In faster flow, *Electra* feeding was greater when *Alcyonidium* colonies were present upstream, and greater still when *Alcyonidium* colonies surrounded *Electra*. Similarly, feeding of *Electra* surrounded by *Flustrellidra* colonies in fast flow was greater than that of isolated *Electra* colonies or of colonies downstream from *Flustrellidra*; there was no apparent difference in *Electra* feeding in the latter two cases. Isolated *Electra* colonies experienced a general reduction in feeding success with increased flow velocity, however, colonies showed a greater propensity to feed as flow velocity increased. The enhanced feeding of *Electra* in association with other colonies in fast flow likely results from the slowing and diverting of flow by *Alcyonidium* and *Flustrellidra*. This study provides evidence that feeding enhancement in encrusting assemblages is an important phenomenon.

Key words: Bryozoan feeding interaction; Colony; Flow velocity

INTRODUCTION

Sessile suspension-feeders depend on flowing water to supply their food resources. Large-scale water movements that introduce food resources to habitats of suspension-feeders are produced by tides, ambient currents, and waves. The subsequent movement of water through local habitats will be influenced in various ways. Patterns of water flow are affected as water interacts with both the bodies of suspension-feeders (Chamberlain & Graus, 1975; Svoboda, 1976; Koehl, 1977a,b; O'Neill, 1978; LaBarbera, 1981; Telford, 1981; Merz, 1984; Okamura, 1984; Patterson, 1984; Denny *et al.*, 1985; McFadden, 1986) and the topography of the substratum (for review, see Nowell &

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Jumars, 1984). The creation of feeding currents by many suspension-feeders further affects the pattern of water movements through aquatic microhabitats.

Sessile suspension-feeders commonly occur in close association (Stebbing, 1973; Buss, 1979; Buss & Jackson, 1979; Kay & Keough, 1981; Rubin, 1982; Russ, 1982), and the movement of water through such assemblages can be complex. The effects of water flow on suspension-feeding have been the focus of several recent investigations (LaBarbera, 1978; Okamura, 1984, 1985; Patterson, 1984; McFadden, 1986; Muschenheim, 1987a,b), however, we are far from understanding patterns of particle capture from flow in composite natural assemblages. For bryozoans, reduced feeding by zooids of an arborescent species occurs when a conspecific colony is present upstream (Okamura, 1984), however, zooids of encrusting colonies experience enhanced feeding under similar conditions (Okamura, 1985). These results may reflect, in part, alterations in small-scale water movements produced by the upstream colonies.

Previous studies of bryozoans feeding from flowing water have focused on interactions between conspecific colonies (Okamura, 1984, 1985). In many assemblages, however, colonies of different species occur in close proximity and often overgrow one another (e.g., Osman, 1977; Buss & Jackson, 1979; Jackson, 1979; Kay & Keough, 1981; Rubin, 1982). Buss (1979) suggested that the outcome of overgrowth interactions between bryozoans may be influenced by competition for food. LaBarbera (1985) argued that suspension-feeding by brachiopods produces food-depleted zones that may preclude the incursion of neighboring suspension-feeders. A growing body of evidence indicates that competition for food frequently occurs among suspension-feeders (Crisp, 1960; Stiven & Kuenzler, 1979; Buss & Jackson, 1981; Peterson, 1982; 1983; 1985; Okamura, 1984; Bertness & Grosholz, 1985; Fréchette & Bourget, 1985).

This paper describes an experimental investigation of the feeding ecology of the encrusting bryozoan *Electra pilosa* (Linnaeus). In particular, I describe how feeding of *Electra* is influenced by variations in ambient flow and by neighboring suspension-feeders. *Electra* is commonly associated with a number of other epifaunal species of the fucoid alga *Fucus serratus* (Linnaeus), which is abundant in the lower intertidal of relatively sheltered shores of the British Isles. The dynamics of the epifaunal community of *Fucus* have been the focus of many investigations (for review, see Seed & O'Connor, 1981; Seed, 1985). Competition for space in this community is evidenced by a well-documented high proportion of overgrowths (Stebbing, 1973; Seed & Boaden, 1977; O'Connor *et al.*, 1980; Wood & Seed, 1980; Oswald & Seed, 1986; Walters & Wethey, 1986). The three most common epifaunal bryozoan species in the area of this study are the encrusting ctenostomes *Flustrellidra hispida* (Fabricius) and *Alcyonidium hirsutum* (Fleming), and the encrusting cheilostome *Electra pilosa*. Encounters among the three bryozoans are frequent, and *Electra* is generally overgrown by both *Flustrellidra* and *Alcyonidium*. Colonies of *Flustrellidra* and *Alcyonidium* are thicker than *Electra* colonies and have larger lophophores, characteristics that have been associated with superior abilities to compete for food and space (Buss, 1979; Best & Thorpe, 1986; Sebens, 1986).

METHODS

FIELD SAMPLING

Fucus plants were collected whole from the shores of the Menai Straits (53° 13'N; 4°9'W) in November 1984, April 1985, and July 1985 to sample distributions and spatial relationships of *Electra* colonies. Data on neighboring organisms were gathered if neighbors were within 5.5 cm of *Electra*. (It was deemed that the very rapid seasonal growth of *Alcyonidium* colonies could result in overgrowth of *Electra* within a radius of 5.5 cm.) If neighbors were > 5.5 cm away, *Electra* colonies were considered to be isolated. Data collected included: the proportions of isolated *Electra* colonies, those with neighbors, and those overgrown, and; the identities, relative positions, and distances of the neighbors or overgrowers.

Initial sampling in November 1984 showed great variation in the number of *Electra* colonies per randomly collected *Fucus* plant (mean = 21.4, SD = 31.3, range = 0-118, $n = 22$), with a high coefficient of dispersion (CD = 45.85) indicative of a clumped distribution (Sokal & Rohlf, 1981). This tendency to aggregate has been noted earlier (Ryland & Stebbing, 1971; Ryland, 1972). Subsequently, in April and July 1985, only heavily encrusted plants were sampled.

LABORATORY FEEDING EXPERIMENTS

Bryozoans were collected on individual fronds of *Fucus* growing in the low intertidal of the Menai Straits. The sloping bedrock of the study area is relatively homogeneous in physical relief and supports dense *Fucus* stands. Due to the narrowness of the Menai Straits, strong bidirectional tidal currents develop. While the intertidal area is exposed to occasional short period, oscillatory water movements from the wakes of boats, the strong tidal currents and surrounding topography damp-out any but perhaps the most severe wind-driven secondary flow effects (Wood & Seed, 1980; pers. obs.). Because *Fucus* fronds are flexible they extend out in the direction of current flow. Colonies on fronds, therefore, experience basically unidirectional flow and also remain in the same position with respect to one another and to flow. [See Wood & Seed (1980) for further description of the study area.] Bryozoans growing on portions of *Fucus* fronds were brought back to the laboratory and mapped for future reference.

Segments of single *Fucus* fronds (6-8 cm in length) with experimental colonies were submerged in a recirculating flow tank by hooking the frond onto a thin wire directed into the working section of the flow tank. [See Okamura (1984, 1985) for further description of flow-tank design.] Experimental colonies all grew on concave surfaces of the fronds and all faced upwards in the flow tank. Earlier studies (Wood & Seed, 1980; Seed *et al.*, 1981) as well as two out of three samples analysed in this study indicate that *Electra* colonies occur in greater number on concave surfaces than on convex surfaces (November 1984; $F_{1,21} = 5.866$, $P < 0.025$, randomized complete block paired comparisons test; April 1985; $t_s = 2.262$, $df = 6$, $0.05 < P < 0.10$, t test for

paired comparisons; July 1985: $t_s = 5.307$, $df = 6$, $0.001 < P < 0.01$, t test for paired comparisons). In the field, concave surfaces of *Fucus* will vary between upward and downward positions depending on the direction of the tidal current.

The flow tank was filled with a suspension of latex particles (polystyrene divinylbenzene calibration standards; Coulter Electronics, Luton, U.K.) with a median diameter of $13.1 \mu\text{m}$ (C.V. < 13). Particles were suspended at an average concentration of $750 \text{ particles} \cdot \text{ml}^{-1}$ (SD = $35 \text{ particles} \cdot \text{ml}^{-1}$, $n = 26$) in filtered seawater. The size of particles was chosen to lie within the range in size of algal cells in bryozoan diets (Winston, 1977), and the concentration of particles lies within the range in concentration of small flagellates measured in the Menai Straits (Jones, 1962; Jones, 1968; Jones & Spencer, 1969). Small flagellates are thought to be particularly important food items for bryozoans (Winston, 1977).

The concentrations of particles during experimental runs were determined by placing samples of the suspension in a 1-ml capacity counting cell (Sedgewick rafter counter) and counting the particles in five randomly chosen transects of 48 mm^3 in each of seven replicate cells. (Mean number of particles counted per cell = 179, SD = 22, range = 116–260, $n = 182$.) ANOVA indicated that the concentration of particles did not vary significantly among the experimental runs ($F_{25,156} = 1.051$, $0.25 < P < 0.50$).

Feeding experiments were performed within a few hours of collecting colonies. Colonies were allowed to feed for 27 min. Gut passage time for *Electra pilosa* has been estimated as 37 min (Winston, 1977). After 27 min colonies were removed from the flow tank and placed in dilute sodium hypochlorite to dissolve their organic contents. This treatment left the exoskeleton of zooids intact as well as the particles consumed. Particles ingested during the experiments could then be clearly seen with a dissecting microscope and were counted. The total number of zooids per colony was also determined. As a measurement of health, only colonies in which more than three zooids fed were sampled. The effect of this practice should not bias the results. Table IV shows that similar proportions of colonies associated with neighbors show this level of feeding in both slow and fast flow, thus there is no evidence that the sampling procedure was highlighting feeding under unusual circumstances.

Data were converted to frequencies of zooids that had consumed different numbers of particles. All feeding zooids were sampled per colony and replicate colonies were run. It is recognized that there is a potential problem in applying contingency table analysis since zooids from the same colonies were pooled, and assumptions of independence may be violated. However, the following considerations indicate that zooids were functionally independent: (1) there was no correlation between feeding rates and colony size (see Table III), therefore no evidence that zooids within a colony were competing for or were otherwise influencing one another in particle capture; (2) within colonies some zooids ingested many particles while many zooids fed on few particles and some did not feed at all; and (3) the volume of the suspension was so large that concentration depletion would be insignificant.

Feeding data were obtained for: (1) isolated *Electra* colonies; (2) *Electra* colonies

downstream from *Alcyonidium* or *Flustrellidra* colonies (neighboring colonies ranged from being 0.5 cm upstream from the edges of *Electra* colonies to directly overgrowing the upstream edges of *Electra*); and (3) *Electra* colonies surrounded by *Alcyonidium* or by *Flustrellidra* colonies. See Fig. 1 for representation of experimental configurations of colonies.

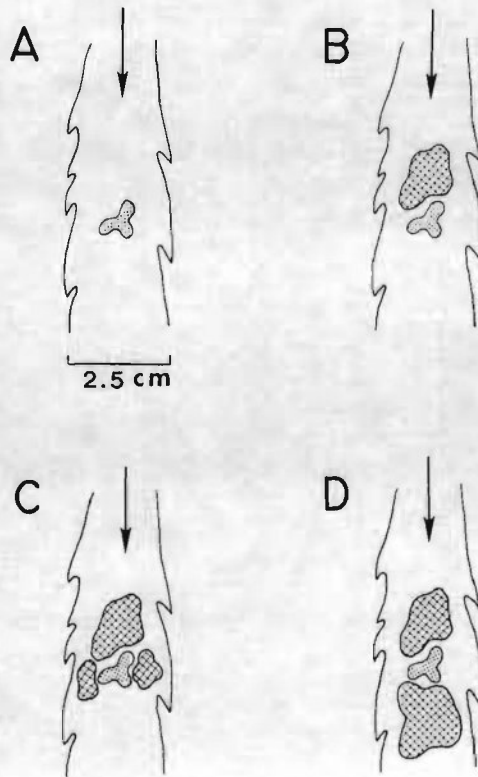


Fig. 1. Schematic representation of experimental colony associations on segments of *Fucus*: isolated *Electra* colonies (A); *Alcyonidium* or *Flustrellidra* present upstream (B); *Alcyonidium* or *Flustrellidra* surrounding *Electra* (C, D).

Feeding was assessed at slow ($0.01\text{--}0.02\text{ m}\cdot\text{s}^{-1}$) and fast ($0.01\text{--}0.12\text{ m}\cdot\text{s}^{-1}$) freestream flow velocities. (Mean freestream velocities were estimated by timing particle movement through 15 cm lengths of the working section of the flow tank.) The relevance of these flow velocities to field conditions is deferred to the discussion. Feeding by *Electra* in still water was also investigated, although not as extensively as feeding from moving water. To obtain these data, *Fucus* fronds with experimental colonies were placed in containers holding particles suspended at a concentration of $750\text{ particles}\cdot\text{ml}^{-1}$ in 2 l seawater. Halfway through experiments particles were resuspended. (Particles were also resuspended in the flow tank to make treatments as similar as possible.)

RESULTS

FIELD SAMPLING

A large proportion of *Electra* colonies were overgrown by or were within 5.5 cm of neighbors other than *Electra* (see Fig. 2). While the proportion of each nearest neighbor or overgrower varied through the year, *Flustrellidra*, *Alcyonidium* and other colonies of *Electra* were consistently the three most common neighbors. The most common overgrowers were *Flustrellidra* and *Alcyonidium*. As Stebbing (1973) previously noted, established *Electra* colonies sent out occasional runner-like chains of zooids that overgrew neighboring colonies of *Alcyonidium* and *Flustrellidra*. In addition and more commonly, *Electra* colonized the surfaces of *Flustrellidra* (no lateral connection with nearby *Electra* colonies being observed). Other overgrowers and neighbors included barnacles, spiror-

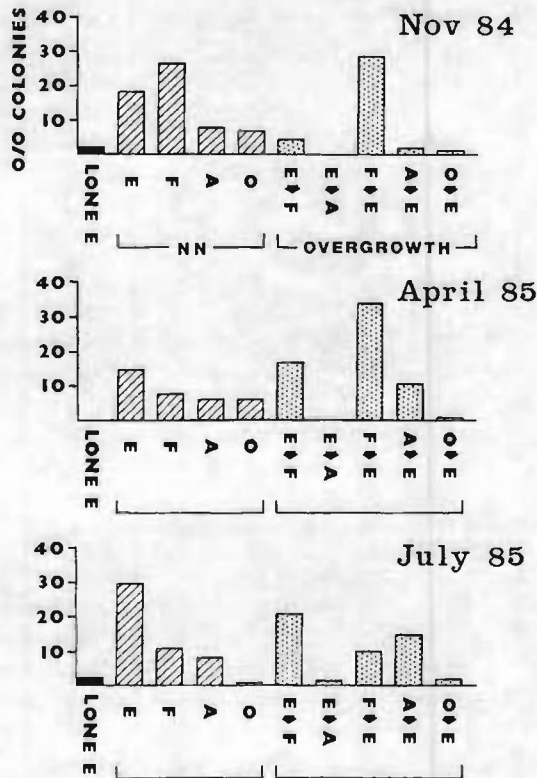


Fig. 2. Spatial relationships of *Electra* colonies on *Fucus* fronds sampled on 7 November 1984 ($n = 472$ *Electra* colonies); 24 April 1985 ($n = 305$); 7 July 1985 ($n = 1114$). Histograms plot percentage of isolated (lone) *Electra* colonies and percentages of colonies with nearest neighbors and overgrowers. (See Methods for definition of isolated colonies and those considered to have nearest neighbors.) E = *Electra*, F = *Flustrellidra*, A = *Alcyonidium*, O = other, NN = nearest neighbor to *Electra*. Overgrowths signified by arrow which points in direction of overgrown colony.

bids, and the bryozoan *Membranipora membranacea* (Linnaeus). The erect hydroid *Dynamena pumila* (Linnaeus) was present occasionally, but was not sampled because: (1) its growing and feeding structures proliferate primarily in a vertical rather than a horizontal direction relative to *Fucus* fronds, and (2) observations indicated that *Electra* grew around its basal attachment.

During all three sampling periods the majority of neighboring *Flustrellidra* and *Alcyonidium* were within 0.5 cm of *Electra* colonies (see Table I). In addition, both *Flustrellidra* and *Alcyonidium* were found to occur most often upstream from *Electra* colonies (see Table II). *Flustrellidra* and *Electra* are found on *Fucus* throughout the year,

TABLE I

Percent (and number) of neighboring *Flustrellidra* and *Alcyonidium* colonies within 0.5 cm of *Electra* colonies during three sampling periods. (Data on neighboring colonies were collected if *Flustrellidra* or *Alcyonidium* were within radius of 5.5 cm of *Electra* colonies. See Methods for further description of sampling.)

	<i>Flustrellidra</i>	<i>Alcyonidium</i>
November 1984	65.4% (83)	82.5% (33)
April 1985	80.0% (20)	68.4% (13)
July 1985	81.9% (99)	57.1% (48)

TABLE II

Percent of *Flustrellidra* ($n = 254$) and *Alcyonidium* ($n = 224$) colonies upstream, downstream, and surrounding *Electra* colonies. Data for *Flustrellidra* were collected in November 1984 and for *Alcyonidium* in July 1985 (sampling dates reflect time course of laboratory studies). (Scores for *Flustrellidra* do not add to 100% as 7.50% of colonies occurred only along sides of *Electra* colonies.) Bryozoans on fronds were isolated enough that scores for one interaction can be assumed to be independent of scores for another.

	Upstream	Downstream	Surrounding	G value
<i>Flustrellidra</i>	53.15%	35.04%	4.33%	178.78*
<i>Alcyonidium</i>	59.82%	14.29%	25.89%	72.99*

* Significant at $P < 0.001$.

while *Alcyonidium* appears in the spring, grows rapidly over the summer and tends to slough away in the autumn (Seed & O'Connor, 1981; pers. obs.). These life histories are reflected in the incidences of the two species as nearest neighbors and overgrowers of *Electra* during the three sampling periods (see Fig. 2).

EFFECT OF NEIGHBORHOOD AND FLOW VELOCITY ON FEEDING SUCCESS

Feeding by zooids of *Electra* was significantly affected by the interacting influences of flow velocity and degree of association with *Alcyonidium* (Fig. 3) (multiway con-

tendency table analysis (Brown, 1983): $G = 272.80$, $P < 0.001$, $df = 46$). In slow flow, isolated colonies experienced greatest success in feeding while colonies surrounded by *Alcyonidium* experienced lowest feeding rates. This can be seen in the greater proportion of zooids from isolated colonies that fed on large numbers of particles in Fig. 3, and by the associated higher value for the mean number of particles captured. In fast flow, the situation reversed: lowest feeding rates were associated with isolated colonies and highest feeding rates with colonies surrounded by *Alcyonidium*. Again, this is seen in the relative shifts of the distributions in Fig. 3 (more zooids fed on greater numbers of particles when surrounded by *Alcyonidium*) and in the associated values for mean numbers of particles captured.

A significant difference was also found in feeding from fast flow by isolated *Electra* colonies and those associated with *Flustrellidra* ($G_{adj} = 69.533$, $P < 0.001$, $df = 36$) (see

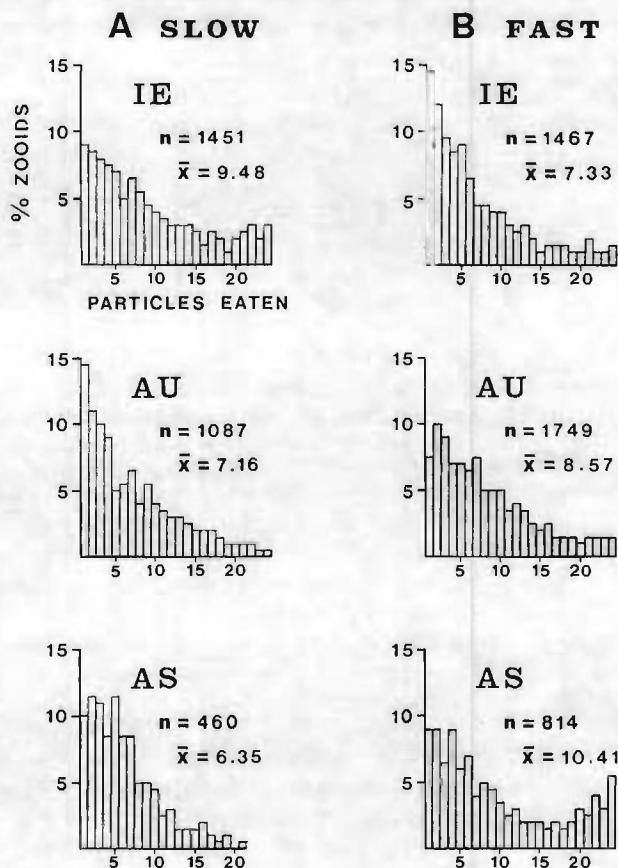


Fig. 3. Percent of zooids that ingested one to ≥ 29 particles in slow (A) and fast (B) ambient flow when *Electra* colonies were isolated (IE), when *Alcyonidium* was present upstream from *Electra* (AU), and when *Alcyonidium* surrounded *Electra* (AS). Analysis required pooling of last four feeding categories to: 21–22, 23–25, 26–28, and ≥ 29 particles \cdot zooid $^{-1}$, respectively. See text for results of analysis.

Fig. 4). Not enough data were collected to analyze the experiments in slow flow. While there appeared to be no consistent difference in the feeding of isolated *Electra* and those downstream from *Flustrellidra*, *Electra* fed slightly better if surrounded by *Flustrellidra* colonies (see associated values for the mean number of particles captured in Fig. 4). The high level of significance may reflect the sensitivity of the test when sample sizes are large to differences in the frequency distributions (e.g., the high number of zooids that ingested five particles when *Flustrellidra* was upstream, and the general trend for greater numbers of particles to be captured when *Electra* was surrounded by *Flustrellidra*).

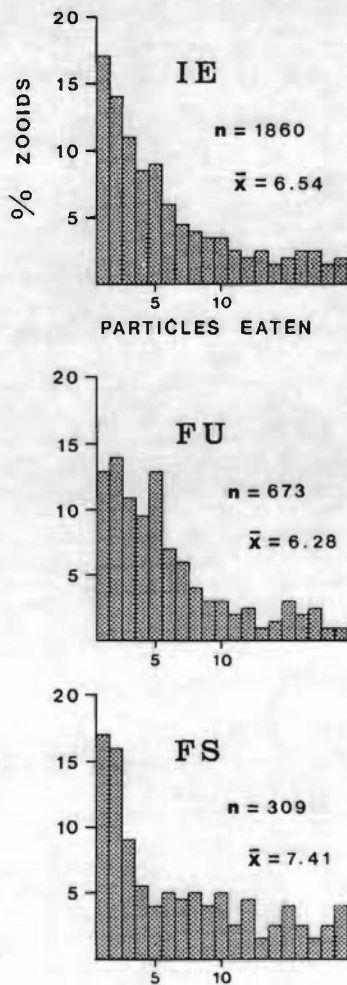


Fig. 4. Proportion of zooids that ingested one to ≥ 25 particles in fast flow when colonies were isolated (IE), when *Flustrellidra* was present upstream (FU), and when surrounded by *Flustrellidra* (FS). Analysis required pooling of last five categories to: 15-16, 17-18, 19-20, 21-24, and ≥ 25 particles \cdot zooid $^{-1}$, respectively. See text for results of analysis.

Data collected on particle capture by *Electra* zooids in still water were not analysed. Fewer colonies actually fed in still water, thus it was deemed that feeding success might be underrepresented.

EFFECT OF COLONY SIZE ON FEEDING SUCCESS

Previous studies of bryozoan feeding showed that feeding from flowing water by species of both arborescent and encrusting bryozoans depended on colony size (Okamura, 1984, 1985). Because it was difficult to maintain constant colony size across experiments in this study, colonies of varying sizes were used; however, ANOVA showed no significant differences among the average sizes of colonies in the experiments [$F_{9,189} = 1.695$, $P > 0.05$, range in size (mm^2) = 3.5–209.2], therefore variation in colony size across experiments should not affect results. Furthermore, for *Electra*, colony size does not explain a significant proportion of the variation in feeding rates (see Table III).

TABLE III

Correlation analysis of colony feeding success (ln-transformed values of number of particles captured averaged for all zooids per colony) and colony size from experiments in fast and slow ambient flow and in still water. Note r^2 values indicate proportion of variation explained by colony size and that none of the correlations is significant.

Flow	r	r^2	n^*
Fast	-0.2374	0.0564	105
Slow	-0.0110	0.0001	61
Still	-0.1752	0.0307	33

* Pools colonies across experimental treatments within each flow category since no significant difference was found among their correlation coefficients (tests of homogeneity among two or more correlation coefficients, Sokal & Rohlf, 1981).

TABLE IV

Number (and percent) of feeding colonies and of these, those that were associated with neighbors in still water and in slow and fast ambient flow velocities after 27 min. Number of colonies is pooled across experiments in each flow regime and includes colonies from experiments not presented due to insufficient data.

Flow velocity	Feeding colonies	Associated with neighbors
Still	35	15
	(28.23)	(142.86)
Slow	89	55
	(34.50)	(62.50)
Fast	124	79
	(55.61)	(63.20)

INDUCTION OF FEEDING BY FLOW

The proportion of colonies (pooled across experiments) that actually fed was influenced by flow (Table IV): significantly more colonies fed as flow velocity increased from still water to fast flow ($G = 32.499$, $P < 0.001$, $df = 2$). The presence of neighbors also appeared to affect the propensity of colonies to feed (see Table IV). More colonies associated with neighbors fed in slow and fast flow, while in still water isolated colonies showed a greater tendency to feed. However, these differences were not significant at the 0.05 level ($G = 4.903$, $0.05 < P < 0.10$, $df = 2$).

DISCUSSION

AMBIENT FLOW VELOCITY AND FEEDING SUCCESS

The narrowness of the Menai Straits at the study site results in particularly strong tidal currents. Nearshore mean current velocities (averaged over 1-m depth intervals) have been measured over 25-h periods near the study site. Peak neap-tide mean current velocities are $\approx 0.70 \text{ m} \cdot \text{s}^{-1}$ at ebb tide and $0.45 \text{ m} \cdot \text{s}^{-1}$ at flood tide (Simpson *et al.*, 1971). Peak current velocities during spring tides are greater (Simpson *et al.*, 1971; data for nearshore sites were not reported). The 25-h record indicates that mean current velocities $< 0.25 \text{ m} \cdot \text{s}^{-1}$ persist for only 3–5 h of the entire neap-tide cycle. The duration of low flows during spring tides can be expected to be even shorter. Flow through *Fucus* stands will likely be less than these measured flow rates due to interactions with the fronds (Kitching *et al.*, 1952; Fonseca *et al.*, 1982; Peterson, 1984) and substratum-related boundary layer effects (Wainwright & Koehl, 1976; Nowell & Jumars, 1984). In addition, flow through *Fucus* plants varies (Seed *et al.*, 1981), thus colonies in various positions along *Fucus* blades will be subject to different flow environments. While no flowmeters were available to measure flow, it is evident that *Fucus* epifauna will be exposed to a wide range in flow. In view of the aforementioned measurements of flow velocities, it seems reasonable to conclude that the experimental flow velocities of $0.01\text{--}0.12 \text{ m} \cdot \text{s}^{-1}$ lie well within the range in flow velocity experienced by epifaunal bryozoans during each tidal cycle. Furthermore, the duration of low-flow periods during the tidal cycle suggests that the experimental slow flows of $0.01\text{--}0.02 \text{ m} \cdot \text{s}^{-1}$ are transient in nature.

Investigations from other areas provide additional support that epifaunal *Electra* colonies largely experience faster flows. *Electra* tended to occur on *Fucus* plants in areas of greater flow in Strangford Lough, Northern Ireland, where flood and ebb-tide currents were 0.6 and $0.4 \text{ m} \cdot \text{s}^{-1}$, respectively (Boaden *et al.*, 1975). In Lough Ine of southern Ireland *Electra* was found to be more abundant on laminarians where currents of $2.5\text{--}3.0 \text{ m} \cdot \text{s}^{-1}$ were measured at the level of fronds (Sloane *et al.*, 1961). Hagerman (1966) noted that *Fucus serratus* and its associated epifauna (including *Electra*) grew only in areas of strong currents in the northern part of the Øresund of Denmark.

The foregoing discussion indicates that for most of the tidal period, isolated *Electra* colonies will experience an inhibition in feeding from faster flows, a result that is in accord with previous experiments with other encrusting bryozoans (Okamura, 1985). This reduction in feeding at higher flow velocities may reflect several phenomena: (1) particles and water moving with greater momentum are more difficult to divert towards the mouth, (2) the greater drag on particles at higher flow velocities may make transfer to the mouth more difficult even after particles have been diverted inside the lophophores. The actual mechanism(s) were not resolved in this study.

FLOW-INDUCED FEEDING

Despite the inhibition in feeding that isolated *Electra* colonies experienced in fast flow, significantly more colonies fed as flow velocity increased. McKinney *et al.* (1986) found zooids of the arborescent bryozoan *Bugula neritina* to be more active in ambient flow up to $0.04 \text{ m} \cdot \text{s}^{-1}$ than they were in still water or in ambient flow $> 0.04 \text{ m} \cdot \text{s}^{-1}$. The reason(s) for flow-induced feeding may only be conjectured. Possibly, the bryozoans respond to water movement itself since moving water will usually carry new food particles, or it may be that a greater flux of particles elicits greater feeding activity.

INFLUENCE OF NEIGHBORS

Neighbors were found to influence feeding by *Electra* in the following ways. (1) In fast flow, feeding was enhanced when *Alcyonidium* and *Flustrellidra* colonies surrounded *Electra*. Feeding was also enhanced when *Alcyonidium* was present upstream, however, the presence of *Flustrellidra* colonies upstream had little effect on feeding. (2) In slow flow, feeding was reduced when *Alcyonidium* colonies surrounded *Electra* or were upstream from *Electra*.

Throughout the year a large proportion of *Electra* colonies were associated with neighboring bryozoan colonies (both *Alcyonidium* and *Flustrellidra*) and thus should experience neighbor-related effects on feeding. Since fast-flow conditions predominate at the study site, enhancement rather than reduction in feeding due to association with neighbors should prevail.

Feeding enhancement may occur because neighboring colonies slow and divert flow down to the level of *Electra*. The movement of dye released in filtered seawater indicated that water entered the region below the level of the extended lophophores of *Alcyonidium* colonies (see Fig. 5) at the upstream end of colonies and was also pumped into this region by the ciliary currents of the lophophores. Once in the sublophophoral region, dye-laden water flowed slowly downstream through the stand of *Alcyonidium* lophophores. *Alcyonidium* was also observed to divert and pump water from much greater distances away from the substratum than *Electra*. This suggests that the relatively strong feeding currents of neighboring *Alcyonidium* colonies allow *Electra* colonies to capture particles from areas otherwise inaccessible. Particle availability and quality has been demonstrated to change with height above the substratum and ambient flow

velocity (Muschenheim, 1987a). At the downstream edge of *Alcyonidium* colonies, water followed the contours of the colony and flowed downwards to the level of the *Electra* colony. Often small areas of turbulence were observed at the downstream edges of the thick *Alcyonidium* colonies, where water was seen to stall and eddy. Eddying regions

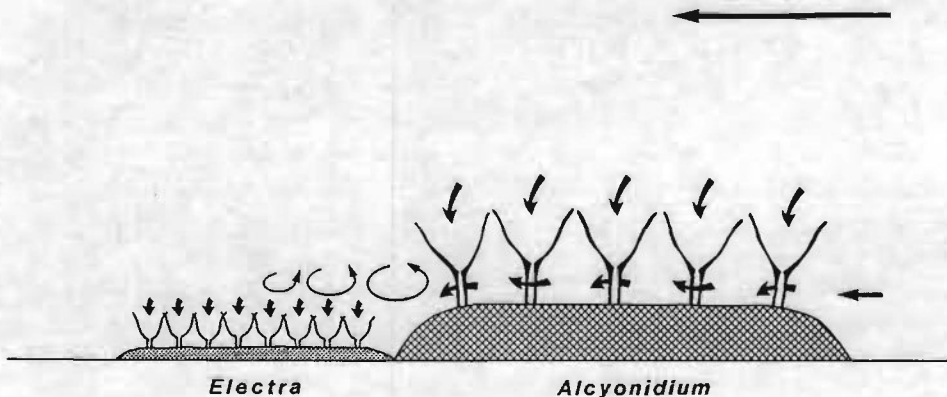


Fig. 5. Schematic representation of flow patterns observed at both experimental flow velocities when a thick *Alcyonidium* colony is present upstream from a thin *Electra* colony. Arrows indicate direction of flow. Note flow meanders through stand of *Alcyonidium* lophophores and forms an eddying wake region over *Electra* colony at downstream edge of *Alcyonidium*. Note also more elevated and stronger feeding currents of *Alcyonidium* that are capable of diverting flow from greater distances above substratum where flow is more rapid (as indicated by large flow arrow at top of illustration).

were also observed to form at the boundaries of *Alcyonidium* colonies that were downstream from *Electra*. Such turbulence undoubtedly illustrates the interaction of fluid flowing over a field of roughness elements, in this case the thick *Alcyonidium* colonies (Monteith, 1973; Nowell & Jumars, 1984). These basic downstream patterns were observed at both experimental flow velocities.

The formation of eddies may allow for greater particle capture by *Electra* because: (1) eddies may represent areas of local particle concentration (Lee & Srinivasan, 1978; Patterson, 1984); (2) flow speeds within eddies may be reduced; and/or, (3) recirculating eddies may present a more even distribution of available particles due to their greater diffusivity in turbulence (Patterson, 1984). This latter effect may be important if feeding rates do not adjust or lag in response time to changes in particle concentration. In contrast, water flowing across isolated *Electra* colonies showed little disruption other than that due to the weak pumping of the lophophores.

Dye streams showed that water followed the contours of *Flustrellidra* colonies and was directed onto *Electra* colonies downstream as described above for *Alcyonidium*. However, the formation of eddying wake regions was not observed. Unlike *Alcyonidium*, *Flustrellidra* did not readily extend dense arrays of lophophores in the flow tank (although all *Flustrellidra* colonies were alive and healthy and extended at least several

lophophores). Flow, therefore, did not encounter and interact with stands of lophophores, and there were many fewer lophophores of *Flustrellidra* creating feeding currents. These considerations suggest that water flowing past *Electra* colonies downstream from *Flustrellidra* would move more rapidly than it would after passing across a colony of *Alcyonidium*. Although no flow measurements at the levels of colonies were made, water moving cross *Flustrellidra* colonies did appear to slow down, possibly due to interactions with *Flustrellidra*'s prominent spines, however, the extent of slowing was not as great as that effected by *Alcyonidium* colonies. Nonetheless, results suggest that when *Electra* is surrounded by *Flustrellidra* colonies the resultant slowing and diversion of flow is great enough to allow for some enhancement of *Electra* feeding. In the field *Flustrellidra* was seen to extend vast arrays of lophophores. This suggests it will likely exert greater effects on the feeding of nearby *Electra* colonies than was evident from the laboratory studies.

Colony thickness appeared to relate to the amount of turbulence produced downstream. Downstream eddies formed behind the relatively thick colonies of *Alcyonidium* but not behind the relatively thinner colonies of *Electra* and *Flustrellidra* (mean thickness (mm) of *Alcyonidium* = 0.995, SD = 0.468, $n = 10$; of *Electra* = 0.140, SD = 0.023, $n = 12$; of *Flustrellidra* = 0.318, SD = 0.032, $n = 11$). Larger wake regions should form downstream of thicker colonies, in keeping with the pattern of flow past blunt objects (Vogel, 1981). Buss (1979) predicted that bryozoans with large zooids will interfere with the feeding of neighboring bryozoans with smaller zooids. In contrast, these results imply that the greater eddying region formed downstream from thick bryozoans with large zooids may actually be advantageous to the feeding of bryozoans with smaller zooids under flow conditions that prevail in the field. The reduction in feeding observed at very low flow velocities in this study is in keeping with Best & Thorpe's (1986) still-water study of competition for food among epifaunal bryozoans of *Fucus serratus*. While results from both studies may well be explained by the mechanism Buss proposed, the biological significance of such reduced feeding is suspect.

In summary, the results of this study indicate that neighbor-associated reduction in feeding of *Electra* is a transient phenomenon associated with low flow velocities. Because fast flow is the prevailing condition, enhancement in feeding among neighbors is the significant interaction. For the epifaunal bryozoans of *Fucus* there is no evidence that competition for food plays an important rôle.

IMPLICATIONS FOR DYNAMICS IN SUSPENSION-FEEDING ASSEMBLAGES

The predominant view to date has been that competition for food is the important feeding interaction among suspension-feeders (Buss, 1979). It is suggested to influence the outcome of overgrowth and hence to play a role in structuring communities of suspension-feeders (Buss, 1979). The notion that suspension-feeders may partition their food resources (Caine, 1977; Winston, 1977; Stuart & Klumpp, 1984) similarly implies that competition for food was important in the evolutionary past and continues to

maintain a partitioning of food resources. However, this study and an earlier investigation (Okamura, 1985) indicate that bryozoans feeding from flowing water do not compete for food, but experience enhanced feeding when associated with neighboring colonies of the same or of different species. Similarly, Laihonen & Furman (1986) inferred that the increased growth of barnacle epibionts near siphonal apertures of mussels was due to the greater availability of food resulting from coordinated feeding currents. A more complete picture of suspension-feeding assemblages thus appears to be one that incorporates facilitation in feeding through mutual feeding activity, as well as exploitative competition for food, and possible resource partitioning. The relative importance of facilitation and competition in feeding may vary depending on the organisms and the flow regime in which they live.

A reduced propensity to feed in slower flows means that waterborne particles have a greater chance to escape ingestion. This could be particularly important to larvae of benthic organisms that must approach and attach to the substratum to metamorphose. The bulk of bryozoan food is thought to be composed of small flagellates and other members of the phytoplankton (Winston, 1977), however, bryozoans have been observed to prey on a variety of organisms (Winston, 1978), and some larvae may be ingested (Jebram, 1977). On occasion, I have observed zooids of the arborescent bryozoan *Bugula neritina* to ingest cyprid larvae. Even if larvae are not ingested they can incur damage during the rejection process. Damage and mortality of larvae that have been rejected by other suspension-feeders has been documented (Mileikovsky, 1974; Cowden *et al.*, 1984; Young & Chia, in press). Larval damage and ingestion by benthic suspension-feeders may exert strong effects in marine assemblages (Woodin, 1976; Wilson, 1980), thus the generality of reduced rates of suspension-feeding during periods of low flow merits further investigation. Settlement by larvae during slack water or very slow flow into suspension-feeding assemblages could reduce rates of predation or damage to larvae, however, settlement behavior under differing flow regimes has received little investigation (Crisp, 1955). A reduction in drag forces that would allow larvae to attach successfully without being swept away would also produce a pattern of greater settlement in lower flow velocities.

Finally, these results suggest that patterns in the distribution and abundance of active suspension-feeders may be related to the strengths of their feeding currents and to flow regimes. In fast flow suspension-feeders with weak feeding currents may be constrained to co-occur with other active suspension-feeders. Such forms may be found in isolation only in habitats of low flow. However, suspension-feeders with stronger feeding currents may be found in isolation over a broad range in flow velocities. Of course there is no reason to believe that any single factor should account for the distribution of suspension feeding forms. Certainly other factors such as larval settlement behavior, competitive ability, and predation will influence distributions and abundances (Jackson, 1983; Buss, 1986). However, the constraints imposed by the interaction of morphology and physiology with physical aspects of the environment may affect distributional patterns to a greater extent than has previously been appreciated.

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