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MEASURING THE FATE OF PATCHES IN THE WATER: LARVAL DISPERSAL

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INTRODUCTION

The aquatic contributions to this volume have focused on the dynamics of either patches on the substratum (benthic communities) or patches in the water column (pelagic communities). This contribution couples these two foci, exploring the importance to benthic organisms of the dynamics of patches in the water. We will outline benthic processes that depend on the transport of materials in the water column. We will describe an empirical technique for quantifying the mixing and transport of patches in nature, and will present some examples of our measurements for wave-swept rocky shores (habitats important in ecological research but difficult to study hydrodynamically). Then we will discuss how future modeling efforts might incorporate these findings.

IMPORTANCE OF THE DYNAMICS OF PATCHES IN THE WATER COLUMN TO BENTHIC ORGANISMS

Benthic organisms often depend on the water moving around them for the transport to their vicinity of dissolved substances (e.g. gases, nutrients) and particulate food, for the removal of wastes, for the transport of gametes (of spawners), and for the dispersal and subsequent return to the shore of propagules (e.g., planktonic larvae, spores). Therefore, if a patch of water is depleted of resources by a benthic organism, or is filled with larvae, gametes, or waste products released by the creature, the fate of that patch can have important consequences for the organism and its neighbors. Such mass transport for organisms on wave-swept rocky shores is poorly understood, in spite of the extensive use of rocky-shore communities for basic ecological research and of the role water movement can play in the ecologically important processes listed above.

Rather than address all of the above processes, let us focus on larval transport. A number of recent reviews of the topic are available (e.g., Norcross and Shaw 1984, Scheltema 1986, Levin 1990, Okubo 1992), so we only mention a few examples here. The supply of larvae is an important factor affecting benthic community structure in some coastal sites (e.g., Bernstein and Jung 1979, Connell 1985, Gaines and Roughgarden 1985, Roughgarden et al. 1987, 1988). Water movement can have important effects on the population dynamics of benthic species with planktonic larval stages, as described by, e.g., Jackson (1986) and Possingham and Roughgarden (1990). Moreover, the transport of larvae by moving water can have significant evolutionary consequences because it is an important determinant of gene flow between populations of marine organisms (e.g., Jackson 1974, Burton and Feldman 1982, Burton 1983, Hedgecock 1979, 1982; Hedgecock et al. 1982, Palumbi 1992). The relationship of larval dispersal to the evolution of life-history strategies of marine organisms has also been considered (e.g., Strathmann, 1974, 1980, 1985; Obrebski 1979; Jackson and Strathmann 1981; Palmer and Strathmann 1981; Jablonski and Lutz 1983).

The role of water motion in transporting marine larvae has been investigated over large and small spatial scales. The effects of oceanic currents on global distributions of species with long-lived larvae have been studied (e.g., Scheltema 1971, 1975, 1986; Scheltema and Carlton 1984). The consequences of coastal circulation (on spatial scales of one to tens of kilometers)

upon geographic distributions of various organisms with planktonic larvae and on their retention in bays and estuaries have also been investigated (e.g., Wood and Hargis 1971, Rothlisberg 1982, Cronin and Forward 1982, Sulkin and van Heukelem 1982, DeWolf 1983, Rothlisberg et al. 1983, Levin 1983, Tegner and Butler 1985, Bakun 1986, Emler 1986, Johnson et al. 1986, Roughgarden et al. 1987, 1988; Boicourt 1988). In addition, the role of internal waves and fronts in cross-shelf transport (spatial scale of tens of meters to kilometers) of larvae has also been considered (Zeldis and Jillett 1982, Shanks 1983, 1986; and Kingsford and Choat 1986). Moreover, water flow on very small spatial scales (mm's to cm's) has been shown to be important to larval settlement (e.g., Crisp 1955, Eckman 1983, 1987; Hannan 1984; Jumars and Nowell 1984; Nowell and Jumars 1984; Butman 1987; Pawlick 1991).

Water motion in nearshore environments on the spatial scale of meters (i.e., 0.1 m to 10 m) connects effects at large and small scales, providing the transport between the small-scale near-substratum flow and the larger-scale circulation patterns whose effects on larval distributions have been studied already. Nonetheless, mass transport on the meter scale along wave-swept rocky shores, and its consequences for larval transport, have received little attention from biologists. Similarly, 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.

It is not surprising that mass transport on the spatial scale of meters has not been studied for wave-swept rocky shores, in spite of the ecological importance of such habitats. 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 current meters, drifters, and other oceanographic instrumentation. We will present here a simple dye-tracking technique that can be used to measure mass transport in this challenging habitat.

TECHNIQUE FOR MEASURING MIXING AND MOVEMENT OF A PATCH OF WATER

All sufficiently small deformable bodies, including parcels of fluid, have only three possible modes of motion (Sommerfeld 1964). First, the body can translate (i.e. the center of mass of the body moves). Second, the body can rotate (e.g. about its center of mass), and third, the body can expand or contract in three mutually orthogonal directions. One can observe directly these three modes of motion in a fluid by labeling a parcel of the fluid with some marker, such as a visible dye like fluorescein, and recording the evolution of the "dye blob" with, for example, a sequence of photographs. The rate of horizontal movement of the center of mass of the fluid blob is commonly called advection by oceanographers and meteorologists. The rate of rotation of the fluid parcel is half its vorticity. The spread of the fluid parcel as it mixes with the adjacent environment is called diffusion -- in this case turbulent diffusion because the molecular processes causing diffusion are much smaller than the mixing effects of fluid turbulence. Such labeling with dye and quantitative tracking (say, via photography) has a venerable history in engineering and oceanography (e.g. Pritchard and Carpenter 1960, Okubo 1971) and provides information about fluid motion similar to that obtained from studies using instrumentation like drifters or current meters (e.g. Lemmin 1991). Note that the tracking of dye is not different in concept from the tracking of features on satellite images to obtain motions of fluid at much larger spatial scales (e.g. Emery et al. 1986, Strub and Powell 1987, and Tokmakian et al. 1990).

Advection, vorticity, and turbulent diffusion rates (on spatial scales of meters to tens of meters) can be measured using the photographic technique reported by Koehl et al. (1987, 1988). A volume of fluorescein dye is released at one instant into the water, and photographs of the dye are taken from a fixed reference point at timed intervals. Dye solution (made using water from the habitat) can be released via a port affixed to the substratum, by gentle pouring, or via rupture of a balloon containing dye; alternatively, a small amount of fluorescein powder can be released directly into the water. The expanding blob of dye is photographed at timed intervals with a camera mounted above the water's surface. The tripod on which the camera is

mounted is outfitted with shaft encoders that indicate the horizontal and vertical angles of the camera. These angles, as well as the time that each photograph is taken, are recorded on a laptop computer. [For those without such equipment, the angle of the camera with the horizontal can be measured using a line level and protractor (Fig. 1,A). The camera must remain unmoved during the sequence of photographs, and the times at which each photo are taken must be recorded by hand. The photographs should include a reference landmark, such as a rock or post, that does not move so that successive photographs can be superimposed.] A photograph must also be taken from each camera location of a size scale on the surface of the water.

The photographs of the dye blobs are projected onto a digitizing tablet and the perimeter of each successive blob is traced. The size scale, reference landmark, and camera angle data are used to correct the coordinates of each point in the blob for parallax (Figs. 1,B and 1,C). By making the simplifying assumption that the dye is evenly dispersed within the blob (see below), we calculate the position of the centroid of the blob at each time (t_1, t_2, \dots, t_n). If Δs_n is the distance the centroid has traveled in the n^{th} time interval (i.e., between t_{n-1} and t_n), then the advective speed (U_n) for the n^{th} time interval is calculated as:

$$U_n = (\Delta s_n) / (t_n - t_{n-1}) \quad (1)$$

as illustrated in Figure 2.

Using Figure 2 as a concrete example, we see that a blob not only spreads, but also rotates about its centroid. If one 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 be separated from those due to rotation. We need a measure of the rate of expansion of the blob that is not confounded by any rotations the blob may have undergone. One method of removing the effects of rotation is to calculate the spread about the two principal axes of the blob. The first principal axis, which we denote by "a", is the direction of greatest spread; the second principal axis, "b", is perpendicular to the first. The identification of principal axes of a solid is a common calculation in rigid body dynamics, described in all physics and engineering mechanics texts (e.g. Marion 1967). A simple and practical way to perform these calculations is to use principal component analysis (PCA; e.g. Chatfield and Collins 1980). The algorithms for PCA are widely available in statistical packages for personal computers. Preisendorfer (1988, Chapter 2) presents a very

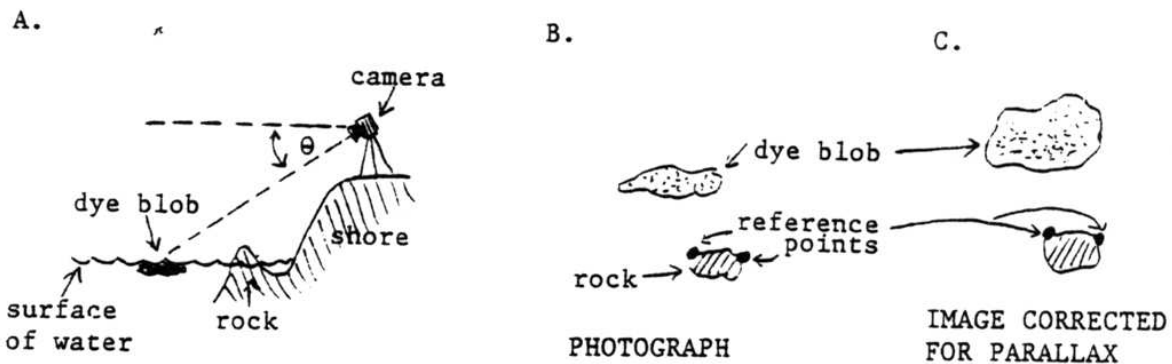


Figure 1. A. Diagram of a camera on the shore used to photograph a blob of dye in the water. The angle between the line of view of the camera and the horizontal (θ) is used in calculating the corrections for parallax. B. Diagram of the photograph taken by the camera in A. Points fixed with respect to the shore (indicated by black dots) are used to align photographs of the same blob taken at later times. C. Diagram of the blob shown in B after correction for parallax.

clear discussion of the use of the technique in a simple two-dimensional problem like the one we consider here, and his results can be readily adapted to our dye blob calculation. Using the terminology of PCA, the eigenvalues associated with these two directions (i.e. the principal axes) measure 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 the best description (in a statistical sense) of the linear dimension of the blob along its direction of greatest spread, and σ_b is that for the perpendicular direction. We further define instantaneous diffusion coefficients (K , diffusivities) for the spread of dye along the first (K_a) and second (K_b) principal axes, respectively, by:

$$K_a = (1/2)d\sigma_a^2/dt \quad (2)$$

$$K_b = (1/2)d\sigma_b^2/dt.$$

In our data analysis we approximate the instantaneous time derivatives above with finite differences:

$$d\sigma^2/dt \approx (\sigma_n^2 - \sigma_{n-1}^2)/(t_n - t_{n-1}) \quad (3)$$

as illustrated in Fig. 3,C. In addition, we determine overall diffusivities (K_A and K_B) for the entire sequence of photographs for a dye blob by calculating linear regressions for plots of σ_a^2 and σ_b^2 versus time (Fig. 3,A). Note that K_a and K_b (or K_A and K_B) relate the flux of some quantity (in this case, dye) to the concentration gradients of that quantity (in this case, again, gradients in dye concentration). Symbolically, one expresses this relationship (called Fick's Law) by

$$F_a = K_a \partial C/\partial x_a \quad (4)$$

F_a is the flux of dye in the "a" direction (units of F_a : grams of dye per unit area per unit time), and C is the concentration of dye (units of C : grams of dye per unit volume). Note that the units of K_a are $(\text{length}^2)/(\text{time})$; see Okubo (1980, Chapter 2).

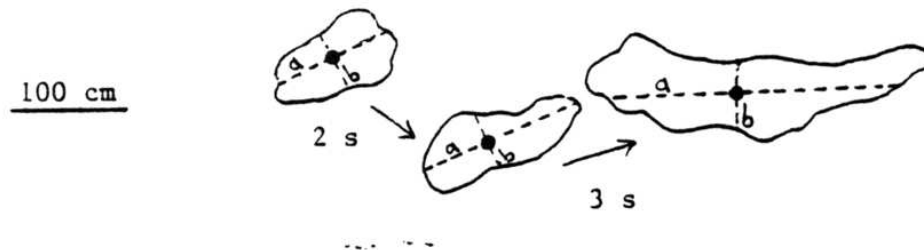


Figure 2. Tracings (corrected for parallax) of the perimeters of a dye patch at three successive times at Toad Point, Tatoosh Island, WA, a wave-swept rocky shore site. The time intervals between tracings are indicated next to the arrows between the tracings. The dark dots indicate the position of the centroid of the dye patch at each time, and the dashed lines indicate the first principal axis ("a", the longer line) and the second principal axis ("b", the shorter line perpendicular to "a" at each time). Note that the blob translates, expands, and rotates slightly.

Our description of the dye-tracking technique has been brief, and we cannot in the space allotted in this volume address all the methodological concerns a reader might have about the reliability of the approach. However, a few questions do demand at least cursory attention. First, the water flows in the rocky shore environments we have studied are decidedly three-dimensional, while the photographic dye-tracking technique gives only a two-dimensional view of the transport. By measuring the concentration of dye in water samples collected at various depths at the same times that photographs of dye blobs were taken, we found that vertical mixing of the dye was very rapid at a shallow site (depth = 1 to 2 m, at Hopkins Marine Station, Pacific Grove, CA; unpubl. data gathered in collaboration with M. Denny). There was no detectable difference between the dye concentrations near the surface and near the bottom within a few seconds of the time of dye release. Accordingly, the 2-D aerial views recorded via photography give a good description of the temporal evolution of the fully three-dimensional patch at such a shallow, wave-swept site. At deeper sites where vertical mixing is of concern, an anchored SCUBA diver or camera can photograph dye blobs from the side, thereby recording the vertical and (one direction of) the horizontal transport and spread of the blob. Such photographs can be analyzed using the technique described above, as we have done for some coral reef sites near Discovery Bay, Jamaica (Koehl and Jackson unpubl. data). A second concern about the dye-tracking technique is whether the transport of a dissolved substance (dye) is a good indicator of the transport of particles in the water, such as larvae, spores, or food. We have addressed this question by simultaneously releasing dye and particles of various sinking or rising velocities in a wave-swept surge channel on Tatoosh Island, WA. Concentrations of dye and particles in water samples taken at stations various distances (0 to 30 m) from the release point show that dye and particles travel together and that their rates of change of concentration at a point are indistinguishable. Hence, the movement of dye is a good marker for the passive movement of particles suspended in the water column, like larvae. At sites with more gentle water motion, however, the dye-tracking technique can only describe the transport of water and dissolved substances, but not that of organisms that sink, rise, or swim rapidly compared with the mixing and advection of the water. Finally, although we have mentioned the possible application of these techniques to calculation (and interpretation) of the changes in vorticity in the fluid as the patch evolves, we defer any discussion of this potentially interesting topic to later articles.

EXAMPLES OF MEASUREMENTS OF WATER TRANSPORT AT WAVE-SWEPT ROCKY SHORES

We have used the technique described above to measure advective transport and turbulent mixing at a variety of coastal sites. We will report here a few examples of our data for wave-swept rocky shores to illustrate the type of information about patch dynamics that can be obtained using this approach.

Figure 3 illustrates data gathered for one dye run in a wave-swept surge channel. Even though instantaneous water velocities in such surge channels can be high (often exceeding 5 m/s, Koehl 1977, 1984) advective velocities (U) are much lower (Fig. 3,B). The water motion in waves is orbital; even though the wave shape moves in one direction with respect to the substratum, a parcel of water moves in the direction of wave motion when in the wave crest, but in the opposite direction when in the wave trough (as described in e.g. Bascom 1980, Koehl 1984, 1986; Denny 1988). The flow over wave-swept rocks and in surge channels is also basically oscillatory when these environments are subjected to breaking waves, that is, water washes up the shore and then returns seaward (Koehl 1977). Although water moves back and forth, there is some net pumping of water in the direction of wave motion (Stokes drift, as described in e.g. LeMehaute 1976). Water motion at wave-swept shores is further complicated by flow oscillations of longer period, such as edge waves (e.g. LeBlond and Mysak 1978, Holman 1983) and tidal currents. A pattern develops of slow net movement of water towards, along, and away from the shore. Since the pattern of this water transport depends on local topography, the dye-tracking technique is a very useful tool for quantifying net water transport to and from particular sites where benthic ecology is being studied. Although the details of

water movement vary from one wave-swept site to another, a general conclusion we can draw from our dye studies is that advective velocities (U) are much lower than instantaneous water velocities. Therefore, although wave-swept habitats appear to be characterized by rapid water movement, this impression is very misleading when considering the net transport of material in such environments.

Our dye blob data also revealed that mixing in these shallow wave-swept habitats is not isotropic. As illustrated in Figure 3,A, the mixing coefficient (K_A) in the direction parallel to the direction of water flow is much greater than the mixing coefficient at right angles to this (K_B). The mechanism responsible for this anisotropy is most likely shear dispersion (for details see e.g. Bowden 1965; Okubo 1968; 1980). Friction with solid boundaries slows nearby water motion, hence velocity gradients (boundary layers) develop in the water between the substratum and the free-stream flow (for further discussion see e.g. Nowell and Jumars 1984). Figures 4,A and B illustrate how such shear in the water can lead to enhanced dispersion along the axis parallel to the freestream velocity. Similarly, pockets of slowly-moving water (e.g. trapped in pools, canopies of organisms, or other topographic irregularities characteristic of complex rocky shores) can also cause anisotropic mixing and slowed advection of patches of water-borne material, as diagrammed in Figures 4,C and D, and described by Okubo (1973).

Our dye studies at a variety of coastal sites have not only shown that assumptions of high transport and isotropic diffusion are not correct for wave-swept shores, but have also revealed that U and K for a particular spot are very sensitive to time in the tidal cycle and to weather (Koehl et al. 1987, 1988). In addition, we have found that U 's and K 's for different sites within the same kilometer stretch of shoreline can differ from each other by orders of magnitude due to the influence of local topography and macrophyte canopies (Koehl et al. 1987; 1988).

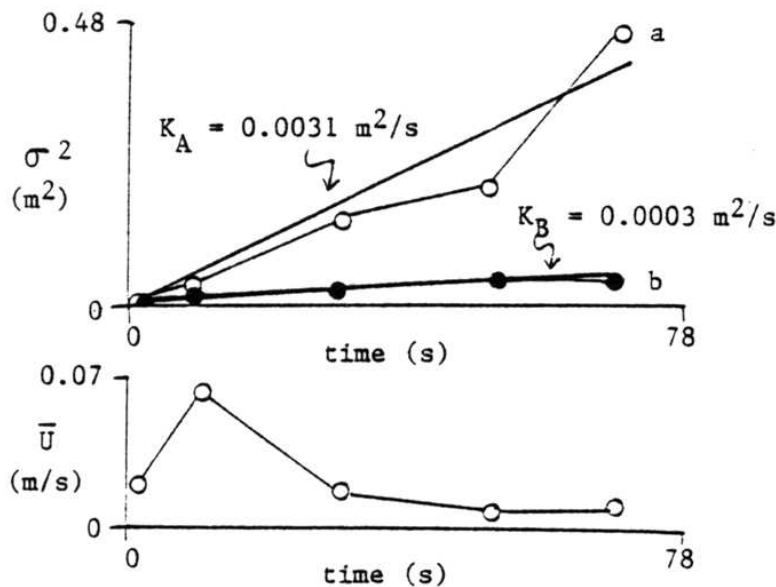


Figure 3. Example of measurements of mass transport in a surge channel on Tatoosh Island, WA, using the dye-tracking technique described in the text. A. The eigenvalues, σ_a^2 and σ_b^2 , (measures of spread of the patch) along the first (open circles) and second (dark circles) principal axes of the dye blob, plotted as functions of time. The straight lines represent the least-squares, best-fit, straight lines (i.e., linear regressions) calculated through these points. The slopes give the overall diffusivities (K_A and K_B) along the two principal axes (parallel to and perpendicular to the direction of greatest spread, respectively, of the blob). B. The speed of advection of the centroid of the blob, plotted as a function of time.

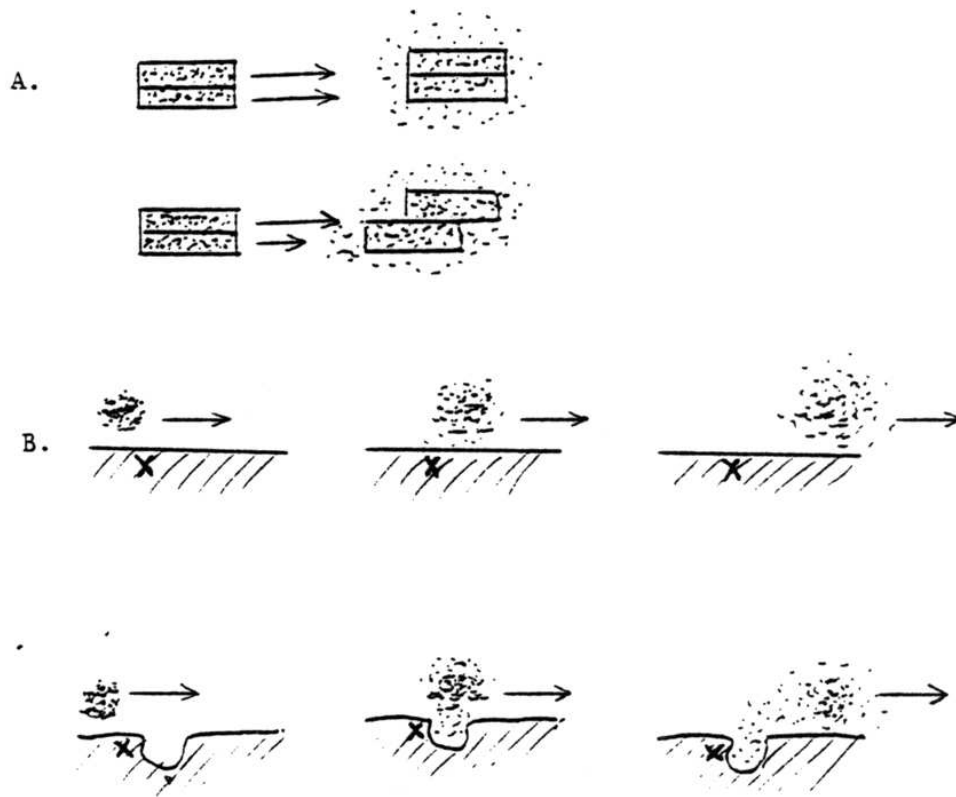


Figure 4. Diagrams of two mechanisms by which anisotropic spreading of a patch of water can occur near a shore. Both mechanisms result in slowed advection of the centroid of the patch because the rear end of the patch is retained for a longer time than it would be if there were no interaction of the patch with the substratum. A patch of water-borne material (e.g., dye molecules) is indicated by the dots, and the direction of the ambient current is indicated by the arrow. A. Diagram of two adjacent slabs of water (indicated by rectangles) whose positions at time 1 are shown on the left, and at time 2 on the right. The upper diagram illustrates adjacent layers of water between which there is no shear, whereas the lower diagram illustrates a layer of water moving more slowly than the layer above it (as would occur, for example, near the substratum). B. Diagram of a patch of material moving past a shore (hatched area) that is smooth (upper diagram) versus a shore with an irregularity (e.g., a pocket of slowly-moving water in a hole, a plant canopy, etc., - lower diagram). Material from the patch mixes into the pocket as the patch moves by, and then continues to mix out of the pocket after the leading edge of the patch has moved further along the shore.

MODELS OF THE DYNAMICS OF PATCHES OF LARVAE

A number of mathematical models have been developed to address various ecological questions that depend on the transport of patches of larvae, as reviewed by Okubo (1992). Most of these deal with populations of pelagic organisms (e.g. fish), and incorporate advection, isotropic diffusion, growth, and sometimes mortality terms. Several models have also been developed for benthic populations. For example, Jackson and Strathmann (1981) considered the role that mixing played in determining the recruitment of larvae into the benthic stages. They did not consider advection or anisotropic diffusion. Further, Possingham and Roughgarden (1990), in an advective-diffusive model of larval dispersal and settlement, allowed absorbing boundaries

(to simulate settlement) and/or reflective boundaries at the shore, in addition to mortality and space limitation on the shore. Diffusion was again assumed to be isotropic. In a model that simulated details of turbulence in the surf zone, Denny and Shibata (1989) examined the effect that vertical turbulent mixing has upon the delivery of the larvae of benthic organisms to the substratum, but they ignored horizontal mixing and advection. However, using Csanady's (1973) turbulent plume formulation, they did consider three-dimensional transport in their model of the fertilization success of eggs and sperm spawned by benthic organisms. Finally, in studies of the dispersal of coral larvae along barrier reefs (Sammarco and Andrews 1988, 1989), Andrews et al. (1989) used a detailed numerical circulation model to study the role that transport plays over both ecological and evolutionary time scales.

In an earlier section of this article we noted that the role of larval transport via water movement has been shown to be important in at least four ecological/evolutionary considerations: 1) the structure of benthic communities; 2) the dynamics of benthic populations that have a planktonic stage; 3) gene flow between such populations of marine organisms; and 4) the evolution of (benthic) life-history strategies. This list is certainly not exhaustive. The models we cited in the previous paragraph (and the many more that we did not cite, e.g. Okubo 1992) are the initial attempts to assess how the details of water flow affect these important ecological and evolutionary considerations. [N.b., although the effects of water motion on population structure have been modeled, so far as we can ascertain no model exists that incorporates the role that water flow plays in determining benthic community structure, though there can be no doubt of its importance. See, e.g., Roughgarden et al. 1985, or Roughgarden et al. 1988.] All of the model studies noted above, though by no means an exhaustive survey, concluded that transport of any kind -- advective, diffusive, turbulent, etc. -- played a substantial role, often the dominant role, in the biological processes under investigation. But few of the (benthic) models incorporated even moderately realistic advection and diffusion characteristics [Andrews's (1989) use of a detailed numerical model is, perhaps, an exception]. One reason for this retreat from realism is the complication that it brings to the modeler's efforts. However, another more important reason is the sad recognition that very few measurements of the relevant transport parameters exist. This state of affairs could change, and should change, rapidly. The dye release techniques we sketched in this article are so simple that they could readily be incorporated into many biological field investigations. In this way important estimates of transport (coarse estimates, to be sure) could accompany the detailed biological data collected by investigators. Furthermore, many such studies in the nearshore, both observational and modeling, could benefit substantially from the addition of realistic transport estimates.

CONCLUSION

The shore environment is a complex mosaic with great variability in transport from site to site over small spatial scales, and from time to time, (even over hours, and certainly over a tidal cycle). Our measurements lead us to the "common sense" conclusion that such spatial and temporal variability can be of considerable ecological and evolutionary importance. We argue that the dye tracking technique provides a simple, quantitative method of classifying various habitats as to their actual transport characteristics. Moreover, the results can be incorporated into the present generation of models of benthic populations and communities.

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