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# Recruitment of *Aurelia aurita* (Cnidaria: Scyphozoa) larvae is position-dependent, and independent of conspecific density, within a settling surface

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ABSTRACT: Aggregated settlement patterns in marine invertebrates are often assumed to result from larval preference for the presence of conspecifics ('gregarious' behaviour). These patterns might also result from larval selection of, or deposition in, particular microhabitats. On smooth, homogeneous surfaces habitat heterogeneity may be produced by the interaction between moving water and a submerged surface. Settlement is aggregated for the larvae of the jellyfish *Aurelia aurita*. I used removal experiments and reciprocal transplants to test whether recruitment occurred as a function of the position of the settlement site within a submerged surface or as a function of the density of conspecifics present. Position determined recruitment rates. The distribution of larvae may be attributable to reductions in local shear stress and increased thickness of the boundary layer. Planulae metamorphose into polyps after settlement, producing patches of varying density. Polyps may grow larger or bud to form clones. Budding rates were not a function of density, but growth rates did decline as density increased. However, high density areas maintained a greater polyp surface area over time than less dense regions, suggesting that food may be as unevenly distributed as larvae within a surface. Thus, position may confound the effect of density on growth and survivorship.

## INTRODUCTION

Three demographic processes control the establishment of populations of sessile marine invertebrates: (1) the number of recruits entering a given area from the plankton, (2) the growth rate of settled individuals, and (3) the rate at which animals multiply asexually. The flow regime affects these factors to the extent that encounter rates for both larvae and food items depend upon water flow patterns around a submerged object (Wainwright & Koehl 1976). Thus the flow regime influences growth rates through food distributions, and may influence dispersion patterns, directly or indirectly, by controlling recruitment and clonal growth rates.

In sessile populations, aggregations of conspecific individuals result when: (1) larvae actively select areas of high conspecific density (behave gregariously), (2) larvae actively select the other biological or physical characteristics of a particular microhabitat, (3) larvae passively accumulate in microhabitats defined by the near-surface features of the flow regime, (4) post-settlement mortality is spatially variable, or (5) rates of asexual multiplication are spatially variable.

The hypothesis that larvae select microhabitats predicts that aggregated settlement results incidentally from a shared larval response to a particular habitat or flow cue. This hypothesis and its not-easily-separable alternate, that larvae act as particles in the water column and are passively deposited in microhabitats created by the near-surface flow regime, are the simplest explanations for aggregated dispersion patterns. These hypotheses sometimes escape examination because aggregations are observed on smooth surfaces with no obvious source of habitat heterogeneity. However, spatially variable characteristics of the boundary layer forming across solid surfaces in moving water may provide such heterogeneity (Nowell & Tumars 1984). These characteristics are proposed determinants of ani-

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mal distributions in soft sediments and are currently under test (Eckman 1983, Hannan 1984). Boundary layer properties which vary with horizontal distance across a submerged surface, and thus might, actively or passively, influence larval dispersion on a smooth flat plate are discussed briefly below, at the end of the 'Introduction'.

If water flow over submerged surfaces creates habitat heterogeneity which influences larval settlement by making physical position within the surface important, then position should also affect growth and survivorship of local sub-populations within a surface. Those flow factors acting on larvae may also act on food distributions, food capture rates and the probability of dislodgement. Highly suitable positions for settlement, as determined by physical processes, may favor survivorship to the extent that persistence of local subpopulations might be less a function of local population density than of physical effects.

This study tested the relationship between larval dispersion patterns and position within a settling plate. The jellyfish *Aurelia aurita* releases sexually produced planula larvae into the waters on the Atlantic coast of North America during June and July. These larvae settle on hard surfaces and metamorphose into feeding scyphistomae (polyps). Polyps may replicate asexually by budding, but eventually differentiate (strobilate) to release ephyrae which develop into pelagic jellyfish. Dispersion of juvenile polyps is aggregated (pers. obs.) and the present study was designed to determine whether such aggregations resulted from (1) larval selection of, or passive deposition in, microhabitats determined by physical processes (e.g. Crisp 1955), or (2) active selection of regions with high conspecific density (gregarious larval behavior, e.g. Williams 1976, Scheltema et al. 1981). Reciprocal transplant and polyp removal experiments were used to test the effects of position and density of conspecifics on recruitment. Within aggregations, polyp growth rates and rates of asexual multiplication were examined as a function of local density.

## Relevant boundary layer properties

When a moving fluid encounters a stationary object, the velocity of the fluid at the surface of the object is zero. Thus, there must be a gradient between the velocity at the surface (zero) and the velocity some distance away from the surface, where the fluid motion is unaffected by the presence of the surface (the 'free-stream' velocity). A boundary layer develops due to the frictional drag of the surface on the flow. It is a region of shear where horizontal velocity increases with vertical distance away from the surface.

As flow moves over a surface the boundary layer attaches at the leading edge, and increases in thickness with distance downstream. The boundary layer thickens downstream because low momentum fluid close to the surface is mixed with higher momentum fluid away from the surface and energy is dissipated as heat in the boundary layer. Vogel (1981, p. 129) gives an operational definition of boundary layer thickness as the vertical distance away from a surface needed for local velocity to reach 99 % of the free-stream velocity.

In a unidirectional steady flow, a laminar boundary layer forms first at the edge of an immersed surface. Downstream, the boundary layer may become turbulent when inertial forces exceed viscous forces in dissipating flow energy (high Reynolds numbers), depending upon water velocity, free-stream turbulence, surface roughness of the object, and the length of the immersed object in the direction of flow. At very high Reynolds numbers, the laminar boundary layer may be infinitesimally small and may even disappear. Vogel (1981, p. 37–38) defines laminar flow as a situation where fluid particles move in smooth paths parallel to each other. The standard deviation of the velocity is small compared to the mean of the velocity. In contrast, the standard deviation of a turbulent flow is large compared to the mean flow velocity. The fluid as a whole moves in a single direction while movement of the fluid particles is irregular. The transition between laminar and turbulent flow occurs abruptly and somewhat unpredictably.

In a laminar boundary layer, molecular diffusion mixes low momentum fluid close to an immersed surface with higher momentum fluid away from the surface. In a turbulent boundary layer, molecular diffusion is restricted to a thin layer close to the object's surface and eddy diffusion operates above this layer. Eddy diffusion mixes the fluid much more effectively than molecular diffusion. The boundary layer thickness defines the extent of the relatively slow-moving flow in which organisms can perceive cues or maneouvre easily. Thus, laminar and turbulent boundary layers differ in the terms of the habitats they provide for organisms: a laminar boundary layer is not as well-stirred as a turbulent one, and the benefits of the refuge it provides may be balanced by the accumulation of wastes and the slow diffusion of nutrients into this semi-stagnant region (Vogel 1981). A turbulent boundary layer, with its thin laminar sub-layer, will be well-stirred but may provide less of a refuge. The role these differences play in determining the composition of fouling panel communities is not well understood, but Nowell & Jumars (1984) suggest that panel-area effects may be confounded by varying boundary layer development.

The boundary shear-stress, the drag force per unit surface area, changes with distance from the leading

edge, decreasing downstream in laminar flow. The local coefficient of skin friction can be calculated on part of the surface and 'provides a useful baseline with which the measured drag or the force needed to dislodge an organism can be compared' (Vogel 1981, p. 135). On a submerged settling plate, horizontal changes in boundary layer thickness and local shear stress have the potential to make both access of larvae to the surface and the forces which larvae must exert to remain in place highly variable and dependent upon position within the plate.

## METHODS

Settling plates were made from 36 unglazed ceramic tiles, each 2.3 × 2.3 cm, arranged in a contiguous 6 by 6 array. Tiles were attached to 16 × 16 cm pieces of galvanized wire mesh in 2 ways: (1) for growth studies of unmanipulated populations and for polyp removal experiments, tiles were glued to the mesh with General Electric silicone adhesive, (2) for experiments where tiles were transplanted from one location to another within a settling plate, Velcro strips were glued to the mesh and to the back of each tile with silicone adhesive.

All plates were suspended subtidally from floating or stationary docks in the Eel Pond at Woods Hole, Massachusetts, USA. The plates were positioned horizontally face-down; the weight of the ceramic tile was sufficient to maintain the horizontal orientation.

**Growth measurements on unmanipulated populations.** Eight replicate plates were set out in June 1981. A number of species subsequently recruited to the plates, including *Aurelia aurita*. Plates were examined every 5 d, with a single exception where there was a 10 d interval between censuses. Plates were otherwise undisturbed. After 14 d of submersion, the density of *A. aurita* polyps sometimes exceeded 50 per tile (5.3 $cm^2$), making exact measurements on every individual impracticable. I randomly chose one plate, and selectively identified 3 high density tiles (polyps: n = 50, 56, 56), 2 intermediate density tiles (n = 18, 22), and 2 low density tiles (n = 0,1). On these tiles, I measured all polyp cup diameters to the nearest 0.03 mm with an ocular micrometer under a dissecting microscope at 30×. I counted the number of buds per polyp and measured bud diameters. Cup diameters were converted to feeding surface areas, exclusive of tentacles, by assuming oral surfaces to be circular. The numbers of *A. aurita* polyps and individuals of all other species present were counted for the first 4 census dates. Plates were replaced randomly after examination and plate orientation (position of edges with respect to direction of water flow) was not controlled.

Time-series size measurements on individual polyps were not obtained because of the difficulties posed by marking individuals. However, measurement of all polyps at each density should have yielded growth data; changes in modal polyp size and in the variance of size distributions with time would provide an index of growth according to density. Two events, continuing recruitment and asexual multiplication, confounded this analysis. Continued recruitment onto high and intermediate density tiles obscured cohorts and augmented the small size classes at some censuses. The effects of asexual multiplication are not as easily identified.

No asexual buds were made until 19 d after plate exposure, and most polyps which made buds did so between 24 and 34 d. I classified polyps as non-budding or as budding individuals at each census. Budding represents a change in classification: the asexual 'parent' polyp was indistinguishable from the other polyps, both before buds appeared and once buds detached. Bud detachment began between Days 29 and 34 of the study, and detached buds, almost always smaller than the 'parent', added to the numbers of polyps in the small and intermediate size classes at these census dates. Clones were identifiable only while buds remained attached to the 'parent'. Thus all estimates dealing with asexual reproduction (% of individuals budding, number of individuals per clone, feeding surface per clone, etc.) were conservative and may underestimate the role of asexual reproduction in population growth.

**Transplant and removal experiments.** Eight settling plates were suspended approximately 0.3 m below the surface from the center of a floating dock during July 1982. *Aurelia aurita* planulae were the most abundant larvae settling at this time. The settling plates, positioned beneath a trap door, were shaded by the dock; thus differential lighting probably did not affect larval behavior. After sampling, plates were always replaced in the original position and orientation, so that any consistent patterns of water movement around the plates would be maintained.

To test whether recruitment was a function of the density of conspecifics on a particular tile or a function of tile position within a settling plate, I reciprocally transplanted tiles with high and low densities of *Aurelia aurita* polyps within plates. Five of the 8 replicate plates, where tiles were attached with Velcro, were submerged for 5 d. All *A. aurita* polyps on each tile were counted and within each replicate plate, tiles were ranked according to the numbers of polyps present. Ten successive highest- and lowest-density tiles were paired within each plate and reciprocal transplants were made between every other one of these pairs (5 pairs transplanted). Thus, the physical position

of tiles of a given density was changed experimentally. The remaining 5 of these 10 high-low density pairs (minimum difference between densities used was 20 polyps per tile) served as treatment controls, and were removed and then replaced at their original location. I transplanted every other pair of tiles so that each transplant could be compared to a control tile of similar density in paired t-tests. Sixteen of the 36 tiles present on each plate were left undisturbed. Plates were returned to the water for 3 d and then censused to estimate the numbers of larval recruits added to each tile.

If larvae behave gregariously, there should be no significant difference between the number of recruits on replaced tiles (controls) and transplanted tiles of the same original density. If recruitment is a function of position within the plate then transplanted high-density tiles, moved to a previously low-density position, should collect only as many larvae as the replaced low-density tiles. Transplanted low-density tiles, moved into positions which had collected high densities of larvae before the experiment, should collect numbers of recruits similar to those on the replaced high density tiles.

A removal experiment was also done to test the role of tile position as a determinant of the density of recruitment. Three replicate plates collected recruits for 5 d, then polyps were removed from the 5 tiles of highest density on each plate. Plates were returned to the water in the same orientation for 3 d and then censused again. If larvae select regions based on conspecific density then cleared tiles should collect few recruits. If position determines settlement, recruitment onto cleared tiles should be comparable to that onto undisturbed dense tiles within each plate.

Rough estimates of the direction of water movement relative to the plates and horizontal water velocity at the study site were made by injecting a carmine suspension (1% weight/volume) into the water. Plates were removed from the water and the carmine stream was injected into the water at plate depth. The time taken for the front of the colored stream to travel a fixed horizontal distance (usually 1 m) was recorded with a stop watch. Direction of water flow was recorded frequently and water speed was estimated on 4 occasions during tidal change and at slack water.

## RESULTS

### Recruitment and growth

After 14 d of plate submersion, polyp densities among tiles within a plate departed significantly from a Poisson distribution ($\chi^2_{35} = 427.5$, $p < 0.001$), while the variance-to-mean ratio (331.9:27.2) indicated that polyps were aggregated. Over time, initially dense areas of the plate collected more recruits than less dense areas (Fig. 1). The number of recruits on each tile at 34 d was highly correlated ($r = 0.96$) with initial density. No significant relation was found between the initial number of polyps on a tile and the area or distribution of other species present.

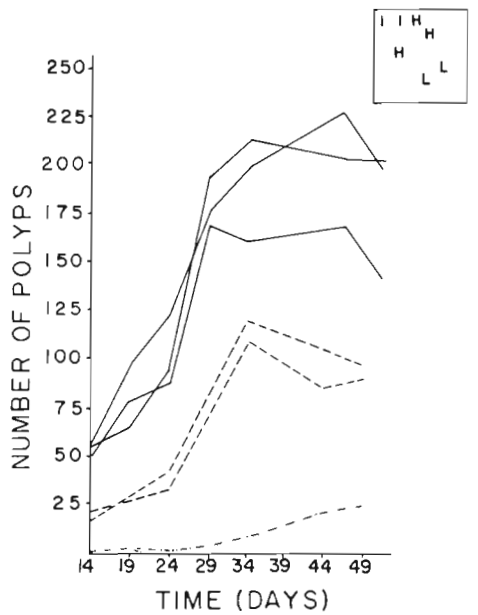


Fig. 1. *Aurelia aurita*. Number of polyps versus time for high (——), intermediate (– – –), and low (– · –) density tiles. Upper right inset shows the location of high (H), intermediate (I), and low (L) density tiles within a settling plate

To compare growth rates according to density I summed the feeding surface areas for all polyps per tile at each time period (Fig. 2). The slopes of least-squares regressions of feeding area versus time from 14 to 34 d (ln area $d^{-1}$) represent rates of increase in area. These slopes increase as density decreases (high density $\bar{x} = 0.10$, SD = 0.01, n = 3; intermediate density $\bar{x} = 0.13$, SD = 0.01, n = 2, low density $\bar{x} = 0.27$, n = 1). Growth on the 2 low density replicates was erratic; rates on one tile declined and polyps disappeared, while polyps were not present on the other tile until Day 19 of the study, then total surface area increased rapidly (Fig. 2). Note that the curves reach asymptotes after 34 d at different total areas depending on density. To examine the relation between growth rate and initial density of polyps I plotted the rate of increase in feeding area from 14 to 34 d against the feeding surface area present at 14 d (Fig. 3). Growth rates declined as feeding surface area present increased (Spearman rank correlation, $r_s = 0.899$, n = 6, $p < 0.05$).

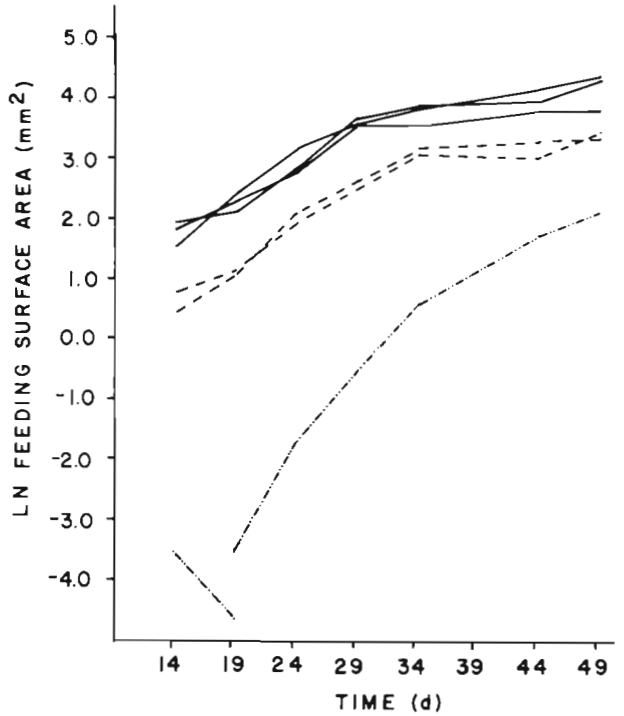


Fig. 2. *Aurelia aurita*. Feeding surface area summed for all polyps present (ln area) at high (——), intermediate (– – –), and low (– · · –) density from 14 to 49 d

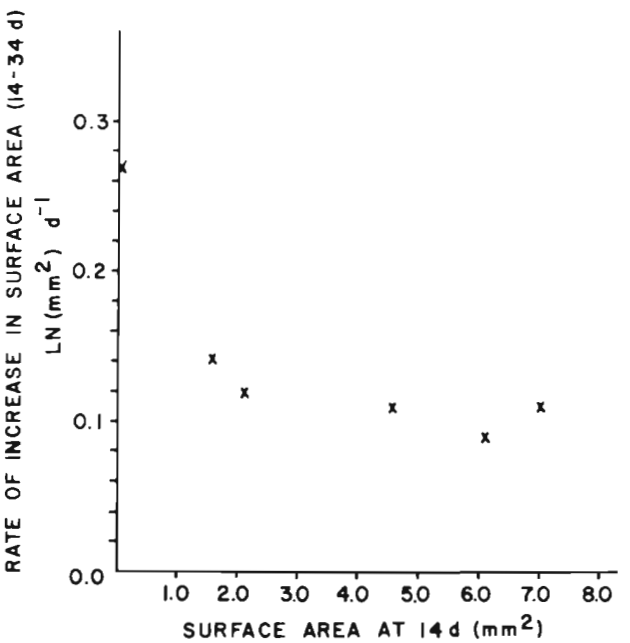


Fig. 3. *Aurelia aurita*. Rates of increase in summed feeding surface area from 14 to 34 d plotted against feeding surface area present at 14 d (n=6)

Mean polyp diameter (Table 1) did not differ among high and intermediate densities (1-way ANOVA, $p > 0.15$). However, for 2 time periods (14 and 43 d) variances were unequal (F-test, $p = 0.02, 0.01$), thus violating the assumptions of ANOVA. Scheffe's multiple comparison (Neter & Wasserman 1974) detected no differences among means for these 2 dates. Mean polyp sizes were comparable at low density (Table 1), but small sample sizes precluded statistical comparisons with high and intermediate densitities.

Table 1. *Aurelia aurita*. Polyp cup diameter ($\bar{x} \pm$ SD) in mm for each census at high and intermediate density (5 tiles pooled) and low density (2 tiles). Number in parentheses is the number of polyps measured

| Day | High and intermediate density (n) | Low density (n) |
|---|---|---|
| 14 | 0.35 ± 0.12 (202) | 0.18 (1) |
| 19 | 0.37 ± 0.14 (302) | 0.14 ± 0.06 (2) |
| 24 | 0.47 ± 0.16 (385) | 0.48 (1) |
| 29 | 0.48 ± 0.17 (692) | 0.42 ± 0.13 (4) |
| 34 | 0.50 ± 0.17 (819) | 0.44 ± 0.14 (11) |
| 43 | 0.54 ± 0.18 (810) | 0.52 ± 0.17 (22) |
| 48 | 0.62 ± 0.23 (746) | 0.64 ± 0.16 (25) |

Growth can occur in 2 ways: polyps can increase in size or produce one or many buds which detach to form clonal patches. Some polyps at all densitites formed buds. There were no significant differences in the percentage of polyps budding at high and intermediate density at 24, 29, or 34 d (Table 2; arcsin transform; ANOVA, $p > 0.05$). Bud separation occurred commonly after 34 d and no estimates of clonal size were made after this point.

Table 2. *Aurelia aurita*. Percent of polyps with buds at each density from 24 to 34 d

| Density | Day | | |
|---|---|---|---|
| | 24 | 29 | 34 |
| High | 10.1 | 13.9 | 23.7 |
| | 14.1 | 22.7 | 18.2 |
| | 17.6 | 18.8 | 14.3 |
| Intermediate | 13.9 | 16.9 | 17.4 |
| | 9.7 | 23.6 | 20.1 |
| Low | • | • | • |
| | 0.0 | 33.3 | 25.0 |

• No polyps present

Most clones were represented by only 2 polyps, but the largest clone comprised 14 polyps. On Day 34 of the study, on high density tiles, an average of 30 clones (SD = 7.5) together accounted for 40 % of polyps and 41 % of the feeding surface area. At intermediate density, an average of 17 clones (SD = 1.4) accounted for 35 % of the polyps and 45 % of the surface area. At low density,

2 clones represented 45 % of the polyps and 52 % of the area. Clonal genotypes have substantially larger feeding areas than genotypes which do not bud (Fig. 4) and clone size was unrelated to polyp density (Fig. 4).

### Patterns of recruitment: transplant and removal experiments

Aggregated settlement produced large variations in density among tiles within a settling plate, but mean polyp size was comparable among tiles of different density. Transplant and removal experiments tested whether location of the tile might account for recruitment and size patterns.

Pre-transplant recruitment patterns were complex, but central areas had the highest densities (Fig. 5). The results of the transplant experiment show that recruitment is primarily determined by tile position, and not by the density of prior recruits (data are summarized in Table 3; paired t-tests used numbers of recruits onto individual tiles, not totals). After transplant, recruitment onto low-density tiles moved to high density positions within the plates was not significantly differ-

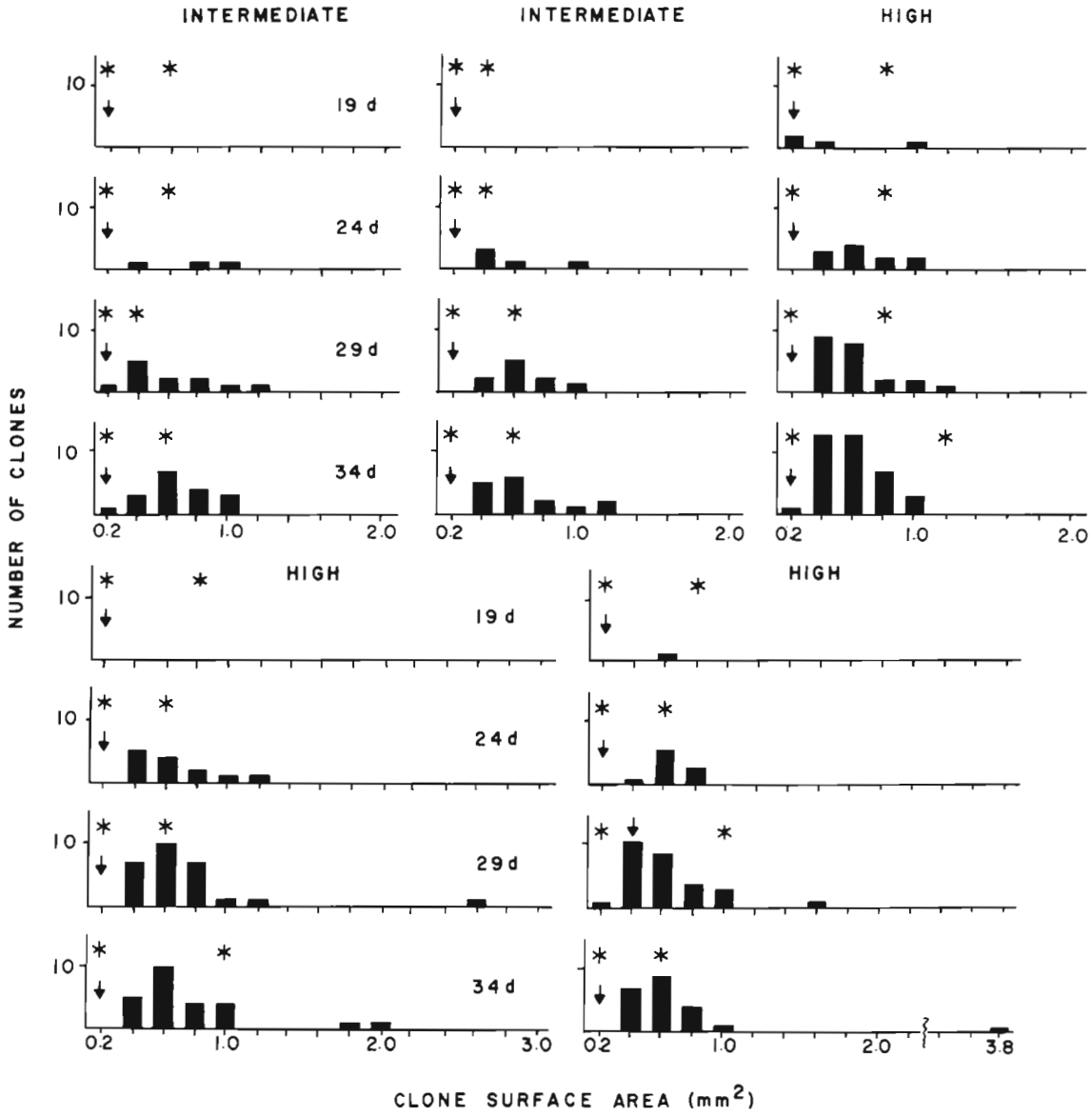


Fig. 4. *Aurelia aurita*. Histograms of clone surface area for each replicate at high and intermediate densities. Time series data are presented from 19 to 34 d. Asterisks indicate the size range of non-budding polyps at each time period. Arrows mark the modal polyp size for non-budding polyps. In most cases budding genotypes achieve a greater surface area than non-budding polyps, although the total feeding area for the genotype is spread over several eventually-separate polyps

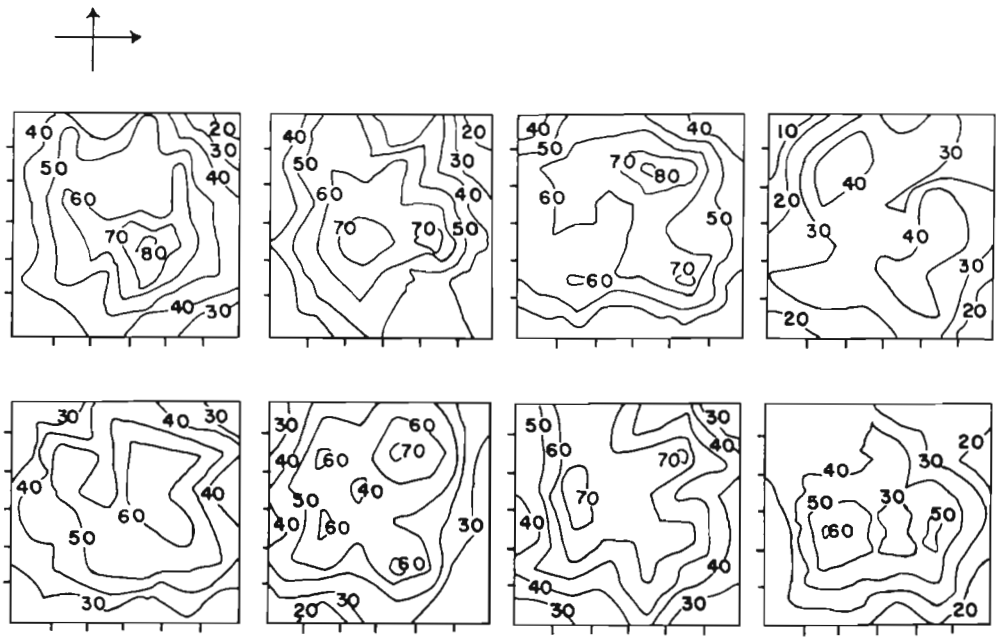

Fig. 5. *Aurelia aurita*. Density isopleths for 5 d old plates. Diagrams were constructed using the number of individuals per tile as a fixed point in the center of each tile and interpolating between points. Plates were made from 36 small tiles and tile boundaries within plates are marked on diagram margins. Arrows in the upper left corner indicate the directions of observed flow

ent from recruitment onto replaced (control) high density tiles (paired t-test: $t = 0.15$, $p = 0.88$). Recruitment onto transplanted low-density tiles was significantly greater than recruitment onto replaced low-density tiles (paired t-test: $t = 3.17$, $p = 0.004$). High-to-low-density transplants collected significantly fewer recruits than control (replaced) high-density tiles ($t = 4.22$, $p = 0.0003$), whereas recruitment in this case did not differ significantly from recruitment onto control (replaced) low-density tiles ($t = 1.95$, $p = 0.06$).

Table 3. *Aurelia aurita*. Total number of larvae recruiting onto tiles of high or low density after transplant or replacement; n = 5 for each replicate in each category. Control tiles of each density were removed and then returned to the same position. Transplanted tiles were removed from their original position, where either many (high density) or few (low density) larvae had settled. Reciprocal transplants were then made, moving experimental high density tiles to previously low density positions and placing experimental low density tiles in previously high density positions

| Replicate | High density control | Transplanted high density | Low density control | Transplanted low density |
|---|---|---|---|---|
| 1 | 227 | 161 | 165 | 245 |
| 2 | 147 | 78 | 146 | 149 |
| 3 | 246 | 139 | 155 | 212 |
| 4 | 153 | 102 | 124 | 163 |
| 5 | 192 | 120 | 136 | 209 |
| Totals | 965 | 600 | 726 | 978 |

The polyp removal experiment was done to test further whether tile location or polyp density was the main determinant of recruitment density. Recruitment was compared between 5 cleared tiles and the 5 undisturbed high-density tiles. There were no significant differences between the numbers of recruits onto cleared and undisturbed tiles (t-test, $t = 0.67$, $p = 0.51$).

### Speed and direction of water flow

Two parameters describing water flow over the plates may be relevant to larval distributions: the local boundary layer thickness and the local shear stress. These parameters have different values for a given mean stream flow velocity, depending upon whether flow over the plate is laminar or turbulent. Reynolds number (Re), indicating the relative importance of inertial and viscous forces, provides a good index of the type of flow expected. If Re is low, flow will be dominated by viscous forces, making velocity gradients very gentle unless large forces are exerted (Vogel 1981).

I recorded water velocities of 0.015 m $s^{-1}$ to 0.02 m $s^{-1}$, and using $2 \times 10^{-2}$ m $s^{-1}$ as the free-stream velocity (U), Re for the maximum length of plate (x) used in the study (13.8 cm) can be calculated from:

$$Re = xU/\nu \quad (1)$$

where $\nu$ = kinematic viscosity of seawater. Here $\nu = 1.07 \times 10^{-6}$ $m^2$ $s^{-1}$. Thus Re for the plates is approxi-

mately $2.6 \times 10^3$. The transition Re at which turbulent flow develops is about $5 \times 10^5$ (Leyton 1975), but, although the plate Re is below this transition value, it may not be reasonable to assume that a laminar boundary layer forms in the field where conditions may vary greatly over time. The qualitative relationship between the coefficient of skin friction and boundary layer thickness (Fig. 6) does not depend on the exact nature of the boundary layer (laminar *vs* turbulent) in the field.

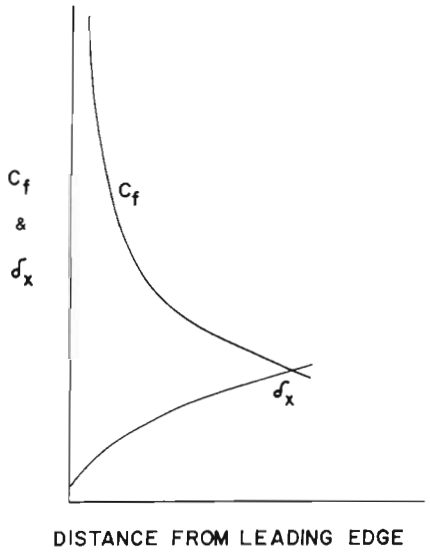


Fig. 6. General form of the relation between the coefficient of local skin friction ($C_f$) and boundary layer thickness ($\delta_x$) with distance from the leading edge of an immersed surface

## DISCUSSION

The density distribution of new recruits of *Aurelia aurita* can be accounted for by tile location within a settling plate. Moreover, the transplant and removal experiments indicated that planula larvae of *A. aurita* recruited to particular tiles based on the location of the tile within a settling plate, rather than prior density *per se*. Later settlers at a given site apparently responded to the same factors that attracted initial settlers, and not to the presence of initial settlers. Thus, while *A. aurita* settlement is aggregated, it cannot be called gregarious. Potential sources of plate heterogeneity likely to affect larval settlement are the distributions of other species on the plates (e.g. competitors) and the water flow regime (which could affect attachment or food availability).

It is unlikely that larvae responded to the presence of other organisms on the plates because settling plates for transplant experiments collected *Aurelia aurita* during their period of peak abundance in the water, and collected few recruits of other organisms.

When growth and asexual multiplication were examined over 40 d, opportunities for biological interactions among settled species and recruiting larvae were possible. Species assemblages developed on initially clean plates and no correlation between polyp density and the distribution of individuals or beginning colonies of other species was found. I hypothesized that *Aurelia aurita* might respond positively to the erect bryozoans (3 species of *Bugula*); the polyps may feed on bryozoans later in the summer. Settlement densities among tiles on new plates did not correlate with *Bugula* presence or absence. However, on older plates or on pilings where *Bugula* colonies were already large, planulae settled in the branches of the bryozoans. On an undisturbed plate, 40 d old, 7.4 % (195/2631) of the polyps were in *Bugula* branches. The polyps are subject to overgrowth by the colonial tunicate *Botryllus schlosseri* and, although planulae do not avoid the tunicate on the tile surface, planulae may use the *Bugula* branches as a refuge from overgrowth. Grosberg (1981) describes *Bugula* as having elevated feeding structures and being generally resistant to tunicate overgrowth. Most settlement by *B. schlosseri* larvae occurs after the peak settlement of *A. aurita*.

On clean, flat, smooth settling plates the only source of habitat heterogeneity is the flow regime. The upstream edge of an immersed settling plate will have a thinner boundary layer and greater shear stresses than the downstream areas, whether flow over the plates is laminar or turbulent. The hypothesis that high larval densities correlate with regions of low shear stress is supported, given that densities of organisms tended to be highest in the center of the plates. Coefficents of skin friction will be greatest near the leading edge (Fig. 6) and decrease toward the center of the plates. The edges are the regions of greatest transition between polyp densities (Fig. 5). However, if flow over the plates is turbulent, then the decrease in values for the coefficient of skin friction away from the leading edge will be much less sharp than in the laminar case (Schlichting 1979).

The exact nature of flow in a field situation may rarely match theoretical predictions, even for plate Reynolds numbers $< 10^5$ (laminar boundary layers are predicted) or Reynolds numbers between $10^5$ and $10^7$ (turbulent boundary layers are predicted). The point at which the boundary layer over a plate becomes turbulent depends upon the level of turbulence in the oncoming flow, the thickness of the leading edge of the plate, the roughness of the plate surface and the angle of incidence with respect to the oncoming flow. All of these factors lead to a destabilization of the boundary layer much further upstream (at Reynolds numbers

$\ll 10^5$) than theoretical calculations would predict. Quantitative values for boundary layer thickness and boundary shear stress would have to be measured directly, although values should still be greatest at the leading edge.

When I introducted a carmine suspension into the water, I observed flow from 2 directions at different times in the Eel Pond. However, given that flow in the Eel Pond is tidally driven, and that recruitment patterns (Fig. 5) commonly show a reduction in density on 3 of the 4 sides, it is possible that multi-directional flows may occur over a tidal cycle.

Flow over the plates in the field is likely heterogeneous, complex and difficult to describe accurately from rough estimates of flow velocity. However, larvae settled more abundantly in central areas of the plates, where the local boundary shear stress is relatively low and the local boundary layer relatively thick. Without laboratory flume experiments it is not possible to predict *a priori* which areas would collect the most larvae, but transplant and removal experiments demonstrated that aggregated larval settlement continued in the same areas on the settling plate.

The absence of significant differences in mean polyp size as a function of density might suggest that, once larvae settled successfully, all positions were equivalent for growth. However, dense aggregations of polyps have the lowest rates of increase in total feeding surface area, in spite of high recruitment rates. Recruitment adds only very small individuals to local populations and negative density-dependent effects are visible in overall growth rates, probably due to food limitation, space pre-emption, or both of these factors. Density is not necessarily well correlated with the total feeding area maintained; a dense area might be composed of many small polyps, whereas large polyps might be present in a low density area. The total feeding area maintained over 34 to 48 d differs with density (asymptotes in Fig. 2), even though total numbers of polyps present at high and intermediate densities are declining over this time period (Fig. 1). High density areas successfully maintain a greater tissue volume although growth occurs at a slower rate. This observation suggests that food organisms might be as unevenly distributed as planulae, allowing each area to sustain populations of different sizes. This hypothesis is supported by the initially poor survival of polyps on low density tiles, but could be tested by following growth and survival of individuals on transplanted tiles. The hypothesis predicts reduced growth of polyps on high density tiles transplanted to previously low density positions in comparison with polyps on replaced high density tiles.

The growth of other species on the plates, especially the erect bryozoans, may greatly alter the flow patterns around the plates and could make previously unsuitable areas available or preferable to larvae. The observation that one of the low density tiles began to collect polyps after 24 d could lend circumstantial support to this hypothesis. Experimental tests controlling the distribution of erect bryozoans and measuring flow patterns are feasible.

Gregarious larval settlement was defined here as larval selection for the presence of conspecifics. Proposed explanations of such behavior are, in general, difficult to test and assume that high density is intrinsically advantageous rather than an incidental result of larval selection for other characteristics of the habitat or passive deposition of larvae in a particular flow regime. Some field studies (Eckman 1983, Hannan 1984) which suggest that deposition patterns due to the flow regime may be controlling small-scale pattern production contrast sharply with field and laboratory experiments (Grosberg 1981, Scheltema et al. 1981, Williams 1976, Young & Chia 1981) where the role of larval behavior seems clear. The relative importance of these 2 processes should be distinguished. If local variation in fitness of sessile organisms is microhabitat-dependent, then the mechanisms used in site recognition should be subject to natural selection. If larval behavior is of adaptive significance, it must be shown to influence dispersion over and above the effects of the flow regime or to occur as a response to characteristics of the flow regime.

Water flow patterns may account for the deposition of larvae in benthic soft sediment communities (Eckman 1979, Eckman 1983, Hannan 1984, Jumars & Nowells 1984). At first glance, settlement on hard substrata appears analogous to deposition onto soft sediments, but it is difficult to use this hypothesis to account for settlement on undersurfaces. Planktonic larvae of infaunal invertebrates rely on gravity (sinking rates) and active larval behaviors to bring them in contact with the sediment surface. Planulae do not sink in order to settle: in many cases, they must overcome their gravitational sinking rate to settle because they occur naturally on the undersides of submerged objects. Although boundary layer formation on lower surfaces should be similar to that on upper surfaces in laminar flow, settlement requires that larvae cross streamlines while moving upward to reach the surface. Thus, larvae reaching the lower surface must be: (1) positively buoyant at all times, (2) actively controlling buoyancy, or (3) capable of controlling position by swimming. Larvae of many species living on undersurfaces are not always positively buoyant (ascidians, bryozoans) and many, including planulae, swim actively. Although larval selection of the flow regime as a feature of the microhabitat has not yet been adequately demonstrated, accounting for the non-random distribution of

larvae on horizontal undersurfaces by merely passive processes is difficult.

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