Hydrodynamic forces on larvae affect their settlement on coral reefs in turbulent, wavedriven flow

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Abstract

This study investigates a key aspect of how ambient flow affects the recruitment of water-dispersed marine larvae onto benthic substrata: the sweeping away of larvae that have landed on surfaces. Through a combination of field and laboratory measurements, we studied how waves interact with a complex substratum to affect hydrodynamic forces encountered by microscopic larvae sitting at different positions on the bottom terrain. We used larvae of the nudibranch *Phestilla sibogae* settling onto coral reefs as the system to address this question. Laser Doppler anemometry was utilized within a laboratory flume to measure water velocities encountered 200 μ m from coral surfaces by microscopic larvae sitting at different locations within a reef of the branching coral *Porites compressa*. Comparing wave-driven flow, based on conditions measured over *P. compressa* reefs in Hawaii, with unidirectional flow of the same mean velocity, we found that peak shear stresses along coral surfaces were ~15 times greater and hydrodynamic forces on larvae were ~10 times higher in wave conditions. Peak forces on larvae sitting on the reef top were 3–10 times greater than on larvae 5–10 cm below the reef top. Intermittent bursts of high velocity, which occurred more often at the reef top than within it, determined the settlement probability for larvae in different reef microhabitats. The faster and more strongly a larva sticks to a surface, the higher the probability of successful settlement. Using values for *P. sibogae* adhesive strength, we predict they can settle only on sheltered surfaces within reefs.

Many benthic marine animals disperse to new habitats by producing planktonic larvae that are transported by ocean currents. For such a larva to colonize a benthic site to which it has been transported, the larva must settle ("settlement" is contact with and attachment to a surface), and recruit ("recruitment" is metamorphosis of a settled larva into a juvenile that survives) (Keough and Downes 1982). The recruitment of larvae to benthic surfaces is an ecologically important process that affects population dynamics and benthic community structure (Eckman 1996; Schiel 2004). Water motion near the substratum not only affects the transport of larvae from the water column to a benthic habitat but also determines whether larvae that have landed on the substratum are swept away (Nowell and Jumars 1984; Abelson and Denny 1997; Koehl 2007).

Water motion affects larval settlement—When moving water interacts with the substratum, a velocity gradient forms between the bed and the free-stream flow, generating a boundary layer (Nowell and Jumars 1984; Schlichting and Gersten 2000). Since water flow in the benthic boundary layer is typically turbulent, eddies mix larvae and other particles contained within the flow and transport this material to and from the benthos. Adjacent to the benthic surface, there is a very thin layer of water (the viscous sublayer) in which the viscosity of the fluid damps the turbulence. The velocity gradient is steepest and the profile is linear with respect to distance from the substratum within the viscous sublayer (Schlichting and Gersten 2000). Although many types of marine invertebrate larvae are small enough (a few hundred microns) to lie fully within the viscous sublayer after they have landed on the substratum, small-scale topographic variability combined with instabilities in the flow due to bursting and sweeping of turbulent eddies can periodically disrupt this viscous sublayer, exposing the larvae to higher instantaneous flow forces (Ligrani 1986; Wright 1989; Crimaldi et al. 2002).

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Most studies of the effects of water flow on larval settlement have been conducted in laboratory flumes in unidirectional currents (reviewed in Koehl 2007), even though shallow coastal habitats are often affected by oscillatory flow due to wave action. Water motion across the benthos at wave-exposed sites is characterized by slow net horizontal transport but high instantaneous velocities, accelerations, and turbulence (Koehl 1977; Koehl and Powell 1994; Koehl and Hadfield 2004). Wave action can have a dramatic effect on the small-scale flow patterns near benthic surfaces and can greatly increase intermittent bed shear stresses compared with those in unidirectional currents (Reidenbach et al. 2007). Furthermore, the oscillatory flow in waves can create flow separation along benthic roughness elements (Sleath 1987), which disrupts the boundary layer by reducing the thickness of the viscous sublayer and increasing turbulence near the bed.

Many studies have shown distinctive spatial patterns of larval settlement relative to the topography and surface texture of the substratum (Koehl 2007). Experiments comparing larvae and inert particles suggest that many larvae settle in crevices and depressions or around the bases of topographic features where flow forces are weaker, enabling passive deposition (Koehl 2007). It has also been suggested that larvae with weak adhesive strength settle in areas of low hydrodynamic stress where they are less likely to be washed away (Wethey 1986; Koehl and Hadfield 2004; Howell and Behrend 2006). In contrast, Abelson and Denny (1997) argue that larvae that can adhere tightly to surfaces should show greater settlement on the peaks of topographic features exposed to faster flow. Although hydrodynamic forces greater than adhesive strengths of larvae have been hypothesized to limit the ability of settling larvae to attach to surfaces (reviewed in Koehl 2007), the adhesive strengths of only a few species have been measured, such as the barnacles Semibalanus balanoides (Yule and Walker 1984) and Balanus amphitrite (Eckman et al. 1990), and the nudibranch Phestilla sibogae (Koehl and Hadfield 2004). We have chosen the latter species to be the model organism used in the study reported here.

Objectives-The goal of the present study was to determine how waves interacting with a complex, rough substratum can affect the flow microhabitats encountered by microscopic larvae sitting at different positions on the bottom terrain. We addressed this question for the case of larvae of the nudibranch *P. sibogae* settling onto coral reefs in habitats exposed to wave-driven water flow. We chose P. sibogae as the research system for our investigation because it has for many years been a model organism in studies of larval settlement and metamorphosis, and thus there is a wealth of background information available about this species. Larvae of *P. sibogae* are induced to sink, adhere to surfaces, and undergo metamorphosis into benthic juveniles by a dissolved chemical cue from their prey, the branching coral Porites compressa (Hadfield and Pennington 1990; Hadfield and Koehl 2004; Koehl and Hadfield 2004). Shallow coral reefs in Hawaii, which are exposed to turbulent, wave-driven flow (Koehl and Hadfield 2004), are dominated by P. compressa (Fig. 1A).



Fig. 1. (A) Coral reef dominated by *Porites compressa* in Kaneohe Bay, Hawaii. (B) "Coral reef" constructed of skeletons of *P. compressa* on the floor of the wave-flume diagrammed in Fig. 2.

We combined field measurements with a flume study to address the question of how waves interact with rough substrata to affect microhabitats of settling larvae. We used a laser Doppler anemometer to measure the time-varying flow that would be encountered by microscopic larvae of *P*. sibogae on coral surfaces at different positions within a reef of P. compressa skeletons in a wave-flume (Reidenbach et al. 2006a, 2007) in which flow conditions mimicked those measured in the field. We also varied flow conditions in the flume to determine how unidirectional vs. wave-dominated flows interact with the coral structure to generate fine-scale turbulent shear and to affect the probability of larval anchoring onto reefs. The specific questions this study sought to answer were (1) How do waves affect the water velocity profiles above and within a reef of branching corals? (2) How does position within a reef affect the instantaneous hydrodynamic forces experienced by a microscopic larva sitting on a coral branch? (3) How do waves affect the water velocities and peak hydrodynamic forces experienced by larvae on surfaces at different positions within a coral reef? (4) What is the probability of larval attachment to surfaces at different positions within a reef, and how is that affected by the strength of larval adhesion to the surface and the time required for larvae to anchor themselves?

Although the goal of our fine-scale flow study is not to document how water flow affects coral reef ecology, larval settlement is certainly one of the important flow-mediated processes affecting benthic community structure (Eckman 1996; Schiel 2004). These fine-scale measurements also provide a link to studies that have focused on the effects of larger-scale water motion on other ecologically important processes in coral reefs (Falter et al. 2004; Lowe et al. 2005; Reidenbach et al. 2006*b*).

Methods

A 2-component laser Doppler anemometer (LDA) was used to measure water velocities 200 μ m from coral branch surfaces at different positions within a coral reef constructed in a laboratory wave-current flume. Flow conditions in the flume were designed to isolate, in a controlled manner, particular aspects of water movement in the field that are critical to the small-scale flow encountered by microscopic organisms on the surfaces of corals: wave frequency, velocity range, and small-scale turbulent motions. These results were used to compute (1) surface shear stresses along coral branches; (2) instantaneous drag, lift, and acceleration reaction forces on a *P. sibogae* larva (approximated as a sphere 200 μ m in diameter) on coral surfaces; and (3) probabilities of larval attachment to different positions within the reef for various unidirectional and wave-dominated flow conditions.

Water velocity measurements in the field—To determine natural flow conditions to simulate over the laboratory reef, fine-scale water velocities were measured using an acoustic Doppler velocimeter (ADV) above a coral reef in Kaneohe Bay on the island of Oahu, Hawaii (21°27'N, 157°47'W). We chose to study patch reefs in Kaneohe Bay, not only because they are known habitat for *P. sibogae*, but also because the wave conditions they experience can be produced in our laboratory flume, whereas the longerperiod large waves hitting the exposed seaward edges of coral reefs cannot. The reef on which we did our detailed ADV measurements experienced flow typical of the patch reefs in Kaneohe Bay (Bathen 1968; Koehl and Hadfield 2004). The dominant coral species at our study site was *Porites compressa* (Fig. 1A).

Water velocities were recorded for periods of 3 min at heights of 2 cm, 4 cm, and 8 cm above the surface of the reef using a Sontek SP-AV10M01 ADV with a measurement volume of ~ 0.25 cm³ and a sampling rate of 25 Hz. A cable from the ADV was run to a boat anchored nearby where the data were recorded on a laptop computer. The distance of the sampling volume above the reef was measured both by the ADV and by ruler (Finelli et al. 1999), and these distances agreed in all cases. The ADV was held in position by a rigid scaffolding placed not to interfere with the flow being recorded.

We measured water velocities above P. compressa throughout the tidal cycle, when water depth above the reef ranged between 0.50 m and 0.80 m. On the days when water velocities were measured, the water temperature was 23- 26° C, mean wind speeds were 6.6–6.8 m s⁻¹, and maximum wind speeds were 9.2-10.8 m s⁻¹. These wind speeds are in the middle of the range of wind speeds recorded that year for Kaneohe Bay (daily mean wind speeds ranged from 1.3 m s⁻¹ to 10.7 m s⁻¹, mean = 4.2 m s⁻¹, SD = 0.2, n= 365 days; mean peak daily wind speeds ranged from 3.1 m s⁻¹ to 17.9 m s⁻¹, mean = 8.9 m s⁻¹, SD = 2.3, n =365 days) (weather station in Kaneohe Bay, Hawaiian Institute of Marine Biology, University of Hawaii). Bathen (1968) described the physical oceanography of Kaneohe Bay, where large ocean swells break at the mouth of the bay, small waves drive water movement across the many patch reefs in the bay, and water exits the bay through two discrete channels. Net water motion across the reef where our study site was located was shoreward at all times in the tidal cycle (Bathen 1968; Hadfield and Koehl 2004).



Fig. 2. (A) Diagram of a side view of the wave-flume containing the "coral reef" made of *Porites compressa* skeletons. Black dots indicate the positions at which LDA measurements were made. (B) Diagram of a top view of the LDA setup. Velocity measurements were made at the point where the 3 laser beams (indicated by black lines) intersected one another over a coral surface in the flume. The photomultiplier tube measures the light scattered from particles moving in the water. By analyzing the Doppler-equivalent frequency of light scattered, the local fluid velocity is computed.

Construction of the coral reef in the flume—A coral reef made of skeletons of P. compressa was constructed in the flume (Fig. 1B). Living corals are difficult to maintain during shipping and in the laboratory; therefore, we used skeletons of P. compressa corals for our flume experiments. This was deemed reasonable since previous measurements by Baird and Atkinson (1997) showed that the roughness Reynolds number (Re*), roughness length scale, and mass transfer coefficient were the same for a reef of living P. compressa and reef of skeletons. The coral skeletons we used were remnants from previous experiments conducted at the University of Hawaii (provided by M. Hadfield, State of Hawaii Collecting Permit No. 1999-05). The coral heads were packed together tightly in the flume, as they are in the field (Fig. 1A), and the constructed reef completely covered the floor of the test section (0.6 m wide \times 3.0 m long) of the flume. The typical size of individual coral heads in the laboratory reef were 15 cm in diameter \times 15 cm in height, with an average branch diameter of 1.8 cm and branch spacing of 0.8 cm (Reidenbach et al. 2006a).

Wave-current flume—Our experiments were conducted in a water flume capable of producing both a mean current and surface waves (Fig. 2) (Reidenbach et al. 2006a, 2007). The flume was 9 m long \times 0.6 m wide, and the mean water depth was 40 cm for all experiments. The unidirectional current in the flume was produced by a centrifugal pump regulated by a digital frequency controller. Waves could be superimposed on the unidirectional current by a plungertype wave maker driven by a 185-W motor. Lowering the wave maker over the weir at the downstream end of the flume prevented water from spilling out of the test section

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and sent a wave propagating upstream through the flume; the wave then reflected off of the upstream end of the flume and returned downstream. The wave maker oscillated up and down at the harmonic resonance of the flume, and wave amplitudes built up over a number of cycles until the waves spilled over the top of the wave maker, at which point the wave amplitude remained constant.

LDA measurements of water velocities—Water velocities in the flume were measured using a Dantec two-component LDA coupled with a Coherent Innova 90 laser operated at 514.5 nm. A detailed description of this system and validation of its velocity measurements is given in Crimaldi (1998). Three laser beams were focused by a lens to form a measuring volume in the flume that was 100 μ m in the vertical and streamwise directions and 1 mm in the crosschannel direction. The LDA system was mounted on a rail traverse by which the streamwise position of the sampling volume was controlled manually, and the vertical and cross-channel location of the sampling volume was positioned by a computer-controlled motorized system with an accuracy of 50 μ m.

For both the unidirectional and wave-dominated flow conditions, we measured water velocities that would have been experienced by microscopic larvae sitting on coral surfaces. Horizontal and vertical velocities were measured at positions 200 μ m above the surfaces of coral branches along the top and at various distances below the top of the reef (diagrammed in Fig. 2B). For each measurement, a relatively flat, horizontal surface at the tip of a coral branch was selected. The LDA system was then positioned so that the midpoint of the sampling volume was 200 μ m above the top of the coral branch. The tip of a coral branch along the top of a coral head located 2 m downstream from the leading edge of the reef was defined as the "top of the reef." Velocities along the tips of branches within the reef at depths of 5 cm, 8 cm, and 10 cm below the top-of-the-reef position were also measured. Velocities at each of these positions were recorded for 30 min at a sampling frequency of 50 Hz.

We also measured water velocity profiles above and within the reef for both the unidirectional and the wavedominated flow conditions in the flume. Measurements were made at 1-cm intervals above and below the "top of the reef" (described above) for comparison with the velocity measurements taken at P. compressa reefs in Kaneohe Bay using an ADV. The within-reef flume measurements were obtained in a gap (2 cm wide) between coral branches through which the LDA laser beams could pass. Therefore, within-reef velocities occurring in narrower or wider gaps within the coral canopy could have been somewhat higher or lower than those we measured. Additional profiles using logarithmically spaced measurements were made directly above the tip of a coral branch along the "top of the reef" to determine friction velocities in the wave-dominated and unidirectional flow.

Calculation of instantaneous hydrodynamic forces on a larva—We used our measurements of water velocities



Fig. 3. (A) Frames of a video of a larva of *Phestilla siobogae* in different postures on a surface. Competent larvae (i.e., larvae developmentally capable of metamorphosis) were gently pipetted into a glass well (14 mm in diameter and 3 mm deep) containing a water sample collected from the spaces within a *Porites compressa* reef (Hadfield and Koehl 2004), which induced them to withdraw their ciliated swimming organ, (the velum), sink, and attach to surfaces (Hadfield and Koehl 2004; Koehl and Hadfield 2004). Larvae were videotaped (60 frames sec⁻¹) using a SPI-Minicam color video camera on a Wild stereomicroscope at a magnification of $50\times$. The larvae were illuminated with transmitted light from the microscope lamp (400-850 nm, with the highest values >600 nm). (B) Diagram of the water flow and forces on a larva. The drag at some instant acts in the same direction as the water velocity relative to the larva at that instant, and the lift acts normal to the water velocity. The acceleration reaction force (a.r.) acts in the direction that the water is accelerating at that instant, so if the water is speeding up, the acceleration reaction acts in the same direction as the flow, but if the water is slowing down, it acts in the opposite direction. The net force on the larva at any instant is the vector sum of these forces.

200 μ m above the surfaces of corals to calculate the hydrodynamic forces that would be encountered by a larva of *Phestilla sibogae* sitting on those surfaces. Such a larva adheres to the substratum with a thin, flattened foot, and its bulbous shell-covered body has a height of about 165–235 μ m, depending on its posture (Fig. 3A). Therefore, for purposes of calculating the forces, we approximated the larva as a sphere with a diameter (*d*) of 200 μ m. The instantaneous velocities (*u*) in the streamwise direction were used to calculate the instantaneous forces on the larva (Fig. 3B).

The instantaneous drag on a larva (D), the force acting parallel to the direction of water flow relative to the larva), is given by Eq. 1, where both the magnitude and direction of the force was approximated as:

$$D = 0.5\rho u^2 S_p C_D u |u|, \tag{1}$$

where $\rho = 1.023$ kg m⁻³ is the density of seawater (salinity = 35) at 25°C, *u* is the instantaneous velocity, and $S_p = 3.14 \times 10^{-8}$ m² is the projected area of the 200- μ m sphere normal to the flow direction. We used the C_D for a sphere sitting on a surface. Values of C_D were obtained from Coleman (1977) and expressed as:

$$C_D = \frac{40}{Re} \quad Re \le 3$$

$$C_D = \frac{27}{Re^{0.63}} \quad Re > 3$$
(2)

where Re = ud/v is the particle Reynolds number, u is the instantaneous velocity of water relative to the particle (i.e., larva), d is particle diameter ($d = 200 \ \mu m$ for a larva of P. *sibogae*), and v is the kinematic viscosity of seawater at 25°C ($1 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$). In our calculations, the C_D was varied with time as the velocity changed, with a typical range of Re between 0 and 10, with episodic events reaching as high as Re = 20.

The instantaneous lift force on a larva (L), the force acting normal to the direction of water flow relative to the larva) is given by:

$$L = 0.5\rho u^2 S_p C_L \tag{3}$$

where $S_p = 3.14 \times 10^{-8} \text{ m}^2$ is the projected area of the 200- μ m sphere parallel to the flow direction, and C_L is the lift coefficient of the larva. A constant value of 0.2 was used for C_L based on a reanalysis of force data (Wiberg and Smith 1987) on sediment grains sitting on surfaces from Chepil (1958). Since the lift force depends upon the gradient in velocity across an object, we assumed that the velocity *u* at the top of the larva was that measured at 200 μ m, and that the velocity at the base of the larva was zero, consistent with the no-slip condition at the surface (Wiberg and Smith 1987).

Because of the oscillatory nature of the velocity in wavy flows, a stationary body in such a flow is subjected to accelerating and decelerating water and experiences a timevarying acceleration reaction force (a.r.), which is proportional to the instantaneous local acceleration past the larva:

$$a.r. = \rho V C_M \frac{\partial u}{\partial t} \tag{4}$$

where $C_M = 1.5$ is the inertial coefficient of a sphere (Denny 1988) and $V = 0.167\pi d^3$ is the volume of the 200- μ m sphere. Because volume generally decreases faster than area with decreasing size, for very small organisms, the acceleration reaction tends to be significantly smaller than drag.

Calculation of shear stress on coral surfaces—A common way of measuring the adhesive strength of larvae, spores, and other microorganisms on surfaces has been to measure the bed shear stress at which these microscopic bodies wash away (Charters et al. 1973; Roegner et al. 1995; Koehl and Hadfield 2004). Similarly, the dislodgement and suspension of sediment particles from the substratum is also often reported in terms of bed shear stress (Wiberg and Smith 1987; McLean et al. 1999). So that we could compare the hydrodynamic stresses on larvae at different positions within a coral reef with these measures of particle or larval dislodgement, we used our instantaneous measurements of water velocities 200 μ m above the surfaces of corals to calculate the instantaneous bed shear stresses along those coral surfaces. The instantaneous bed shear stress was computed by summing the viscous and the turbulent components of stress (Crimaldi et al. 2002):

$$\tau = \mu \frac{\partial u}{\partial z} - \rho u' w' \tag{5}$$

where τ is the bed shear stress and $-\rho u'w'$ is the instantaneous Reynolds or turbulent stress. $\partial u/\partial z$ was estimated as the linear gradient in the flow between u at 200 μ m and the surface of the coral, where u = 0 cm s⁻¹ due to the no-slip boundary condition. This is a reasonable assumption because the thickness of the viscous sublayer (δ_{ν}) , where the velocity profile is linear, was estimated ($\delta_{\nu} =$ 5v u^{-1} ; Kundu 1990) to be on average ~300 μ m over the range of flows we used. Above δ_{v} , the velocity profile becomes logarithmic, but the transition between the linear and logarithmic regions is not abrupt and there is a significant transition zone. In reality, the velocity distribution at and just above δ_{y} lies within a transition region between linear and logarithmic values (Schlichting and Gersten 2000), and therefore, between z = 0 and 200 μ m, a linear approximation was deemed quite appropriate.

Instantaneous Reynolds stresses (i.e., turbulent stresses) were calculated as $-\rho u'w'$, where u' and w' were the instantaneous fluctuations of velocity in the streamwise and vertical directions, respectively. Values of u' and w' were estimated by removing the time-averaged mean component of the velocity (\bar{u}, \bar{w}) as well as the wave component (\tilde{u}, \tilde{w}) as:

$$u' = u - (\bar{u} + \tilde{w})$$

$$w' = w - (\bar{w} + \tilde{w})$$
(6)

To determine the turbulent stresses independent of wave motion, the mean and oscillatory parts of the *u* and *w* velocity signals were first separated from the instantaneous records with the aid of wave height, measured by a capacitance wave gauge (Richard Brancker Research Model WG-30). To do this, wave sets of 20 waves were ensemble averaged to find the mean wave signals, $(\bar{u} + \tilde{u})$ and $(\bar{w} + \tilde{w})$, respectively, which were then subtracted from instantaneous velocity measurements to calculate *u'* and *w'*. This method was found to best preserve the appropriate magnitude of the wave heights and velocities while minimizing errors caused by drift in the phase of the wave-maker signal (Reidenbach et al. 2007).

Calculation of anchoring probabilities—Our calculations of the probabilities of larval attachment to surfaces within the reef were based on a statistical analysis described by Crimaldi et al. (2002). For a larva to successfully anchor to the coral surface, settlement onto the coral must occur during a "stress lull" (L_i), the time interval during which the instantaneous stress is lower than the critical stress (τ_{crit}) required to detach the larva from the surface. Furthermore, the time between when a larva lands on the coral and the end of the lull must be at least as long as the time (t_a) required for the larva to anchor itself. Thus, according to Crimaldi et al. (2002), the probability of a successful anchoring event can be represented by:

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$$P(\tau_{crit}, t_a) = \frac{\sum_{i=1}^{M} \phi_i}{t_1 - t_0}$$
(7)

where *M* is the number of stress lulls, t_0 is the initial time of the first complete lull, t_1 is the time when the last lull ends, and ϕ_i is defined as:

$$\phi_i = \begin{cases} L_i - t_a & \text{if } L_i \ge t_a \\ 0 & \text{if } L_i \le t_a \end{cases}$$
(8)

If stress data are taken at discrete time intervals, Δt , then:

$$\phi_i = \sum_{j=1}^{N_i} H_i(j) \Delta t \tag{9}$$

where N_i is the number of samples in the lull and H_i is defined as

$$H_i(j) = \begin{cases} 1 & \text{if } j < N_i - t_a/\Delta t \\ 0 & \text{if } j \ge N_i - t_a/\Delta t \end{cases}$$
(10)

Note that H_i can only be nonzero if the lull is longer than the required time to anchor. Substituting Eq. 9 into Eq. 7 results in:

$$P(\tau_{crit}, t_a) = \frac{\Delta t}{t_1 - t_0} \sum_{i=1}^{M} \sum_{j=1}^{N_i} H_i(j)$$
(11)

The probability of successfully anchoring to the coral was calculated at various τ_{crit} (between 0.1 Pa and 5 Pa) for a range of t_a (between 1 s and 240 s) at four different locations within the coral canopy (0, 5, 8, 10 cm below the top of the reef).

Results

Flow structure and bed shear stress—One wave-dominated and one unidirectional flow condition were tested in this study. The wavy flow in the flume was generated to closely match both the velocities and scales of turbulent motion of the flow measured over a *P. compressa* reef in Kaneohe Bay, Hawaii (Fig. 4). The oscillatory flow in the flume had a wave period (*T*) of 5 s and a wave orbital velocity amplitude (U_w) of ± 9 cm s⁻¹. These waves were superimposed on a unidirectional current of 7.8 cm s⁻¹. The combination of mean current and oscillatory flow gave a root-mean-squared velocity (U_{rms}) of 9.5 cm s⁻¹. The unidirectional flow condition we used in the flume had a U_{rms} of 9.4 cm s⁻¹, designed to be very similar to U_{rms} of the wave-dominated flow with which it was compared.

Profiles of velocities above and within the reef are shown in Fig. 5A for the unidirectional flow condition. For the unidirectional flow, a logarithmic fit to a velocity profile measured immediately above a coral head 2 m downstream from the beginning of the reef was used to parameterize the friction velocity (u_*) as:

$$U(z) = \frac{u_*}{\kappa} \ln\left(\frac{z}{z_o}\right) \tag{12}$$



Fig. 4. (A) Water velocity (measured using an acoustic Doppler velocimeter, as described in the text) 2 cm above a coral reef in Kaneohe Bay, Hawaii, plotted as a function of time. The positive velocities are in the seaward direction. (B) Water velocity (measured using an LDA, as described in the text) 2 cm above a reef of coral skeletons in the flume. The positive velocities are in the net downstream direction. (C) Turbulence spectrum for water velocities measured for 3 min at a position 2 cm above a reef in Kaneohe Bay (open circles) and for 10 min at a position 2 cm above the "reef" of coral skeletons in the flume (black line).

Using Eq. (12), $u_* = 0.98 \pm 0.11$ cm s⁻¹. This compares well with estimates of u_* calculated using turbulence covariance estimates within the constant stress layer above the reef, where $u_* = \sqrt{-u'w'}$ (Sanford and Lien 1999). These calculations indicate that turbulent velocity fluctuations were roughly 10% of the mean free-stream flow at the outer edge of the boundary layer.

Profiles of velocities above and within the reef for the wave-dominated flow condition are shown in Fig. 5B. Due to the oscillatory nature of the wave-dominated flow, a combined wave-current boundary layer above the reef does not usually follow a logarithmic profile (Grant and Madsen 1979); therefore, Eq. 12 cannot be applied to estimate friction velocity. Instead values of u_* must be calculated from instantaneous bed shear stress (τ) estimates (Eq. 5)



Fig. 5. Profiles of the mean horizontal velocities (solid line with squares) at different heights relative to the top of the reef for the (A) unidirectional and (B) wave-dominated flow conditions. Velocities measured by an LDA were recorded for 30 min at a sampling frequency of 50 Hz. The top of the reef is located at z = 0 cm; positive heights indicate positions in the water column above the reef, and negative heights indicate locations within the reef. Profiles within the reef were made by separating the corals 2 cm to allow passage of the LDA laser beams into the canopy. The dotted lines indicate the average maximum and minimum velocities measured over a 5-s sampling window, which indicate the peak shoreward (+) and seaward (-) velocities during a wave period.

and the relation $\tau = \rho u_*^2$. Using measurements obtained directly above a coral head, 2 m downstream from the leading edge of the reef, the *time-averaged* value of the shear velocity for the wave-dominated flow condition was 0.53 cm s⁻¹, which was lower than the estimate of u_* of 0.98 cm s^{-1} for the unidirectional flow. However, since the wave-dominated flow was oscillatory, the instantaneous u_* varied with the magnitude and direction of wavy flow, and with the periodic bursting and sweeping events of turbulent eddies swirling around the complex topography of the coral branches. Such burst-and-sweep events coincided with specific phases of the wave cycle, such that the highest instantaneous values of u_* tended to occur when flow separation of the boundary layer occurred. Flow separation tended to occur twice every wave cycle, as turbulent eddies were generated during forward wave motion, and as the waves reversed direction. The specific phase of the wave when this separation and high turbulent stresses occurred depended both on the properties of the wave and on the local geometry of the coral branches. During these periods of flow separation, the average magnitude of u_* was 4.0 \pm 0.9 cm s^{-1} , which was approximately 4 times higher than the time-averaged u_* of the unidirectional current.

The degree to which ambient water flow transported momentum within the coral canopy depended on whether the flow was unidirectional or wave dominated. For the unidirectional case, the mean depth into the coral to which flow penetrates was z = -2 cm. Below this depth the mean velocity and turbulent stresses were essentially zero. For the wave-dominated case, the mean flow was nonzero to a depth of z = -6 cm, while the oscillations generated turbulent motions even deeper within the canopy. At water depths between z = -2 cm to z = -5 cm, negative mean velocities occurred, indicating the presence of a recirculation region within the coral branching structure as turbulent eddies penetrated through the shear layer formed at the top of the reef, transporting momentum from the overlying flow into the canopy.

Drag, acceleration reaction, and lift forces on a larva— The sum of streamwise components of the instantaneous drag (D) and acceleration reaction forces (a.r.) on a stationary "larva" (i.e., 200- μ m sphere) sitting on a coral surface exposed to the wave-dominated flow condition are plotted as a function of time in Fig. 6 for positions at the top of the reef, as well as 5 cm and 8 cm below the reef surface. Because the "larvae" were so small, drag forces were on average 50–100 times greater than the acceleration reaction forces. The sum of the instantaneous D and a.r. forces oscillates with the periodicity of the waves between positive (i.e., in the direction of the mean flow) and negative values. Peak forces, which act in the net downstream direction, are much lower on larvae on coral branches within the reef than on the top of the reef.

While drag tends to push a larva along a surface in the direction of the instantaneous water velocity, lift acts perpendicular to the flow direction and tends to pull a larva away from the surface (Fig. 3B). The instantaneous lift (L) on a stationary "larva" sitting on a coral branch at the top of the reef, and at 5 cm and 8 cm below the reef top, are plotted as a function of time in Fig. 7 for the wave-driven flow condition. Lift on a "larva" sitting on the tip of a coral branch at the surface of the reef was much greater than on those sitting on surfaces within the reef. The magnitude of the peak drag plus *a.r.* force was about 20 times greater than the peak lift.

The total instantaneous hydrodynamic force acting on a "larva" was computed as the vector sum of the instanta-



Fig. 6. Sum of instantaneous drag force and acceleration reaction force on a larva in the wave-dominated flow condition sitting on (A) the tip of a coral branch at the top of the reef, (B) 5 cm below the top of the reef, and (C) 8 cm below the top of the reef. Positive forces act in the net downstream flow direction in the flume.

neous lift, drag, and *a.r.* forces. The peak hydrodynamic force during each wave cycle occurred when velocity, and hence and lift and drag, were greatest. For the wave-dominated flow condition, we determined the maximum velocity and the peak hydrodynamic force on a "larva" in each wave (T = 5 s) during a 30-min velocity record. The mean of these maximum velocities (Fig. 8A) and peak hydrodynamic forces (Fig. 8B) on "larvae" were significantly lower within the reef than at the top of the reef.

We compared the flow microhabitats of and the hydrodynamic forces on "larvae" on a reef exposed to the wave-driven flow condition described above with those of "larvae" on the reef subjected to a unidirectional current with a comparable U_{rms} . To make this comparison, we took the peak velocity and peak hydrodynamic force acting on a "larva" during each 5-s interval (equal to one wave period) for both the unidirectional and wave-dominated flow condition. We then used those values to calculate the average of the peak velocities and forces acting on a "larva" over the 30-min sampling period. In the unidirectional flow condition, peak velocities (Fig. 8A) and forces (Fig. 8B) were significantly lower within the reef than at the reef surface. Peak velocities and forces on "larvae" on coral branches at each position on the reef were significantly higher in wave-driven flow than in the unidirectional flow with the same U_{rms} .

Bed shear stress—The mean of the peak instantaneous bed shear stresses (τ) was calculated for each 30-min velocity record for both the wave-dominated and the unidirectional flow conditions (Fig. 8C). Peak estimates of τ were significantly greater at the tips of coral branches on the top of the reef than within the reef, and were significantly greater in wave-driven than in unidirectional flow at each position on the reef. At the top of the reef,



Fig. 7. Instantaneous lift force on a larva in the wavedominated flow condition sitting on the tip of a coral branch at the (A) top of the reef, (B) 5 cm below the top of the reef, and (C) 8 cm below the top of the reef. Positive lift acts upwards.

peak bed shear stresses were 15 times greater for the wavedominated flow than for the equivalent U_{rms} unidirectional flow.

Larval attachment probabilities-Larvae landing on the tips of branches of *Porites compressa* at the top of a healthy reef must adhere to living coral tissue, whereas larvae landing on surfaces within the reef are likely to encounter dead coral skeleton encrusted by organisms such as coralline algae. Koehl and Hadfield (2004) measured the nominal bed shear stress required to dislodge Phestilla sibogae larvae attached to P. compressa coral tissue to be 1.6 Pa, and to coralline algae growing on P. compressa skeletons to be 2.5 Pa. Therefore we used 1.6 Pa as the initial critical bed shear stress (τ_{crit}) required to dislodge a larva in our calculation of the probability of attachment by larvae of P. sibogae at different locations on the reef (Fig. 9). Although the critical stress required for larval detachment has been measured, the time required for larvae of P. sibogae to stick themselves to surfaces has not yet been measured. To determine how temporal variability in stress affects larval attachment, we calculated attachment probabilities for larvae with different anchoring times ranging from 1 s to 240 s. We assumed that if a stress event occurred with a magnitude above the critical stress within the anchoring time needed for attachment, the larva was considered to be washed away. We found that the more quickly a larva can adhere to the reef, the greater its probability of attachment (Fig. 9). Our calculations showed that, for larvae landing on the top of a reef, the probability of attachment was close to zero for all attachment times ≥ 10 s. In contrast, attachment probabilities were much higher for larvae landing within the reef.

To generalize our results beyond the example of *P. sibogae*, we also explored the effects of different larval adhesive strengths on attachment probabilities of larvae on reefs in the wave-driven flow condition. If larvae attach





Fig. 8. Peak (A) velocities, (B) hydrodynamic forces on a larva, and (C) bed shear stresses 200 μ m from coral surfaces, plotted as a function of distance below the top of the reef for the wave-dominated flow condition (black circles) and the unidirectional flow condition (open squares) in the flume. (A) Mean of the peak shoreward velocities measured during each 5-s interval of a 30-min LDA record of instantaneous velocities. (B) Mean of the peak hydrodynamic force (vector sum of drag, lift, and acceleration reaction). (C) Mean of the peak bed shear stresses (τ ; Eq. 5). Peak velocity, force, and τ at different positions within the reef were significantly different from each other (ANOVA, Bonferroni-Dunn, p < 0.05); the exception was that peak velocity, force, and



Fig. 9. Probability of larval attachment to a coral surface (Eq. 11) plotted as a function of the distance of that surface below the top of the reef. Each line represents a different time (t_a) required for the larva to anchor itself. We used 1.6 Pa as the critical bed shear stress (τ_{crit}) required to dislodge a larva.

more strongly to a surface, the critical bed shear stress needed to detach them becomes larger. Although data are not yet available for attachment strengths of larvae of other reef-dwelling animals, bed shear stresses required to dislodge newly settled barnacle cyprids range from 0.2 Pa to 8.7 Pa (calculated from boundary shear velocities reported by Eckman et al. 1990). Therefore, attachment probabilities were calculated for various critical bed shear stress (τ_{crit}) required to dislodge larvae. Attachment probabilities for larva landing on a coral branch at the top of the reef are given in Fig. 10A, and on a coral branch 5 cm below the reef surface are given in Fig. 10B. Results suggest the shorter the attachment time and the stronger the adhesion of the larvae, the greater their probability of attachment is in both locations. Measurements using living P. sibogae larvae exposed to P. compressa surfaces for short durations had attachment strengths that were too low $(\leq 0.2 \text{ Pa})$ to be measured in the flow cell used by Koehl and Hadfield (2004). For such weakly adherent larvae (τ_{crit} = 0.1) only those that stick to the surface very quickly (1 s) have a chance of attaching to the top of the reef. In contrast, larvae with low adhesive strengths and slower attachment times can adhere to surfaces within the reef. Larvae that stick to surfaces more tightly than do P. *sibogae* on coralline algae (i.e., $\tau_{crit} > 2.5$ Pa) have some probability of attaching to the top of the reef and approach a 100% chance of attaching to surfaces within the reef.

The example shown in Table 1 illustrates that the peak hydrodynamic forces and bed shear stresses encountered by larvae in unidirectional flow were lower than in the wavedominated flow, and thus the attachment probabilities of larvae were higher. These differences between the two flow regimes were especially dramatic for larvae on surfaces at the top of the reef.

 $[\]tau$ at 8 cm and 10 cm below the reef top were not significantly different from each other (indicated by line below *x*-axis.)



Fig. 10. Probability of attachment of a larva to a surface (Eq. 11) at (A) the top of a coral reef or (B) 5 cm below the surface of the reef, plotted as a function of the critical bed shear stress (τ_{crit}) required to dislodge a larva. Each line represents a different time (t_a) required for the larva to anchor itself. Maximum measured stress at 5 cm below the top of the reef was 2.51 Pa; therefore, for all critical stresses >2.51 Pa, the probability of attachment is 1.

Discussion

Waves affect water velocity profiles above and within coral reefs—Although most flume studies of larval settlement have been conducted in unidirectional water flow (Abelson and Denny 1997; Koehl 2007), many coastal

habitats where larvae settle are exposed to waves as well as currents. We found that peak phase-averaged boundary shear velocities (u_*) above a coral reef in waves were nearly four times higher than u_* above the reef in a unidirectional current with the same root mean squared velocity. The high instantaneous velocities we measured with each wave cycle correlate with the periodic bursting and sweeping events we measured over the reef using planar laser-induced fluorescence (Reidenbach et al. 2007). We also found that momentum was transported deeper into the porous reef, from the overlying flow, in the wave-dominated flow than in unidirectional flow. Therefore, the transport of larvae and other waterborne materials from the water column to a coral reef, as well as transport through the interstices within the reef, should be much greater in wavy habitats than at sites exposed to unidirectional currents with similar mean free-stream flow velocities. The complex, three-dimensional structure of a coral reef provides habitats for many types of organisms. Our results suggest that waves increase the depth within the reef to which such organisms can be supplied with dissolved gases, nutrients, and particulate food, and from which their wastes, gametes, larvae, or spores can be dispersed.

Hydrodynamic forces on larvae depend on their position within a reef-The hydrodynamic forces that might wash a larva off a surface on which it has landed depend on the local flow velocities that the microscopic larva encounters at that location. LDA enabled us to measure water flow at the height of a larva (200 μ m from a surface) in various microhabitats on and within a coral reef. We found that, even when the free-stream flow above a reef is rapid, there are microhabitats just a few centimeters below the reef surface that are protected from high velocities. Similarly, field measurements have revealed protected microhabitats within aggregations of sea anemones (Koehl 1977) and mussels (Wethey 2004), and within kelp beds (Koehl and Alberte 1988; Jackson 1997; Rosman et al. 2007) and coral reefs (Koehl and Hadfield 2004). Because we could only use the LDA to measure water velocities in regions within the reef where the laser beams could penetrate, we were unable to quantify the flow environments in narrow crevices between closely spaced coral branches deep within the reef. Water velocities in those microhabitats are no doubt much

Table 1. Probability of attachment of larvae in wave-dominated and unidirectional current flow conditions under peak hydrodynamic forces and bed shear stresses.

	Maximum instantaneous drag+ <i>a.r.</i> (μ N) (99th percentile) [•]		Maximum instantaneous bed shear stress (Pa) (99th percentile)‡		Prob. of anchoring $(t_a=30 \text{ s})$ $(\tau_{crit}=1.6 \text{ Pa})$ §	
Flow condition*	reef top	5 cm below	reef top	5 cm below	reef top	5 cm below
$U_{rms} = 9.5 \text{ cm s}^{-1} \text{ (waves)}$ $U_{rms} = 9.4 \text{ cm s}^{-1} \text{ (current only)}$	0.81 0.08	0.27 0.03	1.76 0.12	0.73 0.05	0.018 0.98	0.769 1.00

* Wave-dominated and unidirectional current flow conditions in the flume (described in the text) with similar root-mean-squared horizontal velocity (U_{rms}).
 † Maximum horizontal force (drag plus acceleration reaction, a.r.) on a larva (calculated as magnitude in which 99% of the time the instantaneous force ≤ maximum force) on a surface at the reef top, or 5 cm below the reef top.

[‡] Maximum bed shear stresses (τ , Eq. 5) (99% of the time the instantaneous $\tau \leq \text{maximum } \tau$) on a surface at the reef top or 5 cm below the reef top. [§] Probability of anchoring calculated (Eq. 11) using 1.6 Pa for the critical bed shear stress (τ_{crit}) required to dislodge a larva and 30 s for the time (t_a) required for the larva to anchor itself. slower than the within-reef velocities we were able to measure.

Hydrodynamic forces on a larva sitting on a surface in a coral reef exposed to turbulent currents or waves fluctuate rapidly with time, with peaks occurring during bursting and sweeping events. The position on a reef where a larva lands can have a big effect on the instantaneous hydrodynamic forces it experiences. Not only are maximum forces on larvae at the top of the reef about three times greater than they are just 5 cm below the top of the reef (both in waves and in unidirectional flow), but the frequency at which large forces occur is much higher at the top of the reef than within the reef. Therefore, larvae must be able to attach to surfaces quickly as well as strongly to recruit to the top of a coral reef. Conversely, larvae with low adhesive strengths and larvae that attach themselves to surfaces slowly would be more likely to settle on surfaces within a reef that are shielded from rapid water movement, as suggested by Koehl and Hadfield (2004).

Larval settlement vs. adult location of motile animals— Phestilla sibogae is an example of the many species of motile benthic animals that move around within their habitat but disperse to new sites via planktonic larvae. For such animals, the position within a site at which a larva settles does not determine the location of the juveniles and adults, which can crawl or walk to other locations in the habitat. However, constraints on where larvae can successfully attach to surfaces during settlement can limit the sites that can be colonized by larvae. For example, *P. sibogae* would be unable to settle into a habitat exposed to waves if there were not microhabitats within that site that provided refuges from rapid water motion.

Effects of waves on hydrodynamic forces on larvae—Most shallow coastal areas are exposed to waves, which affect flow along the substratum at depths roughly $\leq 0.5\lambda$, where λ is the crest-to-crest distance between successive waves. In contrast, deeper habitats and sites sheltered from waves experience unidirectional water currents. We found that maximum hydrodynamic forces on larvae on surfaces on the top of and within coral reefs are about 10 times higher in waves than they are in unidirectional flow with a similar U_{rms} . Furthermore, high instantaneous forces occur more often in waves than in unidirectional flow. Although organisms in waves experience higher accelerations, and thus greater acceleration reaction forces (a.r.), than do organisms in unidirectional currents, microscopic larvae are so small that drag is much larger in magnitude than *a.r.* Therefore, the large difference between peak forces on microscopic benthic organisms in waves versus in unidirectional currents is due to the higher instantaneous velocities (and hence higher drag forces) that occur in waves, rather than to the greater accelerations in waves.

Models of larval transport to the benthos by Eckman (1990) and Gross et al. (1992) showed that increasing turbulence raises the rate of larval transport to the substratum. However, Crimaldi et al. (2002) found that the decrease in anchoring probability caused by high turbulence has a larger effect on overall settlement success

than does the increase in larval transport to substratum due to turbulent mixing. Therefore, even though larval transport to coral surfaces should be larger in wave-dominated flow than in less turbulent unidirectional currents, the flow forces imposed on the settling larvae should reduce settlement (i.e., attachment) rates in wave-dominated flows. Thus, the ability of larvae of *P. sibogae* to land on sheltered surfaces within a reef should drastically enhance their probability of settlement success on *Porites compressa* coral in wave-dominated environments.

Factors affecting the probability of larval attachment— We found that the probability of settlement by the larvae of *Phestilla sibogae* was greater in microhabitats within a reef than at the top of the reef. Although the recruitment of *P. sibogae* into coral reefs has been measured (Hadfield et al. 2007), the fine-scale distribution of newly settled larvae (which are microscopic and cryptically colored, and thus cannot be seen within a complex coral reef in the field) has not been reported. However, many other species of larvae settle in crevices and depressions (Koehl 2007), where flow velocities are likely to be low. It has been suggested that larvae with weak adhesive strength settle in such areas of low hydrodynamic stress (Wethey 1986; Howell and Behrend 2006).

We found that the faster a larva can stick itself to a surface, and the greater the strength of its adhesion to the surface, the higher the probability of successful settlement (Fig. 9). Some kinds of larvae increase their adhesive strength with time after landing on a surface (e.g., barnacles, Eckman et al. 1990; *P. sibogae*, Koehl and Hadfield 2004). Crimaldi et al. (2002) found that the ability of larvae to anchor quickly after landing in a clam bed exposed to turbulent unidirectional flow is extremely important to their probability of settlement. Similarly, Eckman et al. (1990) suggested that barnacle larval detachment was linked to when large-amplitude, intermittent bursts of high shear occurred after a larva settled.

The behavior of larvae after they contact a surface can affect where they ultimately settle (Abelson and Denny 1997; Koehl 2007). How long a larva can explore a surface before attaching to it depends on the length of the interval between pulses of hydrodynamic stress large enough to wash it away. Our calculations of settlement probabilities for larvae of *P. sibogae* (Fig. 9) suggest that they have only 1–10 s on top of the reef, but longer within the reef. Larvae of P. sibogae are induced to cease swimming (Hadfield and Koehl 2004) and to adhere to surfaces (Koehl and Hadfield 2004) by a dissolved chemical cue released by the prey of benthic P. sibogae slugs, the coral Porites compressa. Cue concentrations in the water in the interstices within *P*. compressa reefs, and in the water up to 10 cm above the reefs, are high enough to induce competent larvae to sink and stick to surfaces (Hadfield and Koehl 2004; Koehl and Hadfield 2004). Thus, many of the larvae that are washed off surfaces at the top of a reef may well keep sinking into the spaces within the reef where they are likely to land on surfaces exposed to lower, less frequent events that could dislodge them. Furthermore, field experiments measuring where larval mimic particles (particles that sink at the same

rate as *Phestilla sibogae* larvae) first contacted reef surfaces showed that more mimics first bumped into surfaces within the reef than at the top of the reef (Hadfield et al. 2007).

A larva of *P. sibogae* probably sticks to surfaces using mucus secreted by its foot. When larvae of P. sibogae become competent, they develop a propodial mucus gland (Bonar 1974), and when settled larvae are being dislodged from a surface by flowing water, a layer of clear, deformable material that looks like mucus can be observed connecting the foot to the surface (Koehl and Hadfield 2004). The drag on a *P. sibogae* larva tending to push it downstream shears the mucus between the larva's foot and the substratum. When mucus is sheared, it behaves like an elastic solid until the shear stress (force per unit area of its foot) exceeds its "yield stress," after which the mucus flows like a viscous liquid. If the stress is removed, the mucus "heals" back to a solid, and the longer the healing period, the higher the yield stress when the mucus is sheared again (Denny 1984). If we assume that *P. sibogae* larval mucus has a similar yield stress to that of the hydrated mucus of terrestrial slugs (~ 22 N m⁻² for high strain rates; Denny 1984), and if we assume that the foot of a *P. sibogae* larva is circular with a radius of 100 μ m, then a hydrodynamic force of about 0.66 μ N should cause the mucus under the foot of a larva to vield and flow. Comparison of this value with the forces experienced by larvae at different positions on a reef (Fig. 8B) suggests that larvae of P. sibogae are unlikely to stick to the top of a reef, but should be able to settle on surfaces within a reef. This prediction is consistent with the results of our calculations of settlement probabilities for larvae of *P. sibogae* at different heights in a reef (Fig. 9).

Finally, we should point out that our conclusions probably tend to underestimate the probability of recruitment success. This is because our measurements of the adhesive strength of larvae of P. sibogae exposed to steady flow may have underestimated the tenacity of their attachment when exposed to short bursts of high water velocity followed by intervals of slow flow. When larvae of *P. sibogae* are exposed to a steady water current fast enough to detach them from the substratum, first the foot of the larva separates from the surface but the larva remains tethered to the surface by a transparent thread (probably mucus), which then stretches and eventually breaks (Koehl and Hadfield 2004). However, in the turbulent, wave-dominated water flow typical of the reef sites where P. sibogae larvae land in the field, high forces on larvae are intermittent and very brief. While the mucus might not have time to yield and flow if exposed to very brief forces, it can heal back into a solid during the lulls between the short pulses of high force. Thus, mucus that vields, flows, and breaks when subjected to a steady shear stress (as in flow cell measurements of adhesive strength; Koehl and Hadfield 2004) might not fail if the same stress were applied as a series of brief pulses interspersed with intervals of very low or no stress (as occurs in nature). Furthermore, the mucus gluing a larva to the substratum is likely to be stronger (i.e., have a higher yield stress) for larvae at positions within a reef where the lulls between high forces are of long duration than for larvae on the top

of the reef, where the time for the mucus to heal between force pulses is short.

Our results illustrate how brief bursts of high velocity a few hundred micrometers from surfaces can determine the settlement success of larvae in different microhabitats within a complex benthic environment like a coral reef. We also found that waves, which commonly occur in shallow coastal sites, can have a profound effect on the settlement or resuspension of microscopic organisms on the substratum.

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