13 MACROSCOPIC ANIMALS AND PLANTS IN BENTHIC FLOWS

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Macroscopic animals and plants interact in manifold ways with their marine benthic environments. Rhoads's (1974) masterful review consolidated appreciation for interactions among sediments and organisms. Diagenesis and macrofauna have been connected through a range of interactions, from external effects of respiratory currents in radial diffusion to hydrolysis during digestion (chapter 11). Physical transport has long been known to effect large-scale dispersal, but its pervasive influences at smaller scales on larval settlement have been dissected only more recently (Butman, 1987). Vogel's (1994) inspirational book on the multiple roles of moving fluids in the lives of organisms extended appreciation for fluid motion to nearly all ecological processes. A broadly useful idea and null hypothesis has been that organisms in flows behave much like inanimate objects that possess comparable (stillwater) downward velocities with respect to the immediately surrounding fluid. Under this null hypothesis, the field of sediment transport gives good guidance regarding where propagules should be deposited; they should transport much like sediment grains or aggregates that have similar stillwater settling velocities.

Even this brief tour is sufficient to demonstrate that interdisciplinary understanding and appreciation generally have been achieved two disciplines at a time. The 1996 Max Planck Society-sponsored meeting on the Benthic Boundary Layer in Bremen marked an escalation to a new phase in which more than two disciplines often intertwine. Furthermore, the null hypothesis of purely passive behavior has been rejected so many times that it has become a "dead horse, " that is i.e. no longer believable in general. Although useful null hypotheses and experimental controls will still incorporate the notion of passive physical transport, including such sophistications as shape and center-of-gravity effects on passive motion (e.g., Jeffery, 1922; Jonsson et al., 1991; Ellers, 1995a), the interesting alternatives and predictions for continuing research will include active responses on the parts of organisms, using the sensory modalities available to them (Dusenbery, 1992). We therefore, begin with a look at how sensory fields are shaped by benthic boundary layer (BBL) dynamics.

We cite long reviews and books as evidence of progress in understanding of interactions in pairs of disciplines. A review of the full diversity of multidisciplinary interactions in a short chapter is impossible. Indeed, it would be difficult even in the full length of this book. Rather than presenting a necessarily shallow review that is balanced, we have elected to concentrate on three topics that illustrate rapid recent progress when organisms are studied in a multidisciplinary context. We use the chapter to examine current views and to highlight issues that need research attention. There is some logic in our order. We begin with sensory fields as the set of stimuli that allow more than purely passive behaviors in flow. We move to other issues of mass and momentum transfer to or from individuals occurring alone or in groups. We finish the tour with a look at processes that operate at the population level to emphasize that a multidisciplinary look is not useful at the individual level of the ecological hierarchy alone. A repeating theme is that intermediate flow velocities are optimal for most taxa and processes, but positions of the optima vary with taxon and process.

13.1 Flow Modification of Sensory Fields

Perhaps the single most important idea from quantitative sensory ecology is that even a slight bias in finding a goal (e.g., a settlement site for a propagule or a feeding patch for a deposit feeder) can be nearly as effective as perfect ability to aim at that goal; a slightly biased random walk is nearly as good as directed movement (Dusenbery, 1992, fig. 17-2, p. 425). A corollary is that even weak sensory cues may be more useful than intuition might suggest. Flows, through diverse processes of momentum and mass transfer, shape most benthic sensory fields at the same time that they influence paths taken by searchers. We do not attempt a balanced review of the senses, but highlight instead some recent advances in understanding of chemosensing in the marine environment. We do treat the other senses, however, because evolution drives even very "simple" organisms to use multiple sensory modes in "goal" location (Dusenbery, 1996), consonant with our theme that benthic biological oceanography is escalating from "bidisciplinarity" to "multidisciplinarity" in its attack on interesting biological oceanographic questions.

13.1.1 Chemosensing

Water is eminently better suited to transport of a diversity of hydrophilic chemical cues than is air. There are many potential "point" sources of dissolved chemical cues. Exhalent respiratory and feeding currents are obvious ones that might guide parasites, predators (Weissburg and Zimmer-Faust, 1994), or mates to excurrent flows. Induced porewater flows (see chapter 7) from topographic high points are others that might provide useful information on biogeochemical processes below the interface. Less obvious but potentially important to recruitment are dissolved chemical cues emanating from single benthic bacteria or diatoms. Some features of point-source injections into turbulent boundary layers are nearly universal. The near field, like the plume of smoke from the tip of a cigarette, shows very strong gradients on the small scale, whereas in the far field, turbulent and molecular diffusion have had ample opportunity to reduce those gradients. Homogenization is accelerated in the presence of higher turbulence levels, like those under shallow-water waves (see chapter 2). In addition to this decrease in steepness of small-scale gradients downstream and with time, the plume is stretched in the along-stream direction compared to the cross-stream. Because of the no-slip condition at the seabed, the plume travels fastest at its highest extent. Suspended sediments may serve as adsorbents for such plumes, decreasing their half-lives and effective travel distances in solution. Waves both "dither" the geometry of the plume at the length scale of the compressed orbital velocity and contribute to the bottom roughness felt by the flow. Sediment transport further redistributes "tastes, " that is, adsorbed chemical cues that require contact.

Plumes contain both obvious and subtle cues of distance from an odor source. Straining of odor filaments by the flow dominates the near field, but the resulting sharp chemical gradients drive unsteady molecular diffusion quickly to reduce those gradients. Local steepness of the gradient, called *onset slope* to highlight the shape of the signal arriving at a sensor, thus is one cue of proximity (Moore and Atema, 1988). If two sensors are separated by 1–10 cm and detect odor fluctuations at the typical 3–10 Hz (Gomez and Atema, 1996), they can obtain another cue of proximity by differencing the two signals received. In the far field, both should detect the same concentration of odor. In the near field, however, each will receive a sharply different concentration, cueing local search. Although this argument is only qualitative, there is clearly quantitative information contained within the cascade of BBL eddy scales (Zimmer-Faust et al., 1988; Weissburg and Zimmer-Faust, 1994). Very significantly, the high-frequency responses of animal chemosensors (ca. 10 Hz) make less relevant the mean characteristics of plumes which are more easily calculable than are the more stochastic and more difficult to calculate instantaneous features. Good starting points in this direction are with the elegant simplifications of Garrett (1983) and the thorough derivations of Rodeau (1996). It is also possible for signals to escape dilution by packaging in liposomes (Williams et al., 1992), but this hydrophobic form would be easily adsorbed to suspended sediments.

Animals in general use some form of rheotaxis to achieve chemotaxis in BBLs, compounding the feedback between flow and stimulus fields. Known exceptions (e.g., Roe, 1976) wait for intervals of low or no flow (e.g., emersion) to hunt steadier chemical trails. How chemotaxis in flow is accomplished is best worked out for terrestrial insects that use sex pheromones for mate location (e.g., Mafra-Neto and Cardé, 1995). In this case no steady trail exists to follow, and the general strategy is to fly upwind when the odor is detected, but to cast about cross-stream when the odor has been lost. A small insect many body lengths above the ground needs some way to distinguish upwind and down, and the primary cue is thought to be visual referencing to estimate ground speed or velocity. Among macrobenthos, chemotaxis is best understood for some crabs and lobsters that do not leave contact with the bed when they search. In this strong vertical velocity gradient, upstream direction is easier to determine, and the portion of the scent trail in the diffusive sublayer provides a steady trail. Notably, even though its height is large relative to the diffusive sublayer (DBL), a blue crab's body length and width are large relative to plume-edge gradients, and the crab is able to stay in the plume by turning cross-stream in the correct direction when part of its body leaves the plume (Zimmer-Faust et al., 1995).

Perhaps the most provocative finding in benthic chemotaxis is for scavenging, deep-sea (lysianassid) amphipods. They normally seek carrion that has fallen to the seabed. Baited traps placed above the seabed, however, also catch amphipods. The perplexing question is how the traps are found in the absence of any obvious means to tell upstream from down. The higher the trap is placed, up to 100 m or more above the seabed, the more biased is the catch toward larger individuals (e.g., Christiansen, 1996). Jumars and Gallagher (1982) have suggested that larger individuals might search nearer the top of the BBL, where they could effectively scan the largest bottom area for the scent of large bait falls. Another possibility is that larger individuals make larger excursions above the bed, and perhaps in the other two directions as well, in biased random search. Either scenario could explain why individuals trapped higher are on average larger. Because no cues of flow direction are apparent at these greater heights, the mechanism for trap location would appear to be analogous to chemokinesis in bacteria, with turning frequency increasing when the scent becomes weaker or is encountered less frequently.

Signal molecules certainly are diverse, but basic oligopeptides are beginning to emerge as generally useful and often used. Most organisms have the cellular and enzymatic machinery to both synthesize and hydrolyze them. They are hydrophylic and so are carried easily by natural flows and are not particularly susceptible to adsorption. In addition, prelimary work suggests that they are not subject to rapid bacterial uptake (Decho et al., 1998). By contrast, signal molecules in air usually are larger and aromatic. For a chain of length n, 20^n messages are possible from permutations of 20 amino acids. This complex code is used widely both internally and externally in communication. Remarkably, activity in terms of signal response can already be predicted from chemical characteristics of the component amino acids (Hellberg et al., 1987; Browne et al., 1998). Unlike typical, saturating dose-response curves, those for larval settlement of oysters, mud crabs and barnacles and those for phagostimulant activity of adenosine monophosphate in shrimp (Carr and Thompson, 1983) are unimodal, with responses peaking at intermediate concentrations (Browne et al., 1998). Thus, strength and localization of the message depend not only on production and hydrolysis rates of the cue, but also on details of boundary layer mixing. Immediate corollaries are that chemosensing of habitat patches for settlement or foraging will be very scale dependent and that varying source strengths and spatial distributions of individual plumes will yield complex geometries in response isopleths. Field or laboratory manipulations will therefore need to mimic natural field scales or pay the consequences in terms of difficulties in interpretation of observations.

For a diversity of reasons, then, dissolved chemical cues appear to be most effective at intermediate flow velocities. At higher flow speeds, plume dispersion to an ineffectual dose is rapid, and swimming speeds can be overwhelmed. At lower flows, the plume does not extend as far before the signal is degraded chemically.

13.1.2 Other Sensory Cues

Contrary to intuition and to the intuitive notion of the sea as a water bath, thermal cues abound, even in the deep ocean. Demonstrated precision of biological temperature sensors is of order 0.001°C, not far from the accepted precision of thermometers commonly used by physical oceanographers. Terrestrial nematodes, for example, orient in vertical gradients of 10^{-3} °C cm^{-1} (Pline et al., 1988) and respond to temporal changes of 10^{-4} °C s^{-1} (Dusenbery, 1988). The benthic environment is heterogeneous at this scale of resolution, and temperature may be a particularly good indicator of the organism's position with respect to dynamic frontal boundaries. In the intertidal, temperature extremes for emersed organisms are notorious and have long been known to be of ecological significance (e.g., Lewis, 1963), so there is abundant reason to expect a temperature sense. There has been less appreciation of cyclically varying thermal gradients within sediments (Harrison and Phizacklea, 1987). On upwelling shelves, near-bottom temperature drops are reliable indicators of the onset of the upwelling season (e.g., Lentz, 1987). Even in the deep sea (e.g., Ezer and Weatherly, 1991), temperature changes may provide a useful indication of the position of the organism relative to a front, and gamete release on the "correct" side or vertical movement of larvae through an inclined thermal front to reach the "correct" side for recruitment may increase fitness by dispersal to or retention within specific water masses. In shallower water radiative daytime heating and convective nighttime cooling may provide other exploitable cues.

Sound, defined strictly as waves of alternating compression and expansion with no net flow of the medium, is well known to be the only long-distance communications mode that works well in the ocean. Long-distance communication appears to be limited to relatively low acoustic frequencies that do not attenuate rapidly by absorption, and therefore to large animals, such as whales, and to ones that possess air bladders, such as the fishes named *drum* for their resonances. The reason for long-distance efficacy is the existence of a sound channel that focuses the energy and keeps it away from the scattering and absorbing boundaries at the sea surface and bottom (e.g., Clay and Medwin, 1977).

Far more ubiquitous and important to biota living fully within the BBL are smaller scale pressure-velocity fluctuations that are associated with net flow. To the acoustician, this kind of fluctuation is a complicated, one generally found close to the sound generator and called a near-field effect. The natural benthic pressure-velocity field is both noisy and complicated (Heathershaw and Thorne, 1985). Every turbulent vortex produces such fluctuations, as do passing surface waves in shallow water. Although the field is noisy, it contains abundant, potentially useful information. Objects on the bottom shed vortices at Strouhal frequencies characteristic for their size and the flow speed (Nowell and Jumars, 1987). The information contained may be useful in thigmotaxis or in detecting coming erosional events, as increasing flow speeds produce vortices of higher frequency. Similarly, prey and predators both cause pressure-velocity fluctuations when they move that may provide useful information of each other's presence and location. Transmission of mechanical signals through the liquid medium is reasonably well understood in comparison to transmission through two-phase media such as sediments, and at high frequencies sediments are notorious for their capacity to scatter and absorb sound (Stoll, 1989). Nonetheless, it is useful to ask at what distance a burrowing organism can be detected mechanically, and what subtle mechanical signals can be detected.

Diverse organs sense water movements and provide the ability to orient in a flow (e.g., Murray and Willows, 1996). Mechanosensing of periodic disturbances has been documented in relatively few benthic species, however, and quantified in even fewer. Three uses are known. Some of the best quantification of vibrational stimuli traveling along the sediment interface is during emersion for fiddler-crab intraspecific communication (Aicher and Tautz, 1990). A second is timing of swash riding by surf zone clams (Ellers, 1995b) that allows the species to inhabit the intertidal but remain immersed. Mechanosensory prey detection has been documented for several benthic species, including polynoid (Daly, 1973), glycerid (Ockelmann and Vahl, 1970), and hesionid (Oug, 1980) polychaetes and septibranch bivalves (Reid and Reid, 1974), but the stimulus intensity, frequency, and mode of transmission through the water and sediments have not been quantified in any of these cases, and none of these mechanosensing predators has been observed under natural flows. Septibranchs are characteristically deep-water animals, and may be restricted there, in part, by sensitivity to flow noise. It is tempting to speculate as well that shallow-water predators relying on mechanosensory information may be most effective at slack water.

Because water absorbs much more light than does air and because water is also much better at keeping light-scattering particles in suspension and light-absorbing compounds in solution, long-sighted animals are not prevalent in water, especially among the benthos. The ocean has no eagles. In shallow water the benthic light field is especially quickly time varying due to backscatter off both surface waves and the seabed and to high-frequency variation in both (re)suspended sediments (see chapter 4) and phytoplankton populations. Nevertheless, there is evidence that visual predators operate in this environment from very shallow water (Levinton, 1971), at least to shelf depths (Jumars et al., 1996) and probably beyond when and where the intervening water column allows sufficient light to pass. Many taxa in shallow water appear to migrate out of the seabed or out of the turbid layer immediately over the seabed at dusk (e.g., Mauchline, 1980), presumably for reasons similar to those that explain diurnal vertical migration of zooplankton in the open ocean, as well as to find mates (Fincham, 1970). Some near-bed species are able to use quasi-steady spatial variation in light fields (light “shafts”) to maintain stable schools in the presence of flow (Buskey et al., 1995), and light may be a cue for some zonation patterns (Rodgers and Bingham, 1996).

The problem of and solution to avoiding visual predators may be substantially different in shallow water than in the open ocean. Variations in optical properties of near-bed and overpassing water bodies make time variation in benthic light fields difficult to predict or even to summarize from field data (e.g., Jumars et al., 1996). Distance to the refuge from visual predation can be very short, however, which leads to a natural question: do shallow-water migration patterns in and out of the seabed reflect instantaneous ambient light levels or are they more smoothly circadian? The better answer would appear to depend upon the time scale of irradiance variation relative to the time required to reach cover and on the balance of hazard from predation against gain from feeding or sexual encounter in the water column. High-resolution light records near the seabed are rare, as are high-resolution records of vertical migration out from the bottom in shallow water.

Electric sensing appears restricted to a few taxa, in the benthos largely to elasmobranch fishes that can use nervous impulses or impedance irregularities to find even buried prey (Kalmijn, 1988). Thus, we do not treat them further here. Magnetic sensing may be useful in maintaining a course and consequently in search. Other navigational cues are comparatively scarce, and so selection for a magnetic sense may be more intense in this suite of environments than elsewhere. Higher order fluctuations of the electromagnetic field caused by seawater flowing through the earth’s magnetic field again lead to flow-induced complexity in the electromagnetic field that could provide useful information (Paulin, 1995), but we know of no demonstrated benthic uses of these higher order effects.

13.2 Flow Effects on Momentum and Mass Transfer

Flows also supply needs that are less subtle than sensory cues. Macrofauna require O_2, and macrophytes require inorganic carbon. Suspension feeders require an encounter rate with seston. Conversely, animals find their nitrogenous wastes and plants find oxygen toxic at high concentrations. In the context of a macroscopic organism in a BBL, there are two general ways in which transport limitation (see chapters 5 and 14) can be ameliorated; the organism can project upward from the seabed into faster-moving fluid, or it can pump actively. Both active pumping and projecting structures have the capacity to modify BBL structure, with potential effects on downstream individuals (e.g., Eckman, 1987; Eckman et al., 1989; O'Riordan et al., 1993). These themes could be explored in issues as wide ranging as active versus passive suspension feeding, respiratory pumping by infauna (chapter 11) and carbon fixation in macrophytes.

At the opposite extreme from problems of insufficient mass transfer at small scales are catastrophic failures from too much momentum transfer in extreme events. In general, growth upward from the interface greatly increases drag and risks mechanical damage by projecting the organism into faster flows. Infauna under energetic flows risk burial. In particular, oscillatory flows driven by wind-generated surface gravity waves, as well as strong quasisteady currents, can impose extreme forces on macrobenthic organisms and the substratum, with important ecological consequences.

13.2.1 Mass and Momentum Transfer to and from Macrophytes

To photosynthesize, aquatic plants require inorganic carbon to diffuse from the bulk water, through the *diffusive boundary layer* (DBL, also called the *unstirred layer*) over the plant surface, and through a layer of plant tissue before it reaches the site of photosynthesis (chloroplasts). Oxygen is then produced and follows the opposite path. At night, during respiration, the process is reversed. Macroalgae (which lack true roots) obtain nitrogen and phosphorus from the water column (Hanisak, 1983) following the same diffusional path as carbon. This process also applies to benthic microalgae (Ludden et al., 1985) and algal biofilms (Flora et al., 1995) and is addressed in Chapter 15.

Below a saturating velocity (i.e., above a critical DBL thickness) photosynthetic rates decrease with decreasing current speed (fig. 13.1; Wheeler, 1980; Fonseca and Kenworthy, 1987; Koch, 1993a, 1994). This result (left of the dotted line in fig. 13.1) indicates DBL-imposed carbon limitation. Above the critical velocity, uptake is limited by physiological factors such as enzyme concentrations and kinetics (Wheeler, 1980; Koehl and Alberte, 1988; Koch, 1994). The same type of response applies for nutrient uptake (Parker, 1981; Hurd et al., 1996) and therefore is better described by the Hill-Whittingham equation than by Michaelis-Menten kinetics (Smith and Walker, 1980).

The critical (bulk or outer flow) velocity where limitations change from physical mass transfer to physiological capacity depends on the plant species and has been found to be between 2 and 6 cm s^{-1} (Wheeler, 1980; Koch, 1993a, 1994; Gonen et al., 1995; Hurd et al., 1996; van Keulen, 1997). Critical DBL thickness has been estimated to be between 90 and 300 mm, depending on the carbon affinity of the plant (Larkum et al., 1989; Koch, 1994). In contrast, the diffusional path within the plant is only a few micrometers thick (cuticle, cell wall, plasmalemma, and chloroplast membranes). Marine macrophytes may be able to acclimate to different DBL thicknesses (Koch, 1994), but further research on this topic is needed. The mechanism by which an aquatic plant senses its flow environment is also unknown, but may involve chemical cues influenced by transport limitation (Serrao et al., 1996).

Carbon uptake in marine plants is more complex than just summing the distances of the diffusional paths. Permeability of cell components varies with the forms of carbon found in seawater (Larkum et al., 1989). CO_2 is preferred over HCO_3^- in marine plants, but the slow flux of CO_2 through the plant DBL (only small concentrations of CO_2 are

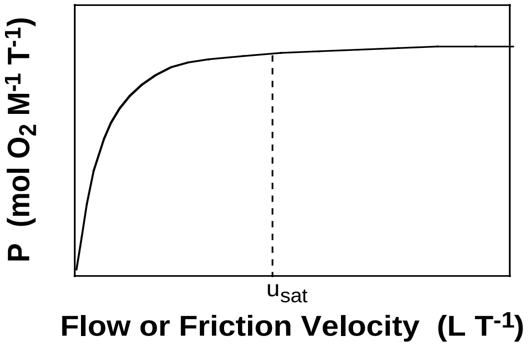

Figure 13.1 Effect of current or friction velocity on photosynthetic rate (P) of a hypothetical macrophyte. Below a saturating flow velocity (u_{sat}, dotted line), photosynthesis is limited by the plant DBL. Above u_{sat}, photosynthesis is limited by physiological capacities.

available) can limit photosynthesis (Beer and Israel, 1990; Beer and Koch, 1996). In contrast, the flux of HCO_3^- through the DBL is higher (higher concentrations in seawater), but the cell membranes have low permeability to HCO_3^-. Various mechanisms have been suggested to overcome these obstacles.

Most marine macroalgae and many seagrasses contain carbonic anhydrase (Millhouse and Strother, 1986; Durako, 1993; Beer, 1994; James and Larkum, 1996; Beer and Rehnberg, 1997) that catalyzes the conversion of HCO_3^- to CO_2. After HCO_3^- diffuses through the DBL and reaches the plant surface, it is transformed into CO_2 which then diffuses into the cells. This mechanism takes advantage of the high HCO_3^- flux through the DBL and solves the problem of low HCO_3^- permeability through the cuticle.

Another mechanism that ameliorates periods of photosynthesis-limiting DBL thicknesses is release of H^+. This process occurs on both surfaces of certain macroalgae (Smith, 1985), but on only one side of the blade (polar leaves) of some freshwater and estuarine flowering plants (Prins et al., 1982). By increasing local (DBL) CO_2 concentration, this process increases the flux of CO_2 into the plant. Both the carbonic anhydrase and the H^+ mechanisms depend on concentrations of these CO_2-enhancing materials in the DBL. Paradoxically, therefore, an increase in current velocity may reduce availability of carbonic anhydrase and H^+ ions (Raven, 1992) and decrease photosynthetic rates (Lucas, 1983). This hypothesis has not been substantiated, but Gonen et al. (1995) suggested that flow-facilitated photosynthesis may not be due to an increased flux of carbon through a thinner plant DBL, but due to the removal of OH^- ions from the surface of the plant. These ions shift the carbon equilibrium in the DBL from CO_2 to HCO_3^-. A third mechanism of HCO_3^- utilization is its direct transport across the plasmalemma as suggested for the macroalga *Ulva* (Beer, 1994) and some seagrasses (Bjork et al., 1997).

Carbon-concentrating mechanisms may also play a vital role in success of marine macrophytes under DBL-limiting conditions (Beer, 1994). Such mechanisms allow the plant to take advantage of times or locations when or where the DBL is reduced in thickness (Koch, 1994) and accumulate the assimilated carbon at the site of photosynthesis. The more efficient this system, the less likely seagrasses and macroalgae will be affected by a thick DBL (Beer, 1997). The macroalga *Ulva lactuca,* which has an efficient carbon uptake system (Drechsler and Beer, 1991), is able to continue photosynthesizing at reduced rates under DBL-limiting conditions for up to 7.5 hr (Koch, 1993a). Additionally, a seagrass from a calm environment with an efficient carbon utilization system was less affected by a thick plant DBL than was a seagrass from a surf zone (Koch, 1994).

Research on the effect of the plant DBL on productivity of marine macrophytes has been conducted under steady flow and with “clean” plants. In situ, plants are exposed to time-varying flows and variable epiphyte cover, which cause the DBL to fluctuate in thickness over time and space (Koch, 1994). Stevens and Hurd (1997) suggested that fluctuations in current velocity can increase nutrient uptake by a factor of 10 by periodically renewing the water in the BBL.

Furthermore, plant leaves rarely occur in isolation. Seagrass shoots and algal fronds, both individually and in groups, reduce flow velocity by extracting momentum (Madsen and Warnke, 1983). Flow velocities under canopies are often reduced by factors of 0.5 –0.1 (Ackerman, 1983, 1986; Gambi et al., 1990; Komatsu and Murakami, 1994), and these beds show a thicker BBL (Eckman, 1987) compared to adjacent unvegetated areas. As a consequence, larvae and juveniles settle and fine sediment particles deposit within macrophyte beds (Scoffin, 1970; Eckman et al., 1989). Nutrient concentrations in the sediments colonized by seagrasses are also higher than those of unvegetated sediments (Kenworthy et al., 1982), perhaps due to lower porewater fluxes through the relatively thick boundary layer and to the trapping of organic particles. The degree to which currents are baffled in canopies of marine plants depends on distance into the canopy (Heller, 1987), current speed (Fonseca and Fisher, 1986; Worcester, 1995) and wave frequency (Heller, 1987). Dependence on density of vegetation is less clear (Gambi et al., 1990). Intertidal seagrass canopies also can trap a thin layer of water (<20 cm) during low tide (Powell and Schaffner, 1991). Although it prevents desiccation of the plants, it also creates stagnant conditions under which carbon can become limiting.

In addition to current velocity, canopies of marine plants have the potential to reduce wave energy. Wave attenuation by marine plants depends on water depth (Mork, 1996) and leaf or stipe/frond length (Fonseca and Cahalan, 1992). As waves propagate over seagrass beds, wave height diminishes and wave energy is lost (Fonseca and Cahalan, 1992; Koch, 1996). Although the same process has been described for kelp forests in the past (Jackson, 1984; Komatsu and Murakami, 1994), the recent work of Elwany et al. (1995), and Mork (1996) suggests that wave attenuation by kelp forests is insignificant at some wave frequencies. This difference in wave attenuation between seagrass beds and kelp forests may be due to the fact that seagrass canopies, which are shorter than most kelp forests, increase drag on the waves, whereas larger kelp stipes and fronds oscillate with the waves, as though embedded in them, imposing little added drag (Seymour, 1996).

Turbulence in canopies of marine macrophytes is not yet well characterized. Studies using a variety of techniques in flumes and in the field observed increased (Gambi et al., 1990; Grizzle et al., 1996), decreased (Eckman et al., 1989; Ackerman and Okubo, 1993), or unchanged (Worcester, 1995) turbulence intensity between sites within marine plant canopies and unvegetated areas. Turbulence among plants can be generated within an otherwise laminar flow, as well as rescaled if the flow is already turbulent (Anderson and Charters, 1982; Gambi et al., 1990; Ackerman and Okubo, 1993; Koch, 1996). By *rescaled* we mean that the size-frequency distribution of turbulent eddies is modified. In addition to production by vortex shedding from the plant structure, turbulence in macrophyte beds can occur through flapping (low-amplitude movement accompanying vortex shedding) of seagrass blades. This motion creates a region of high turbulence at the canopy-water interface, while near the bottom, turbulence intensity is lower but may still exceed that over unvegetated areas (Gambi et al., 1990). This vertical stratification of turbulent energy through the canopy may explain part of the variety in results obtained. The contribution of *monami* (high-amplitude movement due to elasticity of the plants and not the water movement) to turbulence generation is also unclear. Ackerman and Okubo (1993) observed reduced turbulent mixing during monami in a seagrass canopy, whereas Grizzle et al. (1996) observed an increase in turbulent mixing. It is perhaps unreasonable to expect simple generalizations for the diversity of mechanical properties, sizes, shapes, and spacings encountered in plant canopies.

Rescaling of turbulence in macrophyte beds depends on the architecture of the canopy

(Koch, 1996). Flow through a seagrass bed can be compared to flow through a mesh (Anderson and Charters, 1982; Nowell and Jumars, 1984; Ackerman and Okubo, 1993) where the maximum scale of the turbulent eddies approaches the mesh size (or distance between the shoots or fronds). Epiphytes colonizing seagrass blades decrease the mesh size and rescale turbulence to even smaller eddies than those found among clean blades (Koch, 1996). Rescaling of turbulence occurs at the individual (Anderson and Charters, 1982) and at the canopy level (Gambi et al., 1990; Koch, 1996) and may be a mechanism creating mixing lengths of biological importance.

At first glance, hydrodynamic conditions within a macrophyte bed seem to be detrimental to survival of plants (Koch, 1993b): the reduction in flow velocity and attenuation of waves increase the thickness of the plant DBL. Rescaling of turbulence in macrophyte beds may, however, ameliorate local nutrient depletion (Anderson and Charters, 1982; Koch, 1996). Additionally, a decrease in near-bed flow velocities can result in increased deposition (Scoffin, 1970) and nutrients in sediments colonized by macrophytes (Koch, 1993b); reduced current velocities under plant canopies may autofertilize rooted plants. More subtle effects of projecting shoots on porewater advection (see chapter 7) need to be explored. An advantage of this process may be the elimination of phytotoxins from sediments (Koch, 1993b).

Exposure is not without costs, however. Large, wind-generated waves affect most coastal and shelf, and many estuarine and lagoonal, benthic environments. Near-bottom velocities in response to shoaling waves in the nearshore coastal environment can exceed several meters per second (e.g., Denny, 1995). Combined lift and drag forces produced by flows of this magnitude on epibenthic macrophytes and macrofauna can be catastrophic (e.g., Dayton et al., 1984; Paine, 1986), and for this reason wave-induced damage plays a major role in determining abundances, species compositions, and population age structures within hard-substratum communities (Paine and Levin, 1981; Dollar, 1982; Highsmith, 1982; Hughes, 1984; Sousa, 1985; Blanchette, 1996). Surviving plants must have morphologies, mechanical strengths, and flexibilities appropriate to withstand such forces (Koehl, 1986; Niklas, 1992; Vogel, 1994). A change in size or morphology provides an active means to adapt to high drag, whereas collapsing or bending over in the flow is a passive adaptation that reduces instantaneous stresses by reducing both projected area and mean velocity to which the plant surface is exposed (Koehl, 1986).

Macroalgae exposed to high current and wave velocities tend to be flat, long, thick and narrow, whereas plants residing in more quiescent waters tend to be undulate, shorter, thinner, and wider (Koehl, 1986; Gerard, 1987; Kraemer and Chapman, 1991; Dudgeon and Johnson, 1992; Hurd et al., 1996, 1997). Stipes of wave-exposed kelps also thicken, but this response depends on light availability (Sjötun and Fredriksen, 1995). Morphological adaptations of seagrasses to hydrodynamic forces are not well known. Anatomical adaptations of these plants when exposed to strong hydrodynamic forces include smaller lacunae (air spaces within the plants) and thicker fibers (Cooper and McRoy, 1988; Koch, 1993b).

Although higher surface roughness in an alga exposed to slow currents and little wave energy should lead to reduced DBL thickness (Gerard, 1982), this morphology does not appear to result in higher fluxes of nutrients and carbon to plants (Koehl and Alberte, 1988; Hurd et al., 1996, 1997). These data need to be interpreted with caution, due to the possibility that other elements could have been limiting. In some cases, small changes in morphology lead to novel functions, while in other cases, such changes occur without performance consequences (Koehl, 1996). Larned and Atkinson (1997) observed that the alga *Dictyosphaeria cavernosa* is can circumvent DBL limitations under low flow by changing from a flat morphology under high flow conditions to a bubblelike morphology with chambers beneath the thalli. During DBL-limiting conditions, the plant can draw from these chambers, filled with nutrients from the sediments, instead of depending on the water column. Alternatively, fluctuating currents (Stevens and Hurd, 1997) and (or) epiphytes (Koch, 1994) may disrupt the DBL and supply the macrophytes with pulses of nutrient- and carbon-rich water. A thick layer of epiphytes would cause the flow to skim over it, increasing the DBL. Furthermore, epiphytes can compete with seagrasses for light and nutrients.

Passive *drag reduction*, effected by the bending over of algal fronds or seagrass blades, may increase self shading (Fonseca and Kenworthy, 1987; Koehl and Alberte, 1988). When fronds collapse, algae with non-planar blade surfaces may receive more light (Koehl and Alberte, 1988). Additionally, during flapping of the blades, the optimal angle of incident light (normal to the photosynthetic tissue) may occur more often or over a larger area than if the blade were flat. Irradiance reaching the collapsed blades may come in the form of pulses, corresponding to movements of intervening plants and focusing by surface waves (Wing and Patterson, 1993). Therefore, productivity of macrophytes under time-varying irradiance must be addressed along with the hydrodynamics of the habitats that they colonize.

Most work on functional ecology of macrophytes has centered on individual plants. Population and community level research is needed, where individuals at the canopy margin experience different forces and irradiance than those on the inside.

13.2.2 Momentum and Mass Transfer in Other Benthic Settings

Some effects of macrophytes on mass and momentum transfer may be important to corals (Lesser et al., 1994). Nutrient limitation in coral reefs is often severe, implicating mass transfer as an exceedingly important issue (Atkinson and Bilger, 1992; see also chapter 5). Corals often show roughly self-similar or fractal branching that ameliorates transport limitation (Kaandorpe et al., 1996)–an amelioration mode unavailable to flexible organisms in flows. A general problem impeding further understanding of mass and momentum transfer in macrophytes and corals is flow characterization in the complex setting of groups of individuals. Flows are highly 3D and anisotropic near these geometrically irregular arrays, making it difficult to relate larger-scale flow characteristics to the local flow parameters of relevance to diffusional limitations. Corals are also exposed to catastrophic failure, but whereas the breaking or uprooting forces for flexible macrophytes are primarily tensional, those for rigid corals involve cracking failure modes of the projecting cantilever. Although fatal, or morphologically limiting, effects on individuals, populations, and communities are the most obvious and pervasive effects of extreme wave and current energy, beneficial effects also have been noted. In particular, reproduction and dispersal of corals, via fragmentation and transport (Highsmith, 1982), like dispersal of some sediment-dwelling benthos (Palmer, 1984, 1988; Beukema and de Vlas, 1989; Emerson and Grant, 1991; Armonies and Hellwig-Armonies, 1992), may be facilitated by exceptionally strong flows, as is insect dispersal by strong atmospheric events (Burt and Pedgley 1997).

Whereas ecological impacts of waves are obvious to ecologists who study hard-substratum communities, their impacts and those of strong, steady currents may be equally significant to organisms that inhabit shallow marine sediments. Although sediments offer a refuge from direct effects of strong lift and drag forces, the erosion, transport, and redeposition of the upper layer of the substratum is an important source of mortality, and it plays a major role in determining species composition in sedimentary assemblages (e.g., McKnight, 1969; Eagle, 1975; Rees et al., 1977; McCall, 1978; Berg and Alatalo, 1985; Thistle, 1988; Aller 1989, 1997; McCall and Soster, 1990; Thistle et al., 1991; Posey et al., 1996). Ecologically important depositional events may be tied to fluvial discharge, in addition to relaxation after in situ erosion (e.g., Rhoads et al., 1985; Aller and Aller, 1986; Aller and Stupakoff, 1996). Although often highly localized, gravitational events such as turbidity flows and slumping can also have dramatic effects, and the frequency of such disturbances are tied closely to underlying geological structures and overpassing sediment loads.

Topographically induced acceleration of flow apparently is responsible for sediment transport noted on the summits and along the slopes of deeply submerged seamounts in the North Pacific (Lonsdale et al., 1972; Cacchione et al., 1988; Brink, 1989; Noble and Mullineaux, 1989; Levin et al., 1994). Variability in stability of sediments in these topographically complex environments has been invoked as one explanation for among-site heterogeneity in abundances and community composition of benthic fauna (Levin and Thomas, 1989; Levin et al., 1994).

13.3 Benthic Populations and Larval Dynamics

For many benthic species a dispersing phase (larva, spore, or benthic individual dispersing postsettlement) interacts strongly with BBL flows. Both empirical observations (e.g., Connell, 1985; Bertness et al., 1992; Ólafsson et al., 1994) and mathematical models (e.g., Roughgarden et al., 1985, 1988; Levin et al., 1987; Levin and Huggett, 1990; Possingham and Roughgarden, 1990; Pascual and Caswell, 1991) indicate that rates of production, mortality, and intensity settlement of larvae can (but may not always) play key roles in determining abundances and size- and age-frequency structures of benthic populations.

Effects of BBL flow on populations of macrobenthos and their larvae (or spores) by definition are restricted to processes operating near the boundary. Therefore, we consider here only hydrodynamic processes affecting production or immediate dispersal of larvae (spawning, fertilization, and dispersal), and the return of competent larvae to the benthic environment (settlement and recruitment). This review does not consider some key effects of larger scale transport features on dispersal and mortality of larvae, which are reviewed elsewhere (e.g., Shanks, 1995; Eckman, 1996).

13.3.1 Spawning and Fertilization

Entry into the planktonic phase occurs via release of either larvae or gametes from reproductively mature, benthic adults. In the latter case fertilization success, and therefore, rate of larval production, can be affected by BBL processes, because fertilization requires either encounter between egg and sperm within the BBL or transport of sperm through the BBL to a benthic female that carries fertile eggs. Marine benthic invertebrates have evolved diverse means that elevate rates of egg fertilization and larval production. Included are reproductive synchrony (at time scales ranging from seasonal to tidal to diel), and aggregation or swarming of reproductively mature individuals (Levitan, 1995; Morgan, 1995). Of particular significance is understanding how behaviors of spawning individuals can alleviate the problem of dilution and dispersal of gametes within a turbulent BBL. Denny (1988) and Denny and Shibata (1989) provide an elegant theoretical analysis of potential effects of flow, turbulence and animal spacing on fertilization success (fig. 13.2). Using the free-spawning urchin *Strongylocentrotus pupuratus* as a model species, Denny and Shibata (1989) predicted that fertilization success should be typically low (0.01–1%) and should vary positively with rate of sperm release and inversely with flow speed, turbulence intensity, and distance between spawning individuals.

Their results suggest that an optimal reproductive strategy for a species that sheds gametes would be to aggregate in high densities and spawn synchronously at the highest rate (shortest duration) possible under conditions of weak flow. Although such behaviors are observed (Pennington, 1985; Levitan, 1991, 1995; Morgan, 1995), empirical data suggest that the comparatively low fertilization probabilities predicted by Denny and Shibata (1989) may underestimate those achieved in nature. Data collected from the field, including a wide range of taxa, suggest that the probability of fertilization success is much higher and largely falls within a narrower range than predicted by Denny and Shibata (1989) — see Levitan (1995).

For species where both sexes shed gametes, and for those where only males spawn, fertilization success in the field is rarely <5%, often as high as 90%, and as expected, exhibits a strong inverse relationship with distance to the nearest spawning male (fig.

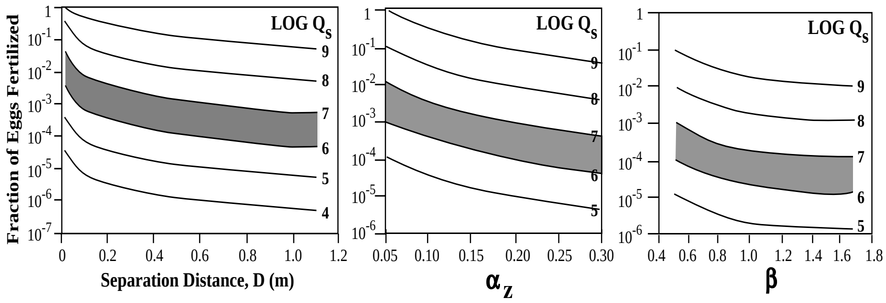

Figure 13.2 Fraction of externally spawned eggs fertilized by externally spawned sperm as functions of distance between spawning individuals (D), rate of sperm release (Q_s), and two coefficients (a_z and b) describing the rate of plume dispersal, according to the model presented by Denny and Shibata (1989), where a_z and b vary directly with flow strength. Shaded regions indicate the probable range of sperm release rate by the urchin *Strongylocentrotus purpuratus*. (Redrawn with permission of University of Chicago Press from fig. 8 in Denny and Shibata [1989])

13.3; table 2 in Levitan, 1995). Where the nearest spawning male is close by (< 1 m distant), fertilization success typically ranges from 20–90%; where males are more distant, it is usually 5–30%.

The contrast between model predictions and empirical data raises some interesting questions. While it is fair to ask whether the simplicity of Denny and Shibata's (1989) mixing model introduces important error, it is equally reasonable to ask whether and how behaviors of spawning individuals, beyond aggregation or animal spacing, for which the model accounts or properties of spawned gametes act to circumvent the problem of gamete dilution in the BBL. For example, one possibility is that an organic matrix enveloping spawned gametes might retard their mixing and dilution by turbulence in the BBL. Any retention of spawned gametes within an organic matrix might maintain higher gamete concentrations, and possibly facilitate merger of gamete streams in the water column, either of which might enhance fertilization success. This and other related possibilities are worthy topics of future research.

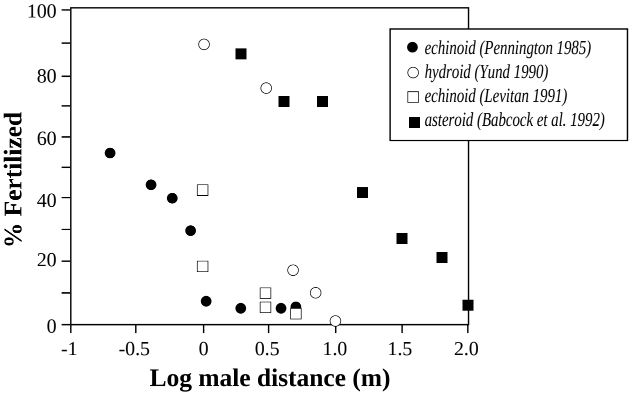

Figure 13.3 Results of four experimental studies in which the percentage of fertilization was measured as a function of distance from a single spawning male. (Redrawn with permission of CRC Press from fig. 1 in Levitan [1995])

13.3.2 Dispersal

For larvae the process of dispersal with all its attendant risks begins with release into the BBL. With the exception of zoeal and megalopal stages of larval crustaceans, swimming speeds of invertebrate larvae and plant zoospores do not exceed a few millimeters per second (Jacoby, 1982; Chia et al., 1984; Butman et al., 1988a). Horizontal current speeds in typical marine boundary layers exceed these low levels even millimeters above the bed (Butman 1986, 1987), implying that larvae have effectively no capacity to overcome horizontal flows in the sea. This simple fact might tempt one to conclude that weakly swimming larvae have little ability to control their dispersal; however, such a conclusion would be erroneous.

Swimming speeds of most planktonic larvae are of comparable magnitude to turbulent fluctuations of flow speed in the vertical direction in typical marine boundary layers. For example,a comparatively strong free-stream horizontal flow of 20 cm s^{-1} should produce a boundary shear velocity of 0.8 cm s^{-1} (Bradshaw, 1971, his fig. 20), sufficient to entrain fine sands from the bed (Miller et al., 1977). Turbulent fluctuations in vertical flow speed would range from a few millimeters to a centimeter per second in such a boundary layer (Bradshaw, 1971), comparable to swimming and sinking speeds of many larvae. Thus, larvae should be capable of directed verticxal movement in BBLs. As a consequence, larval behaviors, either in response to environmental cues or defined by developmental stage or circadian rhythms, afford some control over position in the water column and, thereby, dispersal.

A simple model of diel periodicity in swimming speed demonstrates the capacity of larvae to control vertical position in the water column. A simple, time-dependent, 1D (vertical), advection-diffusion model was constructed to describe a population of weakly swimming larvae in a hypothetical shallow, coastal flow (10 m depth, constant free-stream speed of 20 cm s^{-1}, tides ignored). The model formulation was

$$\frac{\partial c}{\partial t} = -w_s \frac{\partial c}{\partial z} + \frac{\partial}{\partial z}\left(E_z \frac{\partial c}{\partial z} \right) \tag{13.1}$$

where c is the average larval concentration (time and height dependent), t is time, w_s is the sinking or swimming speed of the larva in the vertical dimension, z is vertical location (z = 0 at the bottom), and E_z is the vertical eddy diffusivity.

The larvae are assumed to migrate upward ($w_s = 2$ mm s^{-1}) during darkness and sink passively ($w_s = -2$ mm s^{-1}) during daylight. Turbulence intensity was defined by a diffusivity field, E_z, that produces a maximum at middepth and the well-known linear relationship between diffusivity and height in the lowest portion of the boundary layer (Businger and Arya, 1974; Long, 1981; Middleton and Southard, 1984; Eckman, 1990). The model predicts (fig. 13.4) that two stable distributions of larvae in the water column are achieved within the day-night cycle, and that, as expected, the time scale required to reach equilibrium scales to the ratio of flow depth and larval swim speed, in this example, 1000 cm/0.2 cm s^{-1} = 83 min.

The vertical distribution of larvae is expected to be highly sensitive to interactions between larval swimming or sinking speed and intensity of turbulent mixing. Therefore, features of the water column that might alter mixing intensity (e.g., density stratification) could greatly affect larval distributions. A clear demonstration is provided by Dekshenieks et al. (1996), who illustrate how stratification can interact with ontogenetic changes of oyster larvae to affect larval distributions. Furthermore, larvae may alter swimming patterns in response to changes in water-column properties (e.g., salinity or thermal discontinuities) associated with changes in mixing intensity (Mann and Wolfe, 1983; Mann et al., 1991).

The literature contains numerous examples of behavior-driven temporal changes in vertical distributions of larvae. They range from simple diel or tidally linked vertical migrations (e.g., Wood and Hargis, 1971; Little and Epifanio, 1991; Olmi, 1994; Tankersley and Forward, 1994) to ontogenetic shifts in swimming propensities of lar-

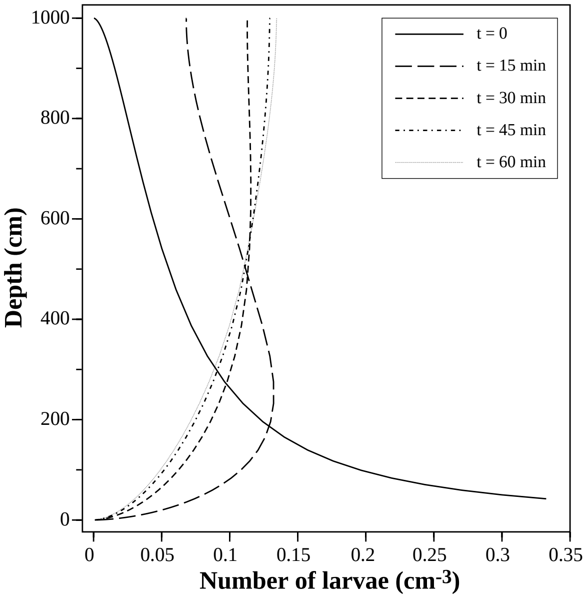

Figure 13.4 Model-simulated vertical migration of a population of larvae with a fixed, depth-integrated density of 100 larvae cm^{-2} in a 10 m water column. Free-stream velocity is 20 cm s^{-1}, producing a shear velocity (u_*) of 0.87 cm s^{-1}. Larvae begin to migrate upward at 2 mm s^{-1} from the stable daytime distribution at the beginning of darkness (t = 0). A stable night-time distribution is achieved at t = 60 min.

vae during development (e.g., Chia et al., 1984; Mann, 1985). Perhaps the most dramatic evidence that these behaviors affect larval dispersal comes from studies of estuarine species whose larvae must face both time-averaged outward flows and strong tidal variations in flow speed and direction. It has been well documented that larvae of oysters (Wood and Hargis, 1971), crabs (De Vries et al., 1994; Olmi, 1994), and many fishes change swimming patterns in response to tidal stage to alter their vertical positions and effect either up-estuary or down-estuary transport.

Dispersal of benthic macroorganisms by BBL flow is not limited to interactions of flow with larva. Benthic macrofauna, ranging from early postset larvae to adults, utilize flow in the BBL to disperse (see Butman, 1987, her table II). In many instances this dispersal is not behaviorally driven, but is primarily a by-product of entrainment and transport of the substratum that the organisms inhabit. This “passive” dispersal is especially common among meiofauna (Palmer and Gust, 1985; Palmer, 1988) and juveniles of macrofauna (Matthiessen, 1960; Grant, 1981; Emerson and Grant, 1991), which must reside close to the sediment surface in order to maintain links to oxygenated waters needed for respiration or food supply. There is clear evidence, in addition, that some species actively utilize the BBL to disperse (e.g., Palmer, 1988; Armonies, 1992). This behavioral phenomenon is especially well documented among molluscs, which employ mechanisms as diverse as “sailing” with secreted mucous or byssal threads (Sigurdsson et al., 1976; Beukema and de Vlas, 1989), buoyancy production (Little and Nix, 1976; Sörlin, 1988), and swimming (Williams and Porter, 1971) to disperse after initial settlement. The clear rhythmical patterns in abundances of benthic individuals dispersing via the BBL (Bell et al., 1988, 1989; Armonies, 1992) confirm that this mechanism of dispersal is behaviorally modulated in many species.

Although the role of BBL flows in facilitating dispersal of both larval and benthic phases has been well documented, there are important shortcomings in knowledge of the significance of this phenomenon. Most important, recognition of the breadth of dispersal mechanisms has not been accompanied by a similarly broad level of appreciation of the role of these processes in the population dynamics of macrobenthic organisms. A fuller appreciation of the importance of dispersal to benthic population dynamics, obtained most efficiently via use of quantitative population dynamic modeling techniques, is an area of research particularly ripe for exploration (Roughgarden et al., 1985, 1988; Possingham and Roughgarden, 1990; Eckman, 1996).

13.3.3 Settlement and Recruitment

Settlement involves interaction of water-borne propagules with the bottom within a boundary layer that is, in most cases, turbulent (Nowell and Jumars, 1984). The ecologically important problem of defining spatial and temporal variability in “rates” of settlement more accurately can be defined as the problem of defining variability in the settlement flux, j_s , the number of organisms settled per unit area of bottom per unit of time. Defining this flux requires solution of two problems: (1) defining the propagule contact flux, j_c, the number of propagule contacts with the bottom per unit area of bottom per unit of time, and (2) defining the probability that a propagule will settle once the bottom is contacted, p_s. Stated more formally,

$$j_c = p_s j_c \tag{13.2}$$

Flow in the BBL can affect settlement by affecting both terms on the right side of equation (13.2). Both the propagule contact flux and the probability of settlement will reflect behavioral interactions of larvae with BBL flow (Butman et al., 1988b; Butman and Grassle, 1992; Grassle et al., 1992).

Larvae or other propagules suspended at any point in the BBL can transit to the bottom by either swimming downward, sinking, or being advected downward in turbulence (Denny, 1988; Denny and Shibata, 1989). Intuitively, the contact flux should depend on the quantity and distribution of larvae suspended in the water column and how rapidly larvae transit toward the bottom. Intuition is supported by results from some field studies, indicating that settlement rates vary directly with concentrations of larvae in the water column (Gaines et al., 1985; Roughgarden et al., 1988; Martel et al., 1994) or their flux past monitored sites (Yund et al., 1991; Bertness et al., 1992).

A formal derivation of the contact flux has been proposed by Eckman (1996) and Eckman and Duggins (1998) that accounts for the distribution of larvae in the turbulent BBL and their tendency for motion in the direction normal to the boundary. For a uniform, flat bottom their arguments lead to the prediction that

$$j_c = \int_0^{\delta_{wc}} \frac{c(z)\,dz}{t_c(z)} \tag{13.3}$$

where δ_{wc} is water column depth, and $t_c(z)$ is the *average* time required for a larva located at height z to transit to the bottom. The ratio $c(z)/t_c(z)$ can be thought of as the average rate of delivery of larvae to a unit area of substratum per unit of thickness of water column, which is a function of height above the bottom. The depth integral of this ratio defines the contact flux. The relative contribution of any location in the water column to the contact flux varies directly with the average concentration of larvae there and inversely with the time required for larvae to travel from the height of that location to the bottom. Because transit times are shortest for points near the bottom ($t_c \to 0$ as $z \to 0$), equation (13.3) leads to the sensible conclusion that the contact flux is dominated by average larval abundances, behavior, and turbulent mixing intensity in the region of the water column closest to the bottom.

The more straightforward problem in solving equation (13.3) is in defining the ver

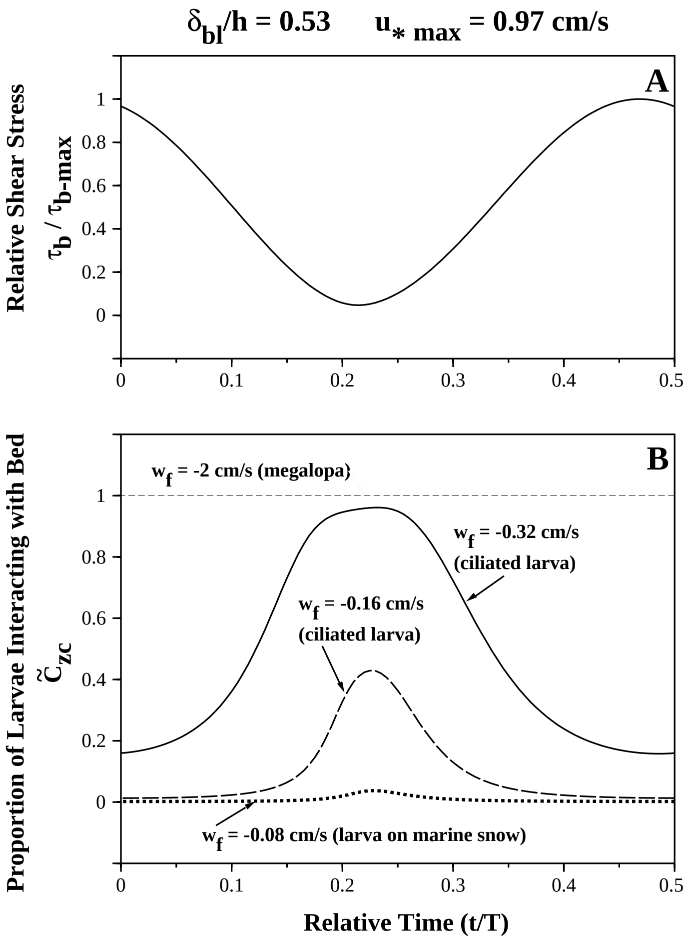

Figure 13.5 A, Boundary shear stress, τ_b, normalized to the maximum shear stress, $\tau_{b\text{-max}}$, as a function of nondimensional time in a semi-diurnal tidal cycle. B, Proportion of suspended larvae capable of interacting with the bed, c_{zc}, as a function of nondimensional time for four cases of larval fall velocity, w_f, according to the model of Gross et al. (1992). Patterns in A and B repeat after 0.5 tidal cycles (t/T = 0.5). Model flow depth (h) was 50 m. (Reprinted with permission of Pergamon Press from Eckman et al. [1994])

tical distribution of larvae, c(z). The theory of sediment transport includes a substantial body of literature devoted to predicting how turbulence in the BBL interacts with the gravitational fall velocity of suspended particles to determine mean particle distribution (e.g., Yalin, 1977; Middleton and Southard, 1984; see chapter 4). This literature can be applied directly to predicting larval distributions by assigning the larval population a mean sinking or swimming speed in the vertical dimension (i.e., Eckman, 1990; Gross et al., 1992; see also eq. [13.1]). Exercises of this nature have led to some important insights. For example, Gross et al. (1992) and Eckman et al. (1994) predict that abundances of many ciliated larvae should vary substantially over a tidal cycle, with most competent larvae being located near the bottom, and most settlement probably occurring during periods of slack or near-slack water (fig. 13.5). The possibility that for some species, much of the total settlement occurs during periods of weakest flow is intriguing and begs for empirical evaluation.

Larval behavior can exert significant effects on contact flux by modifying the larval concentration field, c(z). The substantial body of literature documenting diel, tidal, or ontogenetic shifts in larval position in the water column gives ample testament to the importance of larval swimming behaviors in modifying position and, therefore, the concentration field. Some of these behavioral effects were evaluated quantitatively by Eckman et al. (1994). They demonstrated that changes in the vertical component of larval velocity due to responses to environmental cues (light intensity, pressure, solutes) can drastically alter larval distributions in the water column.

A more difficult problem in solving equation (13.3) is in defining the average propagule transit time to the bottom, $t_c(z)$. This parameter will be governed complexly by larval advection (sinking or swimming), intensity of turbulent motions in the BBL, the vertical distribution of vortex size and intensity of turbulent motions, and viscous damping of turbulence near the boundary. Denny (1988) and Denny and Shibata (1989) derived a method for predicting particle transport times to the substratum in a turbulent boundary layer. Their work has been refined by McNair et al. (1997), who provide an elegant derivation of $t_c(z)$, using a different notation, and correct an apparent error in Denny's earlier derivation. McNair et al. show that the average particle (larval) transit time is greatly affected by the vertical speed of swimming or sinking by the larva. However, in the simple case where larvae are neutrally buoyant ($w_f = 0$)

$$t_c(z) = \int_0^z \left[\frac{(\delta - y)}{E(y)} \right] dz \tag{13.4}$$

The strong dependence of t_c on the vertical advective velocity of the larvae (McNair et al., 1997) indicates that larval transit time can be affected significantly by behavior. Any swimming responses by larvae to environmental cues, in addition to diel, tidal, or ontogenetic changes in swimming patterns, will therefore affect average times of larval transit to the bottom, in addition to changing the distribution of larvae throughout the water column (in fact, the two are interdependent). Because transit times are least from locations near bottom, behaviorally controlled speeds near the boundary should exert especially important effects on the contact flux (see also Eckman et al., 1994). For this reason, documentation of larval swimming responses to recent contacts with the seafloor, to soluble cues released from the substratum (e.g., Tamburri et al., 1992), and interactions of larval swimming with torquing forces in the near-bottom BBL (Jonsson et al., 1991), all can be nominated as especially important topics for future research.

The developing ability to predict larval distributions in the water column, as well as times of larval transport to the seafloor, brings tantalizingly close a capacity to predict rates of larval contacts with potential settlement sites. Because such a capacity would represent an important advance, it is critical that models of larval distribution, transport, and contact be evaluated empirically using both tracer particles and larvae in the flume and field. Furthermore, potentially important effects of bottom roughness on larval contact rates (e.g., Dade et al., 1991) must also be considered.

13.3.4 Settlement Probability

For most species contact with a potential settlement site does not inevitably stimulate metamorphosis. Some exploration or evaluation of the substratum, possibly leading to its rejection, is typical. Factors that influence this decision and, therefore, settlement probability have been the subject of intensive investigations over many decades (reviewed by Crisp, 1976, 1984; Woodin, 1986, 1991; Butman, 1987; Pawlik, 1992; also see Woodin et al., 1993, 1995, 1998). Results of these studies make it clear that a complex suite of chemical, sedimentological or mechanical (e.g., textural) cues may be used by larvae in making the decision to accept or reject a potential settlement site. These behavioral responses operate in the context of, and are modified by, lift and drag forces on larvae in contact with a surface over which water is moving (Denny 1985, 1988; Eckman et al., 1990).,

The critical importance of settlement probability in determining settlement rates and patterns is demonstrated by results of a series flume studies (e.g., Butman et al., 1988b; Butman and Grassle, 1992; Grassle et al., 1992) in which rates of accumulation of settling larvae in closely spaced sediment chambers, containing varied sediment types, were compared with rates of accumulation of inert particles having similar fall speeds. Although the inert particles generally accumulated in equal proportions among different sediment types, larval settlement patterns showed strong biases. The most logical explanation for this discrepancy is that upon encountering unfavorable sediment types, larvae rejected the substratum (p_s small), reentered the flow, and continued testing the bottom until the preferred sediment type was eventually located.

Given the suite of factors that may affect a larva's decision or capacity to accept or reject substratum, and given the wide range in settlement affinities exhibited among different cohorts of apparently "competent" conspecific larvae (Rittschof et al., 1984), the challenge of predicting a priori the probability of a particular larval cohort accepting a particular surface may be vexing. For some species, including those that respond positively to the presence of conspecifics (e.g., some balanoid barnacles [Crisp, 1976, 1984], reef-building sabellariid polychaetes [Pawlik, 1986; Pawlik and Faulkner, 1986]), this settlement probability (p_s) can be well defined, probably approaching unity where the positive cue is encountered (cf. Walters, 1992). If the substratum acceptable to a larva is comparatively rare, one might expect the probability to approach unity when that substratum is encountered. For many other species, however, especially those that inhabit a comparatively common substratum or can tolerate a broad range of substrata, it will almost certainly be necessary to resort to some empirically determined probability of substratum acceptance. This empirically determined probability (p_s) may depend on larval age, and may vary significantly over a range of substrata, especially given the complex suite of negative settlement cues to which a larva might respond (Woodin, 1991; Woodin et al., 1993, 1995, 1998).

13.4 Conclusions

We have by no means touched on all the important interactions of flows with macrobenthos. Instead, we have treated three biologically important classes of flow interactions in boundary layers: flow modulation of sensory fields, flow modulation of mass and momentum transfers to individuals, and flow modulation of the dispersal and settlement of propagules above and on the seabed. The structure of our chapter tempts one to consider these three vignettes as more or less independent because we have chosen to focus, respectively, on large, mobile animals, sessile macrophytes, and dispersing larvae in dealing with these three issues. We can correct this impression by resort to the example of gamete release in the macroalgae *Fucus vesiculosus, Fucus distichus,* and *Pelvetia fastigiata.* They apparently enhance fertilization success by releasing gametes at slack water and sense this flow condition chemically by reduced mass transfer (Serrao et al., 1996).

The major, obvious, important conclusion from this example and our chapter overall is that flow effects are diverse, pervasive, and highly disrespectful of disciplinary bounds. A less obvious conclusion is that both community structure and sedimentary structure provide complementary records of flow history. Introductory texts often assert, based on long-standing correlations between community structure and sedimentary variables that sediment type controls community structure. This and other chapters in this book argue that many of the strong correlations between substratum structure and community structure stem instead from pervasive effects of flow on both.

References

Ackerman, J. D. (1983) Current flow around *Zostera marina* plants and flowers: implications for submarine pollination. Biol. Bull. 5, 504.

Ackerman, J. D. (1986) Mechanistic implications for pollination in the marine angiosperm *Zostera marina*. Aquat. Bot. 24, 343–353.

Ackerman, J. D., and Okubo, A. (1993) Reduced mixing in a marine macrophyte canopy. Funct. Ecol. 7, 305-–309.

Aicher, B., and Tautz, J. (1990) Vibrational communication in the fiddler crab, *Uca pugilator.* I. Signal transmission through the substratum. Jour. Comp. Physiol. A 166, 345–353.

Aller, J. Y. (1989) Quantifying sediment disturbance by bottom currents and its effect on benthic communities in a deep-sea western boundary zone. Deep-Sea Res. 36, 901–934.

Aller, J. Y. (1997) Benthic community response to temporal and spatial gradients in physical disturbance within a deep-sea western boundary region. Deep-Sea Res. 44, 39–69.

Aller, J. Y., and Aller, R. C. (1986) Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic. Deep-Sea Res. 33, 755–790.

Aller, J. Y., and Stupakoff, I. (1996) The distribution and seasonal characteristics of benthic communities on the Amazon shelf as indicators of physical processes. Cont. Shelf Res. 16, 717–751.

Anderson, S. M. and Charters, A. C. (1982) A fluid dynamics study of seawater flow through Gelidium nudifrons. Limnol. Oceanogr. 27, 399–412.

Armonies, W. (1992) Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. Mar. Ecol. Prog. Ser., 83, 197–206.

Armonies, W., and Hellwig-Armonies, M. (1992) Passive settlement of *Macoma balthica* spat on tidal flats of the Wadden Sea and subsequent migration of juveniles. Netherlands Jour. Sea Res. 29, 371–378.

Atkinson, M. J., and Bilger, M. W. (1992) Effects of water velocity on phosphate uptake in coral reef-flat communities. Limnol. Oceanogr. 37, 426–435.

Beer, S. (1994) Mechanism of inorganic carbon acquisition in marine macroalgae (with special reference to the chlorophyta), *in* Progress in Phycological Research (Round, F.E., and Chapman, D.J., eds.), p. 179–207. Biopress, Bristol.

Beer, S. (1997) Inorganic carbon transport in seagrasses, *in* Seagrass Biology: Discussions from an International Workshop (Kuo, J., Phillips, R. C., Walker, D. I., and Kirkman, H., eds.), p. 43-47. Western Australia Museum, Perth. .

Beer, S., and Israel, A. (1990) Photosynthesis of *Ulva lactuca*. IV. pH, carbonic anhydrase and inorganic carbon conversions in the unstirred layer. Plant Cell Env. 13, 555–560.

Beer, S., and Koch, E. W. (1996) Photosynthesis of marine macroalgae and seagrasses in globally changing CO_2 environments. Mar. Ecol. Progr. Ser. 141, 199–204.

Beer, S., and Rehnberg, J. (1997) The acquisition of inorganic carbon by the seagrass *Zostera marina*. Aquat. Bot. 56, 277–283.

Bell, S. S., Hicks, G. R. F., and Walters, K. (1988) Active swimming in meiobenthic copepods of seagrass beds: Geographic comparisons of abundances and reproductive characteristics. Mar. Biol. 98, 351–358.

Bell, S. S., Hicks, G. R. F., and Walters, K. (1989) Experimental investigations of benthic re-entry by migrating meiobenthic copepods. Jour. Exp. Mar. Biol. Ecol. 130, 291–303.

Berg, C. J., Jr., and Alatalo, P. (1985) Biology of the tropical bivalve *Asaphis deflorata* (Linne, 1758). Bull. Mar. Sci. 37, 827–838.

Bertness, M. D., Gaines, S. D., Stephens, E. G., and Yund, P. O. (1992) Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). Jour. Exp. Mar. Biol. Ecol. 156, 199–215.

Beukema, J. J., and de Vlas, J. (1989) Tidal-current transport of thread-drifting post-larval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. Mar. Ecol. Prog. Ser. 52, 193–200.

Bjork, M., Weil, A., Semesi, S., and Beer, S. (1997) Photosynthetic utilization of inorganic carbon by seagrasses from Zanzibar, East Africa. Mar. Biol. 129, 363–366.

Blanchette, C. A. (1996) Seasonal patterns of disturbance influenced recruitment of the sea palm, *Postelsia palmaeformis*. Jour. Exp. Mar. Biol. Ecol. 197, 1–14.

Bradshaw, P. (1971) An Introduction to Turbulence and its Measurement. Pergamon, New York.

Brink, K. H. (1989) The effect of stratification on seamount-trapped waves. Deep-Sea Res. 36, 825–844.

Browne, K. A., Tamburri, M. N., and Zimmer-Faust, R.K. (1998) Modelling quantitative structure-activity relationships between animal behavior and environmental signal molecules. Jour. Exp. Biol. 201, 245_258.

Burt, P. J. A., and Pedgley, D. E. (1997) Nocturnal insect migration: effects of local winds. Adv. Ecol. Res. 27, 61–89.

Businger, J. A., and Arya, S. P. S. (1974) Height of the mixed layer in the stably stratified planetary boundary layer. Adv. Geophys. 18, 73–92.

Buskey, E. J., Peterson, J. O., and Ambler, J. W. (1995). The role of photoreception in the swarming behavior of the copepod *Diothona oculata*. Mar. Freshw. Behav. Physiol. 26, 273–285.

Butman, C. A. (1986) Larval settlement of soft-sediment invertebrates: Some predictions based on an analysis of near-bottom velocity profiles; *in* Marine Interfaces Ecohydrodynamics (Nihoul, J. C. J., ed.), p.487–513. Elsevier, New York.

Butman, C. A. (1987) Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanogr. Mar. Biol. Ann. Rev. 25, 113–165.

Butman, C. A., and Grassle, J. P. (1992) Active habitat selection by *Capitella* sp. I larvae. I. Two-choice experiments in still water and flume flows. Jour. Mar. Res. 50, 669–715

Butman, C. A., Grassle, J. P., and Buskey, E. J. (1988a) Horizontal swimming and gravitational sinking of *Capitella* sp. I (Annelida: Polychaeta) larvae: implications for settlement. Ophelia 29, 43–57.

Butman, C. A., Grassle, J. P., and Webb, C. M. (1988b) Substrate choices made by marine larvae settling in still water and in a flume flow. Nature 333, 771–773.

Cacchione, D. A., Schwab, W. C., Noble, M., and Tate, G. (1988) Internal tides and sediment movement on Horizon Guyot, Mid-Pacific Mountains. Geo-Mar. Lett. 8, 11–17.

Carr, W. E. S., and Thompson, H. W. (1983) Adenosine 5'-monophosphate, an internal regulatory agent, is a potent attractant for a marine shrimp. Jour. Comp. Physiol. 153, 47–53.

Chia, F.-S., Buckland-Nicks, J., and Young, C. M. (1984) Locomotion of marine invertebrate larvae: a review. Can. Jour. Zool. 62, 1205–1222.

Christiansen, B. (1996) Bait-attending amphipods in the deep sea: Comparison of three localities in the north-eastern Atlantic. Jour. Mar. Biol. Assoc. U.K. 76, 345–360.

Clay, C. S., and Medwin, H. (1977) Acoustical Oceanography: Principles and Applications. Wiley, New York.

Connell, J. H. (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. Jour. Exp. Mar. Biol. Ecol. 93, 11–45.

Cooper, L. W., and McRoy, P. (1988) Anatomical adaptations to rocky substrates and surf exposure by the seagrass genus *Phyllospadix*. Aquat. Bot. 32, 365–381.

Crisp, D. J. (1976) Settlement responses in marine organisms, *in* Adaptation to Environment: Essay on the Physiology of Marine Animals (Newell, R. C., ed.), p.83–123. Butterworths, London.

Crisp, D. J. (1984) Overview of research on marine invertebrate larvae, 1940–1980, *in*

Marine Biodeterioration: An Interdisciplinary Study (Costlow, J. D. ,and Tipper, R. C., eds.), p.103–127. Naval Institute Press., Annapolis, Maryland.

Dade, W. B., Nowell, A. R. M., and Jumars, P. A. (1991) Mass arrival mechanisms and clay deposition at the seafloor, *in* The microstructure of fine-grained terrigenous marine sediments — from muds to shale (Bennett, R. H., Bryant, W. R., and Hulbert, M. H., eds.), p.161–164. Springer-Verlag, Heidelberg.

Daly, J. M. (1973) The ability to locate a source of vibrations as a prey-capture mechanism in *Harmothoe imbricata* (Annelida Polychaeta). Mar. Behav. Physiol. 1, 305–322.

Dayton, P. K., Currie, V., Gerrodette, T., Keller, B. D., Rosenthal, R., and Ven Tresca, D. (1984) Patch dynamics and stability of some California kelp communities. Ecol. Monogr. 54, 253–289.

Decho, A. W., Browne K. A., and Zimmer-Faust, R. K. (1998) Chemical cues: why basic peptides are signal molecules in marine environments. Limnol. Oceanogr. 43, 1410–1417.

Dekshenieks, M. M., Hofmann, E. E., Klinck, J. M., and Powell, E. N. (1996) Modeling the vertical distribution of oyster larvae in response to environmental conditions. Mar. Ecol. Prog. Ser. 136, 97–110.

Denny, M. W. (1985) Wave forces on intertidal organisms: a case study. Limnol. Oceanogr. 30, 1171–1187.

Denny, M. W. (1988) Biology and the Mechanics of the Wave-Swept Environment. Princeton University Press, Princeton, N.J.

Denny, M. W. (1995) Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. Ecol. Monogr. 65, 371–418.

Denny, M. W., and Shibata, M. F. (1989) Consequences of surf-zone turbulence for settlement and external fertilization. Amer. Natur. 134, 859–889.

De Vries, M. C., Tankersley, R. A., Forward, R. B., Jr., Kirby-Smith, W. W., and Luettich, R. A., Jr. (1994) Abundance of estuarine crab larvae is associated with tidal hydrologic variables. Mar. Biol. 118, 403–413.

Dollar, S. J. (1982) Wave stress and coral community structure in Hawaii. Coral Reefs 1, 71–81.

Drechsler, Z., and Beer, S. (1991) Utilization of inorganic carbon by *Ulva lactuca*. Plant Phys. 97, 1439–1444.

Dudgeon, S. R., and Johnson, A. S. (1992) Thick vs. thin: thallus morphology and tissue mechanics influence differential drag and dislodgment of two co-dominant seaweeds. Jour. Exp. Mar. Biol. Ecol. 165, 23–43.

Durako, M. (1993) Photosynthetic utilization of CO_2 and HCO_3^- in *Thalassia testudinum* (Hydrocharitaceae). Mar. Biol. 115, 373–380.

Dusenbery, D. B. (1988) Behavioral responses of *Meloidogyne incognita* to small temparature changes. Jour. Nematol. 20, 351–355.

Dusenbery, D. B. (1992) Sensory Ecology. Freeman, New York.

Dusenbery, D. B. (1996) Information is where you find it. Biol Bull. 191, 124–128.

Eagle, R. A. (1975) Natural fluctuations in a soft bottom benthic community. Jour. Mar. Biol. Assoc. U.K. 55, 865–878.

Eckman, J. E. (1987) The role of hydrodynamics in recruitment, growth and survival of *Argopecten irradians* (l.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. Jour. Exp. Mar. Biol. Ecol. 106, 165–191.

Eckman, J. E. (1990) A model of passive settlement by planktonic larvae onto bottoms of differing roughness. Limnol. Oceanogr. 35, 887–901.

Eckman, J. E. (1996) Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. Jour. Exp. Mar. Biol. Ecol. 200, 207–237.

Eckman, J. E. and Duggins, D. O. (1998) Larval settlement in turbulent pipe flows. J. Mar. Res. 56, 1285-1312.

Eckman, J. E., Duggins, D. O., and Sewell, A.T. (1989) Ecology of understory kelp environments. I. Effects of kelps on flow and particle transport near the bottom. Jour. Exp. Mar. Biol. Ecol. 129, 173–187.

Eckman, J. E., Savidge, W. B., and Gross, T. F. (1990) Relationship between duration of cyprid attachment and drag forces associated with detachment of *Balanus amphitrite* cyprids. Mar. Biol. 107, 111–118.

Eckman, J. E., Werner, F. E., and Gross, T. F. (1994) Modelling some effects of behavior on larval settlement in a turbulent boundary layer. Deep Sea Res. 41, 185–208.

Ellers, O. (1995a) Form and motion of *Donax variabilis* in flow. Biol. Bull. 189, 138–147.

Ellers, O. (1995b) Discrimination among wave-generated sounds by a swash-riding clam. Biol. Bull. 189, 128–137.

Elwany, M. H. S., O'Reilly, W. C., Guza, R. T., and Flick, R. E. (1995) Effects of Southern California kelp beds on waves. Jour. Waterw. Port Coast. Ocean Engineer. 121, 143–150.

Emerson, C. W., and Grant, J. (1991) The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. Limnol. Oceanogr. 36, 1288–1300.

Ezer, T., and Weatherly, G. L. (1991) Small-scale spatial structure and long-term variability of near-bottom layers in the HEBBLE area. Mar. Geol. 99, 319–328.

Fincham, A. A. (1970) Rhythmic behaviour of the intertidal amphipod *Bathyporeia pelagica.* Jour. Mar. Biol. Assoc. U.K. 50, 1057–1068.

Flora, J. R. V., Suidan, M. T., Biswas, P., and Sayles, G. G. (1995) Modeling algal biofilms: role of carbon, light, cell surface charge and ionic species. Water Environ. Res. 67, 87–94.

Fonseca, M. S., and Cahalan, J. A. (1992) A preliminary evaluation of wave attenuation by four species of seagrass. Estur. Coast. Shelf Sci. 35, 565–576.

Fonseca, M. S., and Fisher, J. S. (1986) A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. Mar. Ecol. Progr. Ser. 29, 15–22.

Fonseca, M. S., and Kenworthy, W. J. (1987) Effects of current on photosynthesis and distribution of seagrasses. Aquat. Bot. 27, 59–78.

Gaines, S., Brown, S., and Roughgarden, J. (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. Oecologia (Berlin) 67, 267–272.

Gambi, M. C., Nowell, A. R. M., and Jumars, P. A. (1990) Flume observations on flow dynamics in *Zostera marina* (eelgrass) beds. Mar. Ecol. Progr. Ser. 61, 159–169.

Garrett, C. 1983. On the initial streakiness of a dispersing tracer in two- and three-dimensional turbulence. Dyn. Atmos. Oceans 7, 265–277.

Gerard, V. A. (1982) In situ water motion and nutrient uptake by the giant kelp *Macrocystis pyrifera*. Mar. Biol. 69, 51–54.

Gerard, V. A. (1987) Hydrodynamic streamlining of *Laminaria saccharina* Lamour. in response to mechanical stress. Jour. Exp. Mar. Biol. Ecol. 107, 237–244.

Gomez, G., and Atema, J. (1996) Temporal resolution in olfaction: stimulus integration time of lobster chemoreceptor cells. Jour. Exp. Mar. Biol. 199, 1771–1779.

Gonen, Y., Kimmel, E., and Friedlander, M. (1995) Diffusion boundary layer transport in *Gracilaria conferta* (Rhodophyta). Jour. Phycol. 31, 768–773.

Grant, J. (1981) Sediment transport and disturbance on an intertidal sandflat: Infaunal distribution and recolonization. Mar. Ecol. Prog. Ser., 6, 195–206

Grassle, J. P., Butman, C. A., and Mills, S. W. (1992) Active habitat selection by settling *Capitella* sp. I larvae. I. Multiple-choice experiments in flume flows. Jour. Mar. Res. 50, 717–743

Grizzle, R. E., Short, F. T., Newell, C. R., Hoven, H., and Kindblom, L. (1996) Hydrodynamically induced synchronous waving of seagrasses: 'monami' and its possible effects on larval mussel settlement. Jour. Exp. Mar. Biol. Ecol. 206, 165–177.

Gross, T. F., Werner, F. E., and Eckman, J. E. (1992) Numerical modelling of larval settlement in turbulent bottom boundary layers. Jour. Mar. Res. 50, 611–642.

Hanisak, D. M. (1983) The nitrogen relationships of marine macroalgae, *in* Nitrogen in the Marine Environment (Carpenter, E. J., and Capone, D. G., eds.), p. 99–120.

Academic Press.

Harrison, S. J., and Phizacklea, A. P. (1987) Vertical temperature gradients in muddy intertidal sediments in the Forth estuary, Scotland. Limnol. Oceanogr. 32, 954–963.

Heathershaw, A. D., and Thorne, P. D. (1985) Seabed noises reveal role of turbulent bursting phenomenon in sediment transport by tidal currents. Nature 316, 339–342.

Hellberg, S., Sjöström, M., Skagerberg, B., and Wold, S. (1987) Peptide quantitative structure-activity relationships, a multivariate approach. Jour. Med. Chem. 30, 1126–1135.

Heller, D. Y. (1987) Sediment transport through seagrass beds. M.S. thesis, University of Virginia, Charlottesville.

Highsmith, R. C. (1982) Reproduction by fragmentation in corals. Mar. Ecol. Prog. Ser. 7, 207–226.

Hughes, T. P. (1984) Population dynamics based on individual size rather than age: a general model with a reef coral example. Amer. Natur. 123, 778–795.

Hurd, C. L., Harrison, P. J., and Druehl, L. D. (1996) Effect of seawater velocity on inorganic nitrogen uptake by morphologically distinct forms of *Macrocystis integrifolia* from wave-sheltered and exposed sites. Mar. Biol. 126, 205–214.

Hurd, C. L., Stevens, C. L., Laval, B., Lawrence, G. A., and Harrison, P. J. (1997) Visualization of seawater flow around morphologically distinct forms of the giant kelp *Macrocystis integrifolia* from wave-sheltered and exposed sites. Limnol. Oceanogr. 42, 156–163.

Jackson, G. A. (1984) Internal wave attenuation by coastal kelp stands. Jour. Phys. Oceanogr. 14, 1300–1306.

Jacoby, C. A. (1982) Behavioral responses of the larvae of *Cancer magister* Dana (1852) to light, pressure, and gravity. Mar. Behav. Physiol. 8, 267–283.

James, P. L., and Larkum, A. W. D. (1996) Photosynthetic Ci acquisition of *Posidonia australis.* Aquat. Bot. 55, 149–157.

Jeffery, G. B. (1922) The motion of ellipsoidal particles immersed in a viscous fluid. Proc. R. Soc. Lond. 102, 161–179.

Jonsson, P. R., André, C., and Lindegarth, M. (1991) Swimming behaviour of marine bivalve larvae in a flume boundary-layer flow: evidence for near-bottom confinement. Mar. Ecol. Prog. Ser. 79, 67–76.

Jumars, P. A., and Gallagher, E. D. (1982) Deep-sea community structure: three plays on the benthic proscenium, *in* The Environment of the Deep Sea (Ernst, W. G., and Morin, J. G., eds.), p. 217–285. Prentice-Hall, New York.

Jumars, P. A., Jackson, D. R., Gross, T. F., and Sherwood, C. (1996) Acoustic remote sensing of benthic activity: A statistical approach. Limnol. Oceanogr. 41, 1220–1241.

Kaandorp, J. A., Lowe, C. P., Frenkel, D., and Sloot, P. M. A. (1996) Effect of nutrient diffusion and flow on coral morphology. Phys. Rev. Lett. 77, 2328–2331.

Kalmijn, A. J. (1988) Detection of weak electric fields, *in* Sensory Biology of Aquatic Animals (Atema, J., Fay, R. R., Popper, A. N., and Tavolga, W. N., eds.), p. 151–186. Springer-Verlag, Heidelberg.

Kenworthy, W. J., Zieman, J. C., and Thayer, G. W. (1982) Evidence for the influence of seagrasses on the benthic nitrogen cycle in a coastal plain estuary near Beaufort, North Carolina (USA). Oecologia 54, 152–158.

Koch, E. W. (1993a) The effects of water flow on photosynthetic processes of the alga *Ulva lactuca* L. Hydrobiol. 260/261, 457–462.

Koch, E. W. (1993b) Hydrodynamics of flow through seagrass canopies: biological, physical and geochemical interactions. Ph.D. dissertation, University of South Florida, St. Petersburg.

Koch, E. W. (1994) Hydrodynamics, diffusion-boundary layers and photosynthesis of seagrasses *Thalassia testudinum* and *Cymodocea nodosa.* Mar. Biol. 118, 767–776.

Koch, E. W. (1996) Hydrodynamics of a shallow *Thalassia testudinum* bed in Florida, USA, *in* Seagrass Biology: Proceedings of an International Workshop (Kuo, J., Phillips, R. C., Walker, D. I., and Kirkman, H., eds.), p. 105–109. Weatern Australia Museum, Perth.

Koehl, M. A. R. (1986) Seaweeds in moving water: form and mechanical function, *in* On the Economy of Plant Form and Function (Givnish, T. J., ed.), p. 603–634. Cambridge University Press, Cambridge.

Koehl, M. A. R. (1996) When does morphology matter? Annu. Rev. Ecol. Syst. 27, 501–542.

Koehl, M. A. R., and Alberte, R. S. (1988) Flow, flapping and photosynthesis of *Nereocystis luetkeanna*: a functional comparison of undulate and flat blade morphologies. Mar. Biol. 99, 435–444.

Komatsu, T., and Murakami, S.-I. (1994) Influence of a *Sargassum* forest on the spatial distribution of water flow. Fish. Oceanogr. 3, 256–266.

Kraemer, G. P. and Chapman, D. J. (1991) Biomechanics and alginic acid composition during hydrodynamic adaptation by *Egregia menziesii* (Phaeophyta) juveniles. Jour. Phycol. 27, 47–53.

Larkum, A. W. D., Roberts, G., Kuo, J., and Strother, S. (1989) Gaseous movement in seagrasses, *in* Biology of Seagrasses (Larkum, A. W. D., McComb, A. J., and Shepherd, S. A., eds.), p. 686–722. Elsevier, New York.

Larned, S. T., and Atkinson, M. J. (1997) Effects of water velocity on NH_4^+ and PO_4^{3-} uptake and nutrient-limited growth in the macroalga *Dictyosphaeria cavernosa*. Mar. Ecol. Progr. Ser. 157, 295-302.

Lentz, S. J. (1987) A description of the 1981 and 1982 spring transitions over the northern California shelf. Jour. Geophys. Res. 92, 1545–1567.

Lesser, M. P., Weis, V. M., Patterson, M. R., and Jokiel, P. L. (1994) Effects of morphology and water motion on carbon delivery and productivity in the reef coral *Pocillopora damicornis* (Linnaeus): diffusion barriers, inorganic carbon limitation, and biochemical plasticity. Jour. Exp. Mar. Biol. Ecol. 178, 153–179.

Levin, L. A., and Huggett, D. V. (1990) Implications of alternative reproductive modes for seasonality and demography in an estuarine polychaete. Ecol. 71, 2191–2208.

Levin, L. A., and Thomas, C. L. (1989) The influence of hydrodynamic regime on infaunal assemblages inhabiting carbonate sediments on Central Pacific seamounts. Deep-Sea Res. 36, 1897–1915.

Levin, L. A., Caswell, H., DePatra, K. D., and Creed, E. L. (1987) Demographic consequences of larval development mode: Planktotrophy vs. lecithotrophy in *Streblospio benedicti*. Ecol. 68, 1877–1886.

Levin, L. A., Leithold, E. L., Gross, T. F., Huggett, C. L., and DiBacco, C. (1994) Contrasting effects of substrate mobility on infaunal assemblages inhabiting two high-energy settings on Fieberling Guyot. Jour. Mar. Res. 52, 489–522.

Levinton, J. S. (1971) Control of tellinacean (Mollusca: Bivalvia) feeding behavior by predation. Limnol. Oceanogr. 16, 660–662.

Levitan, D. R. (1991) Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. Biol. Bull. 181, 261–268.

Levitan, D. R. (1995) The ecology of fertilization in free-spawning invertebrates, *in* Ecology of Marine Invertebrate Larvae (McEdward, L., ed.), p.123–156. CRC Press, New York.

Lewis, J. R. (1963) Environmental and tissue temperatures of some tropical intertidal marine animals. Biol. Bull. 124, 277–284.

Little, C., and Nix, W. (1976) The burrowing and floating behavior of the gastropod *Hydrobia ulvae*. Estuar. Coastal Mar. Sci. 4, 537–544.

Little, K. T. and Epifanio, C. E. (1991) Mechanism for the reinvasion of the estuary by two species of brachyuran megalopae. Mar. Ecol. Prog. Ser. 68, 235–242.

Long, C. E. (1981): A simple model for time-dependent, stably stratified turbulent boundary layers. Department of Oceanography, University of Washington, Special Report No. 95, Seattle.

Lonsdale, P., Normark, W. R., and Newman, W. A. (1972) Sedimentation and erosion on Horizon Guyot. Geol. Soc. Amer. Bull. 83, 289–316.

Lucas, W. L. (1983) Photosynthetic assimilation of exogenous HCO_3^- by aquatic plants.

Ann. Rev. Plant Physiol. 34, 71–104.

Ludden, E., Admiraal, W. and Colijn, F. (1985) Cyclying of carbon and oxygen in layers of marine microphytes; a simulation model and its eco-physiological implications. Oecologia 66, 50–59.

Madsen, T. V., and Warnke, E. (1983) Velocities of currents around and within submerged aquatic vegetation. Arch. Hydrobiol. 97, 389–394.

Mafra-Neto, A., and Cardé, R. T. (1995) Effect of the fine-scale structure of pheromone plumes: pulse frequency modulates activation and upwind flight of almond moth males. Phys. Entomol. 20, 229–242.

Mann, R. (1985) Seasonal changes in the depth distribution of bivalve larvae on the Southern New England Shelf. Jour. Shellfish Res. 5, 57–64.

Mann, R. and Wolfe, C. C. (1983) Swimming behavior of larvae of the ocean quahog *Arctica icelandica* in response to pressure and temperature. Mar. Ecol. Prog. Ser., 13, 211–218.

Mann, R., Campos, B. M., and Luckenbach, M. W. (1991) Swimming rate and responses of larvae of three mactrid bivalves to salinity discontinuities. Mar. Ecol. Prog. Ser. 68, 257–269.

Martel, A., Mathieu, A. F., Findlay, C. S., Nepszy, S. J., and Leach, J. H. (1994) Daily settlement rates of the Zebra mussel, *Dreissena polymorpha*, on an artificial substrate correlate with veliger abundance. Can. Jour. Fish. Aquat. Sci. 51, 856–861.

Matthiessen, G. C. (1960) Intertidal zonation in populations of *Mya arenaria*. Limnol. Oceanogr. 5, 381–388.

Mauchline, J. (1980) The biology of mysids and euphausiids. Adv. Mar. Biol. 18, 1–681.

McCall, P. L. (1978) Spatial-temporal distributions of Long Island Sound infauna: the role of bottom disturbance in a nearshore marine habitat, *in* Estuarine Interactions (Wiley, M. L., ed.), p.191–220. Academic Press, New York.

McCall, P. L., and Soster, F. M. (1990) Benthos response to disturbance in Western Lake Erie: regional faunal surveys. Can. Jour. Fish. Aquat. Sci. 47, 1996–2009.

McKnight, D. G. (1969) A recent, possibly catastrophic burial in a marine molluscan community. New Zealand Jour. Mar. Freshw. Res. 3, 177–179.

McNair, J. N., Newbold, J. D., and Hart, D. D. (1997) Turbulent transport of suspended particles and dispersing benthic organisms: How long to hit bottom? Jour. Theor. Biol. 188, 29–52

Middleton, G. V., and Southard, J. B. (1984) Mechanics of Sediment Transport, 2nd ed. Society of Economic Paleontologists and Mineralogists, Tulsa, OK.

Miller, M. C., McCave, I. N., and Komar, P. D. (1977) Threshold of sediment motion under unidirectional currents. Sedimentol. 24, 507–527.

Millhouse, J., and Strother, S. (1986) Salt-stimulated bicarbonate-dependent photosynthesis in the marine angiosperm *Zostera muelleri.* Jour. Exp. Mar. Bot. 37, 965–976.

Moore, P. A., and Atema, J. (1988) A model of a temporal filter in chemoreception to extract directional information from a turbulent odor plume. Biol. Bull. 174, 355–363.

Morgan, S. G. (1995) The timing of larval release, *in* Ecology of Marine Invertebrate Larvae (McEdward, L., ed.), p.157–192. CRC Press, New York.

Mork, M. (1996) The effect of kelp in wave damping. Sarsia 80, 323–327.

Murray, J. A., and Willows, A. O. D. (1996) Function of identified nerves in orientation to water flow in *Tritonia diomedea.* Jour. Comp. Physiol. A 178, 201–209.

Niklas, K. J. (1992). Plant Biomechanics. University of Chicago Press, Chicago.

Noble, M., and Mullineaux, L. S. (1989) Internal tidal currents over the summit of Cross Seamount. Deep-Sea Res. 36, 1791–1802.

Nowell, A. R. M., and Jumars, P. A. (1984) Flow environments of aquatic benthos. Ann. Rev. Ecol. Syst. 15, 303–328.

Nowell, A. R. M., and Jumars, P.A. (1987) Flumes: theoretical and experimental considerations for simulation of benthic environments. Oceanogr. Mar. Biol. Ann. Rev.

25, 91–112.

Ockelmann, K. W., and Vahl. O. (1970) On the biology of the polychaete *Glycera alba*, especially its burrowing and feeding. Ophelia 8, 275–294.

Ólafsson, E. B., Peterson, C. H., and Ambrose, W. G., Jr. (1994) Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. Oceanogr. Mar. Biol. Ann. Rev. 32, 65–109.

Olmi, E. J., III (1994) Vertical migration of blue crab *Callinectes sapidus* megalopae: Implications for transport in estuaries. Mar. Ecol. Progr. Ser. 113, 39–54.

O'Riodan, C. A., Monismith, S. G., and Koseff, J. R. (1993) A study of concentration boundary-layer formation over a bed of model bivalves. Limnol. Oceanogr. 38, 1712–1729

Oug, E. (1980) On feeding and behaviour of *Ophiodromus flexuosus* (Delle Chiaje) and *Nereimyra punctata* (O.F. Müller) (Polychaeta, Hesionidae). Ophelia 19, 175–191.

Paine, R. T. (1986) Benthic community-water column coupling during the 1982–1983 El Niño: are community changes at high latitudes attributable to cause or coincidence? Limnol. Oceanogr. 31, 351–360.

Paine, R. T., and Levin, S. A. (1981) Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monogr. 51, 145–178.

Palmer, M. A. (1984) Invertebrate drift: behavioral experiments with intertidal meiobenthos. Mar. Behav. Physiol. 10, 235–253.

Palmer, M. A. (1988) Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. Mar. Ecol. Prog. Ser. 48, 81–91.

Palmer, M. A., and Gust, G. (1985) Dispersal of meiofauna in a turbulent tidal creek. J. Mar. Res. 43, 179–210.

Parker, H. S. (1981) Influence of relative water motion on the growth, ammonium uptake and carbon and nitrogen composition of *Ulva lactuca* (Chlorophyta). Mar. Biol. 63, 309–318.

Pascual, M., and Caswell, H. (1991) The dynamics of a size-classified benthic population with reproductive subsidy. Theor. Pop. Biol. 39, 129–147.

Paulin, M. G. (1995) Electroreception and the compass sense of sharks. Jour. Theor. Biol. 174, 325–339.

Pawlik, J. R. (1986) Chemical induction of larval settlement and metamorphosis in the reef-building tube worm *Phragmatopoma californica* (Sabellariidae: Polychaeta). Mar. Biol. 91, 59–68.

Pawlik, J. R. (1992) Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr. Mar. Biol. Ann. Rev. 30, 273–335

Pawlik, J. R., and Faulkner, D. J. (1986) Specific free fatty acids induce larval settlement and metamorphosis of the reef-building tube worm *Phragmatopoma californica* (Fewkes). Jour. Exp. Mar. Biol. Ecol. 102, 301–310

Pennington, J. T. (1985) The ecology of fertilization of echinoid eggs: The consequence of sperm dilution, adult aggregation, and synchronous spawning. Biol. Bull. 169, 417–430.

Pline, M., Diez, J. A., and Dusenbery, D. B. (1988) Extremely sensitive thermotaxis of the nematode *Meloidogyne incognita*. Jour. Nematol. 20, 605–608.

Posey, M, Lindberg, W., Alphin, T., and Vose, F. (1996) Influence of storm disturbance on an offshore benthic community. Bull. Mar. Sci. 59, 523–529.

Possingham, H. P., and Roughgarden, J. (1990) Spatial population dynamics of a marine organism with a complex life cycle. Ecol. 71, 973–985.

Powell, G. V. N., and Schaffner, F. C. (1991) Water trapping by seagrasses occupying bank habitats in Florida Bay. Estuar. Coast. Shelf Sci. 32, 43–60.

Prins, H. B. A., Snel, J. F. H., Zanstra, P. E., and Helder, R. J. (1982) The mechanism of bicarbonate assimilation by the polar leaves of *Potamogeton* and *Elodea*. CO_2 concentrations at the leaf surface. Plant Cell Environ. 5, 207–214.

Raven, J. A. (1992) How benthic macroalgae cope with flowing freshwater: resource acquisition and retention. Jour. Phycol. 28, 133–146.

Rees, E. I. S., Nicholaidou, A., and Laskaridou, P. (1977) The effects of storms on the dynamics of shallow water benthic associations, *in* Biology of Benthic Organisms (Keegan, B. F., Ceidigh, P. O., and Boaden, P. J. S., eds.), p.465–474. Pergamon Press, New York.

Reid, R. G. B., and Reid, M. (1974) The carnivorous habit of members of the septibranch genus *Cuspidaria* (Mollusca: Bivalvia). Sarsia 56, 47–56.

Rhoads, D. C. (1974) Organism-sediment relations on the muddy sea floor. Oceanogr. Mar. Biol. Ann. Rev. 12, 263–300.

Rhoads, D. C., Boesch, D. F., Zhican, T., Fengshan, X., Liqiang, H., and Nilsen, K. J. (1985) Macrobenthos and sedimentary facies on the Changjiang delta platform and adjacent continental shelf, East China Sea. Cont. Shelf Res. 4, 189–213.

Rittschof, D., Branscomb, E. S., and Costlow, J. D. (1984) Settlement and behavior in relation to flow and surface in larval barnacles, *Balanus amphitrite* Darwin. Jour. Exp. Mar. Biol. Ecol. 82, 131–146.

Rodeau, H. C. (1996) Stochastic Lagrangian models of turbulent diffusion. Meteor. Monogr. 26, 1–84.

Rodgers, S. A., and Bingham, B. L. (1996). Subtidal zonation of the holothurian *Cucumaria lubrica* (Clark). Jour. Exp. Mar. Biol. Ecol. 204, 113–129.

Roe, P. (1976) Life history and predator-prey interactions of the nemertean *Paranemertes peregrina* Coe. Biol. Bull. 150, 80–106.

Roughgarden, J., Iwasa, Y., and Baxter, C. (1985) Demographic theory for an open marine population with space-limited recruitment. Ecol. 66, 54–67.

Roughgarden, J., Gaines, S., and Possingham, H. (1988) Recruitment dynamics in complex life cycles. Science 241, 1460–1466.

Scoffin, T. P. (1970) The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. Jour. Sed. Petrol. 40, 249–273.

Serrao, E. A., Pearson,G., Kautsky, L., and Brawley, S. H. (1996) Successful external fertilization in turbulent environments. Proc. Natl. Acad. Sci. USA 93, 5286–5290.

Seymour, R. J. (1996) Effects of Southern California kelp beds on waves. J. Waterw. Port Coast. Ocean Engineer. 122, 207–208.

Shanks, A. L. (1995) Mechanisms of cross-shelf dispersal of larval invertebrates and fish, *in* Ecology of Marine Invertebrate Larvae (McEdward, L., ed.), p. 323–368. CRC Press, New York.

Sigurdsson, J. B., Titman, C. W., and Davies, P. A. (1976) The dispersal of young post-larval bivalve molluscs by byssus threads. Nature 262, 386–387

Sjötun, K., and Fredriksen, S. (1995) Growth allocation in *Laminaria hyperborea* (Laminariales, Phaeophyceae) in relation to age and wave exposure. Mar. Ecol. Progr. Ser. 126, 213–222.

Smith, F. A. (1985) Biological occurrence and importance of HCO_3^-–utilizing systems: macroalgae (Charophytes), *in* Inorganic Carbon Uptake by Aquatic Photosynthetic Organisms (Lucas, W. J., and Berry, J. A., eds.), p. 1–15. Amer. Soc. Plant Phys., Rockville, Md.

Smith, F. A., and Walker, N. A. (1980) Photosynthesis by aquatic plants: effects of unstirred layers in relation to assimilation of CO_2 and HCO_3^- and to carbon isotopic discrimination. New Phytol. 86, 245–259.

Sörlin, T. (1988) Floating behavior of the tellinid bivalve *Macoma balthica* (L.). Oecologia 77, 273–277.

Sousa, W. P. (1985) The role of disturbance in natural communities. Ann. Rev. Ecol. Syst. 15, 353–391.

Stevens, C. L., and Hurd, C. L. (1997) Boundary-layers around bladed aquatic macrophytes. Hydrobiol. 346, 119–128.

Stoll, R. D. (1989) Sediment Acoustics. Springer-Verlag, Heidelberg.

Tamburri, M. N., Zimmer-Faust, R. K., and Tamplin, M. L. (1992) Natural sources and properties of chemical inducers mediating settlement of oyster larvae: a re-examination. Biol. Bull. 183, 327–338.

Tankersley, R. A., and Forward, R. B., Jr. (1994) Endogenous swimming rhythms in estuarine crab megalopae: implications for flood-tide transport. Mar. Biol. 118, 415–423.

Thistle, D. (1988) A temporal difference in harpacticoid-copepod abundance at a deep-sea site: caused by benthic storms? Deep-Sea Res. 35, 1015–1020.

Thistle, D., Ertman, S. C., and Fauchald, K. (1991) The fauna of the HEBBLE site: patterns in standing stock and sediment-dynamic effects. Mar. Geol. 99, 413–422.

van Keulen, M. (1997) Water Flow in Seagrass Ecosystems, Ph.D. thesis, Murdoch University, Australia.

Vogel, S. (1994) Life in Moving Fluids, 2nd ed. Princeton University Press, Princeton, N.J.

Walters, L. J. (1992) Field settlement locations on subtidal marine hard substrata: is active larval exploration involved? Limnol. Oceanogr. 37, 1101–1107.

Weissburg, M. J., and Zimmer-Faust, R. K. (1994) Odor plumes and how blue crabs use them in finding prey. Jour. Exp. Mar. Biol. Ecol. 197, 349–375.

Wheeler, W. N. (1980) Effect of boundary layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. Mar. Biol. 55, 103–110.

Williams, A. B., and Porter, H. J. (1971) A ten-year study of meroplankton in North Carolina estuaries: occurrence of postmetamorphal bivalves. Chesapeake Sci. 12, 26–32.

Williams, J. D., et al. (1992) Amino acid profiles and liposomes: their role as chemosensory information carriers in the marine environment. Jour. Chem. Ecol. 18, 2107–2115.

Wing, S. R., and Patterson, M. R. (1993) Effects of wave-induced lightflecks in the intertidal zone on photosynthesis in the macroalgae *Postelsia palmaeformis* and *Hedophyllum sessile* (Phaeophyceae). Mar. Biol. 116, 519–525.

Wood, L., and Hargis, W. J., Jr. (1971) Transport of bivalve larvae in a tidal estuary, *in* Fourth European Marine Biology Symposium (Crisp, D. J., ed.), p. 29–44. Cambridge University Press, Cambridge.

Woodin, S. A. (1986) Settlement of infauna: larval choice? Bull. Mar. Sci. 39, 401–407.

Woodin, S. A. (1991) Recruitment of infauna: Positive or negative cues? Amer. Zool. 31, 797–807.

Woodin, S. A., Marinelli, R. L., and Lincoln, D. E. (1993) Allelochemical inhibition of recruitment in a sedimentary assemblage. Jour. Chem. Ecol. 19, 517–530.

Woodin, S. A., Marinelli, R. L., and Lindsay, S. M. (1998) Process-specific cues for recruitment in sedimentary environments: Geochemical signals? Jour. Mar. Res. 56, 535-558.

Woodin, S. A., Wethey, D. S. and Lindsay, S. M. (1995) Process specific recruitment cues in marine sedimentary systems. Biol. Bull. 189, 49–58

Worcester, S. E. (1995) Effects of eelgrass beds on advection and turbulent mixing in low current and low shoot density environments. Mar. Ecol. Progr. Ser. 126, 223–232.

Yalin, M. S. (1977) Mechanics of Sediment Movement, 2nd ed. Pergamon Press, New York.

Yund, P. O., Gaines, S. D., and Bertness, M. D. (1991) Cylindrical tube traps for larval sampling. Limnol. Oceanogr. 36, 1167-1177

Zimmer-Faust, R. K., Finelli, C. M., Pentcheff, N. D., and Wethey, D. S. (1995) Odor plumes and animal navigation in turbulent water flow: a field study. Biol. Bull. 188, 111–116.

Zimmer-Faust, R. K., Stanfill, J. M., and Collard, S. B., III (1988) A fast, multichannel fluorometer for investigating aquatic chemoreception and odor trails. Limnol. Oceanogr. 33, 1586–1595.