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Recruitment of encrusting benthic invertebrates in boundary-layer flows: A deep-water experiment on Cross Seamount

Lauren S. Mullineaux[1] *and Cheryl Ann Butman*
Applied Ocean Physics and Engineering Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543

Abstract

A 48-d field experiment on recruitment of metazoan larvae and other foraminiferal propagules of deep-water, encrusting invertebrates was conducted on the summit of Cross Seamount (central North Pacific, 410-m depth). Experimental substrata were circular flat plates with differing thicknesses and surface characteristics, designed so that larval responses to the plate boundary-layer flow could be evaluated relative to other factors, such as substratum composition and texture. Flume studies indicated that rectangular plates with thin edges (1.5 mm) develop a boundary layer that thickens gradually downstream from the upstream edge, while plates with thick edges (10.0 mm) develop a separation eddy extending 2–3 cm downstream from the leading edge. Dissolution patterns of alabaster disks deployed on Cross Seamount indicated that similar flow patterns developed over plates at the field site. Recruitment of organisms (mostly benthic foraminifers) onto the thin plates was significantly lower very near the edges than near the centers of the plates. Recruits on the thick plates were most abundant 2–3 cm in from the edges of the plates, where the attachment point of the separation eddy was expected to occur most frequently. These results suggest that larval settlement may be a function of very small-scale variations in the boundary-layer flow, reflecting, for example, larval supply to the plate, larval retention on the plate surface, and active larval responses to the flow regime over the plates. Several taxa recruited exclusively onto thick plates covered with finely powdered ferromanganese crust, however, suggesting active selection for substratum composition or texture.

Initial patterns of larval settlement can have important influences on distributions and abundances of organisms living on hard substrata (e.g. Underwood and Denley 1984). In many habitats, early colonists determine subsequent succession, and at any given location species composition may be more strongly influenced by the first larvae to settle than by competition among adults or predation (Grosberg 1982; Keough 1984). In such environments, an understanding of settlement provides insight into the mechanisms structuring communities.

Results of field and laboratory experiments of settlement onto sediment (Eckman 1983; Butman et al. 1988) and hard surfaces (e.g. DeWolf 1973; Munteanu and Maly 1981; Wethey 1986) suggest that the boundary-layer flow regime can have major effects on transport and settlement of propagules. In situations where larval swim speeds are low relative to flow speeds, the flow regime can control paths through the water column and depositional locales (Mileikovsky 1973; Butman 1987). Near a surface, however, larvae may be able to maneuver effectively in the lower velocities within the boundary layer and may actively respond to both hydrodynamic and chemical cues.

Until recently, studies of settlement or recruitment onto hard surfaces were conducted almost exclusively in shallow water. Exceptions include experiments on wood-boring bivalves (Turner 1973, 1977), a series of deep-water corrosion studies (U.S. Naval Oceanogr. Office unpubl. rep.; Mu-

[1] Now in the Biology Department, Woods Hole Oceanographic Institution.

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raoka 1966), and a study at vent sites (Van Dover et al. 1988). Studies of soft-bottom organisms in the deep sea have shown, however, that colonists may have an important influence on community structure (e.g. Smith et al. 1986; Grassle and Morse-Porteous 1987; Kaminski et al. 1988).

A recent experiment conducted at 1,300 m in the Catalina Basin near southern California (Mullineaux 1988) showed that early recruitment of foraminifers onto hard surfaces was strongly influenced by the elevation of the substratum off the seafloor and that several metazoan species actively selected natural ferromanganese surfaces over ceramic models. The possibility that patterns of settlement and recruitment of deep-sea encrusting organisms may be a function of the local flow regime motivated the present study. A deep-water study site was chosen because the flows were not complicated by waves or storms and because the abundance of free space suggested that community structure might be driven by recruitment dynamics rather than by adult interactions.

The purpose of the present study was to investigate processes controlling recruitment of metazoan larvae and foraminiferal propagules onto hard substrata in a deep-water environment. The experiment was specifically designed so that responses of the organisms to the boundary-layer flow over the substratum could be evaluated relative to other factors, such as substratum composition and texture. The experimental substrata were flat plates, chosen for their hydrodynamic simplicity; certain relatively simple flow regimes over plates are well documented theoretically and empirically (e.g. Schlichting 1979) and other, more complicated flows can be described and quantified in a laboratory flume. Furthermore, the boundary-layer flow over a plate could be easily manipulated by changing only the thickness of the leading edge, without changing substratum texture or other potentially confounding substratum characteristics.

When a flat plate is placed in steady, unidirectional flow, a boundary layer of slower moving fluid develops and increases in thickness with distance downstream from the leading edge. For an infinitely thin plate oriented parallel to the mean flow, the thickness of the boundary layer depends on velocity at the height of the plate (u), the distance from the leading edge (x), and the kinematic viscosity (ν) of seawater and is therefore a function of the Reynolds number, $Re = (ux)/\nu$. The downstream growth of the boundary layer can be calculated from empirical equations (e.g. Schlichting 1979). The leading edge of a plate with a finite thickness, however, may act as a bluff body and cause the flow to separate, forming an eddy downstream of the leading edge. Separation over a flat plate occurs when the flow exceeds a threshold edge Reynolds number, where the relevant length scale is the thickness of the plate, rather than distance from the leading edge.

If settlement of propagules is influenced by the local flow regime over surfaces, then density of settlement should vary as a function of distance from the leading edge of a plate, because characteristics of the boundary layer change as it grows downstream. Total settlement of organisms would also be expected to vary between plates differing in separation eddy size and boundary-layer thickness.

Our deep-water experiment on Cross Seamount was designed to determine whether these flow-related phenomena influence settlement of propagules. At the same time, the importance of other factors such as active settlement responses to composition and texture of the substratum was investigated by deploying a set of plates covered with naturally occurring ferromanganese crust. Thus, the magnitudes of propagule responses to substratum composition could be compared with their responses to flow.

The experiment was also designed to evaluate the effect of proximity of potential colonists to the plates. Previous work had shown that early recruitment onto Mn nodules elevated 20 cm off the seafloor was much lower than onto nodules resting on the seafloor (Mullineaux 1988). Thus, in the present study, one set of plates was set directly on the seafloor to test whether elevating a plate excluded taxa that disperse only very near the bottom.

Although these experiments were aimed

at evaluating responses of settling propagules, only patterns of recruitment (sensu Keough and Downes 1982) could be assessed because the plates were left in the field for 7 weeks. We considered this period to be a minimum exposure time to collect sufficient numbers of organisms for statistical tests, given the relatively low abundances of propagules (Wishner 1980) and low rates of colonization (Grassle and Morse-Porteous 1987; Mullineaux 1988) generally found in the deep sea.

Cross Seamount is a flat-topped, submerged peak located ~300 km to the southeast (18°0′N, 158°17′W) of the Hawaiian Islands. The summit rises to within 375 m of the surface and the base is at a depth >4,500 m (topography illustrated by Malahoff 1985). The site chosen for this study was near the center of the summit at a depth of 410 m. All experiments and current measurements were conducted on a rippled sand flat, ~85 m long and 35 m wide. The ripples were <2 cm tall, asymmetric, and spaced ~5 cm apart. They were oriented east–west (crests running north–south) with the steeper face eastward. Small boulders and outcrops of ferromanganese crust surrounded the site, but the surface relief around the perimeter was no greater than 20–30 cm (except for one large basalt block 1 m tall and 3 m long).

For hydrodynamic reasons, a sandflat, rather than a site covered with ferromanganese crust, was selected as the study site. A flat site was needed to ensure that the experimental substrata rested horizontally on the bottom, with the collecting surfaces oriented parallel with the flow (e.g. *see* Nowell and Jumars 1984 for a discussion of boundary-layer flow around tilted plates). The area of this particular site was large enough to position substrata far from seafloor topography which could accelerate and decelerate the flow, shed eddies, or otherwise complicate the flow regime. Experiments and measurements were conducted near the center of the sandflat and well away from the large basalt block and other topographic irregularities. Ripples and other surface relief at this site were relatively small and regularly spaced so that at 6 cm above the seafloor (three times the maximal relief) their influence is reflected in the flow as bed roughness rather than as individual flow disruptions (e.g. Schlichting 1936).

Methods

Flume studies to design recruitment plates—Plates were designed on the basis of laboratory studies performed in the 17-m flume (described by Butman and Chapman 1989; Trowbridge et al. 1989) at Woods Hole Oceanographic Institution. The goal of these studies was to develop plates that generate characterizable flow patterns in current velocities within the range of those expected to occur at the field site. A 2-axis laser Doppler velocimeter (LDV) mounted on the flume was used to measure horizontal and vertical components of the flows. Vertical profiles of mean horizontal velocities were taken over the flume bottom in the flow approaching the plate, and the logarithmic portions of these profiles were used to calculate shear velocity (u_*) (e.g. Gross and Nowell 1983) according to (e.g. Clauser 1956)

$$u(z) = u_*/\kappa \ln z/z_o$$

where $u(z)$ is the mean velocity at height z above the bottom, κ the von Karman's constant (0.40), and z_o the bottom roughness parameter.

Most of the flume measurements were conducted with flows with shear velocities between 0.10 and 1.2 cm s^{-1}, which corresponded to flow speeds of 2.4–20 cm s^{-1}. This range was chosen because although u_* is commonly <1 cm s^{-1} in deep-sea boundary layers (Chriss and Caldwell 1982; Grant et al. 1985), currents can be intensified over topographic features such as seamounts (*see* Roden 1987). Measurements of shear velocity upstream of the plate, in addition to mean velocity at the plate height, were used in this study to characterize the flume flow environment because they better reflect the velocity gradient and turbulence intensity than a single velocity measurement within the boundary layer (e.g. Jumars and Nowell 1984; Nowell and Jumars 1987). We acknowledge that matching bed u_* alone between field and flume may not be sufficient to achieve complete dynamic similarity because mean parameters such as velocity, shear, and turbulence generated by bedforms in the field may differ somewhat from those in the flume. The primary purpose of our flume study, however, was to characterize the plate boundary layer over a range of velocities; within this range, deviations in dynamic similarity of the magnitude expected due to bedform effects are probably negligible. Mean velocity at plate height (plates were elevated 6 cm above the flume bottom) was recorded because both the onset of flow separation and the downstream development of the plate boundary layer depend on $u(z)$ as well as on upstream u_*.

Flow visualizations were combined with LDV measurements to determine the lower threshold velocity for separation at the edge of rectangular glass plates and to characterize the size and shape of the separation eddy over the range of flow velocities. For each plate design, flow velocity was increased until separation was detected visually, and a velocity profile was then measured to calculate the threshold u_*. Separation was detected by introducing fluorescein dye just below the leading edge of the plate with a syringe and drawn-out pipette and observing upward dye movement at the edge or upstream movement along the plate surface toward the leading edge. The presence or absence of separation was verified with the LDV; if velocities measured at 0.5 mm above the plate surface were negative (i.e. flow moving upstream) or zero, separation was confirmed. The size of the eddy was estimated (to ± 0.25 mm) by releasing fluorescein dye upstream and sighting past the eddy onto a ruler. The maximal height of the eddy was also measured with the LDV and was identified as the height at which horizontal velocities reached free-stream values. The length was measured by locating the attachment point at the downstream end of the eddy, where both vertical and horizontal velocities were near zero at 0.5 mm above the plate. Visual estimates of the eddy height and length agreed to within 1 mm with dimensions measured with the LDV. Velocity profiles were also measured at various distances along the plates to characterize boundary-layer development downstream from the leading edge.

Field experiments—Recruitment plates for field deployment were made of polycarbonate (Lexan), a nontoxic plastic commonly used in experiments on chemically sensitive marine organisms, such as larvae and phytoplankton. The plates were shaped into disks (24-cm diam) so that an identical leading edge would be presented to oncoming flows from all directions. This design could be easily and reliably deployed by submersible, but had the possible disadvantage of producing, at higher flow speeds, complicated flow patterns along the sides (e.g. roll vortices). Alternate designs, such as rectangular plates on swivels to orient their edges into the flow, would have had a less complicated flow structure, but were not chosen because of potential unreliability of the swivels for long-term deployments by submersible.

Four different types of plates were fabricated: "thick" (10 mm) and "thin" (1.5 mm) plates, both elevated above the seafloor on legs 6 cm tall, thick plates placed directly on the seafloor ("benthic"), and thick plates elevated and coated with finely powdered ferromanganese crust ("ferromanganese"). The fine ferromanganese powder (silt-size particles) was ground from ferromanganese crust samples that had been dredged in 1984 at a nearby site on Cross Seamount. The powder was affixed to the plates with Tile Clad, a nontoxic adhesive in general use for marine aquaria.

Five replicates of each of the four types of plates (thick, thin, benthic, and ferromanganese) were deployed by the submersible *Pisces V* at the study site in an array of five linear transects (A, B, C, D, and E), each containing all four plate treatments. The transects were to be set out in a rectangular, randomized block, but the irregular shape of the sand flat constrained deployment. Some transects were laid out parallel and others perpendicular to the long axis of the site to ensure that adjacent plates were separated by at least 2 m and that the array was >5 m from the edges of the site. Despite the lack of symmetry in blocks, the transects were arranged so that replicates of a treatment were distributed broadly over the sandflat and thus were not subject to potential biases due to clustering of treatments. Buoyant polypropylene loops were attached at least 30 cm above the plates with fine nylon line (<1-mm diam) for deployment and recovery. Visualizations in the flume indicated that flow disturbances at the plate surface due to the lines and polypropylene loop were negligible.

The plates were preserved in 10% buffered Formalin in seawater on recovery and were later transferred to 80% ethanol for inspection. All eucaryotic organisms visible under a dissecting microscope were counted and identified to the lowest taxonomic group possible. Individuals were counted in 144 subareas on each plate (which was divided into 12 radial sectors, and 12 1-cm-wide concentric rings) for subsequent analyses.

Field flow characterization—Flow patterns near the seamount study site were characterized on two spatial scales, corresponding to the sandflat and the individual plates. Current velocities in the bottom boundary layer at the study site were recorded for 48 d (with a 300-s averaging interval) with a Neil Brown smart acoustic current meter (SACM) moored 1.8 m above the sandflat. Near-bottom flows were measured on three occasions by tracking dye streams as they dissolved from small pellets of fluorescein dye (5–6-mm diam). The pellets were attached at 10-cm intervals on thin vertical lines so that they were suspended 10–50 cm above the seafloor. Flow speeds were estimated from video images of the dye streams, recorded at right angles to the flow direction (as by Cacchione et al. 1978).

Time-integrated patterns of boundary shear stress were measured on the scale of individual recruitment plates by quantifying the dissolution of flat disks of alabaster (crystalline $CaSO_4$). The disks were 15 cm in diameter and 1 cm thick, so even though they were smaller in diameter than the thick recruitment plates, they had the same shape and leading-edge thickness. They were glued to thin plastic bases and coated with Tile Clad along the edges so that only the upper surface of the alabaster was exposed to seawater. Disks were depoloyed on the seafloor at the site for 2 and 3 d. Total dissolution of a disk was measured by weighing it before and after deployment. Dissolution patterns on the surface of each disk were quantified by placing a grid of 90 points over the disk and measuring (in mm) the amount of alabaster dissolved from the upper surface at each point on the grid. Calculations of u_* from dissolution rates were not attempted. Although u_* can be calculated from flush-mounted alabaster plates (Santschi et al. 1983; Opdyke et al. 1987), the applicability of these empirical equations to plates with thick edges and consequent recirculation remains to be tested. The disks used in the Cross Seamount study were intentionally made with thick edges, so that patterns of shear stress relative to the edges of the disks could be compared directly with recruitment patterns on the polycarbonate plates. Spatial patterns of dissolution on the alabaster plates, rather than quantitative estimates of u_*, are of primary interest in this study.

Results

Flume studies—Flow separation was detected at the leading edge of a 1-cm-thick plate supported on legs 6 cm tall for $u_* \geq 0.20$ cm s^{-1} ($u \geq 2.9$ cm s^{-1} at plate height). As the oncoming flow velocity was increased, the eddy grew and attained its maximal size (1.0 cm high, 3.0 cm long) at flows of $u_* \geq 0.43$ cm s^{-1} ($u = 7.8$ cm s^{-1} at plate height). Eddies forming at the edge of a 10-mm-thick plate sitting directly on the flume bottom were similar to those forming on elevated plates, but they were detected only at higher flows of $u_* > 0.3$ cm s^{-1} ($u = 3.5$ cm s^{-1} at plate height) and were consistently smaller than eddies over elevated plates at corresponding upstream shear velocities. No flow separation was detected over the elevated 1.5-mm-thick plate in this range of flows, and a well-behaved boundary layer developed downstream from its leading edge (Fig. 1).

Flow environment—A 46-d record from the current meter showed that near-bottom currents at the study site flowed generally toward the west–northwest with speeds that averaged 9–10 cm s^{-1}, but were at times >25 cm s^{-1} (Fig. 2). Semidiurnal fluctuations dominated the current record, and these currents may have been intensified by interactions between the seamount and internal tides (e.g. Noble et al. 1988). Further analyses of the current record, including a

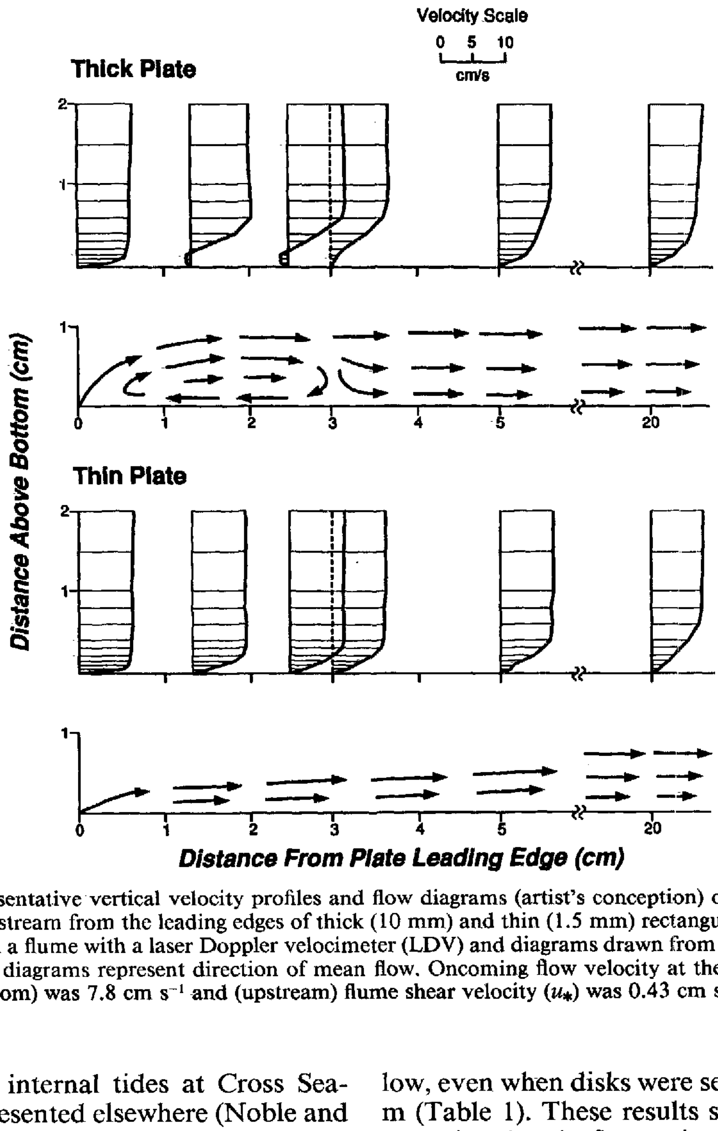

Fig. 1. Representative vertical velocity profiles and flow diagrams (artist's conception) of boundary layers developing downstream from the leading edges of thick (10 mm) and thin (1.5 mm) rectangular plates. Profiles were measured in a flume with a laser Doppler velocimeter (LDV) and diagrams drawn from dye visualizations of flow. Lines in diagrams represent direction of mean flow. Oncoming flow velocity at the plate edge (6 cm above flume bottom) was 7.8 cm s^{-1} and (upstream) flume shear velocity (u_*) was 0.43 cm s^{-1}.

discussion of internal tides at Cross Seamount, are presented elsewhere (Noble and Mullineaux 1989).

Estimates of flow speed near the plate height (10 cm above the bottom) were made on three submersible dives and can be compared directly to current-meter observations. Speeds at 10 cm above the bottom were <1, 3.5, and 4–6 cm s^{-1} corresponding to 5-min velocity averages of 6, 10, and 12 cm s^{-1} recorded by the current meter.

The alabaster disks dissolved at a mean rate of 0.29 g h^{-1} (SD = 0.05) during the first deployment and 0.57 g h^{-1} (SD = 0.03) during the second. The variability between disks within each deployment was relatively low, even when disks were separated by >8 m (Table 1). These results support our assumption that the flow regime over the study site is horizontally homogeneous. The weight loss of one disk that was carried to the study site by submersible but not deployed, was low (<3 g), indicating that relatively little dissolution (~10% of the total) occurs during transit between the study site and the surface. The disks, therefore, predominantly reflect shear stress at the study site, rather than shear stress during transit.

Dissolution of the surface of all six alabaster disks was greater at the edges than near the center of the top surface (Fig. 3). No more than 1 mm of alabaster dissolved

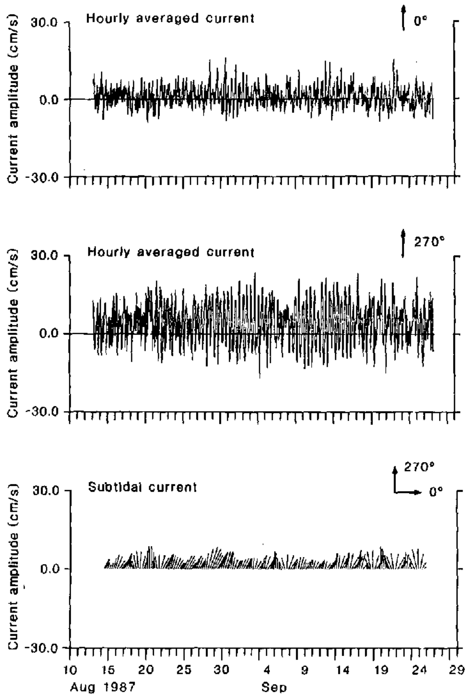

Fig. 2. Hourly averages of flow velocity from the current meter deployed 1.8 m above the summit of Cross Seamount. Currents are divided into north–south and east–west components. Subtidal currents are low-pass filtered to show the current directions without tidal influences (retaining all frequencies lower than 0.015 cph).

from any portion of the disks, however, indicating that flow over the disk probably was not substantially altered by its surface topography. Dissolution patterns were not symmetric, however; dissolution of each disk was consistently higher along one edge than along the opposite edge. Unfortunately, the orientation of the alabaster disks with respect to the mean current was not recorded, because a strongly directional flow was not anticipated.

Larval recruitment—Fourteen plates were recovered during the September cruise, including three replicates of the thick, thin, and benthic treatments, and five of the ferromanganese treatment. The remaining plates had been overturned during deployment and were not recovered. Two of the five ferromanganese plates were chosen at random and excluded in order to have an equal number of replicates per treatment.

Table 1. Dissolution of alabaster (crystalline $CaSO_4$) disks. Four disks were set out for 3 d during the August cruise (A1–A4) and two for 2 d during the September cruise (S1–S2). A1–A4 were spaced 1 m apart and S1 was spaced >8 m from S2.

Disk	Dissolution (g)	Deployment (h)	Spacing (m)
A1	19.6	70	1
A2	19.6	70	1
A3	16.1	70	1
A4	19.6	70	1
S1	27.7	47	8
S2	25.4	47	8
S3*	2.9	6	

* Carried to site, but not deployed.

The majority of organisms (>90%) recruiting onto the 12 plates included in the analyses were agglutinated foraminifers with trochoidal coiling (Table 2). They were originally identified as *Trochammina* sp., but a recent revision of taxa in the superfamily Trochamminacea (Brönnimann and Whittaker 1988) prompted the use of the more conservative term "trochamminacean" because diagnostic characters of *Trochammina* were not observed in some of the smaller individuals. Other taxa, especially metazoans, were too rare to analyze separately for patterns within plates, so recruitment of all individuals combined was used to test for propagule responses to the flow-related treatments.

All experimental plates were deployed within 2 d of each other, remained on the site for 46–50 d, and were recovered within 2 d of each other. An average deployment duration of 48 d is used in the following analyses. The maximal error from this approximation is <5%, and, because plates were deployed and recovered in blocks (transects), the error in duration does not introduce a systematic bias into the analysis of treatments.

The areal density of recruits varied as a function of distance from the edge of both the thick and thin polycarbonate plates (Fig. 4). Recruitment onto the thin plates was low at the edge, but relatively uniform over the interior. Recruitment onto the thick plates was low at the edge of all three replicates. In two of the replicates, densities were highest in the ring 2–3 cm from the edge, but in the third, recruitment continued to increase

Alabaster Dissolution

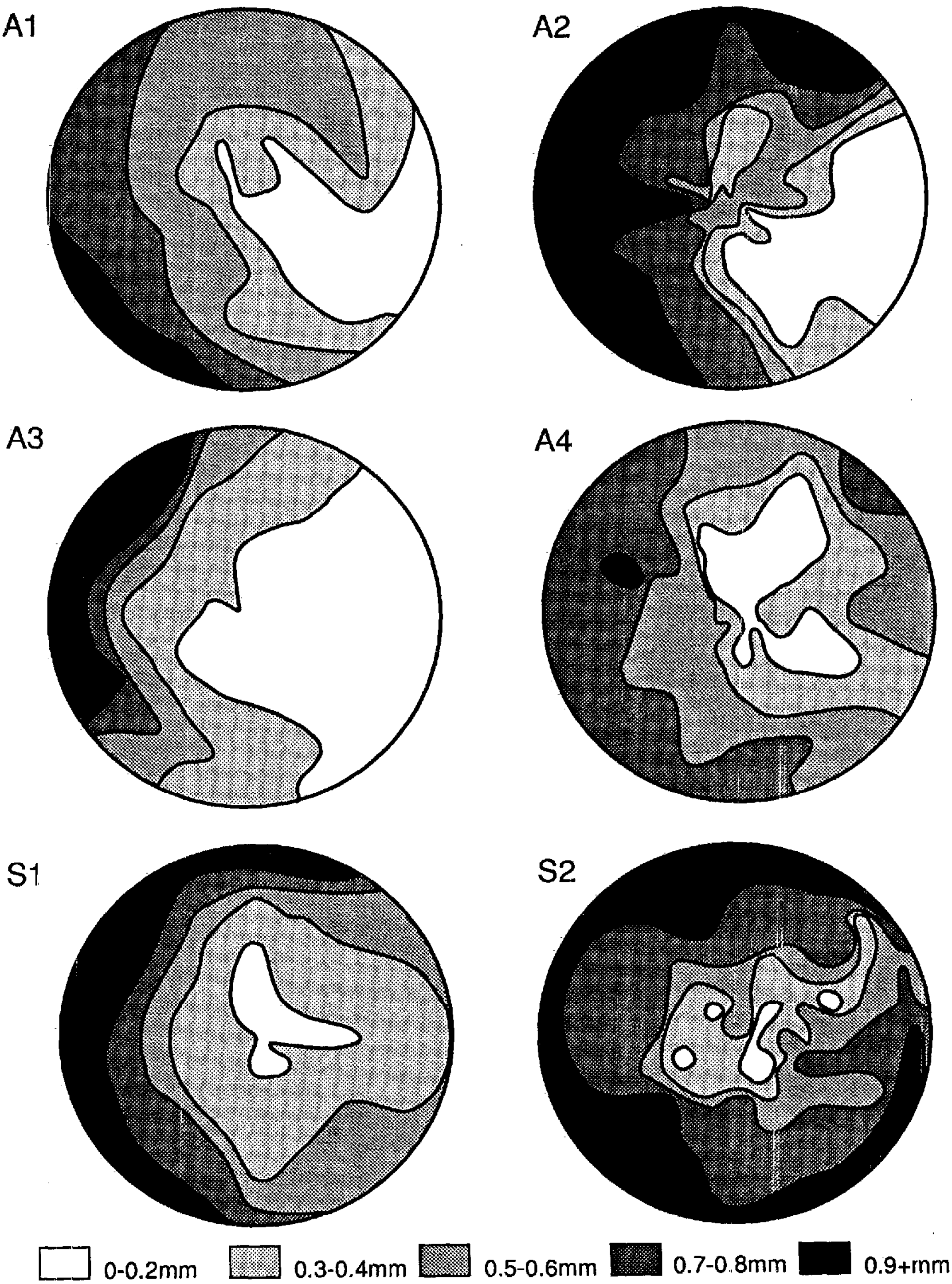

Table 2. Numbers of individuals recruiting onto three replicates of each plate treatment. Thick treatment was a 10-mm-thick polycarbonate disk supported on legs 6 cm tall. Other treatments differed in that thin plates were 1.5 mm thick, Ferro-Mn plates were coated with finely powdered ferromanganese crusts, and benthic plates lacked legs. Plates are identified by transect (A–E).

	Thick			Thin			Ferro-Mn			Benthic		
	B	C	D	A	B	C	A	C	E	A	C	D
Foraminifers												
Allogromid sp. a										1		
Allogromid sp. b							5	6	7			2
Tube with base	1											
Tube				1		2			1			
Branched tube		7		1	16							
Hemisphaerammina sp.									7			
Ammodiscus sp.							1					
Rhizammina sp.									4			
Trochamminaceans	222	457	193	160	118	144	181	182	137	128	107	127
Cibicides sp.	2	1		1	2		1	9	4	1	1	1
Rosalina sp.		3			1		11	16	21			1
Total foraminifers	225	468	193	163	137	146	199	213	181	130	108	131
Metazoans												
Sponge	1								1			
Hydroid	1											
Solitary coral	2	3		2	1	11	1	2		7	1	4
Anemone		1			3							1
Polychaete tube a							1	1	1			
Polychaete tube b								2	1			
Tubicolous copepod									1			
Tunicate sp. a								1		2		
Tunicate sp. b							2					
Unknown metazoans	2			1				1				
Total metazoans	6	4		3	4	11	4	7	3	9	1	5

toward the center of the plate. These recruitment patterns were analyzed with paired-comparison t-tests on selected rings. The rings were selected a priori on the basis of flume studies, which showed steep downstream gradients in the boundary layer within 2 cm from the leading edge of the thin plate and within 4 cm from the leading edge of the thick plate (Fig. 1). Densities in each ring were normalized by total number of individuals on the plate and $\log(x + 1)$-transformed to achieve homoscedasticity. These analyses showed that recruitment onto the outermost ring of the thin plate was significantly lower than onto the ring 1 cm inward from the edge ($P < 0.05$, $n = 3$). Recruitment onto the outermost ring of the thick plate was significantly lower than onto the ring 3 cm in from the edge, but not the rings 2 and 4 cm from the edge ($P < 0.016$; used to correct for multiple comparisons, $n = 3$).

The unusually high recruitment onto the center of the thick plate from one transect cannot be explained hydrodynamically. Other plates from this part of the study site did not show unusually high densities of recruits. Local reproduction may have been responsible for high recruitment, although evidence for this process, such as single-species aggregations or large individuals with many smaller individuals around them, was not observed on any of the plates.

Although recruitment onto both the thick

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Fig. 3. Dissolution of alabaster disks contoured in 0.2-mm intervals below the original surface. Disks were 15 cm in diameter and 1 cm thick. Disks A1-A4 were deployed on the August cruise; S1 and S2 were deployed in September (*see Table 1 for details*). Field orientations of the disks with respect to flow are unknown, and figures are arbitrarily oriented with greatest dissolution at the left.

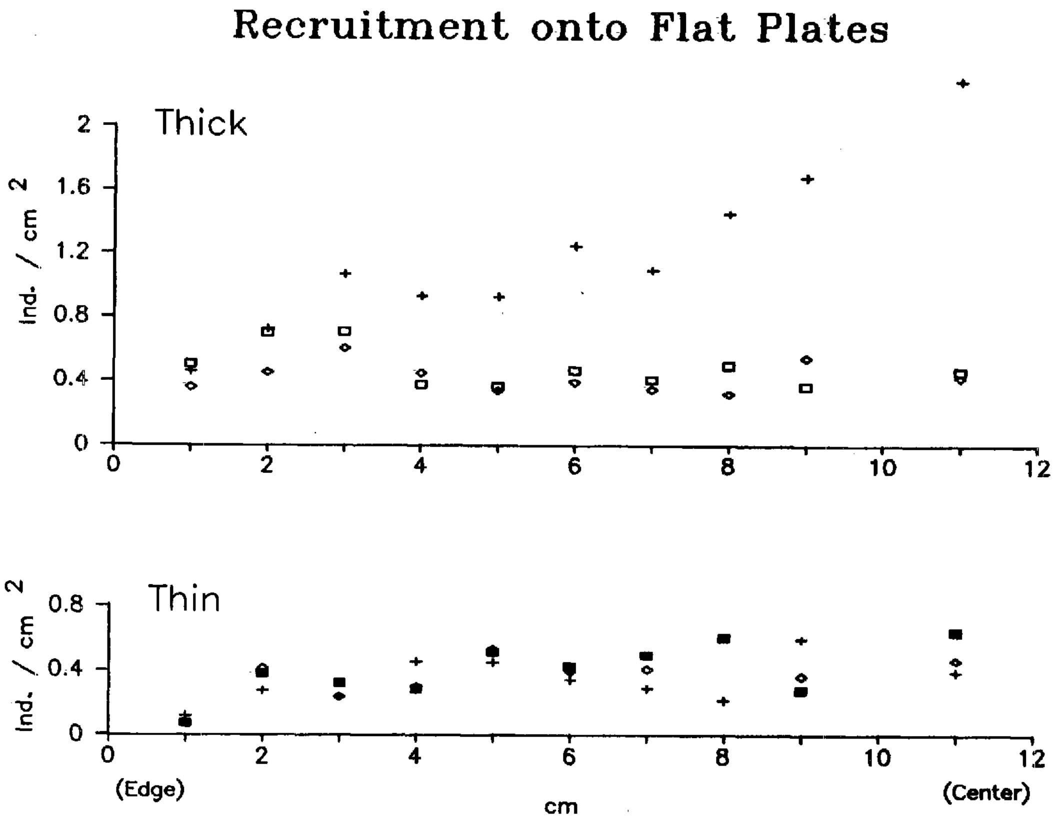

Fig. 4. Density of recruits in rings 1 cm wide on three replicate thick and thin plates. Plates are labeled by transect: A—■; B—◇; C—+; D—□. Densities include all taxa found on the plates, but predominantly reflect distributions of the trochamminaceans—a group of foraminiferal genera.

and thin plates varied with distance from the edge, there was also substantial variability among the 12 sectors of each plate. Because the mean current was directional, predominantly toward the northwest, asymmetry in the recruitment patterns (such as that found in alabaster dissolution, Fig. 3) would be predicted for organisms recruiting in response to flow. For instance, the density maximum in the 2–3-cm ring would be most prominent on the side of a thick plate that was most frequently oriented into the flow. Similarly, the density minimum in the outermost ring would be most noticeable on the side of a thin plate that was most frequently upstream. Unfortunately, the plates' orientations relative to the mean flow were not recorded, so alignment of recruitment patterns with flow direction can only be inferred. Asymmetry is evident in contoured diagrams of recruitment (Fig. 5) and a general pattern can be detected if the three replicates of the thick and thin plates are pooled (Fig. 6). Pooling was accomplished by matching the quadrant (three adjacent sectors) on each plate with the strongest leading-edge patterns (density max at 2–3 cm for thick plates, density min at 0–1 cm for thin plates).

Total numbers of attached individuals on thick and thin plates were also used in the comparison of recruitment onto elevated, benthic, and ferromanganese plates. Foraminifers were much more abundant than metazoans on all plate treatments (Table 2). Total recruitment onto the thick plates was significantly higher than onto the thin plates [model 1 ANOVA and Duncan's a posteriori test of the log(x + 1)-transformed abundance data; F = 5.2, P < 0.05], and

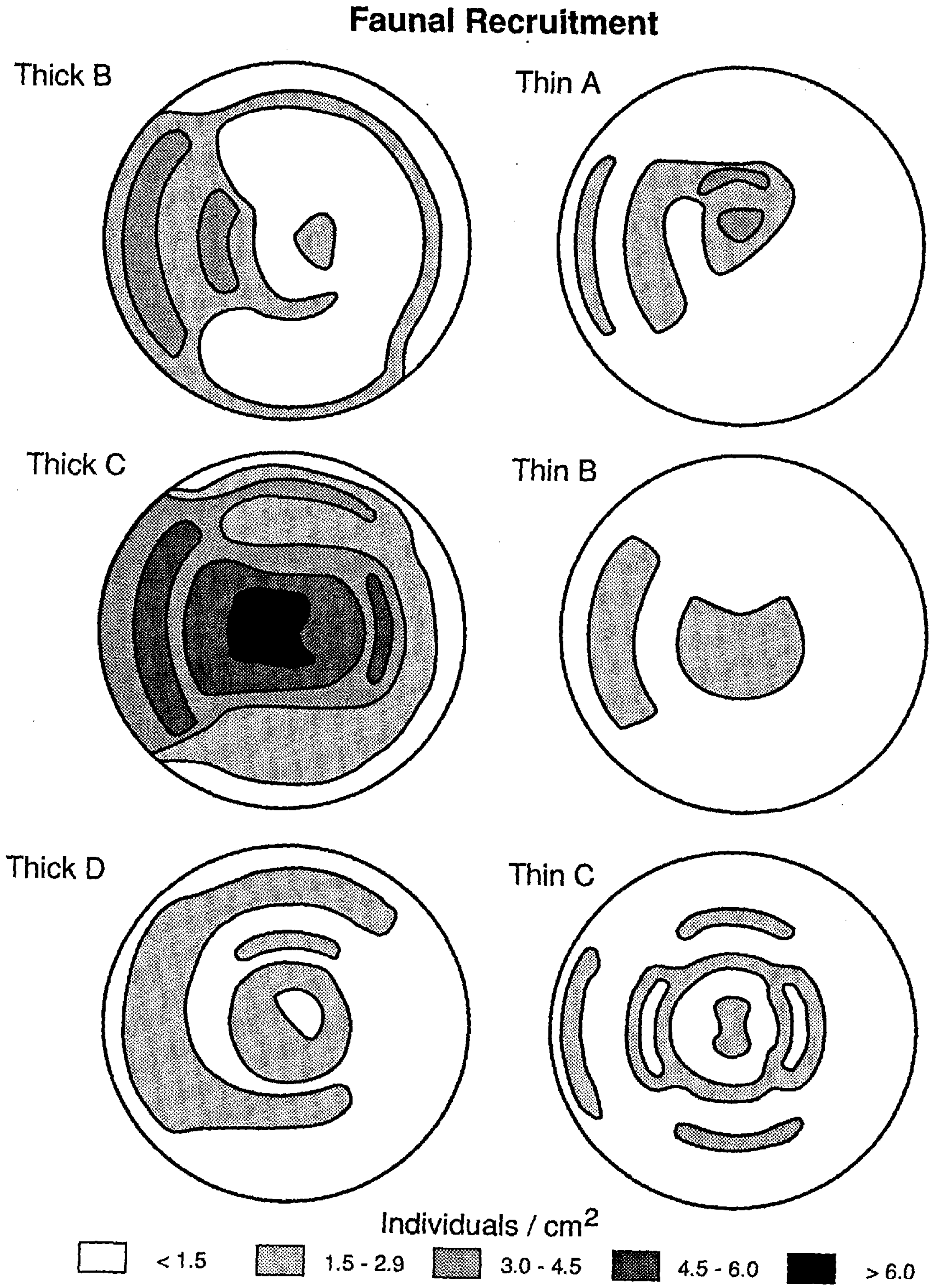

Fig. 5. Density of recruits contoured in four quadrants of rings 1 cm wide on 24-cm-diameter plates. Field orientations of plates with respect to flow are unknown, and figures are arbitrarily oriented with highest recruitment at the left.

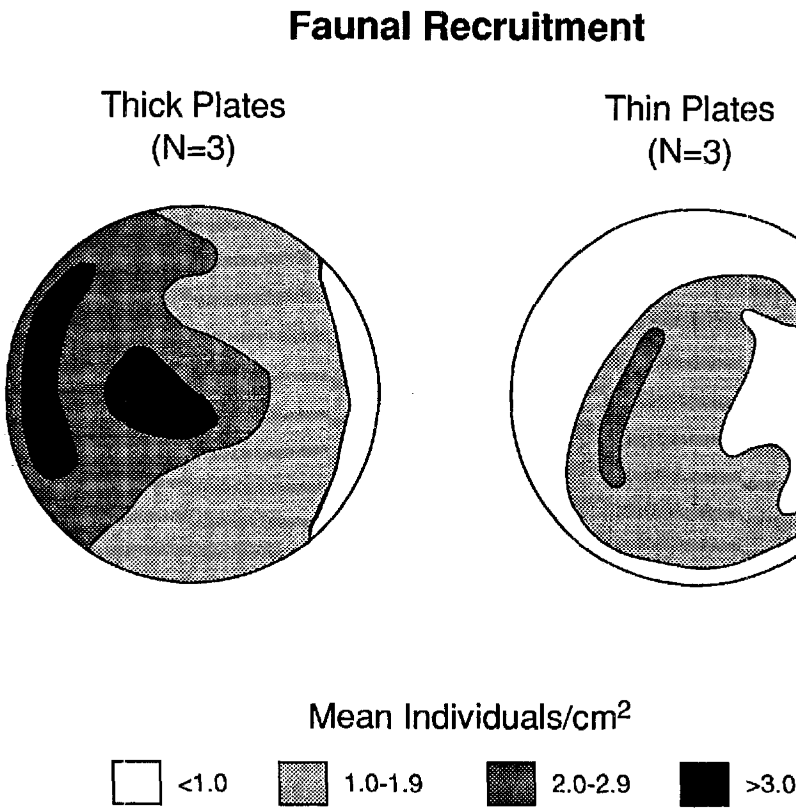

Fig. 6. Density of recruits averaged from three replicate thick and thin plates to show recruitment asymmetry (*see text*).

recruitment onto both the thick plates and the ferromanganese plates was greater than onto the benthic plates. Evidence for predation (mucus and radula tracks) was found on all benthic plates, and the low faunal densities on these plates may be due to post-settlement mortality rather than low settlement. Because of this potential predation, the benthic plates could not be used as intended to test for possible exclusion of larvae by the elevated plates.

Trochamminacean densities accounted for most of the variability in the analyses of total recruits and are responsible for the distance-from-edge patterns as well as significant differences between total recruitment onto thick, thin, and ferromanganese plates. A few of the rarer taxa, however, recruited exclusively or in relatively high abundances onto the ferromanganese plates. Of the nine metazoan species that could be identified to phylum, both of the tube-dwelling polychaetes, one of the tunicates, and one individual tubicolous harpacticoid copepod were found only on ferromanganese plates. Of the foraminifers, *Hemisphaerammina* sp., *Rhizammina* sp., and one individual *Ammodiscus* sp. were found only on ferromanganese plates, and *Cibicides* sp., *Rosalina* sp., and allogromid sp. b were all noticeably more abundant. Only one taxon, an individual hydroid, recruited exclusively onto a thick plate, and allogromid sp. a was the only taxon recruiting uniquely onto the benthic plates.

Discussion

The summit of Cross Seamount is subject to strong currents relative to open-ocean sites at similar depths. Flow speeds recorded from dye streams 10 cm above the bottom indicated that flow speeds near the field plates were within the range of flows used in the laboratory flume. Although field flows of 28 cm s^{-1} were measured at 1.8 m above the study site, it is unlikely that flows at plate height (7 cm) exceeded the 20 cm s^{-1} flows used in the flume.

Greater loss at the edges than at the centers of alabaster disks suggested that the boundary shear stress near the edges was greater than in the center (*see* Opdyke et al. 1987 for a discussion of the relation between dissolution and shear stress). High shear stress at the edge of the disks may have been a consequence of the thin boundary layer at the leading edge. An asymmetric dissolution pattern can be predicted from the mean directionality observed in the near-bottom currents. If the currents had been omnidirectional, the expected dissolution patterns would have been radially symmetric, with the greatest dissolution occurring around the entire perimeter of the disk. Because disk orientations were not recorded, we can only suggest that the greatest alabaster dissolution occurred on the side oriented into the mean current. If propagules are indeed affected by or are responding to boundary shear stress (or a correlated parameter such as turbulence intensity) over the recruitment plates, then recruitment patterns should vary with distance from the edge and be asymmetric.

Total recruitment, which reflects predominantly recruitment of trochamminaceans, did vary with distance from the edge of the thin plates in patterns that suggest a response to the gradual development of the boundary layer. Densities also varied with distance from the edge of thick plates, but the high recruitment between 2 and 3 cm from the edge suggests that the organisms were responding to an abrupt change in the boundary layer (the attachment point of the leading edge eddy, Fig. 1). The observed asymmetry in recruitment patterns provides additional evidence that the organisms may have been responding to flow rather than to some unidentified factor that also varied with distance from the edge of plates.

Benthic encrusting foraminifers can colonize new habitats in several ways. The original adult cell may divide sexually to produce small amoebalike propagules or sexually to produce tiny, flagellated swarmer cells (Grell 1967). Both propagule types can disperse through the water column, although the asexual forms may stay very close to the bottom and the adult. Once the propagule attaches to a surface, it constructs a cyst composed of organic cement as well as inorganic and organic particles. This cyst holds the foraminifer onto the surface, but if conditions become favorable, the foraminifer can dissolve it and move as an adult (Lipps 1983).

One explanation for the patterns observed on both the thick and thin plates is that recruitment is a function of the hydrodynamically controlled supply of propagules to the surface. Propagules acting as passive particles may not come into frequent contact with the outer edges of the upper surface of plates because the boundary layer is thin and only those recruits passing within a few millimeters above the plate could be mixed into contact with it. Recruitment would be expected to increase downstream, where the boundary layer thickens, because more recruits (from a thicker layer of the water column) would be brought into contact with the plate. On the thick plates, the region of low recruitment would be confined to a relatively narrow zone at the edge because the boundary layer grows thicker over a shorter distance than on the thin plates. High recruitment would be expected at the attachment point of the eddy because the downward velocities should bring more recruits into contact with the plate at that point than elsewhere.

The recruitment patterns observed on the thick and thin plates are consistent with this supply model. Another possibility is that low recruitment results from low retention of propagules at the edges of the plates due to high shear stresses (e.g. Crisp 1955; Keen 1987). This explanation is plausible, and the supply and retention mechanisms may operate separately or in concert. In addition, the patterns of recruitment could have been due to active responses of the larvae to the flow environments over the plates. Thus, although much of the variation in recruitment onto a plate can be attributed to flow patterns, the specific mechanisms producing the response are still subject to speculation.

The anomalously high recruitment in the center of thick plate C might be a result of in situ reproduction of early recruits on the plate. Lifespans of deep-sea foraminifers have been estimated to last between a few months and a year (Lipps 1983), so recruits could have become reproductively mature during the 7-week experiment. There is, however, no other evidence for local reproduction on plate C, such as patchy distributions or more than one size class of individuals.

The substantial number of taxa recruiting exclusively onto ferromanganese-covered plates suggests that these organisms are actively selecting their natural substratum over polycarbonate. The polycarbonate and ferromanganese plates varied, however, in both composition and texture. Although the silt-size ferromanganese particles were too small (less than the thickness of the viscous sublayer) to affect the boundary-layer flow characteristics significantly, they did create surface texture that could possibly be detected by a propagule. The elevated densities on ferromanganese plates could be simply a response to surface texture, but this interpretation is considered unlikely in light of previous results (Mullineaux 1988). In the previous study, organisms recruiting onto nodules with different textures showed no textural preferences, but did show a response to surface composition. Several taxa settled exclusively onto natural Mn nodules, avoiding ceramic mimics with surface textures similar to the nodules.

The observation that, in a relatively simple physical system, much of the variation in recruitment of hard-substratum organisms in deep water can be attributed to the flow environment may prove to be useful in predicting recruitment in complex, natural deep-water habitats and in understanding the structure of deep-water communities. These communities may be particularly suited to this appraoch since the majority of initial colonists are small single-celled foraminifers, which are more likely to disperse and settle as passive particles than are the larger, evolutionarily more advanced and complex invertebrates.

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