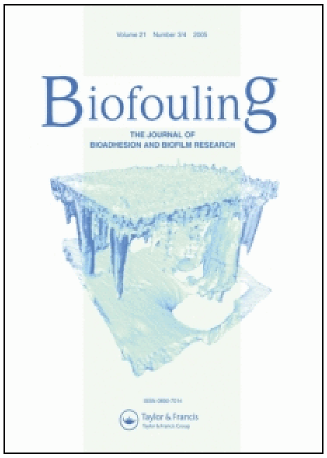

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Mini review: Hydrodynamics of larval settlement into fouling communities

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Mini review: Hydrodynamics of larval settlement into fouling communities

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Abstract

Flowing water delivers planktonic larvae to surfaces, but also dislodges them. This paper reviews experiments in the field and in laboratory flumes, as well as mathematical models, which have revealed how the interaction of ambient water motion with a developing fouling community affects larval settlement. Although mean current velocities across fouling communities in harbours are low, instantaneous velocities can be much higher due to turbulence and to the velocity oscillations of wind chop and ship wakes. As a fouling community develops, its topography becomes more complex and the range of flow microhabitats on the spatial scale of larvae increases. In spite of the prevalence of waves in shallow coastal habitats, and in spite of the importance to settlement of the fine-scale instantaneous velocities encountered by larvae, most studies of flow effects on larval settlement have focused on unidirectional currents and on temporally- and spatially-averaged aspects of the flow.

Keywords: *Biofouling, larvae, hydrodynamics, settlement, boundary layer, turbulence, flow*

Introduction

Many of the organisms in marine fouling communities are sessile invertebrates such as sponges, hydrozoans, tube-building polychaete worms, bivalved molluscs, bryozoans, barnacles, and tunicates. These animals produce, via sexual reproduction, planktonic larvae that are transported by ambient currents and colonise new surfaces. The recruitment of larvae to benthic sites is a critical process affecting population dynamics and community structure (reviewed by Ólafsson et al. 1994; Eckman, 1996; Schiel, 2004).

To colonise a surface, a larva must be transported to that surface, settle ('settlement' is contact with and attachment to a surface by a larva), and recruit ('recruitment' is metamorphosis of a settled larva into a juvenile and survival until counted by an observer) (Keough & Downes, 1982). Water motion on large spatial scales plays an important role in determining spatial and temporal patterns in recruitment by transporting marine larvae between sites and from offshore waters to the coast (e.g. reviewed by Roughgarden et al. 1991; Rothlisberg & Church, 1994; Shanks, 1995). Post-settlement processes affecting larval and juvenile mortality can also be critical in determining when and where recruitment occurs (e.g. reviewed by Ólafsson et al. 1994).

The focus of this review is the process of settlement. The initial contact of larvae with a surface is often due to water flow near that surface (e.g. Hannan, 1984; Harvey et al. 1995; Wethey, 1986; Havenhand & Svane, 1991). However, the positions where larvae settle can also be affected by their behavior after contact (e.g. Rittschof et al. 1984; Butman, 1989; Grassle & Butman, 1989; Mullineaux & Butman, 1991; Pawlik & Butman, 1993; Snelgrove et al. 1993; Walters et al. 1997).

The assemblages of organisms living on hard surfaces in estuaries and harbours ('fouling communities') have long served as model systems for studying ecological succession, the processes by which communities are established and develop over time (e.g. Sutherland & Karlson, 1977). Typically, surfaces are first colonised by a biofilm of bacteria and other microorganisms, and then by larger multicellular organisms. As community succession proceeds with time, free space on the substratum decreases and the surface relief of the community

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increases as settlers accumulate and grow. The successional stage of a fouling community can affect larval settlement into the community for some species (e.g. bryozoans: Hurlbut, 1991; Walters et al. 1999; barnacles: Miron et al. 2000; bivalves, polychaetes, Hurlbut, 1991), but not for others (e.g. ascidians, Hurlbut, 1991). This review explores how the interaction of ambient water motion with a developing fouling community affects larval settlement.

Small-scale water flow near surfaces

When water moves past a stationary solid surface, a velocity gradient develops in the water between the surface and free-stream ambient flow (the 'boundary layer') (Figure 1A). The water flowing in the boundary layer not only delivers water-borne larvae and particles to the substratum, but also dislodges them from it (e.g. reviewed by Nowell & Jumars, 1984; Allen, 1985; Butman, 1987; Wright, 1989; Eckman et al. 1990; Abelson & Denny, 1997; Crimaldi et al. 2002; Koehl & Hadfield, 2004). The greater the distance from the leading edge of a body (e.g. a ship, dock, or fouling plate), the thicker the boundary layer (e.g. Vogel, 1994). Boundary layers in marine habitats over macroscopic surfaces are turbulent, although there is a very thin layer (the 'viscous sublayer') of water next to smooth surfaces in which the viscosity (resistance to being sheared) of the water damps the turbulence (Figure 1A) (e.g. Nowell & Jumars, 1984; Wright, 1989; Vogel, 1994). Bumps on rough surfaces can disrupt the viscous sublayer (e.g. reviewed by Nowell & Jumars, 1984; Ligrani, 1989; Wright, 1989), as will be discussed below. The velocity gradient in a turbulent boundary layer is steepest close to the solid surface. As eddies swirl around in a turbulent boundary layer, water and the materials it carries (e.g. larvae, particles, dissolved chemical cues) are transported to and from the surface.

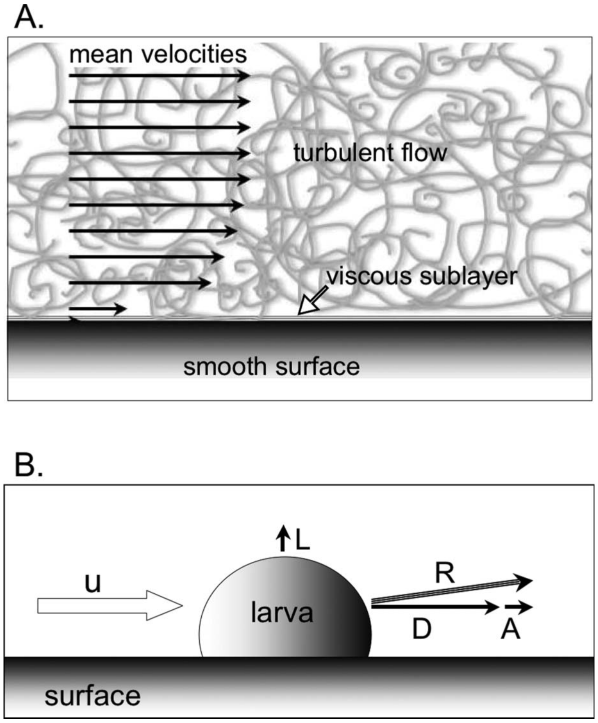

Figure 1. (A) Diagram of a turbulent boundary layer along a smooth surface past which a water current is flowing from left to right. The black arrows show the time-averaged velocities at different distances (z) from the surface, grey swirls represent turbulent flow, and the grey layer near the surface indicates the viscous sublayer. (B) Diagram of the instantaneous hydrodynamic forces on a larva exposed to an instantaneous velocity u: L = lift, D = drag, A = acceleration reaction (at the instant shown in this example the flow is accelerating and A acts in the same direction as drag; at instants when the flow is decelerating, A acts in the opposite direction as drag), R = net instantaneous hydrodynamic force on the larva (r is the vector sum of L, D, and A). For details, see text.

Dispersal of dissolved chemical cues from the surface

The larvae of many species of marine animals are induced to metamorphose into benthic juveniles by dissolved chemicals released by organisms (e.g. prey, conspecifics) living on the substratum (reviewed by Hadfield & Paul, 2001). A few studies have also shown that dissolved chemical cues can affect the swimming behavior of larvae in the water column (e.g. Boudreau et al. 1993; Welch et al. 1997; Hadfield & Koehl, 2004), and can affect their motion towards the substratum in unidirectional flow (Turner et al. 1994; Tamburri et al. 1996; Finelli & Wethey, 2003), and in waves (Koehl et al. 2007).

Past analyses of the effect on larval settlement of dissolved chemicals released from the substratum have assumed a diffuse concentration gradient of chemical cue in the water near a surface (e.g. Crisp, 1974; Eckman et al. 1994). However, recent flume studies using planar laser-induced fluorescence (PLIF) have revealed the concentrations of dissolved substances in flowing water on the fine spatial and rapid temporal scales relevant to microscopic larvae by video imaging of fluorescent dye released from the substratum and illuminated by a thin sheet of laser light. Such PLIF studies of benthic boundary layers have shown that chemical cues from flat or rough surfaces are dispersed in the water above the substratum as fine filaments of high concentration swirling in cue-free water (Crimaldi & Koseff, 2006; Koehl, 2006; Koehl et al. 2007). As a microscopic larva swims or sinks through such a rapidly-changing, filamentous cue distribution, it experiences a series of on/off encounters with the cue, which become more frequent as the larva nears the surface (Koehl et al. 2007).

Hydrodynamic forces on settling larvae

A body, such as a larva or particle, settling on a substratum exposed to flowing water experiences hydrodynamic forces tending to wash it off the surface (e.g. Koehl, 1977; Allen, 1985; Denny, 1988; Abelson & Denny, 1997). Drag (D) pushes a larva in the direction of the instantaneous velocity (u) of the water relative to the larva, while lift (L) acts at right angles to the flow direction past the larva (Figure 1B):

$$\mathrm{D} = 0.5\rho \mathrm{S}\mathrm{C}_{\mathrm{D}}u^2 \tag{1}$$

$$\mathrm{L} = 0.5\rho \mathrm{S}\mathrm{C}_{\mathrm{L}}u^2 \tag{2}$$

where ρ is the water density, S is the projected area of the larva normal to the direction of the force, and $\mathrm{C_D}$ (drag coefficient) and $\mathrm{C_L}$ (lift coefficient) depend on the shape of the larva (e.g. Koehl, 1977; Denny, 1988; Vogel, 1994). If the water velocity fluctuates, as it does in turbulent flow and in waves, D and L (both proportional to u^2) can vary greatly from one instant to the next. A body exposed to rapidly fluctuating water velocities can also experience acceleration reaction force (A), which is proportional to the instantaneous local acceleration of the water past the body ($\mathrm{d}u/\mathrm{dt}$):

$$\mathrm{A} = \rho \mathrm{V}\mathrm{C}_{\mathrm{M}}\mathrm{d}u/\mathrm{dt} \tag{3}$$

where V is the volume of the body and $\mathrm{C_M}$ (inertia coefficient) depends on the shape of the body (e.g. Koehl, 1977; Denny, 1988). The relative magnitudes of the various forces on a settling larva depend on the size and shape of the larva and the water velocities and accelerations it encounters. In general, for very small bodies such as larvae, the acceleration reaction is small compared with drag. The instantaneous force on an organism on the substratum can be calculated as the vector sum of the instantaneous lift, drag, and acceleration reaction (Figure 1B) (e.g. Koehl, 1977; Denny, 1988). For a small larva sitting on a surface, those instantaneous forces depend on the water velocities experienced by the larva, i.e. the velocities a few hundred microns from the surface. Furthermore, a larva resting on a surface can be exposed to a velocity gradient (Figure 1A), which can roll it along the substratum if it is not attached to the surface (Abelson & Denny, 1997).

The instantaneous forces tending to dislodge a larva or particle from a surface exposed to turbulent flowing water can also be represented by the instantaneous Reynolds shear stress at the location of the larva (Crimaldi et al. 2002). Water in the boundary layer along a surface is sheared; 'shear stress' (τ) is the force per unit area tangential to the surface acting in the direction of the flow. The faster the ambient flow, the steeper the velocity gradient and the greater the shear stresses in the boundary layer (for quantitative details, see Cantwell, 1981; Allen, 1985; Wright, 1989; Crimaldi et al. 2002). Turbulence transports momentum across the boundary layer as swirling eddies carry rapidly-moving parcels of water towards the stationary surface and low-momentum water away from it (e.g. Cantwell, 1981; Allen, 1985). Turbulent eddies sometimes 'sweep' through the thin viscous sublayer along a surface, and water near the surface can 'burst' up into the overlying flow. The faster the free-stream velocity, the more frequent these random burst-sweeps and the higher the instantaneous shear stresses on the surface when they occur, and thus the greater the chance that particles and larvae on the bottom will be rolled along or swept away (Eckman et al. 1990; Abelson & Denny, 1997; Crimaldi et al. 2002). The Reynolds shear stress is a measure of the momentum transfer across a boundary layer by turbulent eddies. As eddies swirl in turbulent flow, the velocity measured at a point fluctuates. That velocity record is composed of the mean streamwise velocity (U) and the mean velocity normal to the substratum (W), and the time-varying deviations from those means (u' and w', respectively). The more turbulent the flow, the more often those deviations are large. The time-varying magnitudes of the instantaneous Reynolds shear stresses (τ_{inst}) at a point in the water just above a substratum have been used to calculate the probability of settlement onto the surface by larvae that require different periods of time to stick to the surface (Crimaldi et al. 2002):

$$\tau_{\mathrm{inst}} = \rho \mathrm{u}'\mathrm{w}' \tag{4}$$

where τ_{inst} correlates the instantaneous streamwise velocity fluctuation u' with the simultaneous velocity fluctuation w' normal to the substratum.

Water flow affects larval settlement

Experiments in the field and in laboratory flumes, as well as mathematical models, have shown that water motion affects larval settlement of benthic marine animals (e.g. reviewed by Butman, 1987; Eckman, 1990; Eckman et al. 1994; Gross et al. 1992; Abelson & Denny, 1997; Eckman & Duggins, 1998; Crimaldi et al. 2002; Koehl et al. 2007). Larvae contact surfaces more often in rapid flow (barnacles: Mullineaux & Butman, 1991), while shear in the steep velocity gradient right along a surface tumbles larvae and keeps them near the surface (bivalves: Jonsson et al. 1991). However, settling larvae are more likely to be resuspended off the substratum in rapid currents (e.g. Jonsson et al. 1991). Experimental studies in flumes, pipes, and the field have shown that increases in velocity, turbulence, or boundary shear stress enhance the settlement of some species (e.g. hydroids: Mullineaux & Garland, 1993; Judge & Craig, 1997; barnacles: Judge & Craig, 1997; Qian et al. 1999; 2000; bryozoans: Mullineaux & Garland, 1993), but decrease the settlement of others (e.g. other species of hydroids: Mullineaux & Garland, 1993; bryozoans: Mullineaux & Garland, 1993; Qian et al. 1999; 2000; barnacles: Mullineaux & Butman, 1991; Mullineaux & Garland, 1993; bivalves: Judge & Craig, 1997; polychaetes: Qian et al. 1999; 2000). Because the ways in which water flow was produced and measured differ greatly between these various studies, it is difficult to discern general patterns in the results. Water flow can also affect the mortality of settling larvae (bivalves: Lindegarth et al. 2002).

Much attention has focused on the issue of whether marine larvae are simply transported like passive particles by moving water, or exercise active habitat selection (e.g. reviewed by Butman, 1987; Woodin, 1991; Jumars, 1993). Larval behavior while being transported in the water flowing near surfaces can affect their transport to the surfaces (bivalves: Tamburri et al. 1996; Finelli & Wethey, 2003; gastropods: Koehl et al. 2007). Some types of larvae actively explore surfaces after they land and choose the spot on which to settle (e.g. hydroids: Walters & Wethey, 1996; Lemire & Bourget, 1996; bryozoans: Walters, 1992a; 1992b; Walters & Wethey, 1996; barnacles: Miron et al. 1996; Lemire & Bourget, 1996; Walters & Wethey, 1996; crabs: Lee et al. 2004). Larvae that have landed can reject surfaces and resume swimming (reviewed by Krug, 2006), and some species do so more frequently in faster flow (barnacles: Mullineaux & Butman, 1991; Jonsson et al. 2004; Larsson & Jonsson, 2006). Although barnacle larvae have been observed to explore more surface area in flowing than in still water (Walters et al. 1999), post-contact exploration of surfaces by larvae can be restricted or prevented by rapid water motion (e.g. reviewed by Butman, 1987; bivalves: Lindegarth et al. 2002; Pernet et al. 2003; Kobak, 2005; bryozoans: Walters et al. 1999). A model of larval settlement in flowing water predicts that behavioral responses by larvae on the bottom to the fluid forces they experience can alter settlement rates by an order of magnitude (Eckman et al. 1994).

It has long been thought that hydrodynamic forces limit the ability of settling larvae to attach to surfaces (e.g. Crisp, 1955; Jonsson et al. 2004). Although the adhesive strengths of the larvae of only a few species have been measured (barnacle cyprids: Yule & Crisp, 1983; Yule & Walker, 1984a; 1984b; Eckman et al. 1990; sea slug veligers: Koehl & Hadfield, 2004), the importance of the adhesive strength of larvae in limiting where they are able to settle in complex habitats exposed to turbulent water flow has been discussed (e.g. Abelson et al. 1994; Abelson & Denny, 1997; Crimaldi et al. 2002).

Water flow near fouling communities: importance of waves and turbulence to larval settlement

Although mean current velocities in harbours are low, measurements of velocity as a function of time near fouled surfaces on docks revealed that instantaneous velocities can be much higher due to turbulence and to the velocity oscillations of wind chop and the wakes of boats and ships (Okamura, 1984; Hunter, 1988; Schabes, 1992; Koehl & Cooper, unpublished data) (Figure 2). As explained above, in turbulent flow, high instantaneous shear stresses occur along surfaces when eddies 'sweep'

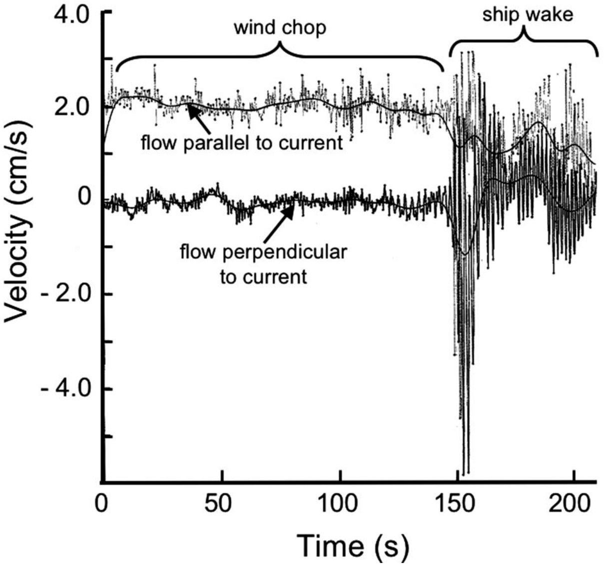

Figure 2. Water velocities measured by an electromagnetic flowmeter (Marsh-McBirney Model #523) as a function of time at a distance of 16 cm from a flat panel covered with tube worms (*H. elegans*) at a depth of 0.3 m in Pearl Harbor, HI. The upper tracing is the flow velocity in the direction of the net ambient current, and the lower tracing is the flow normal to the surface of the panel. The oscillations in water velocity at the beginning of this record were due to small wind-driven waves ('wind chop'), and the large oscillations at the end of the tracing were due to the wake of a ship. The smooth line running through each tracing, which was produced by passing the data through a low-pass filter with a cut-off frequency of 0.1 Hz to eliminate the waves, provides a measure of the slow net velocity of water transport past the worm-covered panel (Koehl & Cooper, unpublished data).

through the thin viscous sublayer along the surface while water near the surface 'bursts' up into the overlying flow (e.g. Eckman et al. 1990; Abelson & Denny, 1997; Crimaldi et al. 2002). Such instantaneous peaks in hydrodynamic force on settling larvae can have profound consequences to their probability of settlement at a spot on the substratum, and the rapidity with which larvae can attach themselves to a surface relative to the frequency of high hydrodynamic stresses also determines the likelihood of settling (Crimaldi et al. 2002).

In spite of the importance of waves in shallow coastal habitats, most studies of flow effects on larval settlement have focused on unidirectional currents. A few mathematical models have explored the consequences of waves to the transport of larvae to the substratum (e.g. Denny & Shibata, 1989; Gross et al. 1992; Koehl & Powell, 1994; Koehl et al. 2007), but not wave effects on post-contact adhesion to surfaces. Waves should affect larval settlement because shear stresses along the bottom are higher in waves, which are more effective at washing particles off surfaces than is unidirectional flow at the same mean free-stream velocity (e.g. reviewed by Wright, 1989; Koehl & Hadfield, 2004). In addition, filaments of dissolved chemical cues released from the substratum tend to be mixed farther from the substratum in waves than in unidirectional flow, and to be wider and higher in concentration (reviewed by Koehl, 2006).

Although the effects of waves should be incorporated into studies of the settlement of fouling organisms onto surfaces in harbours, unidirectional turbulent flow past surfaces can be used to study the hydrodynamics of attached larvae and juveniles on the hulls of moving ships (e.g. Schultz et al. 2003).

Small-scale topography affects water motion

As fouling communities develop, the rugosity of the assemblage of organisms increases. Microscopic larvae settling onto surfaces on which macroscopic organisms are living experience water flow that is affected by the presence of those organisms. Since the sizes, shapes, and spacing of attached organisms ('roughness elements') changes as a fouling community develops, the Reynolds shear stresses encountered by larvae settling into fouling communities at early successional stages might well be different from those experienced by larvae settling into more mature communities.

Turbulent flows over rough surfaces are more complex than over smooth substrata (e.g. reviewed in Nowell & Jumars, 1984; Ligrani, 1989). For example, the periods between high Reynolds shear stresses can be shorter (Krogstad et al. 1992) and the velocities of bursts of water movement away from the wall can be greater (Grass, 1971) when fluid flows over rough surfaces than over smooth ones. Furthermore, when rough substrata are subjected to waves (as are surfaces in harbours exposed to wind chop and ship wakes), these effects of bed roughness are enhanced (Grant & Madsen, 1986).

Turbulence structure is sensitive to the details of the roughness type, thus a challenge to making statistical generalisations about turbulence structure over rough surfaces is that there are too many possible roughness patterns to investigate (Carpenter, 1997). Therefore, many studies of turbulent flow have focused on geometrically regular grids (e.g. Krogstad et al. 1992), parallel grooves (e.g. Bandyopadhyay, 1987), or uniform spheres (e.g. Ligrani & Moffat, 1986; Schultz & Flack, 2005). Studies of flow over complex types of roughness such as gravel beds (e.g. Mulhearn & Finnigan, 1978) have shown that the turbulence statistics very close to the bed become spatially variable due to the local variability in the roughness. At the small scales affecting larval settlement, local flow patterns around individual roughness elements on a surface are probably the most important features of the boundary layer to determine. For example, a larva landing in a crevice between barnacles might experience different forces from one landing on top of an oyster in the same fouling community.

Flow microhabitats within communities of organisms can be quite different from the freestream flow across a site. For example, field measurements reveal that individuals within aggregations of sea anemones (Koehl, 1977) and mussels (Wethey, 2004) were protected by their neighbours from high hydrodynamic forces. Other studies have shown that the spacing between biological roughness elements (e.g. worm tubes, barnacles) affects the water flow between them as well as where ambient water currents deposit particles or sweep them off the substratum (Eckman, 1985; Johnson, 1990; Thomason et al. 1998).

Small-scale topography can affect larval settlement

The effects that topographic features of surfaces have on larval settlement depend on their size relative to the larvae (many marine invertebrate larvae have body lengths of the order of 100 μm to 1 mm) and to the velocity gradient in the boundary layer (reviewed by Howell & Behrends, 2006). There is little consistency in the literature on larval settlement about whether or how to report the spatial scales of roughness elements or textures of surfaces. Therefore, in this review, roughness elements and topographic features that are large enough to disrupt the viscous sublayer will be discussed in the section on small-scale topography, while surface features that are small relative both to larvae and to the viscous sublayer will be addressed in the section on microtexture.

Although the roughness or small-scale topography of a surface does not appear to affect where the larvae of some species settle (e.g. hydroids: Orlov, 1996; ascidians: Hurlbut, 1991), surface rugosity can have striking effects on the larval settlement of many other species (reviewed in Howell & Behrends, 2006). For example, a number of studies have shown higher larval settlement on rough surfaces than on smooth surfaces (barnacles: Mullineaux & Butman, 1991; Hills & Thomason, 1998; Wright & Boxshall, 1999; Skinner & Coutinho, 2005; polychaetes: Hurlbut, 1991; Walters et al. 1997; bivalves: Bologna & Heck, 2000; Czarnoleski et al. 2004; crabs: Lee et al. 2004), although cases of higher larval settlement on smooth surfaces than on rough surfaces have also been reported (barnacles: Berntsson et al. 2000; 2004;: Osman & Whitlatch, 1995a; 1995b; ascidians, bryozoans, polychaetes: Osman & Whitlatch, 1995a; 1995b). Some species preferentially settle on the peaks of bumps on the substratum (hydrozoans: Lemire & Bourget, 1996; barnacles: Chabot & Bourget, 1988; LeTourneaux & Bourget, 1988; Miron et al. 1996; bryozoans: Walters & Wethey, 1991). In contrast, many other species tend to settle in greater numbers in pits, crevices, and grooves, and around the bases of bumps or attached organisms (sponges: Maldonado & Uriz, 1998; hydroids: Walters & Wethey, 1996; bryozoans: Walters & Wethey, 1991; 1996; Walters 1992a; 1992b; bivalves: Kobak, 2005; gastropods: Underwood, 2004; polychaetes: Walters et al. 1997; barnacles: Chabot & Bourget, 1988; LeTourneaux & Bourget, 1988; Lemire & Bourget, 1996).

A variety of biological mechanisms that could produce the patterns of larval settlement on rough surfaces have been suggested. For example, surface roughness can affect larval behavior. Larvae of one species of barnacle spent more time exploring macrofouled surfaces than smooth ones (Walters et al. 1999), whereas larvae of another species spent less time exploring textured surfaces than smooth ones (Berntsson et al. 2000). The tendency for settlement to be high around the bases of benthic organisms such as barnacles and oysters has been explained as the result of space usurpation by those animals, which forces larvae with limited mobility to settle on adjacent surfaces (larvae of polychaetes, barnacles, bryozoans, and ascidians: Osman et al. 1989; Osman & Whitlatch, 1995b). Animals on the substratum can also affect the fine-scale spatial patterns of larval settlement by actively producing water currents (e.g. Ertman & Jumars, 1988), by preying on larvae (e.g. Andre & Rosenberg, 1991: Andre et al. 1993), or by producing chemicals that either repel larvae or induce them to settle (reviewed by Woodin, 1991; Hadfield & Paul, 2001; Krug, 2006). Roughness can enhance the development of bacterial biofilms on surfaces (e.g. Kerr & Cowling, 2003; Howell & Behrends, 2006), and such biofilms can enhance or reduce settlement by invertebrate larvae (reviewed in Maki et al. 2000; Hadfield & Paul, 2001; Krug, 2006; Dobretsov et al. 2006).

A number of hydrodynamic mechanisms have also been proposed for the effects of surface rugosity on larval settlement. For example, mathematical modeling of how larvae are carried by the water in a turbulent boundary layer indicates that surface roughness enhances turbulence, which in turn increases transport of larvae to the substratum (Eckman, 1990). Furthermore, experiments in which spatial patterns of larval settlement are compared with that of inert particles suggest that many types of larvae settle around the bases of benthic organisms, in crevices, in depressions, and at other topographic features where they are passively deposited (hydroids: Harvey & Bourget, 1997; bivalves: Harvey et al. 1995; Harvey & Bourget, 1997; Lindegarth et al. 2002; Kobak, 2005; gastropods: Boxshall, 2000; bryozoans: Harvey & Bourget, 1997; polychaetes: Hannan, 1984; Harvey & Bourget, 1997; barnacles: Wethey, 1986; ascidians: Havenhand & Svane, 1991). It has been suggested that larvae whose initial adhesive strength is low should tend to settle in such areas of low hydrodynamic stress, where they are less likely to be washed away (e.g. Wethey, 1986; Abelson & Denny, 1997; Koehl & Hadfield, 2004; Howell & Behrends, 2006). In contrast, since larvae carried in ambient currents are likely to encounter exposed bumps more frequently than protected crevices, Abelson and Denny (1997) argue that species with strong adhesive devices should show greater settlement on the peaks of surface roughness elements.

Physical and biological factors can interact to affect larval settlement on rough surfaces. For instance, Kobak (2005) observed that surface roughness affects settlement of bivalve larvae in flowing water, but not in still water. Furthermore, larvae can respond to physical and chemical cues on rough surfaces simultaneously. For example, barnacle larvae settled in pits, but at greater rates in those with chemical settlement cues than in those without such cues (Hills et al. 1998). Hydrodynamics can also produce indirect biological effects on larval settlement. Barnacle larvae attached more tightly to surfaces covered with biofilms that developed when the surfaces were exposed to high-shear water flow than they did to biofilms that had been grown in low-shear flow (Neal & Yule, 1994; Neal et al. 1996).

Mounting evidence that the interaction of water flow with surface roughness affects larval settlement indicates that a detailed analysis of the small-scale hydrodynamics of developing fouling communities is an essential component to working out the mechanisms affecting larval settlement into fouling communities at different stages of succession.

Surface microtexture can affect larval settlement

Surface roughness elements that are smaller than larvae and that do not disrupt the viscous sublayer can still affect larval settlement *via* a number of mechanisms. For example, larvae that glue themselves to the substratum may form stronger bonds with rough surfaces than with smooth ones if the bioadhesives the larvae secrete can flow into the interstices between bumps before hardening (Howell & Behrends, 2006). In contrast, some textured surfaces such as whale skin (Baum et al. 2002) and the shells of certain crabs, bivalves, and egg cases (Bers & Wahl, 2004; Scardino & de Nys, 2004; Guenther & de Nys, 2006) may be self-cleaning (i.e. fouling organisms adhere weakly and slough off easily). Although surfaces cast from such natural microtopographies did not affect the recruitment of bivalves, ophiuroids, or polychaetes, they did reduce barnacle recruitment (Bers & Wahl, 2004). Microtextured surfaces can have a major effect on the recruitment of fouling organisms much smaller than invertebrate larvae (e.g. bacteria: Kerr & Cowling, 2003; protozoans: Bers & Wahl, 2004: algal zoospores: Callow et al. 2002; Carman et al. 2006), especially if their diameters are similar in size to the widths of grooves or pockets in the surface (reviewed by Howell & Behrends, 2006). Therefore, microtextured surfaces might indirectly influence the settlement of larvae that are attracted or repelled by such single-celled colonists.

Measuring water flow on the spatial and temporal scales experienced by settling larvae in the field

The water movement experienced by a microscopic larva near a surface affects whether or not it will contact that surface, and the hydrodynamic forces on a larva on a surface determine whether or not it will wash away. Most studies of the effects of water movement on larval settlement have focused on average aspects of the flow, such as mean velocity, volume flow rate, or boundary shear velocity, and most flume studies of larvae settling in flowing water have been conducted in unidirectional flow. However, to unravel physical mechanisms that affect the spatial patterns of larval settlement into fouling communities, it is necessary to quantify the ambient water flow encountered by surfaces in the field. Even in harbours, the flow across fouling communities is turbulent and is affected by the velocity oscillations due to waves (wind chop, ship wakes) (Figure 2). Such realistic conditions can be produced in wave-current flumes, where the details of time-varying water velocities (Figure 3) and instantaneous Reynolds shear stresses can be measured on the spatial and temporal scales relevant to settling larvae.

In laboratory flumes it is now technically possible to measure the fluctuating water velocities that would be experienced by larvae on spatial scales of hundreds of microns and temporal scales of fractions of a second using laser-Doppler velocimetry (LDV). A laser-Doppler velocimeter is a non-invasive, optically-based instrument that has a very small measurement volume and fast temporal response, and the measurement volume can be placed close to a solid boundary. LDV measurements have been used to study the transport of phytoplankton in

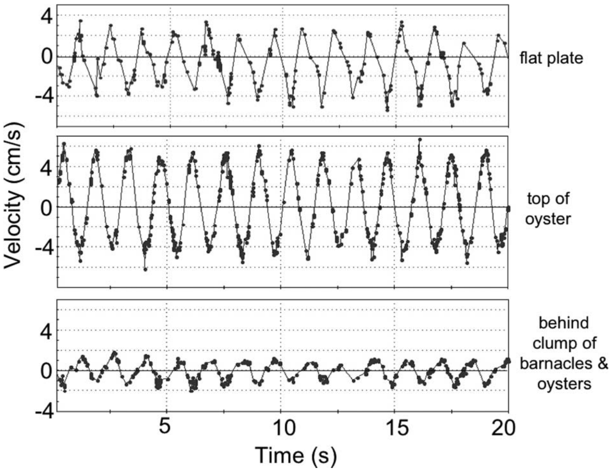

Figure 3. Laser-Doppler velocimeter (LDV) measurements of water velocities measured on the spatial scale of a settling larva. Horizontal velocity as a function of time measured 500 μm above the surface of a flat plate on the floor of a flume (top panel), 500 μm above the top of an oyster in a fouling community on the floor of the flume (middle panel), and 500 μm above the substratum, in a crevice behind a clump of barnacles and oysters in the same fouling community (lower panel). The flow conditions in the flume were designed to mimic the water velocity profiles, turbulence spectra, and waves measured along surfaces in Pearl Harbor, HI. The flume flow in this example mimics field conditions when a ship wake hits a dock (see Figure 2). As this example illustrates, the range of flow microhabitats a settling larva might encounter is much greater in a complex fouling community than on an unfouled, flat surface, and the instantaneous velocity peaks are much larger than the average flow speed past the surface (Crimaldi, Dombroski & Koehl, unpublished data).

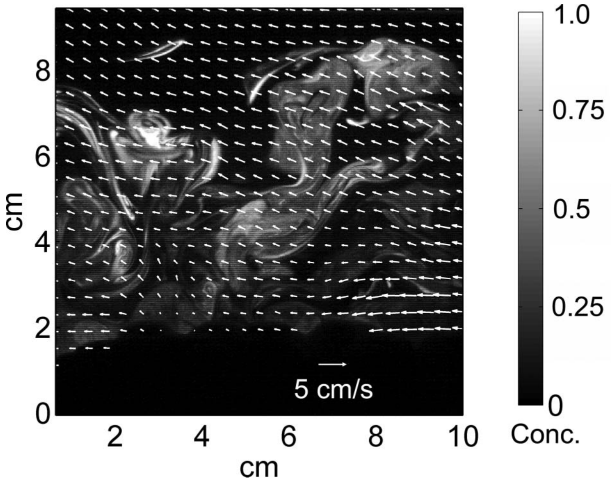

Figure 4. Example of simultaneous PIV and PLIF measurements over *Porites compressa* coral (shown in black at the bottom of the image) in wave-dominated flow in a flume (Reidenbach, unpublished data). The flow was oscillatory with a mean freestream velocity (from left to right in the image) of $U = 5$ cm s^{-1} and superimposed waves with a period of 5 s and orbital wave velocity amplitude of $+/-10$ cm s^{-1}. The image shown here was collected when the oscillatory flow was reversing the current from right to left. The brightness of the pixels in the PLIF image is proportional to the scaled concentration (normalised from 0 to 1) of fluorescein dye, an analogue for dissolved settlement cue released by the coral, at that position in the water (for details, see Koehl et al. 2007). The velocity vectors of water motion (measured using PIV) that occurred during this interval are shown in white.

a turbulent boundary layer above a rough bed of benthic suspension feeders (Crimaldi et al. 2007), and to determine the effect of local turbulent stresses on sediment transport (Nelson et al. 1995) and larval settlement in unidirectional water currents (Crimaldi et al. 2002) and in waves (Figure 3). These studies revealed that episodic peak stresses a few hundred microns from surfaces can be several orders of magnitude larger than the local mean stress. The importance of instantaneous high stresses on larvae to their probability of settlement (e.g. Crimaldi et al. 2002) indicates that future measurements of larval adhesive abilities should focus in large, brief forces rather than the steady force application used to measure larval adhesive strength in the past (e.g reviewed in Koehl & Hadfield, 2004).

Particle image velocimetry (PIV) is another technique that can be used to study the instantaneous fine-scale structure of the complex water velocity field near a surface on which larvae settle. Using PIV, maps of instantaneous velocity vectors are calculated from video records of the movements of neutrally-buoyant marker particles carried in fluid illuminated by a sheet of laser light (details described in e.g. Cowen & Monismith, 1997; Grant, 1997; Liu, 2000). This technique has been used to investigate the effects of surface roughness on boundary layer flow (e.g. Keirsbulck et al. 2002), and has been employed to measure flow in benthic boundary layers in the field (e.g. Bertuccioli et al. 1999; Doron et al. 2001). Combined PIV and PLIF measurements are currently being used in a flume to study the fine-scale flow of water and dissolved settlement cues for larvae in the water over coral reefs in waves (Figure 4); this approach could be used to address similar issues for natural fouling communities and man-made antifouling surfaces.

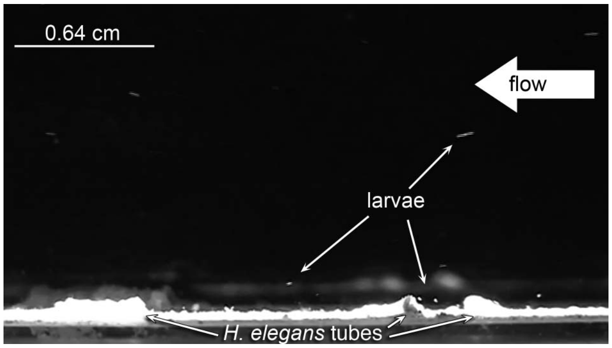

Figure 5. Frame of a video of competent larvae of the tube worm *H. elegans* swimming in wave-driven flow in a small wave-current flume (Sischo, Koehl, Hata, Cooper & Hadfield, unpublished data). The flow 2 cm above the floor of the flume was designed to mimic the flow measured 2 cm from dock surfaces in Pearl Harbor, HI (Koehl & Cooper, unpublished data). The substratum of the flume in this experiment was a glass slide on which a biofilm and adult *H. elegans* were living. The slowly-moving larvae near the substratum look like look like white dots in this image, while those carried in the faster flow higher in the water appear as white streaks. Frame-by-frame analysis of such videos permits us to measure larval trajectories and velocities, as well as the locations, durations, and frequencies of their touchdowns on the bottom for different types of surfaces and flow conditions.

In laboratory flumes, it is also possible to use high-magnification video records of the trajectories and behaviors of larvae encountering different types of surfaces exposed to realistic water flow conditions (Figure 5). Coupling such behavioral studies of living larvae with fine-scale LDV or PIV measurements of time-varying flow should enable the determination of the mechanisms underlying the spatial patterns of larval settlement that occur during the succession of fouling communities.

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