Turbulent Transport of Larvae near Wave-Swept Rocky Shores: Does Water Motion Overwhelm Larval Sinking?

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ABSTRACT We investigated the potential role that the vertical motion of marine larvae through the water (via sinking or swimming) might play in their dispersal on spatial scales of meters near wave-swept rocky shores. Field releases of particles of different sinking velocities as models of larvae and of dye to track water mixing and transport showed that dilution rates of larvae and dye were similar and that they traveled together across the habitat. Our data suggest that larval vertical motion is overwhelmed by turbulent mixing near wave-beaten shores. Although instantaneous water velocities at wave-swept sites can be quite high (meters per second), the rates of horizontal transport of water and particles across such habitats are much slower (tenths of meters per second).

Introduction

Larval Transport by Moving Water

Benthic marine animals often depend on the water moving around them to disperse their larvae, as described in a number of reviews (e.g., Crisp, 1984; Norcross and Shaw, 1984; Scheltema, 1986; Butman, 1987; Young and Chia, 1987; Levin, 1990; Okubo, in press). Such larval dispersal can have important effects on the population dynamics of benthic species (e.g., Jackson, 1986; Possingham and Roughgarden, 1990) as well as on the gene flow between populations (e.g., Jackson, 1974; Burton and Feldman, 1982; Burton, 1983; Hedgecock, 1979, 1982; Palumbi, 1992). The supply of larvae is also an important factor affecting benthic community structure at some coastal sites (e.g., Bernstein and Jung, 1979; Connell, 1985; Gaines and Roughgarden, 1985; Roughgarden et al., 1987, 1988).

The role of water motion in transporting marine larvae has been investigated at small and large spatial scales. Small-scale water flow (millimeters to centimeters) near the substratum has been shown to affect where larvae settle (e.g., Crisp, 1955; Eckman, 1983, 1987; Hannan, 1984; Butman, 1987), although active substratum selection by settling larvae in flowing water can also play an important role at these small scales (Butman, 1987; Butman et al., 1988; Pawlik et al., 1991). Water flow on larger scales (e.g., internal waves and fronts on spatial scales of tens of meters to kilometers) can be responsible for cross-shelf transport of larvae (Zeldis and Jillet, 1982; Shanks, 1983, 1986; Kingsford and Choat, 1986; Pineda, 1991). Coastal circulation (on spatial scales of one to tens of kilometers) determines the regional distributions of various organisms with planktonic larvae and their retention in bays and estuaries (e.g., Wood and Hargis, 1971;

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Rothlisberg, 1982; Cronin and Forward, 1982; Sulkin and van Heukelem, 1982; DeWolf, 1983; Rothlisberg et al., 1983; Levin, 1983; Tegner and Butler, 1985; Emlet, 1986; Johnson et al., 1986; Roughgarden et al., 1987, 1988; Boicourt, 1988). On very large spatial scales, oceanic currents can affect the global distributions of species with long-lived larvae (e.g., Scheltema, 1971, 1975, 1986; Scheltema and Carlton, 1984).

Evidence for the importance of passive dispersal by moving water versus active substratum choice by larvae in determining spatial patterns of invertebrate settlement has been reviewed by Butman (1987) and Pawlik (1992). Butman (1987) suggested that hydrodynamic processes determine larval distributions on large spatial scales (tens of meters to tens of kilometers), whereas active larval behavior can also play a role at small scales (centimeters to meters) near the substratum.`

In spite of this wealth of information about hydrodynamic effects on larval dispersal, relatively little is known about the role of water motion in near-shore environments on the spatial scale of meters (0.1–10 m). This scale of water motion provides the transport between the small-scale near-substratum flow and the larger-scale circulation patterns whose effects on larval distributions have been studied already. In spite of the extensive use of rocky-shore communities for basic ecological research, transport on the scale of meters for organisms on wave-swept rocky shores is poorly understood. Furthermore, even physical studies of mechanisms of mass transport in the ocean, such as dispersal of pollutants (e.g., Myers and Harding, 1983) or transport of beach sand (e.g., Bascom, 1980; Basco, 1983), have not focused on the spatial scale of meters near wave-beaten rocks.

## Transport of Water and Larvae near Wave-Swept Shores

It is not surprising that water transport on the spatial scale of meters has not been studied for wave-swept rocky shores: water flow at such sites is complicated by the interaction of waves, tidal currents, and complex topography (e.g., Koehl, 1977, 1982, 1984, 1986; Denny, 1988), and waves crashing onto rocks provide a very hostile environment for instrumentation such as current meters or drifters.

One straightforward way of measuring the movement of water and waterborne materials (e.g., dissolved substances, particles, larvae) in challenging environments is by tracking water labeled with dye (e.g., Pritchard and Carpenter, 1960; Okubo, 1971; Riempa, 1985). A patch of water in the ocean (and the materials it carries) can translate and rotate with respect to the substratum (Fig. 20.1a); the patch can also mix with the surrounding water (thereby expanding while becoming more dilute). The rate of horizontal movement of the center of mass of the patch of water is commonly called "advection" by oceanographers. The spread of the patch as it mixes with the adjacent water is called "diffusion," or "turbulent diffusion" (this mixing of the water by turbulent eddies should not be confused with molecular diffusion, due to the random thermal motion of molecules, which is a much slower process).

We have developed a simple dye-tracking technique that can be used to measure such advection and turbulent mixing in the field on the spatial scale of meters (Koehl et al., 1987, 1988, 1993). Although our technique permits us to quantify the transport of dissolved substances carried by the water, we must determine for each habitat whether the transport of dye can provide information about the transport of larvae, which may sink or swim through the water.

It is generally thought that larval swimming is too weak to overcome horizontal currents directly, but that the vertical swimming or sinking of larvae can affect their horizontal transport indirectly by moving them into layers of the water column traveling in different directions or
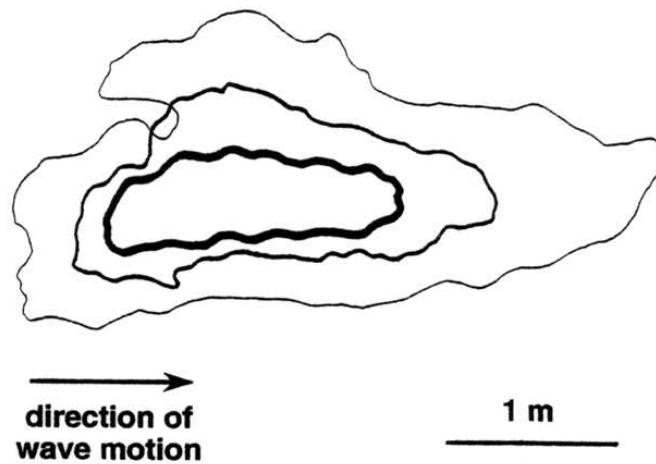
A.

ΔS_n

σ^2_A

σ^2_B

t_{n-1} t_n

B.

→
**direction of
wave motion**

1 m
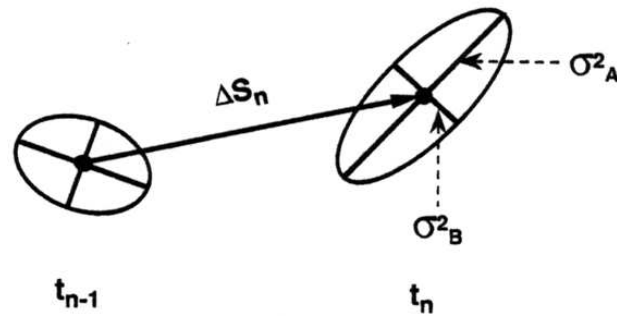
FIGURE 20.1. The fate of patches of waterborne material, such as dye. a. Simplified diagram of a patch at two successive times, t_{n-1} and t_n. The centroid of the patch is indicated by the dot, and the distance the centroid traveled is Δs_n. The patch has rotated; hence its spread is indicated by the eigenvalues of the first (σ^2_A) and the second (σ^2_B) principal component axes, as described in the text. b. Tracings of the perimeter of an actual dye patch at 2-s intervals (indicated by successively thinner lines) in the surge channel on a calm day (6 August 1989). Expansion of the patch was greatest along the axis of the oscillating flow in the channel, and the patch advected slowly in the direction of wave motion (from left to right in this diagram).

speeds (reviewed in Mileikovsky, 1973; Crisp, 1984; Chia et al., 1984; Young and Chia, 1987; Pawlik, 1992). The speed of sinking and the direction and speed of larval swimming can change as they develop (reviewed by Chia et al., 1984; Young and Chia, 1987). A number of studies have shown that such ontogenetic changes in vertical swimming or sinking by larvae can determine whether they are retained in estuaries (e.g., Graham, 1972; Smith et al., 1978; Boicourt, 1988; Cronin and Forward, 1982; Sulkin and van Heukelem, 1982; Norcross and Shaw, 1984; Laprose and Dodson, 1989; Jacobson et al., 1990). Moreover, the vertical distribution of larvae in the water column can, under calm water conditions, affect the tidal height at which they settle (Grosberg, 1982).

On the other hand, the water motion on wave-swept shores is so rapid and turbulent that we might expect this flow to overwhelm any vertical motion of the larvae. In a well-stirred water column, turbulence is able to counteract the tendency of particles to settle (Csanady, 1983). Evidence that rocky, wave-swept sites are well mixed is provided by the observation that vertical mixing of dye released at the water surface is so rapid that dye concentrations near the bottom (2 m below) can equal those at the surface in a few seconds (Koehl et al., in press). Moreover, analysis

of the variation over depth of turbulent kinetic energy in the surf zone suggests strong vertical mixing due to large-scale turbulent vortices (Svendsen, 1987).

The purpose of this study was to determine whether the sinking or downward swimming of larvae in a wave-swept habitat can affect their horizontal dispersal on spatial scales of meters (the scale that determines whether they leave the neighborhood of their parents and enter the larger-scale flows whose effects on larval dispersal have already been studied). Another goal of this work was to assess whether the dispersal of dye is a reasonable tool for estimating the dispersal of particles or larvae in wave-swept habitats.

Materials and Methods

To study the dispersal of waterborne materials in waves, we conducted a series of experiments in which we released dye and particles into the habitat and then tracked their transport and dilution. Because of the technical difficulty of rearing and labeling enough larvae for such field studies, we used particles with different sinking speeds as models of larvae that are negatively buoyant or that swim downward.

Measurement of Particle Sinking Velocities

We chose several types of easily recognizable particles (poppy seeds, glitter [Craft House], and snapdragon seeds) that could be obtained in large quantities and that had sinking velocities similar to those of various marine larvae. We measured particle sinking speeds in sea water (salinity of 33‰) in a cylindrical glass container 16 cm in diameter. Measurements were made in a cold room at 10°C to mimic the temperature of the water at the field site where the particle release experiments were conducted (described below). A jar of each type of particle was well shaken, and then twenty particles were haphazardly picked out of the jar with forceps and placed in sea water. A Pasteur pipette was used to gently deposit a particle below the water surface in the large cylinder. The time for the particle to fall a distance of 5 cm through each of three successive marked intervals in the cylinder was measured to the nearest 0.1 s using a digital stopwatch. All particles had reached terminal velocity before sinking into the first interval, and the mean of the times to fall through the three intervals was used to calculate the sinking speed for each particle. Ten other particles of each type were selected as described above, and the longest dimension of each was measured to the nearest 0.01 mm using an ocular micrometer in a Wild dissecting microscope.

Field Releases of Particles and Fluorescein

All field measurements were made in a large surge channel on Tatoosh Island, Washington, in which the advection and turbulent diffusion were fairly typical of wave-swept rocky shores not subjected to strong unidirectional currents (e.g., Koehl et al., 1993). By confining our measurements to a single channel, ambient flow varied from one experiment to the next while all other parameters could be held constant (i.e., we essentially used that channel as a field version of laboratory wave tank). Water temperature, measured in the channel during each experiment, was 10°C. Experiments were conducted at times during the tidal cycle when water depth in the channel was 2–3 m. Six people ("samplers") were stationed at mapped positions along the south and north shores of the channel.

A mixture of concentrated dye and particles was prepared by placing 55 ml each of dry poppy seeds, glitter, and snapdragon seeds into a can attached to the end of a wooden handle (2 m long) and then adding 220 ml of a solution of fluorescein in sea water (30 g/l of seawater freshly collected from the surge channel); this mixture was stirred until the air bubbles were removed. The

can was lowered below the water surface at a defined position in the surge channel (the "zero position," which was one of the six sampling positions mentioned above). The can was then turned over to release its contents and was gently pulled out of the water. A digital stopwatch was started at the instant that the can was turned over, and a signal was called out to the six samplers at 60, 150, 240, 330, and 420 s after dye release. Only one such release was performed per day to assure that dye and particles from earlier experiments had been cleared from the channel. (Indeed, we found that samples of water taken from the channel before each experiment contained no seeds, glitter, or measurable dye.) Experiments were performed on five different days during August and September 1989 to cover a variety of wave and tidal conditions.

Each sampler was equipped with six nets and a wooden handle (2 m long) to which each net could be attached. The sampling nets were small plankton nets (mouth diameter 20 cm, length 50 cm, mesh size 345 μm), each with a 15-ml screw-cap test tube at the downstream end. During each experiment, samples were taken at each of the six positions in the channel at each of the times listed above, and a sample was also taken at the zero position before the mixture of particles and dye was released. A net on the end of the handle was pushed through the water just below the surface for a distance of 2 m; hence the volume of water sampled was about 6.3×10^{-2} m^3. Samples were taken between waves to minimize the effects of ambient flow on the volume of water processed during a sweep of the net; nets were pushed in the opposite direction from the direction of wave movement. After each sample was taken, a cap was immediately put on the test tube, and the net was removed from the handle and rolled up so that no particles could be lost.

At the end of each experiment, all the particles in each net were washed into a paper filter (Mr. Coffee, 8–12 cup size) supported by a wire strainer. A glass grid was laid over each filter, and all the poppy seeds, glitter, and snapdragon seeds on the filter were counted. The test tubes were removed from the nets and stored in the dark until the concentration of fluorescein in the water samples was measured using a Perkin-Elmer Fluorescence Spectrophotometer 204 Å (emission wavelength was 495 nm, excitation wavelength was 513 nm, and both emission and excitation bandpass widths were 10 nm). Any particles in the test tubes were counted and removed before a water sample was put in the spectrophotometer. Samples of water collected from the surge channel before the dye release were used as the blanks for each experiment.

Quantification of Advection and Turbulent Diffusion

We measured advection and turbulent diffusion of the water in the surge channel (on spatial scales of meters to tens of meters) during the particle and fluorescein release experiments described above using the photographic technique reported by Koehl et al. (1993). The expanding blob of fluorescein was photographed at timed intervals from a fixed position on the cliff above the channel. The angle of the camera with the horizontal was measured using a line level and protractor (the camera remained unmoved during the sequence of photographs). The photographs of the dye blobs were projected onto a digitizing tablet (Jandel), the perimeter of each successive blob was traced, and the camera angle was used to correct the coordinates of each point within the blob for parallax (Fig. 20.1b). By making the simplifying assumption that the dye was evenly dispersed within the blob, we calculated the position of the centroid of the blob at each time (t_1, t_2, . . . , t_n). If Δs_n is the distance the centroid has traveled in the nth time interval (i.e., between t_{n-1} and t_n), then the advective speed (U_n) for the nth time interval is calculated as:

$$U_n = (\Delta s_n)/(t_n - t_{n-1})$$
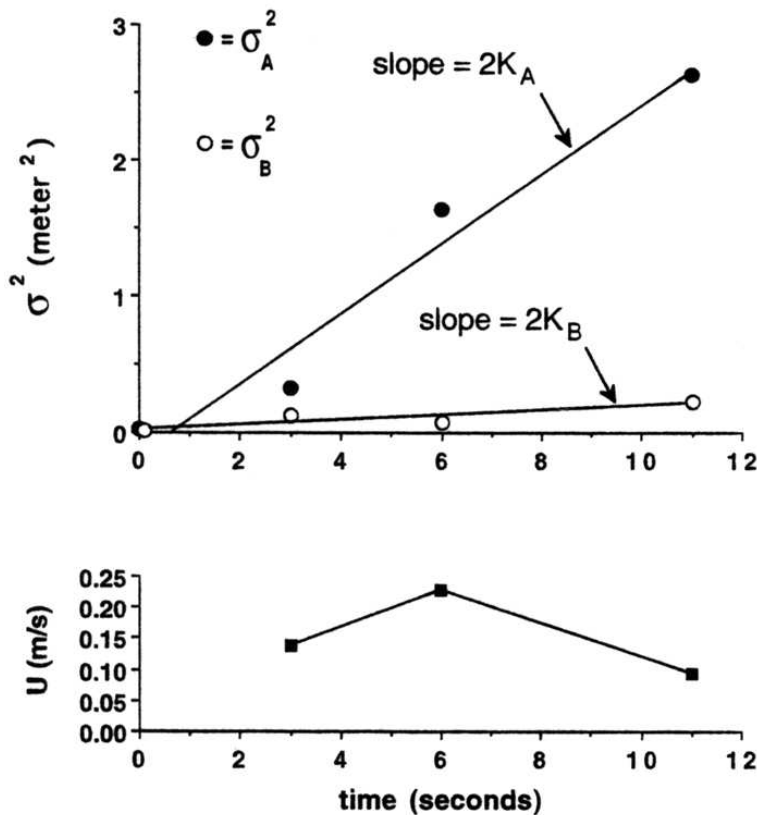
as illustrated in Figure 20.1a.

FIGURE 20.2. Example of measurements of mass transport in a surge channel on Tatoosh Island, Washington, using the dye-tracking technique described in the text. The upper graph shows the eigenvalues, σ_A^2 and σ_B^2 (measures of spread of the patch) along the first (dark circles) and second (open circles) principal axes of the dye patch, plotted as functions of time. The lines represent the least-squares, best-fit, straight lines (i.e., linear regressions) calculated through these points. One-half of the slope of such a regression gives the overall diffusivity (K): K_A is the mixing coefficient along the axis of greatest spread of the dye blob, and K_B is the mixing coefficient along the axis perpendicular to the direction of greatest spread. The lower graph shows the speed of advection (U) of the centroid of the patch, plotted as a function of time.

Each dye blob not only spread, but also might have rotated about its centroid (Fig. 20.1a). If we had calculated the rate of spread of the blob with respect to fixed (i.e., non-rotating) axes, then the effects due to expansion could not have been separated from those due to rotation. Therefore, we removed the effect of rotation by using principal component analysis (PCA; e.g., Chatfield and Collins, 1980; Preisendorfer, 1988) to calculate the spread along the two principal axes of the blob. The first principal axis, which we denoted by A, was the direction of greatest spread; the second principal axis, B, was perpendicular to the first. Using the terminology of PCA, the eigenvalues associated with these two directions (i.e., the principal axes) measured the variance (i.e., the spread) along these two axes. We call these two eigenvalues σ_A^2 and σ_B^2; σ_A is a statistical measure of the linear dimension of the blob along its direction of greatest spread, and σ_B is that for the perpendicular direction. We determined overall mixing coefficients (K_A and K_B) for the entire sequence of photographs of a dye blob by calculating linear regressions for plots of σ_A^2 and σ_B^2 versus time (Fig. 20.2); the slopes of these regression lines equal $2K_A$ and $2K_B$, respectively (Okubo, 1980; Koehl et al., 1993).

Results and Discussion
Sinking Rates of Particles

The sinking rates and sizes of the particles we used are given in Table 20.1, where examples of types of larvae that sink or swim at similar speeds are listed.

Table 20.1. Particle sizes and sinking rates, along with larvae with similar speeds

Particle	Width (S.D.) (N = 10) (mm)	Sinking speed (S.D.) (N = 20) (cm · s⁻¹)	Larvae with similar speeds[a]	
			Sinking	Swimming[b]
Poppy seed	1.4(0.11)	1.2(0.29)	Crab zoea	Crab zoea (d,h,u)
				Ascidian tadpole
Glitter	1.1(0.07)	1.1(0.13)	Crab zoea	Crab zoea (h)
				Ascidian tadpole
				Sponge amphiblastula (h)
			Bivalve veliger	Bivalve veliger
Snapdragon seed	1.0(0.11)	0.3(0.47)	Coral planula	Coral planula (h,u)
			Bivalve veliger	Bivalve veliger (u)
				Annelid trochophore
			Barnacle cypris	Barnacle nauplius (h,u)
			Crab zoea	Crab zoea (d,h,u)
			Crab megalopa	Crab megalopa
				Lobster phyllosoma (d,u)
				Bryozoan cyphonautes
				Ascidian tadpole

[a]From Chia et al. (1984), who review speed data for particular species.
[b]With direction of swimming indicated (if reported): d = down, h = horizontal, u = up.

Concentrations of Particles and Fluorescein

We released and collected particles and fluorescein near the water surface. If particles had been sinking out of the surface water, we would expect their concentrations in our samples to decrease at a greater rate than that of the dye. In contrast, if the vertical motion of the particles was overwhelmed by the turbulent mixing of the water in the surge channel, we would expect the dye and the particles to be diluted at the same rate by this mixing, and we would expect particles and dye to travel together horizontally.

An example of the changes in concentration (C) of particles and fluorescein at one of the positions in the surge channel is illustrated in Figure 20.3. Both particles and dye showed exponential rates of loss at each position:

$$C_t/C_0 = e^{\lambda t}$$

where C_t is the concentration at time t, C_0 is the highest concentration reached at that position, and λ is the slope of a linear regression of $\ln(C_t/C_0)$ as a function of time (Fig. 20.3), starting at the time when C_0 was measured. We compared the λ's (decay, or loss constants) of the different particles and the dye; we considered that these slopes were significantly different from each other if their 95 percent confidence intervals did not overlap. We only compared loss rates of the different materials within a position on a single day. In seventy of the seventy-five comparisons we made, we found no significant differences between the loss rates of particles with different sinking speeds, or between the particles and the dye. (Note that 95 percent confidence limits imply that, out of seventy-five comparisons selected at random, four should show disagreement simply by chance alone.) Furthermore, in the few cases where the loss rates of certain materials did differ from each other, there was no pattern in the types of materials that showed different λ's, or in the sites or days on which the differences occurred. Therefore, we conclude that there was no
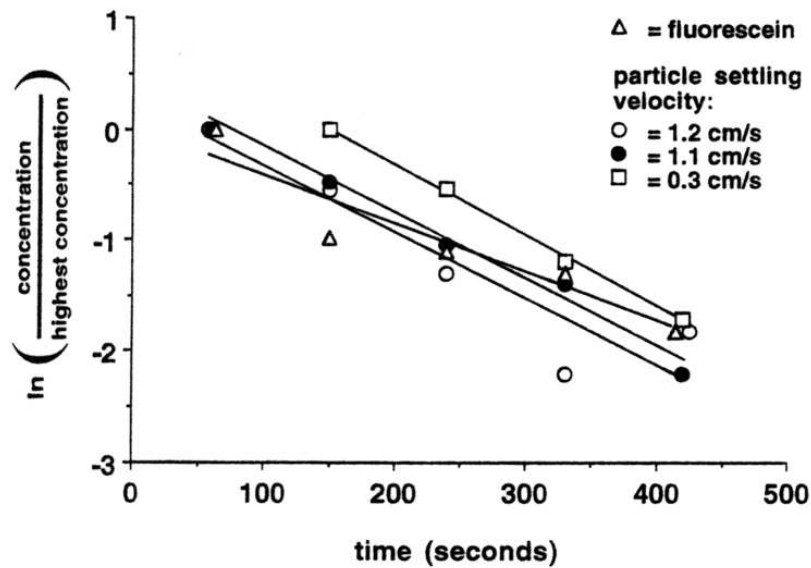
FIGURE 20.3. Plot of the natural log (ln) of the concentration of waterborne material as a function of time at one of the positions (4.5 m from the release point) on 18 August 1989. The concentrations of the particles are given in number per cubic meter of water, whereas the concentration of fluorescein is given in milligrams per cubic meter; all the concentrations are normalized by dividing them by their highest concentration on that day at that position in the channel. The lines represent linear regressions for each type of material (fluorescein: $r^2 = 0.88$, $\lambda = -0.0044$ s^{-1}, 95 percent confidence interval = 0.0019; poppy seeds (settling velocity = 1.2 cm·s^{-1}): $r^2 = 0.85$, $\lambda = -0.0059$ s^{-1}, 95 percent confidence interval = 0.0028; glitter (1.1 cm·s^{-1}): $r^2 = 0.98$, $\lambda = -0.0059$ s^{-1}, 95 percent confidence interval = 0.0010; snapdragon seeds (0.3 cm·s^{-1}): $r^2 = 0.92$, $\lambda = -0.0065$ s^{-1}, 95 percent confidence interval = 0.0004).

systematic statistical difference in the loss rates of the dye and of the different types of particles.

An example of how particle and fluorescein concentrations varied spatially with time is given in Figure 20.4. Such plots indicate that the dyed patch of water and the particles traveled together across the habitat. These observations, coupled with the similarity of the λ's for dye and particles, suggest that tracking dye blobs should give a reasonable measure of the transport of particles or larvae at turbulent, wave-swept habitats such as our surge channel. These results also suggest that the vertical motion of larvae does not play an important role in their transport on the scale of meters near wave-exposed rocky shores where turbulent mixing is great enough to overwhelm larval motion. This contrasts with the important role that vertical swimming or sinking can play in larval transport in less turbulent waters and with the important role that larval behavior can play at the smaller scale of settlement events, as discussed in the Introduction.

Advection and Turbulent Diffusion

We quantified the transport of water in the wave-swept surge channel by measuring the dispersal of patches of dye. Figure 20.1b illustrates an example of the spread and the horizontal translation of a blob of dye, and Figure 20.2 shows how σ^2 (spread) and U (advective velocity) varied with time. Mixing coefficients (K_A and K_B) and advective velocities for each of our experiments are listed in Table 20.2.

The advective velocities we measured were much lower than the instantaneous water velocities in surge channels on Tatoosh (which often exceed 5 m·s^{-1}; Koehl, 1977, 1984). We have observed this phenomenon at other wave-swept sites as well (Koehl et al., 1987, 1988, 1993). Such slow advection is not surprising if we consider that water oscillates back and forth as a wave shape moves across the habitat (e.g., Bascom 1980; Koehl, 1984, 1986; Denny, 1988), while there is some net pumping of water in the direction of wave motion (i.e., Stokes drift; see
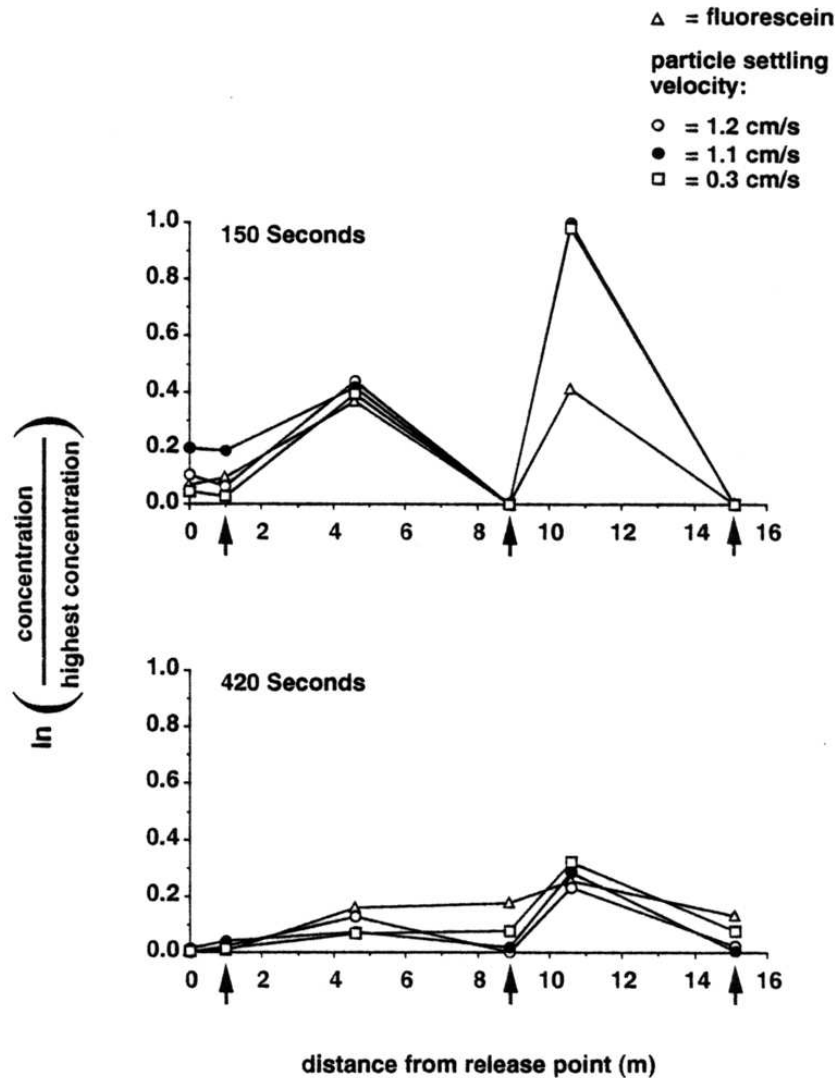
FIGURE 20.4. Plot of the concentration of particles (number per cubic meter) and fluorescein (milligrams per cubic meter) at different positions in the surge channel at 150 s (upper graph) and 420 s (lower graph) after the mixture of fluorescein and particles was released on 18 August 1989. All the concentrations have been normalized by dividing them by their highest concentration on that day. The dye and particles were released from a position (0 m) on one side of the channel; positions indicated by arrows were along the opposite side of the channel from that release point. Note that material was initially (150 s) transported along one side of the channel, but eventually (420 s) mixed over to the opposite side. (Although the highest concentrations of dye and particles at the 150 s sampling time all co-occurred at the 10.5-m position (indicating that they were traveling together), the relative concentration of dye was lower there than were the relative concentrations of the particles. Since only one sample per position could be taken at each time, we do not know the uncertainty of these concentration measurements and hence cannot evaluate whether this difference was significant. Furthermore, we observed no consistent pattern in our 150 samples as to which type of material showed higher or lower concentrations at particular positions.)

LeMehaute, 1976). Therefore, although wave-swept habitats appear to be characterized by rapid water movement, this impression is quite misleading when considering the net transport of material in such environments.

Our dye patch data in this and in previous studies (Koehl et al., 1987, 1988, 1993) also revealed that mixing in shallow wave-swept habitats was not isotropic. As illustrated in Figure 20.2, the mixing coefficient (K_A) in the direction parallel to the axis of the oscillatory water flow in the channel was much greater than the mixing coefficient (K_B) at right angles to this. One mechanism responsible for this anisotropy is probably shear dispersion (as explained in, e.g., Bowden, 1965; Okubo, 1968, 1980; Koehl et al., 1993).

Table 20.2 Mixing coefficients and advective velocity for experimental conditions

Date (conditions)	Mean loss constant, λ (s^{-1})	(range of λ's)[a] (s^{-1})	Mixing coefficient (m$^2 \cdot$ s^{-1}) K_A	K_B	Advective velocity, U (m $\cdot$ s^{-1})
8/17/89 (Calm; slack high tide)	−0.010	(−0.002 to −0.022)	0.05	0.02	0.11
8/18/89 (Moderate waves; flooding tide)	−0.007	(−0.003 to −0.013)	0.13	0.01	0.15
9/14/89 (Big waves; ebbing tide)	−0.010	(−0.004 to −0.020)	[b]	[b]	[b]
9/15/89 (Big waves; ebbing tide)	−0.007	(−0.002 to −0.013)	0.15	0.02	0.19
9/16/89 (Calm; flooding tide)	−0.009	(−0.004 to −0.020)	0.05	0.01	0.11

[a]Data for fluorescein and particles at all six sampling sites summarized.
[b]No data due to camera malfunction.

Summary

Flowing water plays an important role in the dispersal of the larvae of benthic animals. The effects of small-scale near-substratum flow and of larger-scale circulation patterns on larval dispersal have been well studied, but water motion on the spatial scale of meters to tens of meters, which provides the transport between these two flow regimes, is less well understood. We have developed a simple dye-tracking technique to quantify water transport at this spatial scale and have used it to characterize the flow at wave-swept rocky shores, where we found advection velocities to be an order of magnitude lower than instantaneous water velocities in waves. By comparing the transport of dye with that of particles of different sinking velocities (which mimic those of various larvae), we ascertained that tracking dye should give a reasonable measure of the transport of larvae at wave-exposed shores. Our data also suggest that the vertical motion of larvae does not play an important role in their transport on spatial scales of meters near wave-swept shores where turbulent mixing is great enough to overwhelm larval motion.

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