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SETTLEMENT OF MARINE ORGANISMS IN FLOW

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ABSTRACT

A feature common to many benthic marine plants and animals is the release of propagules that serve as the organism's only mechanism of dispersal. Successful dispersal depends to a large extent on the process of settlement—the transient phase between the pelagic life of the propagule and the benthic existence of the adult. The flow of water may affect settlement on three levels: 1. Flow can act by exerting hydrodynamic forces on settling propagules. These forces may affect the propagule's encounter with the substratum, its behavior following encounter, or both. 2. Flow may provide a settlement cue that induces active behavior of motile propagules. 3. Flow may act to mediate various settlement cues (e.g. sediment load and the concentration of attractants). We discuss these three levels of flow effects as a means of examining the potential importance of flow in the settlement process, and then we explore the ecological consequences of settlement in different flow-regimes in light of the direct effects of flow and flow-derived factors.

INTRODUCTION

Evidence is accumulating for the significant involvement of water motion in diverse biological and ecological processes in the sea (e.g. 13, 24, 39, 62). These effects include the flux of nutrients, food, and wastes to and from organisms, external fertilization of gametes, disturbance by hydrodynamic forces of benthic organisms, and the ability of organisms to detect scents. In addition,

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flow may control or strongly regulate the dispersal of benthic species. A feature common to many benthic plants and animals is the release of propagules (e.g. spores and larvae), which are, in most cases, the organism's only mechanism of dispersal. Several possible advantages accrue to a life history that includes dispersing propagules: wide distribution of offspring, gene flow, and coexistence with disturbance (39, 73). Fulfilment of these tasks depends to a large extent on the process of settlement—the transient phase between the pelagic dispersal phase and the sessile existence of the adult. During this phase propagules must first encounter the substratum. Following its arrival at the seabed, a propagule must determine the adequacy of the substratum for adult requirements by using a variety of settlement cues, which may include surface contour (17, 95), substratum type (15), chemistry (55, 65), the presence of a microbial film (82), and flow conditions (e.g. 58, 100). Finally, the propagule must effectively attach, thereby allowing metamorphosis and development into a reproductive adult.

Flow may affect settlement of marine organisms on three levels. First, flow may act as an agent exerting hydrodynamic forces on settling propagules, which may affect either the propagule's encounter with the substratum, the propagule's behavior (passive or active) following encounter, or both. Second, flow may act as a settlement cue that induces active behavior of motile propagules. Only a few studies (most of which deal with invertebrate larvae) have examined the role of flow regime in determining site selection by propagules (e.g. 4, 58). Finally, flow may act as a mediating factor affecting various settlement cues (e.g. sedimentation, chemical distribution, and light intensity).

There are three approaches to the study of flow effects on settlement. The first, and probably the most common, is to monitor settlement on substrata in the field (e.g. 27, 56, 57). By characterizing the flow pattern induced by substrata, and comparing this to the settlement distribution of larvae, one can indirectly relate the settlement pattern to flow. The primary problem with this approach, however, is a practical one; it is difficult to observe the behavior of propagules under natural flow conditions. The second approach circumvents this observational problem by directly observing settlement behavior in the laboratory under controlled flow conditions (e.g. 4, 15, 21, 58). The disadvantage of this approach is that it cannot simulate the exact flow conditions experienced by propagules in the field. The third method employs numerical modeling of flow conditions prevailing in the field and of propagules' behavior during dispersal and settlement (e.g. 25, 28, 34). This last approach depends largely on data obtained by the other two to supply realistic values for parameters and boundary conditions. To be mathematically tractable, models must often be simplistic. Despite this limitation, models may reveal neglected aspects of empirical studies and can provide new directions of research. A synthesis of all three approaches is likely best to augment understanding of the effects of flow on the settlement of propagules.

In the present review we examine the three levels of flow effects and the various structural and behavioral features of propagules that may interact with flow during settlement. We then explore the ecological consequences of settlement as they are affected by the flow characteristics of differing substratum types.

SUBSTRATUM TYPES AND FLOW PATTERNS

The vast majority of studies that deal with settlement, whether in the field, in the lab, or on a computer, examine behavior and settlement patterns over planar substrata. In nature, however, the surfaces available for settlement (e.g. coral reefs, kelp forests, and artificial reefs and other engineered structures) include a diversity of shapes. To understand flow effects on settlement and to assess the flow-generated forces that a propagule must withstand, we first must characterize the flow patterns associated with common substrata in the sea. To this end we briefly describe the flow patterns induced by three major substratum types: planar surfaces, protruding bodies, and depressions. Our qualitative description is based on the simplifying assumption that the undisturbed, mainstream flow is steady. In the field, however, it is not uncommon to find flow that is unsteady due to tides and/or wave action (for a more thorough description of benthic flow environments, see 62).

Planar Substrata

Examples of planar surfaces are numerous in the marine environment and include substrata of limited area, such as rock faces, as well as more spacious substrata, such as soft bottoms. If we assume that the flow is steady over a planar substratum oriented parallel to the direction of water motion, the flow near the substratum (in the benthic boundary layer) is similarly steady. The boundary layer over a planar substratum develops from a very thin, laminar flow just downstream of the leading edge of the surface, to a turbulent, thick boundary layer further along the surface at a certain distance downstream from the edge (Figure 1). If the planar substratum is spacious and hydrodynamically smooth, a fully developed boundary layer is characterized by three zones: a thin viscous sublayer adjacent to the seafloor, a turbulence-dominated layer adjacent to the mainstream flow, and a buffer layer between the two (Figure 1). Although the ocean floor is seldom smooth, viscous sublayers that may exist there (16) can be up to 6 mm thick. For purposes of calculating the forces acting on small propagules during settlement, the relevant zone is this thin sublayer.

Protruding Bodies

The surfaces of marine substrata are frequently rough, and the flow over rough substrata can be divided into various flow regimes (54, 97, 98). Some of these involve "protruding bodies," those elements or bodies that project above their

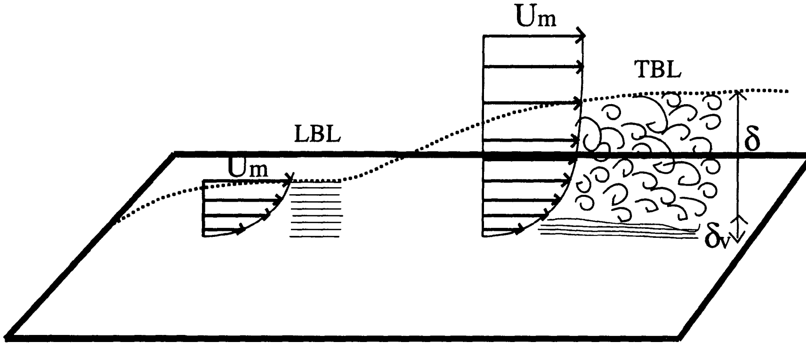

Figure 1 Schematic representation of the flow regimes in the vicinity of planar substratum. The laminar boundary layer (LBL) is indicated by solid lines. The fully turbulent boundary layer (TBL) is characterized by eddies and sweeps (indicated by curliques). The buffer layer is indicated by small eddies over the viscous sublayer. Um = free-stream flow; the broken line indicates the outer edge of the boundary layer, the thickness of which is δ; arrows indicate the flow, and their length proportional to flow velocity. δ_v = thickness of the viscous sublayer.

neighbors and the presence of which alters the flow pattern: kelp stipes, coral branches, rocks, and manmade structures such as pilings and artificial reefs. Although protruding bodies offer less surface area than do planar ones, they nonetheless form an important component of the substratum in many marine environments. In our analysis of flow pattern in the vicinity of protruding bodies, we use a circular cylinder as a simple model (Figure 2).

The presence of a cylinder causes flow to accelerate as water moves toward its widest cross-section (at $\theta = 90°$ for the circular cylinder in Figure 2), and flow near the cylinder can reach velocities twice that of mainstream. On the downstream side of the cylinder, flow decelerates. Due to the adverse pressure gradient associated with the deceleration, a separation zone is induced resulting in a downstream wake (Figure 2).

Depressions

Depressions (e.g. pits and crevices) are abundant on the surfaces of submerged substrata including organisms, manmade structures, and both soft bottoms and hard bottoms. Generally speaking, depressions have the opposite effect from protruding bodies—they increase the cross-sectional area through which water flows, and water consequently slows when flowing over and into a depression (62). The decreasing velocity leads to an adverse pressure gradient that results in a separation of the flow at the upstream edge of the depression and a vortical flow within the cavity itself (Figure 3). Flow often reattaches to the substratum at the downstream rim (96; Figure 3*C*).

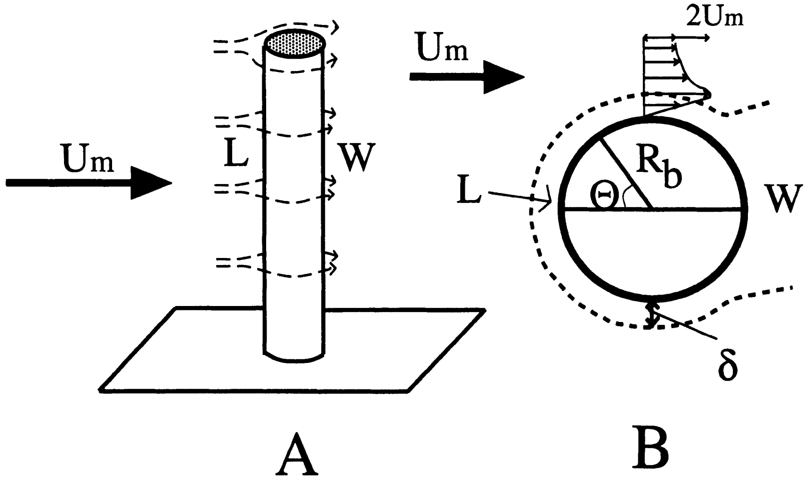

Figure 2 Schematic representation of a protruding body (*A*), its cross section (*B*), and the flow regime in its vicinity. The flow pattern induced by protruding bodies (in high Reynolds numbers) is of two zone types: accelerated laminar, thin boundary layer flow (L) in upstream turns, and retarded turbulent flow in downstream wakes (W). *Um* = free-stream flow (note that the velocity at the boundary-layer edge can reach 2 Um); *broken lines* indicate the outer edge of the boundary layers; *broken arrows* indicate streamlines, and *full arrows* flow velocity where length is proportional to velocity. Rb = body radius, θ = angle between a given point and the upstream stagnation point; δ = thickness of the boundary layer.

The maximum tangential velocities of vortices within depressions are approximately one tenth the mainstream flow velocity and do not exceed two tenths mainstream velocity (e.g. 40, 77, 91). Periodically, the vortex within the cavity becomes unstable and is shed from the cavity. This vortex-shedding leads to bulk replacement of fluid within the depression and, thereby, potentially to the bulk delivery of propagules to the cavity. The shedding of vortices is strongly enhanced by the presence of a distinct downstream edge to the cavity (69).

Most studies dealing with cavity flow have examined depressions below a planar substratum, in which case sharply defined vortices are the dominant patterns of cavity flow. Depressions in hard substrata may be formed, however, from walls raised above the local topography, and they may produce a different pattern of cavity flow (A Abelson, personal observation). This flow pattern includes a relatively slow entrainment of fluid out of the cavity by the "mainstream flow" (an outward current that occupies more than three quarters of the cavity cross section), and a rapid inward current near the downstream lip (Figure 3*C*). Delivery of propagules to the cavity under such circumstances

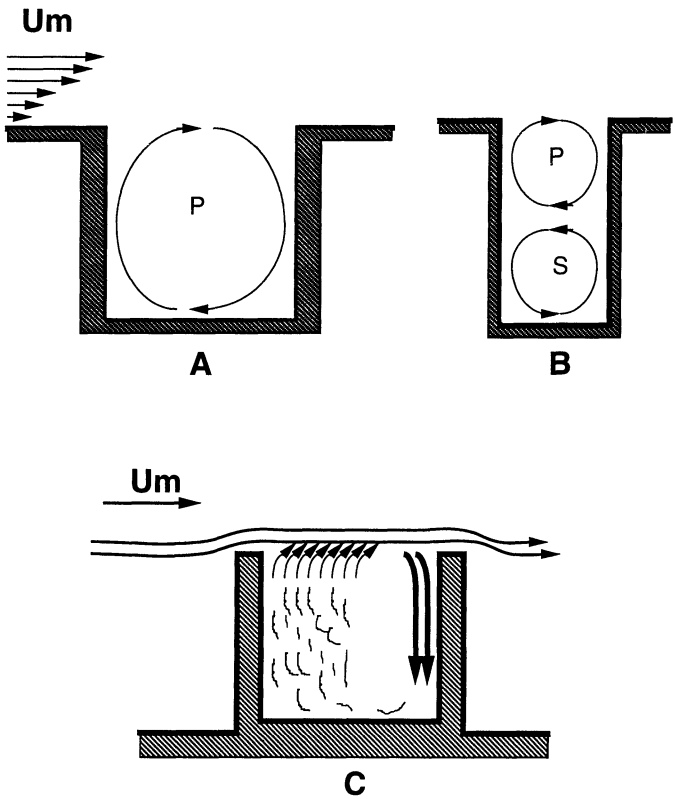

Figure 3 Schematic representation of a shallow depression (*A*) (where the depression's depth is equal to or less than its length in the direction of flow) and deep depressions (*B*, *C*) (where depth is greater than length) and the flow regimes in their vicinity. Separation and reattachment points are illustrated by the streamlines (in *C*). *Solid arrows* indicate flow direction; *arrow thickness* indicates relative flow velocity; *wavy lines* indicate the zone of slow outward current; *Um* = free-stream flow; *P* = primary vortex; *S* = secondary vortex.

may be enhanced by the inward, rapid current, while passive escape of propagules is unlikely because the outward current is slower than the propagules sink. Unfortunately, no quantitative study has yet addressed the transport rates to cavities under these circumstances.

FLOW AS A FORCING AGENT

Settlement can be divided into two critical stages: the delivery of propagules to the substratum, and the subsequent establishment of the larvae or spores, a stage that includes both attachment and metamorphosis. Here, we describe possible effects of flow as a physical forcing mechanism that acts on settling propagules during these two stages. Transport mechanisms of propagules to each substratum type are listed, along with the relevant problems each poses for propagules. We then examine problems that propagules might encounter in exploring the substratum and achieving a residence time sufficient for the creation of a firm attachment—a process that is a function of time (e.g. 29).

Mechanisms of Propagule Transport To Substrata

Delivery of propagules to the substratum can be achieved through active swimming, passive transport by the ambient flow, or both. Passive, flow-mediated delivery may be divided into two major categories depending on whether the flow is laminar or turbulent.

DELIVERY BY ACTIVE SWIMMING Marine propagules can be classified according to their ability to transport themselves. Nonmotile propagules include various bacteria, bacterial capsules, fungal and algal spores, larvae of some invertebrate species, dispersive fragments of both plants and animals, and the slow-moving juveniles and adults of tiny species. Motile propagules include some algal spores and (primarily) invertebrate larvae. These motile propagules can reach 5 mm in length (10) but are frequently much smaller, whereas the nonmotile fragments can be much larger—up to several centimeters long (e.g. 35).

Among propagules that are nominally motile, most are weak swimmers, capable of maintaining speeds of less than 1 cm/s (19, 51). This speed is less than the flow speeds common near ocean substrata (e.g. 13), suggesting that the flow may limit the maneuverability of most self-propelled propagules. Accordingly, we assume that under most prevailing turbulent flow conditions, transport of propagules to the substratum is due to passive motion.

DELIVERY BY LAMINAR FLOW The basic mechanisms by which particles can be delivered to the substratum in laminar flow were introduced to the biological literature by Rubenstein & Koehl (72) in the context of aerosol filtration theory. Subsequently, a number of studies (e.g. 8, 42, 75) have contributed to our understanding of the mechanisms controlling particle entrapment by marine organisms. Four of these mechanisms may also operate to transport propagules to substrata: 1. Direct interception, in which neutrally buoyant particles follow streamlines; if particles are carried within one particle radius of the substratum, they encounter it. 2. Inertial impaction, in which particles that are denser than the fluid diverge from streamlines as flow is accelerated while passing around a protruding body; under appropriate circumstances, dense particles move in the direction of the substratum. 3. Gravitational deposition, a mechanism similar to inertial impaction, but one in which deviation from a streamline is caused by a gravity. 4. Diffusional deposition, in which very tiny propagules may exhibit random, Brownian motion, thereby causing them to encounter the substratum.

DELIVERY BY TURBULENT TRANSPORT The nature of turbulent flows near the bed is characterized by an alternating sequence of "ejections" and "sweeps," which are random in space and time (84). The ejection phase is a slow movement of vortices that creates horseshoe-shaped structures in the flow, which move away from the substratum. The sweep phase is characterized by high-speed flow that penetrates the viscous sublayer as fluid moves toward the substratum. Sweeps have been suggested to be a mechanism by which propagules are carried through the viscous sublayer to the substratum (18). To date, information on the efficiency of sweeps as a transport mechanism, and on the encounter rates of particles transported by sweeps, is lacking, and we must rely on the traditional theory of turbulent diffusion for a qualitative estimation of the efficiency by which turbulence transports propagules (e.g. 25, 28).

TRANSPORT TO DIFFERENT SUBSTRATUM TYPES The transport of passive propagules to horizontal, planar substrata is dominated by turbulent transport, gravitational deposition, and downward swimming (e.g. 24, 30, 34). Turbulence intensity (an index of the efficacy of turbulent transport) is a function of both flow velocity (24) and whether the flow is accelerating (50). At high mainstream velocities in decelerating or steady flows, turbulence intensity is typically high, and the dominant transport mechanism to a planar substratum is likely to be turbulent transport regardless of propagule size. However, under conditions of very low turbulence intensities (e.g. slow and accelerating flows), transport may instead be dominated by gravitational deposition (especially for large propagules that consequently sink fast) and downward swimming. Given the vast area of planar substrata in the sea and the variety of effective transport mechanisms that can combine to maintain high encounter rates over a wide range of flow velocities and propagule sizes, it can be argued that, among the three substratum types, the chances of a propagule encountering planar substrata are the highest.

A preliminary model of transport to protruding bodies suggests that direct interception is the dominant mechanism (A Abelson, unpublished data). The efficiency of direct interception is proportional to both flow velocity and propagule size (42, 72). Therefore, the transport rates of propagules (which are typically small) in the low-flow velocities common in the marine environment are expected to be low.

The separated flow in a depression inhibits most of the transport mechanisms that prevail outside cavities. The sole exception, as suggested by Yager et al (96), is gravitational deposition, which, in this case, is coupled to the process of vortex-shedding. Particles can effectively settle only in the interim between shedding events. The frequency with which vortices are shed is determined by the flow velocity, cavity dimension, and a dimensionless index (the Strouhal number), which is a function of the cavity shape and Reynolds number (92).

Gravitational deposition is likely to be the dominant mechanism transporting propagules into depressions. One should bear in mind, however, that particle dynamics in vortices can be complicated and are not well understood. For example, submicron particles can segregate from the flow due to the rotational motion of the flow (33), a process for which a physical explanation is lacking. In deep depressions with low flow-velocities, diffusional deposition and directed swimming may also be important.

The Limits to Exploration and Attachment

Once a propagule encounters the substratum, the next step in settlement is either exploration of the surface or immediate attachment. In either case, the propagule must be able to control its position in space, whether to stay in one spot for time sufficient to establish a permanent attachment or to move in search of an optimal site.

The ability of a propagule to control its position depends on whether it can resist the hydrodynamic forces imposed on it. Under steady flow conditions, a propagule on the substratum is exposed to drag and lift forces, and if the flow accelerates either spatially or temporally, an acceleration reaction is also imposed. In addition, the velocity gradient in the benthic boundary layer exerts a torque on the propagule, a "rotary force" that rolls the propagule along the substratum (A Abelson, P Sanjines, S Monismith, submitted).

In the absence of adhesion, even the slightest forces are sufficient to dislodge passive particles from the substratum, with the result that nonadhesive propagules are likely to settle only where the flow is exceedingly slow (e.g. in depressions). Under such benign flow conditions, directed swimming may also be effective in allowing a propagule to maintain its position.

Assuming that the surfaces of substrata are equally rough, the relative forces on given propagule sizes at the substratum surface may depend on the substratum type. Protruding bodies induce the largest hydrodynamic forces among the three substratum types. These relatively strong forces are due primarily to the steep velocity gradients over the protruding-body surfaces, as well as to the increased flow velocity along the sides of the body (which, in cases of circular cylinders, may reach values twice the mainstream flow velocity; Figure 2). An additional force, the acceleration reaction, may play an important role in determining the resultant force on relatively large propagules. Planar substrata present intermediate values of mean forces exerted on settling propagules. These forces are lower than those exerted by the flow in the vicinity of protruding bodies but higher than these in depressions. Propagules settling on planar substrata, however, can experience instantaneous shear stresses due to sweeps that may exceed 30 times the average (26).

Proposed Solutions To Force-Related Problems

In the discussion above, we identified two factors that can act as potential barriers to the settlement of marine propagules—the inefficient manner in which they are delivered to protruding bodies and the need to resist hydrodynamic forces while maintaining a position on the substratum. The solutions to these problems are of two kinds: mechanisms that increase the probability of encounter with the substratum, and mechanisms of temporary, instantaneous attachment (or adhesion), which enable the propagule to achieve the residence time required for a permanent attachment.

As has been noted, the efficiency of transport to protruding bodies is positively correlated with propagule size; hence, an obvious mechanism to increase the probability of a propagule encountering a protruding body is to increase the propagule's size. However, large propagules experience large flow-related forces that can detach them from the substratum. Likewise, large propagules are costly to produce. Therefore, the optimal solution should be one that increases the propagule's effective size prior to encounter but does not increase the force exerted after encounter.

The evolved solutions to this problem are based on the use of flexible appendages or other temporary devices that increase the propagule's volume. For example, mucus sheaths envelope the propagules of red algae (12) and diatoms (E Gaiser, personal communication); the sheath of a red-algal spore may increase its actual volume by nearly an order of magnitude (Figure 4*A*). Another strategy is to extend projections from the propagule's body (Figure 4*B*), a solution found in bacterial capsules (20) and pili (60), fungal spores (38), and the dispersive fragments of red algae (47) and soft corals (Y Benayahu, personal communication). These fragments produce sticky crowns of rhizoids.

Attachment devices that cover the whole surface area of the propagule body or a large portion of it might be impractical for motile propagules, which in many cases utilize their body surface for locomotion (by cilia, for instance). Motile propagules such as larvae and dispersive juveniles or adults of invertebrates are more likely to use a single, projecting appendage which, due to the continuous reorientation of the propagule in flow, may nonetheless occupy a much larger effective space than a propagule without an appendage (4) (Figure 4*C*). Projecting appendages include the mucous threads secreted by larvae of hydrozoans (37; A Abelson, unpublished information), sea anemones (76), corals (4, 88), and polychaetes (32), and by juveniles and small dispersive adults of snails (49, 90) and bivalves (23, 87).

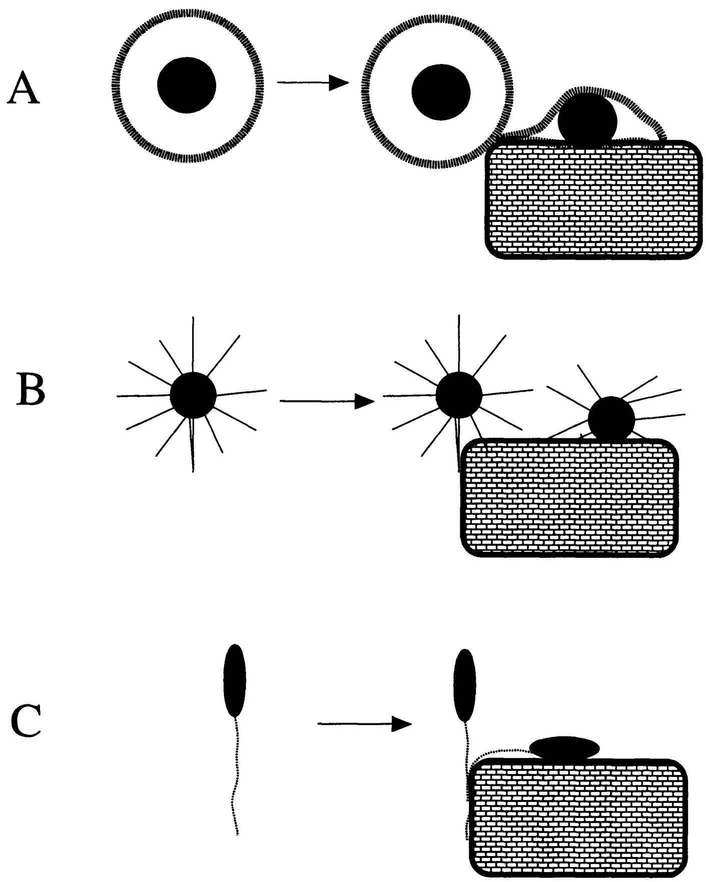

Figure 4 Attachment devices of propagules. (*A*) mucous sheath; (*B*) surface projections (e.g. bacterial pili); (*C*) threads (e.g. mucous and byssus).

Single projecting appendages have been observed in a flow tank to give rise to enhanced encounter rates of larvae with protruding bodies (4). However, the increased probability of encounter is largely dependent on the orientation of the propagule and its appendage relative to the protruding body. The orientation of appendage-bearing propagules may be affected, among other factors, by their aspect ratio and the turbulent dissipation energy (e.g. 41).

After the propagule has reached the substratum, it has two potential remaining problems. If it is to settle there permanently, it must maintain its position until a permanent attachment is made. Alternatively, it may be advantageous to explore the substratum in search of a more appropriate site. In both cases, some form of adhesion is required.

Often an adhesive is secreted prior to the organism's encounter with the substratum, examples being the mucous threads and sheaths described above. These allow the propagule to adhere instantly upon contact with the substratum. If the point of contact is inappropriate, some propagules can cut themselves off the substratum and return to the flow (4). This trial-and-error strategy may be an inefficient means of searching for a favorable site to settle. Alternatively, adhesion can be effected by devices that enable the propagule to move while keeping its attachment. The most prominent example is the barnacle cypris larva, which uses its antennular attachment organs to hold itself on the substratum while it explores (e.g. 21, 99). The exact adhesive mechanism of these antennules is not clear, but it seems that the larva can control the adhesiveness of its antennules. A similar role is played by the pyriform organ of the cyphonautes larva of bryozoans. This organ is reported to secrete a thin mucus sheet that aids locomotion and helps to fasten the larva temporarily to the substratum (83); larvae of the bryozoan *Membranipora membranacea* have been observed to explore substrata in flow (1), although the exact mechanism of locomotion in cyphonautes larvae is not yet clear.

The morphology of a larva can affect its exploratory locomotion when the organism is exposed to flow. This effect has been examined using three morphological models (spheres, symmetrical elongated models, and asymmetrical elongated models) in a flow tank (A Abelson, P Sanjines, S Monismith, submitted). The three morphologies behave differently when exposed to the shear flow of a benthic boundary layer. Specifically, spherical models were subjected to torque levels stronger than the forces most larvae can generate; they rolled along the substratum. Thus, spherical larvae may have trouble controlling their orientation. The symmetrical elongated models autorotated in a pattern that included two weak equilibrium positions, so larvae of this shape may also have problems controlling their orientation. The asymmetrically elongated models kept a stable position parallel to the flow direction and seemed to have the morphology best suited for locomotion.

FLOW AS A SETTLEMENT CUE

It is reasonable to assume that the various effects of flow on settling organisms may have led to the utilization of the local flow regime as a settlement cue. Indeed, some field studies show active site selection by larvae that may be attributed to larval response to different flows (e.g. 57, 93). The role of flow may be indirect, acting through its effect on other environmental parameters (see the following section). Nevertheless, the few studies on active behavior of settling propagules in response to flow show that larvae can select settlement sites by somehow sensing the local flow regime (e.g. 4, 43, 58).

Parameters that may be used by larvae to characterize the flow regime in their vicinity include: flow direction, shear stress, pressure gradient (adverse or favorable gradients), turbulence intensity, boundary-layer or viscous sublayer thickness, and acceleration. These flow parameters are often interrelated (e.g. shear stress is a function of the boundary layer thickness, and turbulence intensity may be linked to acceleration). As a consequence, it can be difficult to determine which parameter is affecting behavior. For example, Crisp (21) studied the behavior of barnacle larvae in tubes and on rotating plates. He demonstrated that larvae tend to move actively against the flow both by swimming and by using their adhesive antennules. Crisp argued that the velocity gradient close to the substratum is the flow parameter that affects the attachment of larvae of sessile species, and the nominal speed of the water is important only for its influence on the velocity gradient. In the same study, however, when referring to the exploratory behavior of larvae before attachment, Crisp related larval migration to flow direction rather than to the velocity gradient along the substratum. Unfortunately, the experimental design in Crisp's study did not enable discrimination between larval response to flow direction and velocity gradient.

In another study of settlement, coral larvae were shown to actively select settlement sites that differ from other sites only in their flow regime (4). Although the coral larvae select sites that can be characterized by different accelerations (acceleration, steady flow, deceleration), the precise flow parameters used to select preferred sites were not clear.

The studies cited above failed to isolate the specific flow parameters responsible for the observed larval behavior. It is possible, however, to isolate the effects of flow parameters by using substrata that induce distinct flow regimes. For example, it is possible to discriminate between larval responses to flow direction and shear stress using circular cylinders and flat plates in a flow tank. A cylinder affects the flow such that shear stress increases in the direction of flow because the flow accelerates. In contrast, on a flat plate the shear decreases in the direction of flow because the boundary layer grows. It was found that cyphonautes larvae respond to flow direction rather than to changing trends in shear stress (1).

FLOW AS A MEDIATING FACTOR AFFECTING SETTLEMENT CUES

Flow affects various environmental parameters, some of which are used as settlement cues by propagules of benthic marine organisms. Despite the likelihood of such indirect effects of flow on settlement, this is probably the least studied aspect of the role of flow in settlement. The most prominent environmental factors that are affected by flow and used as settlement cues are the concentration of chemical attractants or settlement inducers, the magnitude of sediment load, the grain size distribution of soft-substrata, and the characteristics of the microfilm.

Flow and Chemical Cue Distribution

Numerous studies (for reviews, see 55, 65) describe the induction and/or enhancement of settlement in invertebrate larvae in response to chemical factors produced by conspecific adults, host and prey species, and microbial films. On the other hand, very few studies have examined the effect of chemicals on settling propagules under flow conditions (67, 89), and, to the best of our knowledge, only one study has examined the combined effects of water-soluble chemical cues and flow on settling propagules (89).

Despite our poor knowledge of larval response to waterborne chemicals under flow conditions, it is generally accepted that chemotaxis toward a preferred substratum in flow is unlikely to play a role in settlement (e.g. 22, 65). This conclusion is based on three lines of reasoning. First, turbulent flow over a body releasing a waterborne substance is expected to dilute the substance to negligible concentrations within a short distance from the source (65). Second, the small sizes of larvae would seem to make orientation and navigation in a concentration gradient unlikely (22). Finally, given the limited locomotory capabilities of larvae, it has been assumed that they do not move upstream (see, for example, 7). Because waterborne chemicals cannot be tracked by downstream exploration, the possibility of tracking settlement sites along gradients of waterborne chemicals would appear to be impractical.

It is always dangerous to underestimate the abilities of organisms, however, and the advantage of being able to track waterborne chemicals would seem to be large. For example, many organisms inhabit spatially limited, specific substrata (e.g. the bodies of host organisms), and for them the probability of encountering the appropriate substratum without any remote indicator is likely to be extremely low. The ability of dispersed chemicals to indicate at a distance the presence of the required substratum could be used by a capable larva to move toward its host. Indeed, we believe that larvae that settle in association with other organisms may (while on the substratum) possess the capacity to track waterborne settlement inducers toward their preferred substratum under flow conditions. We base our view on the following considerations.

First, while the expectation is that turbulence rapidly mixes chemical plumes, it must be remembered that mixing near the wall is relatively weak, so that plumes might remain coherent for substantial distances (52). Additionally, while low concentrations might be measured in the mean in turbulent flow, these are generally the result of intermittent pulses of high concentration, rather than of a steady supply of mixed fluid (64). Relatively strong chemical cues may thus be available occasionally to guide settlement. Crabs track waterborne odors from distances of 0.5 m and 1 m in a turbulent flow (94).

Second, the arguments against the ability of larvae to orient and navigate in a concentration gradient are not grounded in experimental results. Moore et al (53) suggested that if significant spatial differences in chemical signal structure consistently occur at spatial scales of a few hundred mm, as they found in their study, then directional and distance information from odor plumes could be derived via differential sensory input between paired sensors in small organisms. Furthermore, the case against chemotaxis in larvae is at odds with a large body of evidence of chemotaxis in other, much smaller organisms (e.g. 5, 8). For example, neutrophil cells (a type of phagocytic white blood cells) are able to detect very low concentrations (ca 10^{-10} M) of a specific chemoattractant and can detect a 1% difference in the concentration across the cell, allowing them to migrate up a chemical gradient (5).

Finally, some larvae can explore substrata in the upstream direction. Crisp (21) found that barnacle larvae can actively move against the flow by swimming extremely fast (4–5 cm/s) and using their adhesive antennules. Crisp's results have been criticized for the experimental design, which did not simulate the natural conditions of larvae (58). However, it is reasonable to assume that barnacle larvae are capable of locomoting against the stream. The cyphonautes larvae of *Membranipora membranacea* can explore substrata against currents that are much faster than their locomotion speeds by crawling over mucus sheets that attach them to the substratum (1).

In summary, we suggest that larvae of benthic marine organisms may be tracking waterborne settlement cues under flow conditions. However, a future study will have to resolve this issue by examining whether plumes carrying chemical settlement cues can induce upstream substratum exploration by propagules that utilize these cues to track their preferred habitats.

Flow and Sediment Load

Sedimentation exerts harmful effects on hard-bottom dwellers in diverse manners (e.g. 70). Sediment grains in flow may abrade the organism's tissue; suspended grains can interfere with filter feeding; and deposited particles can cover organisms, preventing them from carrying out various vital processes. In light of the deleterious effects of sediment on organisms inhabiting hard substrata, sediment load is likely to have an influence on the habitat choice of settling larvae. This issue has not been explored in depth, but in certain cases settlement rate has been shown to be reduced in areas with high sediment loads (e.g. 36, 86).

Sediment load is the outcome of two counteracting processes, sediment erosion (or entrainment) and deposition. Flow is a dominant agent governing these sedimentological processes and therefore is likely to be an important indirect factor affecting propagule site selection and settlement.

Flow and Soft-Substratum Type

Size of sediment grains is an important parameter in the biology and ecology of soft-bottom dwellers (e.g. 79). Grain size may affect particle selection by deposit feeders (74), and grain size may determine the amount of organic matter in the sediment and consequently the feeding efficiency of deposit feeders (e.g. 85). The effects of grain size on soft-bottom dwellers explains what has been known for decades—that sediment grain size can determine site selection, settlement, and metamorphosis of soft-bottom dwellers (reviews in 13, 79).

Flow characteristics (e.g. turbulence intensity and shear stress) are crucial in determining the grade and structure of deposited sediments at a given site (within the limiting frame of the sediment-grain coomposition of the potential sources; e.g. 6). Combining the role of flow in sediment distribution and the role of grain size in site selection, we can argue that flow probably plays an important role mediating larval settlement in response to grain size.

Flow and Biofilm Type

There is mounting evidence for the role of flow in bacterial attachment, removal, growth, and spatial density, as well as for its effect on metabolic activity of biofilm communities (11, 45, 100). Flow causing different shear stresses may induce bacterial films of different morphology and structure. Biofilm communities function as pioneer communities developed during the first stages of succession on a newly cleared substratum, and they act both as an attractant and as the actual substrate upon which algae and animals subsequently settle. For example, barnacle larvae of two species respond differently to each of two films (61). Flow can thus indirectly affect late settlers by its effect on pioneer communities of microorganisms.

CONCLUSIONS AND SPECULATIONS

Active Versus Passive Behavior in Settlement

Most models of propagular settlement assume, for simplicity, that when a larva encounters the substratum, it immediately adheres and settles (e.g. 25, 78). Similarly, models of benthic invertebrate recruitment treat larvae as passive particles (e.g. 71). Butman and coworkers (58, 67) pointed out that such studies disregard the importance of behavior in settlement, supporting their argument with results clearly showing that active behavior may greatly affect recruitment patterns. Currently, the accepted paradigm is that settlement is a combined result of both flow effects and larval behavior (e.g. 30). It seems that the delivery of larvae to potential habitats is governed mainly by flow-related processes, whereas exploratory larval behavior may be important over small spatial scales after the initial encounter with the substratum (e.g. 13, 67, 93).

Nonmotile and motile propagules exhibit major difference in behavior during settlement. Nonmotile propagules, by definition, do not actively explore the substratum and can select an optimal habitat only by initiating permanent adhesion when they come across a suitable site. Although motile propagules are able to explore and select an appropriate settlement site, a wide range of flow regimes exist under which these organisms are unable to explore the surface. Support for this assumption is given, for example, by Pawlik & Butman (66), who have observed "erosion" of larvae from the bed at shear velocities (shear velocity is a measure of the magnitude and correlation of turbulent fluctuations in velocity near the substratum) higher than 1.03 cm s^{-1}. In such flow conditions, swimming of motile propagules can be considered ineffective.

We therefore suggest that differential settlement (i.e. deviation from the settlement distribution predicted from the distribution of initial contacts of propagules with the substratum) under conditions of hydrodynamic forces higher than the propagule swimming forces is due to desertion of unfavorable sites rather than to exploration and active selection of an appropriate site. Invertebrate larvae have been observed to desert substrates following encounter in flow tanks (e.g. 4, 14, 58). Moreover, larvae reportedly have deserted their settlement site after settlement and metamorphosis due to unfavorable conditions (e.g. 68).

An alternative explanation for differential settlement in flow is provided by the "adhere and explore" mechanisms of barnacles and bryozoans. These mechanisms may explain deviations of settlement distribution from encounter distributions of barnacles and bryozoans under flow conditions (as was found by Walters, 93). The potential importance of "adhere and explore" mechanisms is that they save the propagule the need to return to the flow if it encounters unfavorable sites.

Ecological Significance of Settlement in Environments of Different Flow Conditions

Flow causes food particles to be distributed nonhomogeneously in sites that differ in height, or over morphologically different substrata of benthic habitats (3, 59), and organisms may be distributed in accordance with their potential food distribution (2). Larvae of sessile particle-feeders may settle in flow patterns that enhance the concentration of their "preferred" food.

In this sense, larvae of suspension-, bedload- and deposit-feeding species (for definitions, see 3, 42, 48) are expected to select distinct microhabitats that differ in their flow patterns and, as a consequence, their prevailing particle compositions. Specifically, larvae that feed on fine, suspended particles may have evolved mechanisms (e.g. adhesive appendages) that allow them to settle on protruding bodies where the fluxes of fine, suspended particles are the highest and where the potentially disturbing coarse bedload particles are in relatively low quantities. On the other hand, propagules of bedload- and deposit-feeders would be expected to have evolved without these mechanisms because, for example, adhesive appendages might stick them to sites unfavorable in terms of food supply. The larvae of bedload-feeders are expected to favor sites on planar substrata in which the bedload fluxes are the highest, whereas deposit-feeders are more likely to prefer depressions.

Larvae that tend to settle in depressions may recognize differences in flow conditions that result from different pit sizes (80). Likewise, larvae of different species, or of the same species in different seas, may differ in their responses to the same pit under the same flow conditions (17, 80). Alternatively, depressions may be chosen not only for the flow pattern they induce. For instance, small depressions, equal in size to or smaller than many propagules and with little effect on flow, may be chosen as preferred settlement sites, possibly because they provide firm attachment (46).

Postsettlement strategies also exist that enable organisms to persist and grow on a wide range of substratum types. For example, the flow pattern in the organisms' vicinity can be altered. This can be accomplished either by changing the substratum morphology (an option open mainly to soft-bottom dwellers, e.g. the ampharetid polychaete *Amphicteis scaphobranchiata*; 63), or by building a body that changes the flow pattern experienced by the organism's feeding devices (e.g. diverse coral species; 2).

CONCLUDING REMARKS

We have presented several themes regarding the effects of flow on settling propagules that should receive more attention in studies of benthic ecology. First, not all substrata are planar. The morphology of the substratum is of great importance in determining the flow pattern in its vicinity and consequently may play a pivotal role in affecting the species composition of settling propagules. The studies of Mullineaux & Butman (57, 58), for instance, clearly show the distinctive effects of induced flow patterns over substrata on the distribution of larvae at settlement. These studies have concentrated, however, on planar substrata and do not deal with other substrata of great importance (but see 80). The neglect of substratum morphology and its resultant flow regime is exemplified by field studies that attempt to explain the distribution of organisms on cylindrical bodies (such as mangrove prop roots) by examining differential settlement on planar substrata (e.g. ceramic tiles; 9). Studies with different substratum morphologies are necessary to assess the exact role of morphology on site selection of propagules and survivorship of the developing recruits.

Second, flow can simultaneously play a role as a settlement cue (which may influence active behavior of motile propagules) and as a factor preventing or disturbing the settlement process. Distinguishing between these two roles is important for understanding the settlement process. No significant attempt has been made to characterize environments in which active exploration is possible and those in which active locomotion is prevented by excessive hydrodynamic forces.

Third, where differential settlement is correlated with flow conditions, flow is often considered to be the sole factor directly affecting the distribution of settling propagules. Flow, however, may affect diverse settlement cues. Parameters other than flow but influenced by flow may determine the differential settlement. These factors include biofilm structure, sediment load, substratum type, distribution of chemicals, and light intensity (due to turbidity).

Finally, further work should be conducted to examine the hypothesis that projecting appendages or other adhesive devices are associated with propagules of species inhabiting substrata characterized by high velocities of flow (e.g. protruding bodies). The corollary here is that species lacking these appendages are likely to settle in sites with low flow velocity (e.g. depressions). Some support for this hypothesis is provided by settlement patterns of several coral species that were found to be correlated to the adult distribution that match their food-particle distribution (4). The differences in settlement patterns of these species can be related to mechanisms affecting larval encounter with and attachment to the substratum. Most mechanisms that facilitate settlement on protruding bodies have been previously described in contexts other than settlement in flow and have elicited various explanations as to their role in the biology and ecology of propagules. The most widely accepted explanations for the role of projecting appendages on larvae concern their role in drifting and dispersion (e.g. 44, 90), in feeding (e.g. 31), and in creating aggregations (20). Strathmann (81) argues that there is no evidence that projecting appendages are used to maintain larvae in suspension, as is often suggested. Likewise, the presence of projecting appendages among tiny propagules that exhibit very low settling velocities is not likely to affect dramatically their dispersal range, especially for motile propagules that can maintain their vertical position by swimming. We do not deny alternative explanations for the roles of projecting appendages. However, many organisms possessing them are apparently able to settle on protruding bodies and in other environments of strong, accelerating flow.

In summary, the information of previous studies suggests that flow may act on settling propagules through one or more of three levels: as an agent exerting hydrodynamic forces, as a settlement cue, and as a mediating factor affecting various other settlement cues. A limitation to interpreting the exact role of each level is that discrimination among the three levels requires a complicated experimental setup that in many cases may pose "unresolved" technical problems. Of the three levels, flow as a mediating factor affecting various settlement cues seems to be the least studied. The role of flow as an agent exerting hydrodynamic forces on settling propagules has been clearly shown in various studies. Likewise, there is increasing evidence for the use of flow by propagules (mainly larvae) in selecting preferred sites that fit the adult requirements. To use the flow as a settlement cue, propagules should possess mechanisms to cope with force-related problems. Here we have explored such mechanisms whose effectiveness remains to be examined. Taking into account the significant involvement of flow in diverse biological and ecological processes in the sea, it is reasonable to argue that whatever the relative weight of each level, the overall effect of flow may be crucial for many benthic species.

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