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Diffusion and Ecological Problems: Modern Perspectives

Second Edition

With 114 Illustrations

2002



Springer

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Passive Diffusion in Ecosystems

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Preface: *In writing this revision, we endeavored to include information and directions contained in Akira's notes. He suggested most of the new sections, and we included other new ones based on our understanding of his interests and scientific concerns. We dedicate this effort to a teacher, advisor, mentor, and friend.*

JDA would like to acknowledge the assistance of Julia Bolton for her efforts in many aspects of this work, Trent Hoover for rendering crude sketches into figures, Nicole Bock of the Interlibrary loan office for ordering the mountains of articles, and NSERC for research support. DPS would like to acknowledge the assistance of Karin Limburg, who made helpful comments on sections of the manuscript, and Christoph Humborg, Sven Blomqvist, and Christopher Post, who suggested several references and helped with the literature search.

In this chapter we consider several aspects of passive diffusion in the environment. In this book, *passive diffusion* is defined to be the diffusion of chiefly abiotic objects that are not capable of performing random motion without the help of environmental turbulence. Likewise, *active diffusion* is defined to be the diffusion of objects, chiefly animals, that perform motion by themselves.

Wolfenbarger (1975) introduced the following definition: When transportation is supplied by energy from within the organism, the dispersion is termed "active", and when it is supplied by energy from outside the body, the dispersion is called "passive".

The smaller the organism, the more it is subject to the effect of environmental turbulence. Thus, the diffusion of small animals should be considered as partly passive and partly active. For instance, bacteria and pollen in the air and phytoplankton in the water diffuse almost passively, while many insects in flight undergo varying proportions of passive and active diffusion, according to the degree of movement of the environmental fluid.

Theories of turbulent diffusion are expected to hold approximately for organisms that diffuse in an essentially passive manner. In this case, however, attention must be paid to the fact that, depending on the organism's size, certain components (i.e., small-scale motions of the environmental turbulence) will not be effective agents of dispersion. The effect of falling or

rising must be considered when the density of the organism differs significantly from that of the surrounding medium. Moreover, given sufficient time, behavioral responses of small organisms, including phototaxis and geotaxis, may lead to patterns of dispersion that differ from that of the fluid. Remember that dispersion in turbulent fluids is both directional and random: (1) directional in the direction of advection of the fluid; and (2) random or chaotic-like within the eddies associated with the turbulence.

3.1 Diffusion Within and Above Plant Canopies

Plant canopies are of particular importance in the ecology of many organisms, in that they provide structure, habitat, shelter, and resources (Russell et al., 1989). For example, one need only consider that most of the principal agricultural crops are species that form canopies (Heiser, 1990) to understand the implications to human societies. Plant canopies modify local environments and thereby provide the constituent elements for the formation of terrestrial (e.g., grasslands, forests) and aquatic ecosystems (e.g., marshes, weed beds, kelps). While many of the fluid dynamic factors related to diffusion within and above plant canopies (Raupach and Thom, 1981; Raupach et al., 1991; Finnigan, 2000) are similar regardless of the environment, there are sufficient differences such that both terrestrial and aquatic ecosystems are treated separately here.

3.1.1 Terrestrial Plant Canopies

The wind distribution above plant canopies, when the atmosphere is neutrally stable, is represented by a modified logarithmic law (i.e., the law of the wall; refer to Sect. 2.6.1),

$$u(z) = \frac{u_*}{k} \ln \left\{ \frac{z-d}{z_0} \right\}, \quad z > H > d + z_0. \quad (3.1)$$

This form accounts for the roughness of the surface and displacement of flow due to the presence of plants (Inoue, 1963; Thom, 1975; Grace, 1977); H is the mean plant height, d is called the datum-level displacement, or zero plane displacement, and the other quantities were already defined in Sect. 2.6.1. The wind expressed in (3.1) is a mean quantity; thus, it should have been written \bar{u} . The overbar is omitted for simplicity, a convention that is used frequently throughout this book.

Expression (3.1) provides a model for the boundary layer above the plant canopy. The canopy boundary layer can be subdivided into (1) a *roughness sublayer* extending 1 to $2H$ from the top of the canopy, (2) an *inertial* or *logarithmic sublayer* above the smaller *roughness sublayer*, and (3) an *outer sublayer* that extends to the region where u approaches the free-stream velocity within that region of the planetary boundary layer (i.e., that region

within ≈ 1 km of the earth's surface). Typically, velocity measurements made within the inertial sublayer can be used to estimate u_* , d , and z_0 (e.g., Monteith and Unsworth, 1990).

As a rule of thumb for a typical agricultural crop, the roughness parameter, z_0 , is 10% of the length of the surface protuberances, and the zero plane displacement, d , is 60% to 70% of the height of the plant (Grace, 1977). Takeda (1965, 1966) derived a theoretical relation between d and z_0 . Later, Maki (1969, 1976) extended the concept to obtain a new relationship, which better fits the data taken from various canopies with different leaf-area indexes. Numerical investigations confirmed these results and included the effects of the density and distribution of vegetation within the canopy on d and z_0 (Shaw and Pereira, 1982). Both d and z_0 show some dependence on wind speed since the canopy is distorted and smoothed with increasing wind speed (Finnigan and Mulhearn, 1978). Some empirically determined values for z_0 range from 0.1 to 9 cm for mowed and 50-cm-long grass canopies, to greater than 120 cm for coniferous forests (Campbell and Norman, 1998).

Within the plant canopy, on the other hand, we must make allowance for the resistance of plant leaves to the wind. By analogy to the law of resistance of an object placed in a field of turbulence (Tani, 1951; Imai, 1970; Prandtl and Tietjens, 1957), the plant resistance per unit volume, F , may be given by

$$F = \frac{1}{2} C_d B \rho u^2, \quad (3.2)$$

where C_d is a resistance coefficient, B is the leaf-area density (i.e., leaf area per unit volume), and ρ is the density of air.

This resistance force balances the vertical variation of the tangential shearing stress due to the wind, τ . We thus have

$$\frac{d\tau}{dz} = \frac{1}{2} C_d B \rho u^2. \quad (3.3)$$

According to turbulent transport theory (Hinze, 1959; Ogura, 1955), the stress can be expressed as

$$\tau = \rho A_v \frac{du}{dz} \quad (3.4)$$

with the use of the eddy viscosity A_v . The mixing-length concept gives

$$A_v = \ell_z^2 \left| \frac{du}{dz} \right|, \quad (3.5)$$

where ℓ_z is the mixing length (Hinze, 1959).

Substituting (3.4) and (3.5) into (3.3), we obtain

$$\frac{d}{dz} \left\{ \ell_z^2 \left(\frac{du}{dz} \right)^2 \right\} = \frac{1}{2} C_d B u^2. \quad (3.6)$$

While a degree of uncertainty remains about whether or not the concept behind (3.3)–(3.5) is valid within terrestrial plant canopies (Saito et al., 1970), some success has been achieved in submerged macrophyte canopies (Ackerman and Okubo, 1993; see below).

Inoue (1963) solved (3.6) assuming that, for plant communities where the foliage distribution is reasonably uniform, ℓ_z is constant except in the immediate vicinity of the ground. The result is

$$u = u_H \exp\left\{-\alpha\left(1 - \frac{z}{H}\right)\right\}, \quad (3.7)$$

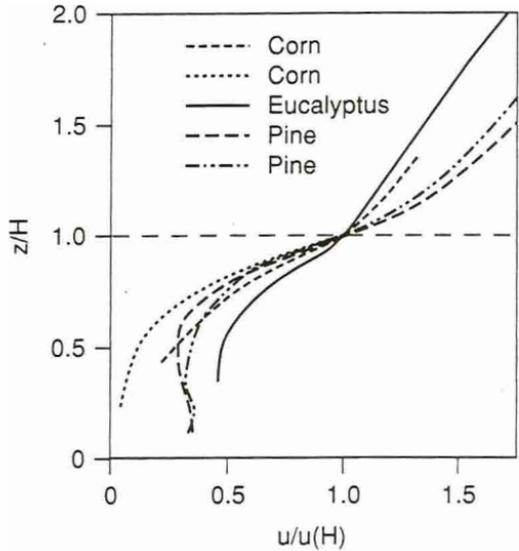
where u_H is the wind velocity at the “height” (top) of the plant canopy $z = H$, and α is an attenuation coefficient defined by $\alpha = H(C_d B/2\ell_z^2)^{1/2}$. Wind profiles within a corn canopy observed by Shaw et al. (1974) agree well with (3.7), with an α -value of about 2.2. The wind velocity within the canopy thus decreases exponentially toward the ground. A logarithmic profile will develop immediately above the ground with new d - and z_0 -values characteristic of the soil.

Cionco (1965) computed a mixing-length solution, which showed that the mixing length ℓ_z was nearly constant throughout most of the canopy’s vertical extent; this lends support to Inoue’s hypothesis. Cionco developed a refined model (Cionco, 1965), which takes into account the variation of ℓ_z in the vicinity of the ground, and found that the simulated canopy wind profiles agree quite well with the observed canopy wind data from a cornfield. Other wind profiles, which are more or less similar to each other, have been proposed. Thus, Landsberg and James (1971) semiempirically derived an analytical form for wind profile which is the same as Thom’s (1971). Equation (3.6) can also be applied to the top portion (e.g., within 30%–40%) of canopies with nonuniformly distributed vegetation (e.g., trees; Campbell and Norman, 1998).

Kondo and Akashi (1976) developed a model for two-dimensional horizontal flow in canopy layers which includes the pressure gradient and Coriolis forces.

The structure of *turbulence* in plant canopies has been the object of much study. Some typical velocity profiles obtained from studies within wind tunnels, crops, and forests are presented in Fig. 3.1. The figure shows a point of inflection in the normalized velocity at the top of the canopy ($z/H = 1$). The (1) inflection point, (2) negative skewness in the vertical direction and positive skewness in the horizontal velocity components, and (3) integral length scales on the order of H appear to be consistent features of the turbulence with plant canopies (Finnigan and Brunet, 1995). Historically, it was believed that the high level of turbulence in canopies was the result of the eddy shed downstream of the vegetation. Recent advances in sensors, fluid dynamic modeling including Lagrangian models and higher-order closures of wind field, have led to the conclusion that large-scale, intermittent turbulent eddies are responsible for the transfer of momentum in canopies (Finnigan and

FIGURE 3.1. Velocity profiles through model, cereal, and forest canopies (after Finnigan and Brunet, 1995).



Brunet, 1995). It would appear that turbulence within and just above the canopy is characterized as a region with a broad and continuous eddy spectrum.

Three ranges of eddy vertical length scales (L_w) are of importance: (1) eddies with $L_w \gg H$, the canopy height; (2) eddies with $L_w \sim H$; and (3) eddies with $L_w \ll H$. The largest eddies provide little to the vertical mixing in the canopy, in contrast to eddies of $L_w \sim H$, which contribute most of the momentum transfer. This can best be seen in Fig. 3.2, which depicts the energy spectrum within the canopy as a function of κ , the wavenumber. The principal peak in energy is due to shear production at κ on the order of the reciprocal of the Eulerian length scale (i.e., $1/H$), and these are followed by a cascade, i.e., $\kappa^{-5/3}$, due to viscous dissipation beyond the Kolmogorov microscale ($\lambda = \text{mm}$). The canopy-scale eddies that lead to shear production also cause the *honami* (*ho* = cereal, *nami* = wave; Inoue, 1955) or cowlick patterns observed in cereal fields on windy days. Honami are generated by downward gusts (eddies), whose energy is transferred to the plants through drag, which result in the transfer of momentum (i.e., shear production). After the gust passes, the plants rebound from their deflected position due to the mechanical properties of their tissues and oscillate leading to the waving phenomena (Finnigan, 1979a, b). Honami may contribute to a more rapid dissipation of energy in the canopy (i.e., spectral shortcut in Fig. 3.2) through the splitting of eddies in the wakes of plant materials (i.e., stem wake turbulence) and the oscillatory motion; however, this contributes relatively little to the overall momentum transfer in the canopy (Raupach et al., 1996).

The various, and sometimes deleterious, effects of winds and turbulence

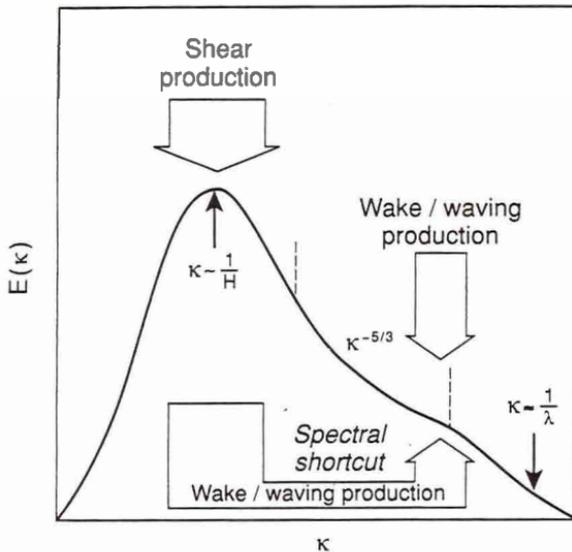


FIGURE 3.2. Schematic diagram of the energy spectrum E through plant canopies as a function of κ , the wavenumber. H : canopy height, λ : Kolmogorov microscale (after Finnigan and Brunet, 1995).

on the mechanics, physiology, ecology, and management of trees have been addressed in a recent multidisciplinary volume (Coutts and Grace, 1995).

Of late, Finnigan and Brunet (1995) suggested that the fluid dynamic interactions—specifically, the active turbulence and coherent motions—near the top of canopies are characteristic of a *plane mixing layer*. The *plane mixing layer* model appears to explain many features associated with canopy turbulence better than boundary layer models (Raupach et al., 1996). Turbulent flow below the top portion of the canopy is less well defined and is a function of the vegetation density profile (i.e., leaf-area density), especially in canopies that are nonuniform in this regard. For more details on the development of ideas related to the turbulence in plant canopies, readers may consult Cionco (1972), Kawatani and Meroney (1970), Baines (1972), Saito et al. (1970), Isobe (1972), Arkin and Perrier (1974), Shaw et al. (1974), Grace (1977), Seginer et al. (1976), Raupach and Thom (1981), Raupach et al. (1991, 1996), Finnigan and Brunet (1995), and Finnigan (2000), among others.

A discussion of the diffusion of CO_2 within canopies may commence with (2.16). For the interior of the plant canopy, away from its periphery, we may ignore the horizontal advection and diffusion of CO_2 and the vertical advective flow. Only the vertical diffusion and nonconservative processes become relevant to the problem. We thus have

$$\frac{\partial S}{\partial t} = \frac{\partial}{\partial z} \left(K_z \frac{\partial S}{\partial z} \right) - (\epsilon I - r)B, \quad (3.8)$$

where S, ε, I , and r denote, respectively, the CO_2 concentration, photosynthetic efficiency, incident light intensity, and respiration rate (Inoue, 1965). The last term of (3.8) provides an appropriate expression of \bar{R} in (2.16) for the problem of concern.

For steady-state conditions, (3.8) yields

$$\frac{\partial}{\partial z} \left(K_z \frac{\partial S}{\partial z} \right) = (\varepsilon I - r)B. \quad (3.9)$$

Inoue (1965), assuming that K_z is equal to A_v and that l_z is constant, and using the wind profile (3.7) obtained from (3.5)

$$K_z = K_H \exp \left\{ -\alpha \left(1 - \frac{z}{H} \right) \right\} \quad (3.10)$$

where K_H is the value of K_z at the height of the plant canopy, i.e., at $z = H$. Furthermore, if the leaf-area density is invariant with height, Inoue (1965) gives the incident light intensity as

$$I = I_H \exp \left\{ -\beta \left(1 - \frac{z}{H} \right) \right\}, \quad (3.11)$$

where I_H is the incident light intensity at height H , and β is a constant of light attenuation that depends on the leaf-area density.

In the upper part of plant canopies, the photosynthetic rate is assumed to overcome the rate of respiration, i.e., $\varepsilon I \gg r$. Neglecting r compared with εI in (3.9)–(3.11), we integrate (3.9) to obtain

$$S = S_H - \frac{H^2 \varepsilon B I_H}{\beta(\beta - \alpha) K_H} \left[1 - \exp \left\{ -(\beta - \alpha) \left(1 - \frac{z}{H} \right) \right\} \right],$$

where S_H is the CO_2 concentration at height H .

In the lower part of plant canopies, on the other hand, the respiration overcomes the photosynthesis, i.e., $r \gg \varepsilon I$, and we may neglect the term εI . We also neglect the height variation of K_z , i.e., $K_z = \text{constant}$. The solution of (3.9) is then given by

$$S = S_0 - \frac{J_0}{K_z} z - \frac{rB}{2K_z} z^2,$$

where S_0 is the concentration of CO_2 at the ground, $z = 0$, and J_0 is the flux of CO_2 through the ground due to soil respiration: $J_0 = -(K_z \partial S / \partial z)_{z=0}$. (Note that (3.9) in combination with (3.10) and (3.11) can be integrated in general without Inoue's assumption.)

Figure 3.3 shows examples of vertical profiles of CO_2 within crop canopies. The concentration of CO_2 increases upward in the upper part of the canopy, and it also increases downward in the lower part of the canopy. The increase toward the ground is due both to plant respiration and to the supply

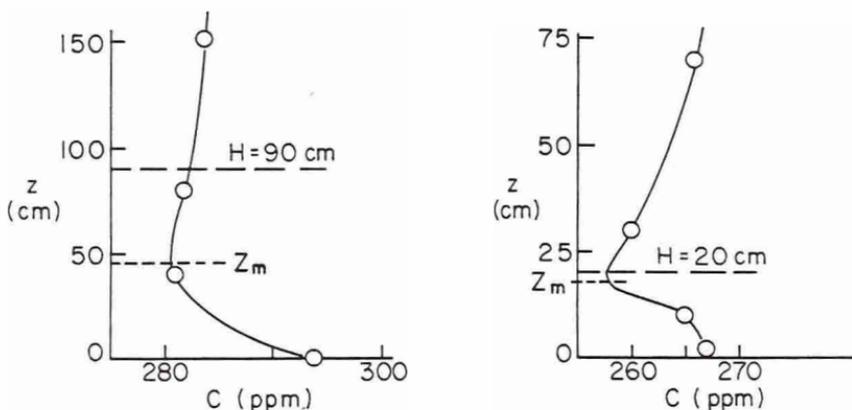


FIGURE 3.3. Vertical profiles of carbon dioxide within and above crop canopies. C: CO₂ concentration, z: height, H: plant height, z_m: height of minimum CO₂ (Inoue, 1965).

of CO₂ from soil respiration. The minimum concentration of CO₂ is found to be within the canopy at $z = z_m$. The compensation height, $z = z_c$, where the photosynthetic assimilation balances the rate of respiration, is seen to be below the height of minimum concentration (Noble, 1983).

There are one direct and two indirect methods for determining CO₂ fluxes (or other scalars) above and within the top portions of uniform canopies (Monteith and Unsworth, 1990). The direct method known as *eddy correlation* involves considerable sophistication in the simultaneous measurement of velocity and CO₂ fluctuations (i.e., turbulence) at small spatial and temporal scales (e.g., Katul et al., 1998). The indirect methods include (1) the *aerodynamic method* proposed by Inoue et al. (1958), which uses measurements of CO₂ concentrations at two heights and an integral exchange coefficient that depends on the wind profile and the stability of a column of air to determine the flux, and (2) the *Bowen ratio method*, which uses an energy balance model (e.g., heat balance) to estimate the flux. The aerodynamic method is advantageous in estimating the CO₂ flux, and accordingly the photosynthetic fixation of CO₂ by plants, without artificial disturbances to the plant and environment. Since the introduction of the aerodynamic method, Japanese scientists at the National Institute of Agricultural Sciences in Tokyo have made much progress in developing more advanced methods (Inoue et al., 1968; Uchijima, 1970; Uchijima et al., 1970; Uchijima and Inoue, 1970). Barring limitations in the measurement of some types of scalars (Percy et al., 1989), recent advances in electronics, remote sensing, and statistical measurements of turbulence may lead to dominance of the direct method (i.e., eddy correlation; Finnigan and Brunet, 1995; Raupach et al., 1996).

3.1.2 Aquatic Plant Canopies

A number of different experimental and theoretical approaches have been applied to the study of water flow above and within aquatic plant or macrophyte canopies. This is due, in part, to the taxonomic (e.g., algae, pteridophytes, angiosperms) and morphological diversity of macrophytes, which include (1) emergent canopies where the top of the canopy is exposed to the atmosphere (e.g., rushes and marsh grasses), (2) submerged canopies of marine and freshwater plants (e.g., pondweeds and seagrasses), and (3) submerged kelp forests. It is intriguing to postulate analogies between pondweeds/seagrasses and cereals, and between kelps and trees, but the fluid media pose important constraints (Denny, 1993) related directly to the attenuation and, therefore, the acquisition of light (Niklas, 1997). By necessity, terrestrial plants are composed of mechanically reinforced structures that act against gravity, whereas aquatic plants are flexible organisms that use specialized gas-filled tissues (e.g., lacuna, aerenchyma, pneumatocysts) as a means of buoyancy. Notwithstanding these differences in growth form, in general, the study of water flow and turbulence above and within macrophyte canopies is less developed than what was observed above for terrestrial plant canopies.

We will begin our discussion of flow within and above macrophyte canopies by examining the kelps, which can form forests many tens of meters tall (up to 47.5 m!). Kelps create important ecosystems in coastal temperate waters. One of the largest kelp forests (*Macrocystis pyrifera*) is about 7 km long and 1 to 1.5 km wide adjacent to Point Loma (San Diego), California (Fig. 3.4). Ocean currents introduce nutrient, plankton, larvae, and other waterborne materials into the kelp ecosystem. Jackson and Winant (1983) demonstrated that the currents measured in the kelp forest were approxi-

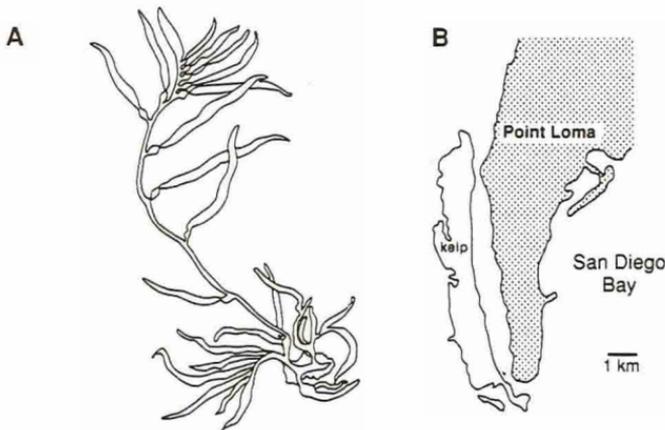


FIGURE 3.4. Kelp forest ecosystems in southern California. A—sketch of the giant kelp, *Macrocystis*. B—Map of the Point Loma forest (after Jackson, 1998).

mately one-third slower than those measured at similar locations outside the forest. The distance over which the longshore current was found to penetrate the kelp canopy (i.e., assuming flow within the kelp) was determined by balancing the advective momentum of the flow with the drag of the plants using

$$u \frac{\partial u}{\partial x} = -(C_d D q) u^2,$$

where C_d is the drag coefficient (0.5), D is the diameter of the kelp stipe (0.2 m), and q is the plant density (0.1 kelp/m²) (Jackson and Winant, 1983). The solution subject to $u = u_0$, the free-stream velocity, at $x = 0$, the leading edge is

$$u = u_0 \exp(-(C_d D q)x),$$

with a scale length of $\approx (C_d D q)^{-1}$ or approximately 100 m. In other words, the longshore currents are expected to penetrate on the order of 100 m into the kelp forest, which is too little to be of importance for fluid exchange given the 7-km length of the forest.

Jackson (1998) determined the relative importance of the cross-shore currents from the variance in the velocities measured in the cross-shore direction and the first empirical orthogonal function (EOF; a form of principal component analysis) of velocity ($e_{u,1}$). Since the cross-shore velocity was linearly related to the cross-shore distance ($y = -1000$ m), i.e., $u_1 = a(t)y$, it was possible to express u_1 as a function of $e_{u,1}$:

$$u_1(t) = \frac{\sigma}{L} e_{u,1}(t)y,$$

where σ is the standard deviation of velocity and $y = L$. An integration of $u = dy/dt$ leads to the following result:

$$y = y_0 e^{\sigma/L} \int_0^t e_{u,1}(t) dt,$$

which, when solved using field data, indicates that currents frequently penetrate more than 400 m into the Point Loma kelp forest (Fig. 3.4) on a daily basis (Jackson, 1998). In other words, the cross-shore exchange of water is substantial given the width of the forest (1 km) and therefore is of greater importance than the longshore exchange.

In addition to the reduction in flow into the kelp forest due to drag, which is about 10 times higher in the kelp forest compared to outside it, Jackson (1984, 1988) demonstrated that the size of the forest is comparable to the wavelengths of suprainertial-frequency Kelvin waves. This leads to a reduction and dampening of coastal-trapped waves in the region. Jackson (1998) also noted that the kelp forests dampen high-frequency waves and surface gravity waves and slow low-frequency waves. The flexibility of the kelp and

their response to the currents are likely responsible for this reduction in turbulence (see below). Koehl (1986) recognized that kelps have an advantage of being both flexible and long relative to other subtidal and intertidal organisms in energetic environments where fluid dynamic forces can be damaging or fatal (see Denny, 1988). Long and flexible organisms may be able to reduce the drag they experience by moving with the fluid (i.e., to "go with the flow") and thereby decreasing the water velocity relative to their tissues. While this concept has merit, it does not account for the dynamic loading (i.e., dynamic drag, acceleration reaction: virtual buoyancy and mass) due to the acceleration and deceleration of kelp over the period of a wave. Denny et al. (1998) recently examined the effects of dynamic loading of kelps and other organisms in energetic tidal environments through numerical and empirical studies. They introduced the *Jerk number* (J), a dimensionless number, which is the ratio of the maximum inertial force acting on a moving system to the maximum hydrodynamic force that a stationary object encounters:

$$J = \frac{\sqrt{km}}{K_D u_{x,m}},$$

where k is stiffness of the material ($k \approx 3EI/L^3$, where EI is the flexural stiffness and L is the length), m is the mass, K_D is the drag divided by the square of the velocity ($K_D = 1/2C_d\rho A$, where A is the area), and $u_{x,m}$ is the maximum horizontal velocity of the fluid relative to the bottom. It is possible to estimate the overall forces experienced by an organism when J is combined with the dimensionless frequency (f), which is the ratio of the frequency of oscillation of the wave force (ω) to the natural frequency of the organism's movements,

$$f = \frac{\omega}{\sqrt{km}}.$$

Going with the flow reduces the overall force when J and f are small, whereas under large J and f , flexibility is predicted to increase the overall force experienced (Denny et al., 1998). For example, when this type of approach was applied to the understory kelps *Eisenia* and *Pterygophora*, going with the flow was predicted to be advantageous for plants greater than 1 m tall, at depths deeper than 10 m and under waves less than 2 m in height (Gaylord and Denny, 1997).

There are a number of other coastal plants of smaller scale, which are cosmopolitan in the range of coastal habitats in which they are found (den Hartog, 1970; Dawes, 1998). The seagrasses and their freshwater relatives are the aquatic analogue of terrestrial cereals. These aquatic plants create coastal and inland ecosystems of ecological and economic importance, where water velocities and turbulence are reduced, and where sedimentation is enhanced (see Ackerman and Okubo, 1993). In general, there has been greater emphasis on flow in seagrass canopies; they will be presented here,

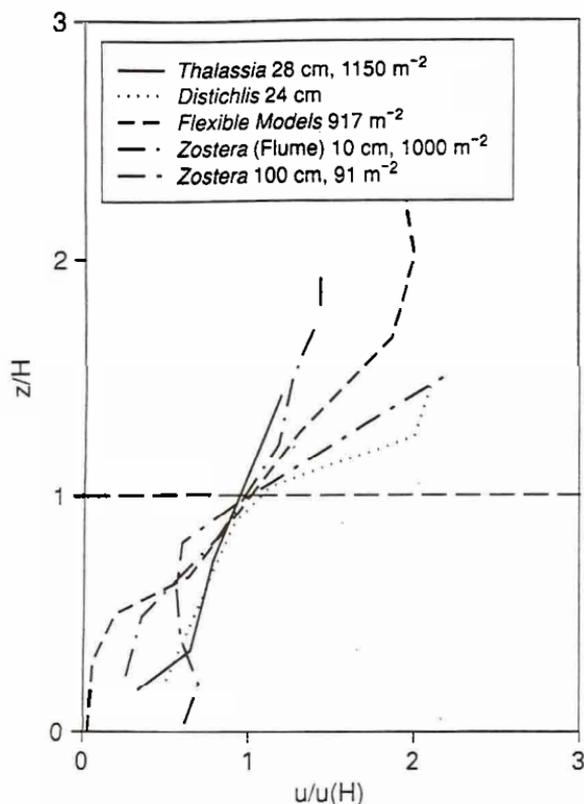


FIGURE 3.5. Velocity profiles through model, marsh, and seagrass canopies. H : canopy height, z : height, u : velocity.

but readers may also consult Dawson and Robinson (1984), Marshall and Westlake (1990), Sand-Jensen and Mebus (1996), Lopez and Garcia (1997), and Sand-Jensen and Pedersen (1999).

Flow is reduced at the top of seagrass canopies (Fig. 3.5), but friction velocities (u_*) may be ten times that of nonvegetative areas (Gambi et al., 1990). Estimated friction factors for the top of the canopy were found to decrease with increasing canopy Reynolds numbers (Re) for seagrasses with ribbon-shaped leaves (Fonseca and Fisher, 1986), and the sedimentation of clays and organic materials was also found to decrease under higher Re (Fonseca et al., 1983). Strong unidirectional flows may lead to a reduction in the canopy friction due to the horizontal deflection of leaves (Fonseca et al., 1982; Ackerman, 1986). Flow within a 1-m-tall eelgrass (*Zostera marina*) canopy at 5.5-m depth closely matched the vegetative profile of the plants (Fig. 3.5) (Ackerman and Okubo, 1993). Ackerman and Okubo (1993) estimated the eddy viscosity (K) and mixing lengths within the canopy by combining (1) the canopy drag [$F(z)$] as a function of resistance exerted by

the leaves on the fluid [cf. (3.2)],

$$F(z) = \frac{1}{2} C(z) \rho u^2 L(z),$$

where C is the drag coefficient and L is the leaf-area index, with (2) the shear stress (τ) from turbulent transport theory [cf. (3.3)],

$$\tau = \rho K \left(\frac{du}{dz} \right).$$

In this case,

$$K(z) = 1 / \left(\frac{du}{dz} \right) \frac{1}{2} \int_0^z C(z) L(z) u(z)^2 dz,$$

provided vertical eddy viscosities on the order of 10^{-5} to 10^{-4} m^2/s , which are less than one-quarter the magnitude predicted from models that do not account for vegetation (i.e., $K = \kappa u_* z$, where κ is the von Karman constant). These results were consistent with particle diffusivities measured in the same canopy (Ackerman, 1989). Worcester (1995) estimated horizontal K on the order of 10^{-3} to 10^{-2} m^2/s in shallow seagrass canopies, where the canopy height (H) was similar to the water depth (Z), under slow flow conditions ($u < 5$ cm/s) using a dye-tracking technique. The lack of difference in K estimated in the canopy and in nonvegetative sites draws Worcester's (1995) results into question because they were obtained so close to the free surface, where thermal convective and wind-driven movements would enhance mixing.

The effect of external turbulence on canopy flow was also found to be important by Ackerman and Okubo (1993), who referred to the wavelike oscillations of an eelgrass canopy as *monami* (*mo* = aquatic plant, *nami* = wave). Monami are mechanically different from the honami observed in cereals. In the former case, water deflects the flexible plants horizontally, and the buoyancy created by gas-filled lacunae leads to the return to the vertical (i.e., a hydroelastic response). In the latter case, winds deflect the stiff stems horizontally by loading the panicles, and the stiff elastic tissues in the stem return the plants to the vertical (i.e., a mechanical response). While monami effect the physiology of aquatic plants, Grizzle et al. (1996) also demonstrated that monami affect the settlement of bivalve larvae.

As in the case of terrestrial canopies, shear production is of importance to the overall canopy turbulence in model canopies when flow is unconfined (e.g., $Z/H > 1$) (Nepf and Vivoni, 1999). When the flow is confined by the free surface (i.e., $Z/H \leq 1$), pressure-gradient flow and wake turbulence are of greater importance to the overall turbulence. Energy spectra within seagrass canopies have been found to be consistent with the plant movements (i.e., monami) in that fundamental frequencies were distinct from external conditions (Ackerman and Okubo, 1993). Koch (1996) and Koch and Gust (1999) found that seagrass canopies attenuate wave energy, but

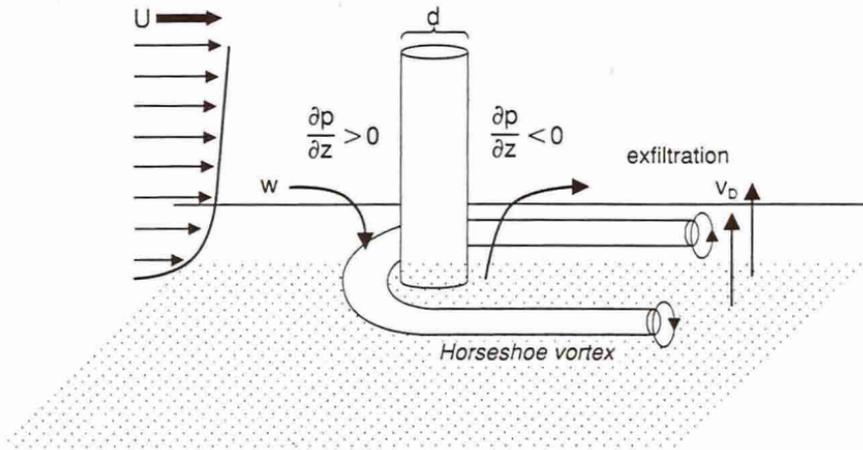


FIGURE 3.6. Secondary flows around aquatic plants. U : horizontal velocity, w : vertical velocity, V_D : exfiltration velocity, p : pressure, z : height, d : diameter.

they did not report distinct plant responses in the velocity spectra. However, careful scrutiny of their results reveals distinct frequencies in the canopy (i.e., fluctuations of 2.5 and 5.5 s) that are consistent with monami (i.e., too long for wake turbulence). Given these results, it is evident that seagrasses reduce and modify the flow within their canopies. Care must be taken, however, in the comparison of results from different studies given differences in vegetative profiles and canopy-to-water depth ratios (i.e., Z/H).

Vertical secondary flows also occur in macrophyte canopies (Nepf and Koch, 1999). These flows are due to the pressure difference upstream and downstream of cylindrical obstructions (diameter d), which lead to downward flows on the upstream face and upward flows on the downstream face of the obstruction (Fig. 3.6). Given hydrostatic flows in the boundary layer, the secondary flow in the vertical [$w(z)$] is given by

$$w(z) = u_* d \frac{\ln(z/z_0)}{8\kappa^3 z}.$$

The upward-oriented flows downstream of the plant models are thought to be of importance for the exfiltration of nutrient and other materials from the sediments. Nepf and Koch (1999) estimated the exfiltration velocity (V_D) from Darcy's equation

$$V_D = K_{\text{hyd}} \frac{\partial p / \partial s}{\rho g} = \frac{K_{\text{hyd}} u_{z \sim 0}^2}{g d},$$

where K_{hyd} is the hydraulic conductivity, $\partial p / \partial s$ is the pressure gradient between the extremes of pressure along the obstruction, and $u_{z \sim 0}$ is the near-bottom velocity. Results of theoretical and empirical models were consistent using these relationships.

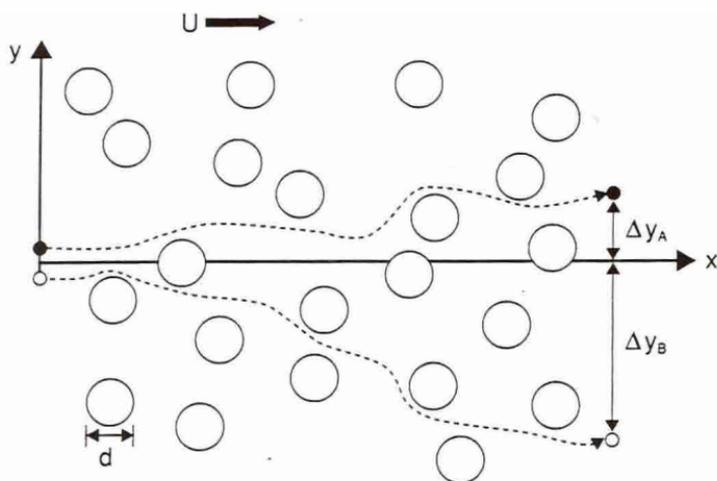


FIGURE 3.7. Mechanical turbulence in emergent plant canopies. Dashed lines represent different fluid paths. (After Nepf, 1999).

As described above, confined flow in macrophyte canopies is characterized by stem wake turbulence rather than shear production. This also applies to the more mechanically rigid emergent plants found in marshes and salt marshes (e.g., sedges, rushes, and grasses). Flow conditions in emergent plant canopies include the reduction of velocity, which matches the vegetative density profile (see Fig. 3.5), and the production of small-scale turbulence by the vortices shed in the downstream wakes (Leonard and Luther, 1995) when stem $Re > 200$ (Nepf, 1999). This leads to a nonlinear response in the turbulence as velocity is increased. In addition, there is significant anisotropy in the turbulence, with horizontal turbulence accounting for four times that of the vertical component in model canopies (Nepf et al., 1997).

Diffusion in emergent plant canopies was found to be a function of the approaching flow (U) and the plant density (q). Nepf (1999) recognized that *mechanical diffusion* (D_{mech}), which causes the fluid to move laterally due to the physical obstruction of the flow by stems (Fig. 3.7), is also present. Mechanical diffusion increases the total diffusion (D_{total}) over that of molecular diffusion (D_{mol}) when the stem $Re < 200$, and while much smaller in scale than the turbulent diffusion (D_{turb}) in the stem wakes, D_{mech} does contribute to the D_{total} when stem $Re > 200$. In both of these situations, an increase in the population density (= fractional volume of the flow occupied by plants; ad , where a is the stem density) leads to increased D_{mech} and D_{turb} . The D_{total} scales through the addition of D_{turb} and D_{mech} according to

$$D_{\text{total}} \approx E_k^{1/2} l + [ad] Ud,$$

where E_k is the turbulent kinetic energy, and l is the mixing length. In turn, E_k scales with the addition of the turbulence due to shear production and

stem wake production according to

$$E_k \sim (1 - ad)C_B U^2 + [\bar{C}_D ad]^{2/3} U^2,$$

where C_B is the bed drag coefficient, and \bar{C}_D is the bulk drag coefficient (Nepf, 1999). These scaling relationships provide an opportunity to assess the effect of plant spacing and density on the diffusion within emergent plant canopies, which should be of considerable importance given the ecological relevance of emergent macrophyte canopies (i.e., marshes and wetlands) and the increasing emphasis of wetlands in environmental engineering.

The nature of the motion of fluids immediately around the leaves and fronds of macrophytes has been of interest because it controls mass transfer in aquatic ecosystems. Anderson and Charters (1982) examined the flow through the bushy intertidal algae *Gelidium*, which was found to reduce the velocity and suppress the turbulence of the approaching flow. Associated with these changes was the generation of stem wake turbulence generated at velocities ranging from 6 to 12 cm/s, depending on the diameter and spatial density of the branches.

As mentioned above, the transition in flow induced by the branches of a marine plant is probably a phenomenon of considerable adaptive significance because the turbulence generated by the plant itself, or by neighboring plants, may be the only turbulence that is of the right scale to enhance nutrient uptake and affect the exchange of dissolved gases and solutes. Wheeler (1980) noted an analogous phenomenon in the giant kelp (*Macrocystis pyrifera*), where turbulent boundary layers were observed on fronds at low flows (e.g., 1 cm/s) as a result of the rugosities and spines on the surface of fronds. Hurd and Stevens (1997) confirmed this finding in their examination of the flow around ten types of marine algae. The transition to turbulence occurred at relatively low flows (<3 cm/s), although the transition was much higher (e.g., 12–14 cm/s) on bushy algae like *Gelidium* as a consequence of the stem wake turbulence.

The transport of inorganic carbon within the viscous sublayer (δ_V) of the boundary layer directly next to macrophytes can be modeled using Fick's law (see Sect. 2.4),

$$J = -D \frac{\partial C}{\partial z} \quad \text{or} \quad J = \frac{D}{\delta} (C_\infty - C_0),$$

where J is the flux, D is the molecular diffusivity, C is the concentration (in the free stream C_∞ and at the substratum C_0), z is distance, and δ is the boundary layer thickness (e.g., Wheeler, 1980). The mass transport of inorganic carbon may be limited by δ if the uptake by the plant exceeds the delivery (Wheeler, 1988; Neushul et al., 1992; Falkowski and Raven, 1997). Such *diffusional* or *mass transport stress* occurs at velocities <10 cm/s (Wheeler, 1988; Hurd et al., 1996) equivalent to leaf and frond $Re \ll 10^4$ (Ackerman, 1998a), which may also lead to ^{13}C isotope enrichment in their tissues (France and Holmquist, 1997; Keough et al., 1998). This carbon

isotope enrichment has been directly related to boundary layer resistance (Smith and Walker, 1980) although the hypothesis has not been examined explicitly. Higher velocities lead to enhanced productivity due to increased nutrient flux (Wheeler, 1988; Ackerman and Okubo, 1993; Hurd et al., 1996; Stevens and Hurd, 1997). At extremely high velocities, nutrient uptake may be limited by a threshold dictated by enzymatic function (Wheeler, 1980; Koch, 1994) and/or drag-induced damage to tissues (Koehl, 1986). Ackerman (1998a) reviewed the effect of velocity on photosynthesis and growth of macrophytes. He found that the *velocity effect* also occurred for other ecophysiological processes in a diverse range of aquatic plants and animals.

Stevens and Hurd (1997) modeled the boundary layers around macrophytes under steady and oscillatory flows. They questioned the use of the flat plate approximation (e.g., Wheeler, 1980) since it ignores the complex morphologies of macrophytes and leads to an underestimation of the diffusional boundary layer thickness (δ_D), which lies within the viscous sublayer of the boundary layer. When realistic measures of u_*/U obtained from direct measurements on macrophytes (e.g., Koehl and Alberte, 1988) are used, advection may balance diffusion, i.e., $\delta_D \rightarrow \delta_V$. Moreover, under oscillatory flow, periodic removal of the nutrient gradient (ΔC) by external shear at frequencies of $1/t'$, where t' is the time scale for replenishment, can increase the time-averaged flux (\bar{J})

$$\bar{J} = D \frac{\Delta C}{\delta_D} + \frac{2\Delta C\delta_V}{t'} \sum_{n=1}^{\infty} \left(\frac{1 - e^{-Dn^2\pi^2 t'/\delta_V^2}}{n^2\pi^2} \right)$$

tenfold over the expectation from the equilibrium flux

$$J_v = D \frac{\Delta C}{\delta_v}.$$

The strong influence of macrophyte morphology on u_*/U in these models indicates the need for further laboratory and field study.

3.2 Diffusion of Nutrients in the Sea

Nutrients are chemical elements within marine ecosystems that are directly responsible for the activity of primary producers. At the largest scales, nutrient transport is driven by the advective "oceanic conveyor belt" that constitutes the general circulation (Gordon, 1986; Broecker, 1991). In the open ocean, mesoscale eddies (≈ 100 km) are also significant, episodic drivers of nutrient transport (Falkowski et al., 1991; McGillicuddy et al., 1998; Oschlies and Garcon, 1998). Vertical advection is generally impeded by a strong density gradient (pycnocline) that exists between a well-mixed surface layer and the deep ocean (except in the upwelling areas of coastal regions and at the equator). Turbulent diffusion transports nutrients (e.g., NO_3) across the pycnocline to phytoplankton in the surface layer. In addi-

tion to the physical processes of advection and diffusion, the distribution of nutrients is controlled by the nonconservative terms in the balance equation. These include the uptake of nutrients by phytoplankton in the upper mixed layer, much of which lies in the euphotic zone, and the remineralization of organic matter (the remains of planktonic organisms) in the deeper layers of water. This process of nutrient sequestration into organic "bundles" which then sink into deeper layers where they are remineralized is sometimes referred to as a "biological pump" of carbon and other nutrients (cf. Longhurst, 1991). Thus, the concentration of nutrients such as NO_3 , PO_4 , and SiO_3 is small in the surface layer, increases with depth, reaches a maximum at a deep layer, and decreases toward the bottom of the ocean.

If the near-surface nutrient profile is described by a simple advection-diffusion model for the vertical distribution of nutrients, assuming steady state and constant values of vertical diffusivity, K_z and vertical advection, w , we find from (2.16) that

$$K_z \frac{d^2 S}{dz^2} - w \frac{dS}{dz} + R = 0, \quad (3.12)$$

where S is the concentration of nutrients and the z -axis is taken downward from the sea surface. Equation (3.12) deals only with the gross features of nutrient distribution, disregarding, for instance, the seasonal variation of nutrients in the upper layer.

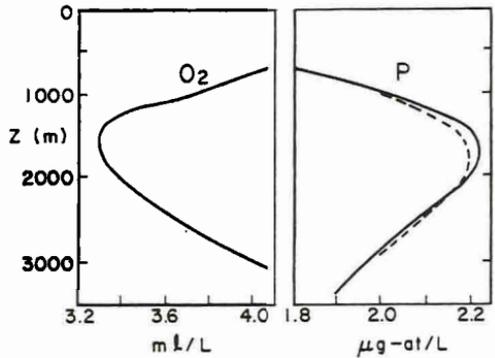
Munk (1966), Wyrтки (1962), and Tsunogai (1972a) found (3.12) to be applicable to distributions in deep layers, at depths of perhaps 1 to 5 km, of the interior ocean such as the Pacific, where the estimated values $w = -1.4 \times 10^{-5}$ cm/s and $K_z = 1.3$ cm²/s are considered reasonable. In other words, the deep water of the interior oceans, while being mixed and diffuse, gradually rises at a speed of 4.4 m per year. The upward flux of mass in the Pacific then amounts to 6×10^{32} g per year. This flux is supplied by the Antarctic Bottom Water, which flows through the South Pacific, thus completing the general circulation.

In deep water the regeneration of nutrients (R) from the remains of organisms (remineralization) causes R to be positive. Thus, Riley (1951), Wyrтки (1962), Tsunogai (1972a), Grill (1970), and Shaffer (1996) all assumed

$$R = R_0 e^{-\alpha z} \quad (3.13)$$

as an analytical expression for the nonconservative term. [Okubo (1954, 1956) obtained a purely theoretical profile for R , the form of which is close to an exponential function. See also Lerman and Lal (1977) and Pond et al., (1971).] Power-law relationships derived from sediment trap data have also been used (Martin et al., 1987). The downward decrease of R is likely due to the facts that the remineralization process starts at an upper layer and that the organic remains sink as they decompose. For the special case of $\alpha = 0$, the regeneration rate, $R = R_0$ (= constant).

FIGURE 3.8. Vertical distribution of dissolved oxygen (O_2), and inorganic phosphorus (P) in the Coral Sea. Observed (—) and theoretical (---) distributions (from Wyrтки, 1962).



Substituting (3.13) into (3.12) and solving the resulting equation, we obtain

$$S = A + Be^{wz/Kz} + \frac{R_0 e^{-\alpha z}}{K_z \alpha^2 (1 + w/K_z \alpha)}, \quad (3.14)$$

with constants A and B to be determined from boundary conditions. Thus, if we know the boundary values $S = S_1$ at $z = z_1$ (upper layer) and $S = S_2$ at $z = z_2$ (lower layer), we can evaluate A and B .

Wyrтки (1962) found that the theoretical profile (3.14), with $\alpha = 0$, agreed with the observed vertical profile of inorganic phosphorus in the Coral Sea, with a maximum concentration of P (phosphorus) occurring at a depth of about 2000 m (Fig. 3.8). More recently, Shaffer (1996) obtained excellent fits of theoretical profiles of NO_3 and PO_4 to data obtained from cruises in northern latitudes. In this case, different nonzero values of α were obtained for NO_3 and PO_4 profiles.

It seems unreasonable to assume that (3.12) also holds in the upper layer, especially at high latitudes, where seasonal variations, effects due to horizontal mixing, and wide fluctuations in the values of K_z and w exist, and where difficulties in the formulation of the nonconservative term become formidable. Nevertheless, Grill (1970) met with some success in applying (3.12) to the vertical distribution of inorganic silicate in the surface layer of the sea.

The vertical flux of nitrate across the pycnocline in the upper layer of the oligotrophic open ocean imposes a rigorous constraint on the rate of export of organic carbon from the surface layer of the sea ("new" production). Assuming horizontal fluxes to be small in relation to vertical fluxes,

$$\frac{\partial S}{\partial t} = \frac{\partial}{\partial z} \left(K_z \frac{dS}{dz} \right) - bS,$$

the rate of change of local nitrate concentration is equal to the turbulent diffusion of S and loss (biological sink) rate in the form of algal uptake. At

steady state, and assuming constant K_z ,

$$K_z \frac{d^2 S}{dz^2} - bS = 0.$$

Near-surface nitrate distributions in the open ocean, generally observed to increase exponentially with depth, are consistent with this first-order, concentration-dependent uptake by phytoplankton and a diffusional supply in the vertical direction. Even this simple model demonstrates that phytoplankton uptake exerts a control on both the vertical nitrate flux and gradient (Lewis et al., 1986). However, the specific rate of uptake, b , may itself vary with depth. If b follows the exponential profile of irradiance in the surface layer (Beer's law), then the steady-state relation becomes

$$K_z \frac{d^2 S}{dz^2} - aI_0 e^{-kz} S = 0.$$

Lewis et al. (1986) solved this equation subject to $dS/dz = 0$ (no nitrate flux at the sea surface) and $S = S_0$ at $z = 0$:

$$\begin{aligned} S(z) &= S_0 \frac{\mathbf{K}_1(\beta) \mathbf{I}_0(\xi) + \mathbf{I}_1(\beta) \mathbf{K}_0(\xi)}{\mathbf{K}_1(\beta) \mathbf{I}_0(\beta) + \mathbf{I}_1(\beta) \mathbf{K}_0(\beta)} \\ &= S_0 \beta (\mathbf{K}_1(\beta) \mathbf{I}_0(\xi) + \mathbf{I}_1(\beta) \mathbf{K}_0(\xi)), \end{aligned}$$

where $\beta = (2/k)(aI_0/K_z)^{1/2}$, $\xi = \beta \exp(-1/2kz)$, and \mathbf{I}_m , \mathbf{K}_m are modified Bessel functions of order m . The shape of this concentration profile increases approximately exponentially with depth, and a nonlinear fit of the parameters β and S_0 to the observed nitrate profile match the data well. The corresponding value of vertical nitrate flux (supply) agrees reasonably well with independent estimates of new production (i.e., production not fed by recycled NH_3) based on ^{15}N uptake, though the 95% confidence interval spans a relatively wide range.

Coastal areas are often characterized by marked upwelling of water caused by Ekman pumping (i.e., interactions of wind and the Coriolis force driving vertical advection; Mann and Lazier, 1996). The supply of nutrients by upwelling and their effect on primary productivity are among the central issues of marine ecology. Several international, multidisciplinary research efforts have addressed the interactions of physical and biological processes of coastal upwelling ecosystems (*Deep-Sea Research*, 24(1), 1977; Dengler, 1985; MacIsaac et al., 1985). In principle, Lewis et al.'s (1986) steady-state equation could be extended to include the advective flux of nutrients due to upwelling (or downwelling). The addition of an advective term with velocity w (positive downward) to their equation yields

$$K_z \frac{d^2 S}{dz^2} - w \frac{dS}{dz} - aI_0 e^{-kz} S = 0,$$

which, using their boundary conditions, is satisfied by

$$S(z) = S_0 \xi^{-\text{Pe}} \beta^{1+\text{Pe}} (\mathbf{K}_{\text{Pe}-1}(\beta) \mathbf{I}_{\text{Pe}}(\xi) + \mathbf{I}_{\text{Pe}-1}(\beta) \mathbf{K}_{\text{Pe}}(\xi)),$$

where $\text{Pe} = \text{Peclet number} (= w/(kK_z)$, a dimensionless parameter expressing the relative importance of advection and turbulent diffusion over the length scale, k^{-1}). For no advection, $w = 0$, and the solution reduces to that of Lewis et al. (1986). Upwelling reduces the proportion of nutrient demand in the euphotic zone met by eddy diffusion, and the concentration profile becomes relatively flat (Swaney, unpublished).

While our understanding of the nutrient dynamics of the sea has been advanced by one-dimensional, linear models like those presented above, and their analytical solutions continue to give insight (e.g., Shaffer and Sarmiento, 1995; Shaffer, 1996), some caution should be used when using random walk models to simulate these processes, especially when the diffusivity varies spatially (see Visser, 1997). Importantly, knowledge of the biochemical reaction kinetics of oceanic nutrients has greatly progressed so that the non-conservative term, R , is often evaluated using more complex nonlinear forms. Anderson et al. (1978) constructed a diffusion-reaction model for the vertical distribution of anaerobic NO_2 in the sea that incorporates advective and diffusive processes with Michaelis–Menten reaction kinetics for NO_2 in the following equation:

$$\frac{\partial S}{\partial t} = K_z \frac{\partial^2 S}{\partial z^2} - w \frac{\partial S}{\partial z} + P(z) \left(1 - \lambda \frac{S}{S + M} \right),$$

where $P(z)$ represents the rate of oxidation of organic matter by denitrifying bacteria, λ is the mean ratio of the potential rate of NO_2 reduction to the potential rate of NO_3 reduction by denitrifying bacteria, and M is the Michaelis–Menten constant for NO_2 uptake. Anderson et al. (1978) successfully applied this model to interpret the observed pattern of anaerobic NO_2 in the eastern tropic North Pacific Ocean.

Michaelis–Menten kinetics have been used in many other studies to analyze, for example, the status of Si as a limiting nutrient in diatoms (Nelson and Treguer, 1992; Dugdale et al., 1995), the inhibition of NO_3 uptake by NH_4 and the effect on production (Harrison et al., 1996; Elskens et al., 1997), and effects of resource competition among multiple species (Fong et al., 1994). Mathematical modeling in recent years (e.g., Fasham et al., 1990; Sarmiento et al., 1993; Doney et al., 1996; Hurtt and Armstrong, 1996) frequently rely on such nonlinear nutrient kinetics. Increasingly, ecological relationships are being incorporated into these models, which make them analytically intractable but behaviorally rich [e.g., (1) allometrically scaled nutrient uptake and other organism size-based parameters (Armstrong, 1994) and (2) resource-ratio arguments that help explain the relationships between multiple nutrient profiles and biological production (Carpenter et al., 1992; Tilman et al., 1982)]. Much remains to be learned of the interplay

between diffusion of nutrients and these biological processes (Owens, 1993; Jumars, 1993; Mann and Lazier, 1996).

Before ending this section, we note that Eq. (3.12), or the corresponding time-varying version,

$$\frac{\partial S}{\partial t} = K_z \frac{\partial^2 S}{\partial z^2} - w \frac{\partial S}{\partial z} + R,$$

can also be used as a model for the distribution of dissolved oxygen in water bodies. A boundary condition makes oxygen flux at the surface (reaeration) proportional to the difference between ambient concentration (O_2) and the atmospheric equilibrium value (O_{2s}):

$$F_{O_2} = v(O_{2s} - O_2)|_{z=\text{surface}}.$$

The constant of proportionality (mass transfer velocity) is generally assumed to be strongly dependent on wind speed at the surface (Liss and Merlivat, 1986; Wanninkhof, 1992).

In investigations of lake and river water quality, a solution of a simple form of Eq. (3.12) has a venerable history in water-quality engineering as the dissolved oxygen "sag" curve response to a point source of oxygen-consuming organic waste in which the water is being reoxygenated from the surface (Streeter and Phelps, 1925). This topic is covered thoroughly by Thomann and Mueller (1987).

In the sea and other bodies of water, phytoplankton in the photic zone produce oxygen, and predation and decomposition of organic matter by heterotrophs imply the regeneration of nutrients and the consumption of oxygen (Wyrтки, 1962; Tsunogai, 1972b). In addition, near the sea surface, an oxygen concentration in excess of the atmospheric equilibrium concentration by about 2% to 3% can result from bubble injection from wind-driven breaking waves in addition to biological production (Broecker and Peng, 1982; Liss and Merlivat, 1986; Craig and Hayward, 1987). The balance between these processes tends to result in a net production of oxygen during the daylight hours near the surface of the water column ($R > 0$) and a net consumption at depth ($R < 0$). Integrating the time-varying form of Eq. (3.12) over the water column results in a direct relationship between the change in the average oxygen content, the diffusion of oxygen at the boundaries, and the depth-integrated net production in the water column. This is the basis of the whole-ecosystem productivity estimation method introduced by Odum (1956) and since used by many others (e.g., Odum and Hoskin, 1958; Nixon and Oviatt, 1972; Kemp and Boynton, 1980; Emerson et al., 1993; DeGrandpre et al., 1997). Stigebrandt (1991) used the relationship between the oxygen flux boundary condition at the sea surface, oxygen concentration, and primary production in order to estimate depth-integrated production in the Baltic.

As far as the oceanic dispersion process is concerned, both oxygen and nutrients behave in the same manner, with the difference in boundary con-

ditions, primarily at the sea surface, being largely responsible for the discrepancy between nutrient and oxygen profiles. Accordingly, it might be expected that there would be a close agreement in deep water between the amount of nutrients such as phosphate and the oxygen depletion. In reality, the matter is not so simple.

The layer of maximum PO_4 and other nutrients does not necessarily coincide with that of minimum oxygen (Fig. 3.8). A simple plot of the phosphate content against the "apparent oxygen utilization" may not reveal the expected relationship of chemical equivalence, as the effect of diffusion must be taken into consideration (Sugiura, 1964; Sugiura and Yoshimura, 1964). Also, "fractionation" effects occur that change the relative proportions of oxygen and nutrients with depth because of progressive change in the stoichiometric ratios of nutrients and oxygen in sinking organic matter as it is remineralized (Shaffer, 1996). Reactions closer to and within sediments are discussed below.

3.2.1 *Subsurface Productivity and Chlorophyll Maximum*

In the absence of other factors, the profile of chlorophyll production in the sea could be expected to be related directly to productivity, and therefore to the balance between corresponding light profiles and nutrient profiles (e.g., Wolf and Woods, 1988). For example, a nitrite maximum in the vertical is commonly associated with the chlorophyll maximum at the base of the euphotic zone (French et al., 1983). French et al. (1983) showed diel changes in nitrite concentration in which the nitrite maximum is produced mainly by phytoplankton during the day by reduction of nitrate. They used the vertical balance equation (3.12) for estimating K_z and w from temperature or salinity data ($R = 0$) combined with the rate (R) estimate of chlorophyll a or ATP. Gorfield et al. (1983) found that a subsurface maximum in electron transport system (ETS) activity (microbial activity) was associated with the (secondary) nitrite maximum and particle maximum.

Other factors also influence the chlorophyll depth profile. First, the ambient light conditions near the surface may actually inhibit production in shade- (depth-) adapted phytoplankton (Neale et al., 1991). Higher chlorophyll levels present in low-light-adapted species can result in a separation between the depth of the chlorophyll maximum and the productivity maximum (Venrick, 1982; Jumars, 1993).

Second, phytoplankton sinking through the water column transport chlorophyll to depths below that of chlorophyll production. Conversely, phytoplankton can be transported upward by advection (upwelling) or turbulent diffusion (Takahashi et al., 1985). These rates of transport may not be constant with depth as sinking rate can be an active response of phytoplankton to a reduction in light level with depth (Steele and Yentsch, 1960; Bienfang, 1993). Resistance to sinking by the pycnocline at the bottom of the mixed layer (cf. Roman et al., 1986; Vandeveldel et al., 1987) and to variations in

turbulent diffusion with depth (Jamart et al., 1977; 1979) can affect the position of the chlorophyll maximum.

Finally, predation by zooplankton and other organisms can affect the shape of the chlorophyll profile. Evidence exists for zooplankton density maxima that are coincident with either the productivity maximum (Roman et al., 1986) or the chlorophyll maximum. Tsuda et al. (1989) estimated that 56% to 100% of chlorophyll production at the chlorophyll maximum was consumed by microzooplankton ($<95 \mu\text{m}$) at a site in the subtropical North Pacific. Revelante and Gilmartin (1990) observed a maximum of ciliated protozoa coincident with the subsurface chlorophyll maximum and oxygen maximum in the Northern Adriatic. Herman (1989) observed maximum copepod densities coincident with the subsurface productivity maximum, and not at the chlorophyll maximum, in the Eastern subtropical Pacific. Townsend et al. (1984) observed highest copepod densities at the depth of the chlorophyll maximum in the Gulf of Maine. It may be true that both the chlorophyll and productivity maxima are preferred sites for grazing, depending on the season and the size of the grazer (Le Fevre and Frontier, 1988; Mann and Lazier, 1996).

3.2.2 *Flocs, Aggregates, and Marine Snow*

The nature of organic and inorganic matter in aquatic systems is directly related to the availability and diffusion of nutrients discussed above. As much of this material exists as particulate organic matter (POM) in aggregates $>500 \mu\text{m}$ in diameter comprised of microorganisms, inorganic particles, transparent exopolymer particles (TEM), and detritus, it is prudent to examine the nature and formation of these aggregations, which are also known as *flocs* and *marine snow*. Aggregates lead to temporal and spatial patchiness in the environment and consequently are of importance for nutrient cycling (Posedel and Faganeli, 1991; Brzezinski et al., 1997), microbial activity (Silver et al., 1998), and the downward flux and potential retention of autotrophic production in the euphotic zone (Kjørboe et al., 1998). Ultimately, aggregates contribute to the downward flux of material in the water column and, therefore, remove nutrients from aquatic ecosystems (Fowler and Knauer, 1986).

There are historical accounts of bathyscaphe observations of relatively large particles in suspension, which were referred to as marine snow. Nishizawa et al. (1954) provided photographic evidence of such material a decade before Riley (1963) described 5- μm - to mm-sized organic aggregates in Long Island Sound. These aggregates were interpreted to have formed on surfaces, including those on air bubbles, from the agglutination of organic material from live and dead phytoplankton cells. In subsequent reports, Riley et al. (1964, 1965) noted variability in aggregate distribution both in space, which was strongly correlated to phytoplankton abundance in upwelling regions,

and in depth, for which a decline was observed with distance from the surface, but concentrations remained consistent below depths of 3000 m.

The role of physical processes in the formation of aggregates as noted by Riley (1963) involved the accumulation of organic and inorganic materials. Sea-surface slicks, which are areas of accumulations of such materials (Poseidel and Faganeli, 1991), may provide some of the material that eventually becomes incorporated into aggregates. Slick formation was directly related to periods when wind speeds were less than 7 m/s, which was quite frequent even in areas considered to be highly energetic (Romano and Marquet, 1991). Carlson (1987) noted that the microlayers associated with slicks can be extremely viscous. Issues related to the bulk properties of these conditions and those found in aggregations are presented in Jenkinson and Biddanda (1995). In addition to physical processes, there are important biological contributions to the formation and nature of aggregates, which were noted from careful in situ observation and collection (Silver et al., 1978).

The composition of marine aggregates may be primarily organic, diatomaceous due to the intrinsic stickiness of diatoms (Kjørboe et al., 1998), or mucous due to the castoff mucous feeding apparatus of pelagic zooplankters (e.g., larvaceans; Hansen et al., 1996; Kjørboe et al., 1996; also see Halloway and Cowen, 1997). In the cases of larvacean mucous, house-derived aggregates can be many dm in length and while spatially rare may contribute significantly to the POM distribution in marine waters (Silver et al., 1998). Early observations of POM in coastal inlets noted temporal and spatial variability in the composition and content of aggregates (Kranck, 1980). Similar diversity in lake aggregates was found by Grossart et al. (1997). They noted four types of aggregates in Lake Constance: (1) algal-derived; (2) zooplankton exoskeleton-derived; (3) cyanobacterial-derived; and (4) those of indeterminate derivation. Conversely, riverine aggregates appear to be both detrital and inorganic material packed within a bacterial-derived microfibril matrix (Droppo et al., 1997). In this case, the bacterial composition of extracellular polymers is of significance, as is the morphology (i.e., porosity and water content) of the aggregate. Similar observations have been made for marine aggregates (Alldredge and Silver, 1988). The shape of aggregates is fractal, especially with respect to length and mass relationships, which is important for aggregation formation as described by coagulation theory (Jackson and Burd, 1998). The fractal dimension (D) of marine snow is generally around 1.7, which is less than a value of 3 predicted for a sphere (Logan and Wilkinson, 1990). Aggregates smaller than 200 μm also appear to be fractal with values ranging from 1.7 to 2.3 depending on the sampling location and the technique used to estimate D (Jackson et al., 1997; Li et al., 1998). Importantly, Li et al. (1998) interpreted the low value of D for small aggregates to be a consequence of formation through coagulation, which would make them similar to marine snow.

Droppo et al. (1997) noted the complexity in the formation of riverine

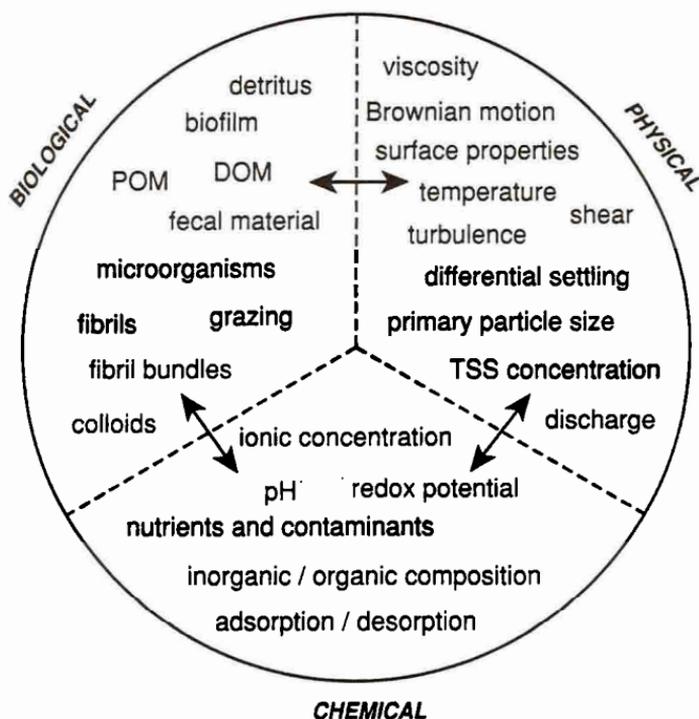


FIGURE 3.9. Biological, chemical, and physical factors influencing the aggregation and fragmentation of freshwater flocks (after Droppo et al., 1997).

aggregates involving biological, chemical, and physical factors (Fig. 3.9). Many of these factors also apply to marine aggregates. With respect to the physical processes, Jackson (1990) modeled the formation of algal flocs during algal blooms using a coagulation process, in which shear coagulation is thought to be of importance in the formation of aggregates in the upper ocean (McCave, 1984). Coagulation theory models collision rates via Brownian motion, fluid shear, and differential sedimentation of particles. Jackson (1990) predicted that there would be a two-stage process of aggregate formation, including low aggregate formation during the development and decline of the bloom, and high aggregate formation during the peak of the algal bloom. The rapid transition between the two stages, as indicated by a critical algal concentration, was predicted to be related inversely to the fluid shear, size of the cell, and stickiness of the cell surface. Importantly, aggregate size was predicted to influence the chemotaxis and attachment of bacteria to aggregates (Jackson, 1989). Mesocosm studies have supported the predictions of coagulation theory (e.g., Dam and Drapeau, 1995), and modeling theory has been refined (Jackson and Lochmann, 1993; see Jackson and Burd, 1998). Field studies by Riebesell (1991) confirmed the two-stage process of aggregate formation in his study of algal blooms in the

North Sea, where biological processes and shear were found to affect aggregate formation.

Shear stress can be estimated from wind speeds at 10 m (w_{10}) that create wind stress on the water surface and that lead to friction velocity (u_*) via

$$u_* = (C_d \rho_{\text{air}} / \rho_{\text{water}})^{1/2} w_{10},$$

where ρ_{air} and ρ_{water} are the density of the air and the water, respectively. The turbulent energy dissipation rate (ε) in the mixed layer in the upper ocean is a function of u_* :

$$\varepsilon = a u_*^2 f \exp[z/(b u_* / f)],$$

where a and b are constants (53.5 and 0.068, respectively) and f is the Coriolis parameter ($f = 2 \times 7.29 \cdot 10^{-5} \sin \phi$, where ϕ is the latitude). The shear rate (γ) is a function of ε and the kinematic viscosity (ν):

$$\gamma = (\varepsilon / \nu)^{1/2}.$$

The smallest eddies associated with these conditions are determined via the Kolmogorov length scale (λ)

$$\lambda = (\nu^3 / \varepsilon)^{1/4},$$

which is on the order of mm in the open ocean (Mitchell et al., 1985). Hill et al. (1992) examined the encounter rates of particles via eddies and determined that the relative velocity between particles was more important than viscous forces even though the spatial scales affecting encounters (e.g., λ) indicated viscous conditions.

While fluid shear contributes to the collision rate necessary for the coagulation process leading to the creation of aggregates, it may also lead to the disaggregation of established aggregates. The loss of aggregates is thought to occur due to sedimentation, consumption and degradation by organisms, dissolution, and fragmentation via surface erosion, pressure fluctuations, and filament fracture (Aldredge et al., 1990). Aldredge et al. (1990) examined the strength of four types of marine aggregates under different shears (γ). They discovered that, while fragmentation was possible via pressure fluctuations and filament fracture, the γ required to fragment aggregates were seldom found in nature (i.e., the turbulent energy dissipation rate, ε , was too low). They suggested that animal grazers are likely responsible for the vertical distribution of POM in the water column. Kiørboe's (2000) recent evaluation of the colonization of marine aggregates by invertebrate zooplankton supports this assertion.

High temporal resolution sampling of marine aggregates revealed seasonal as well as diel variation (day > night) in marine snow concentration measured at 270-m depth (Lampitt et al., 1993). This variation is thought to be driven by diel variation in (1) phytoplankton production due to solar inputs, (2) grazing by vertically migrating zooplankton, and/or (3) turbulence-induced fragmentation. Turbulence is generally reduced in the upper mixed

layer during the day due to stratification caused by solar warming. The release of this potential energy at night leads to increased turbulent kinetic energy (i.e., shear). Ruiz (1997) modeled the growth dynamics of marine aggregate concentration (C) as

$$dC/dt = \text{aggregation} - \text{fragmentation} + \text{growth} - \text{grazing} - \text{sedimentation}$$

using parameter values measured or estimated from observations. Neither diel variation in phytoplankton growth nor diel variation in zooplankton grazing resulted in diel variation in C . Diel variation in turbulence, however, led to diel oscillations in the concentration of marine aggregates. Diel variation in the turbulent energy dissipation rate, where values of ε between 10^{-9} and $7 \times 10^{-8} \text{ m}^2/\text{s}^3$, reduced C through fragmentation at a greater rate than was produced through coagulation. This is because fragmentation scales with $\varepsilon^{1/2}$, whereas coagulation scales with $\varepsilon^{1/3}$ for large particles (i.e., $>0.01 \text{ cm}$) (see Hill et al., 1992). In other words, the nightly increase in ε results in more than eight times more fragmentation of large particles at night compared to the day, which is approximately twice the rate of coagulation of smaller particles over the same period. The magnitude of these ε -values are at least an order of magnitude less than the ε required to fragment marine aggregates in the laboratory as reported above (Alldredge et al., 1990).

Aggregates appear to accumulate at physical discontinuities in the water column associated with density stratification (MacIntyre et al., 1995). The likely cause of this phenomenon is water column shear caused by velocity gradients ($\partial u/\partial z$), horizontal intrusions, and turbulent mixing. This phenomenon was modeled via the accumulation of aggregates due to density-related sedimentation and accumulation due to interactions with turbulent flow. In the first model, the sinking speed (u_z) of an aggregate of radius r is given by

$$u_z = \sqrt{c\Delta\rho},$$

where $c = 2grC_d\rho_{\text{water}}$, g is gravity, and $\Delta\rho$ is the density difference (i.e., excess density). The density difference is a function of the solid (f_s), porosity (f_p), and mucous (f_m) content of the aggregate such that $f_s + f_p + f_m = 1$,

$$\Delta\rho = f_s\Delta\rho_s + f_p\Delta\rho_{af} + f_m\Delta\rho_{mf},$$

where $\Delta\rho_s$ and $\Delta\rho_{af}$ is the density difference with respect to the solid and aggregate interstitial fluid (e.g., mucous), respectively. The model predicts that u_z would be reduced for highly porous aggregates with moderate $\Delta\rho$.

The duration of the reduction in u_z on approaching the density discontinuity was examined through a comparison of the time scales related to molecular diffusion ($t_D = r^2/2D$, where D is the diffusion coefficient), pressure-driven flow through the aggregate ($t_p = 2r/u_I$, where the interstitial flow $u_I = 3Pu/2r^2$ and P is the porosity), and shear-driven flow through the boundary layer ($t_\tau = \theta r/u_s$, where θ is angle subtending the boundary layer,

and the maximum shear-driven flow $u_s = 3P^{1/2}u/2r$). For compact detrital marine snow, MacIntyre et al. (1995) determined that t_D for heat was more rapid than either t_p or t_r , but it was also much slower for t_D for salt. Thus, the sinking velocity would be reduced near the halocline. For larger and more porous diatom aggregates, t_D for heat was more rapid than either t_p or t_r , which were comparable to t_D for salt, indicating that the aggregate would have to be located within the halocline for a reduction in u_z . The higher the mucous content of the aggregate, the longer the duration of reduced u_z was predicted. In general, the salinity difference of the stratification was determined to be of greater importance than were the temperature differences.

In the second model of accumulation, MacIntyre et al. (1995) used random walk models to demonstrate that low-porosity aggregates accumulated due to the turbulent mixing at the discontinuity. High-turbulence intensities were predicted to disrupt the accumulation and fracture large porous aggregates. Regardless of the mechanism involved, the persistence of aggregates at discontinuities may be on the order of hours to days, which would have important ecological implications for trophic transfer.

3.2.3 *Benthic–Pelagic Coupling*

As noted above, marine snow and other detritus falling from the productive surface layer through the water column are acted upon by a variety of pelagic organisms, which regenerate mineral nutrients. Much of this regenerated material takes the form of fecal particles, which play an important role in transporting organic matter (i.e., nutrients) into deeper water. For example, Deibel (1990) provides settling velocities for fecal matter from neritic salps and dolioids, which eventually reaches the benthos, thereby coupling the benthic and pelagic zones.

The issue of benthic–pelagic coupling in the nearshore has received considerable attention by marine ecologists, especially with respect to bivalve ecosystems as presented below. This is due, in part, to the question of whether aquatic ecosystems are controlled by limits to primary production by phytoplankton or by consumption by grazers (e.g., bottom-up and top-down controls, respectively; Fretwell, 1987; Menge, 1992; Wildish and Kristmanson, 1997; Gili and Coma, 1998). In the former, a lack of nutrients limits phytoplankton growth, while in the latter, pelagic grazing is the limiting factor. Benthic suspension feeders may also contribute to the consumption of phytoplankton, depending on the water depth, water column mixing, and phytoplankton concentrations. These issues have been examined under unidirectional conditions in numerical, laboratory, and field studies (reviewed by Dame, 1996; Wildish and Kristmanson, 1997). The situation in lakes is complicated by the interaction of other forcing functions such as wind-generated waves, stratification, and surface-gravitational seiching (see Fischer et al., 1979; but see Ackerman et al., 2001).

Benthic bivalves are perhaps one of the most significant taxa of benthic

suspension feeders, and consequently, benthic–pelagic coupling is best known in these systems (see Dame, 1996). Research on these and other suspension-feeding invertebrates has been recently reviewed by Wildish and Kristmanson (1997). The strongest case for benthic–pelagic coupling is provided by the detection of concentration boundary layers that have been observed over marine bivalves in estuaries (Dame, 1996). The modeling of these systems has confirmed that turbulent transport is the key physical process supplying phytoplankton to the bivalves (Fréchette et al., 1989). Evidence of suspension feeding-induced concentration boundary layers has also been observed in lakes (e.g., Ackerman et al., 2000; 2001). Similar reductions in phytoplankton biomass near coral reefs have also been reported (Yahel et al., 1998).

The mass transport of waterborne material (i.e., seston) to suspension-feeding bivalves is influenced by fluid dynamics (Cloern, 1991; Koseff et al., 1993; O’Riordan et al., 1995). For example, velocity has a positive effect on suspension-feeding rates measured at low velocities and a negative one at higher flow rates (Wildish and Kristmanson 1997; see review in Ackerman, 1999). While the positive effects at low velocity may be due to the local replenishment of resources, the mechanisms responsible for the decline in feeding at higher flows may be due to dynamic pressure differences in the flow and lift–drag effects that lead to behavioral responses in the bivalves (Ackerman, 1998a, 1999).

At larger scales, an increased velocity would replenish depleted resources with fresh seston as a function of the ambient flow and mixing within the water column. Physical modeling of siphonal flow in laboratory flow is consistent with this conclusion and suggests that there may also be significant refiltration in bivalve beds (Monismith et al., 1990; O’Riordan et al., 1995). The seston concentration (C_l) at bivalve beds has been modeled as

$$U \frac{\partial C_l}{\partial x} + w_s \frac{\partial C_l}{\partial z} - \frac{\partial}{\partial z} \left(K \frac{\partial C_l}{\partial z} \right) = \Psi(Q, C_\infty, E, H),$$

where U is velocity, w_s is the settling of seston, Q is the pumping rate, E is the filtering efficiency, H is the intake height, and Ψ is the filter feeding (O’Riordan et al., 1995). This model relates the physical mixing processes affecting the delivery of seston, to the physiology of filter feeding (Koseff et al., 1993; Butman et al., 1994; Wildish and Kristmanson, 1997). It requires information on the physical mixing processes and the ability of the bivalves to feed under these conditions. Neither the physical mixing of coastal waters nor the bivalve-filter-feeding physiology in them is well understood (Dame, 1996; Wildish and Kristmanson, 1997). This situation is similar for other taxonomic groups.

Benthic–pelagic coupling, depending on the context, may also refer to the relationships between the deposition of sediments from the water column to the sea floor and the benthic foodweb, the effect of benthic oxygen demand on pelagic primary production (Hargrave, 1973), the relationship between

diagenetic processes and nutrient availability, or the effect of benthic predators on pelagic populations. Graf (1992) reviewed many of these processes. All of these phenomena are related to the coupling of the benthic to the pelagic zones in a narrower sense—the magnitudes of advective and diffusive terms in a mass-balance equation describing the transport of nutrients and organisms across the interface. In a sense, the mixed layer of the benthic zone (\approx top 10 cm) plays a role analogous to the mixed layer at the surface of the water column. It is a region of active biogeochemical processes and may serve as a source or sink of nutrients to the water column above it. The level of activity of this zone depends on the degree of advective transport (sediment accumulation at the surface) and the degree of turbulent and biodiffusion.

While the top 10 cm or so of the sediment profile is a mixed layer subject to the mechanical mixing of sediments by organisms (bioturbation; Sect. 3.5.2), and the thin layer just below the surface (Brinkman layer) is subject to the effects of shear, generated in the overlying waters, most transport in the sediment profile is due to porewater diffusion, dispersion, and advection (see Fig. 3.10; Boudreau, 1997). Immediately above the sediment surface are boundary layers similar to those of the atmosphere (Sect. 2.6.1) in which the presence of the benthic surface is manifested by the effects of diffusion and shear on the composition and velocity profiles of the overlying waters (Thibodeaux, 1996). In the diffusive sublayer, a linear concentration profile of dissolved materials exists between the top of the layer and the benthic surface. The lowest layers are frequently associated with a benthic nepheloid (cloudy) zone in which benthic material is continually or episodically re-

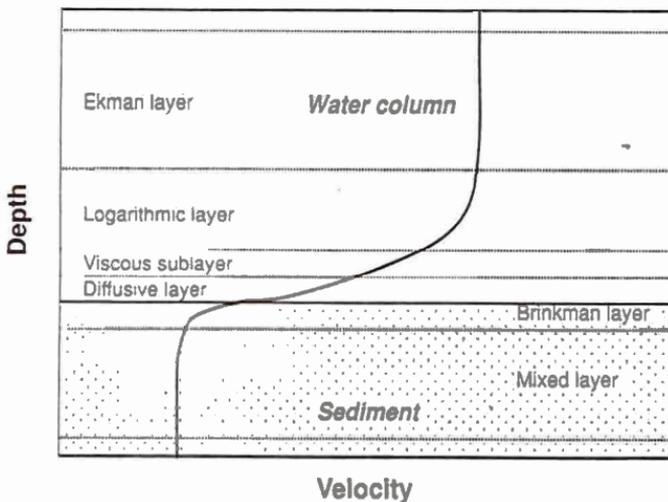


FIGURE 3.10. Velocity profile and various boundary layer features above and below the seafloor (not to scale) (after Svensson and Rahm, 1991).

suspended by benthic organisms or flow events (cf. Richardson et al., 1993; Pudsey and King, 1997; Pilskałn et al., 1998).

From the standpoint of benthic diagenesis as described by advection-diffusion-reaction equations, the coupling between the benthic and pelagic zones occurs in the relationship between the deposition rate of sediments falling to the benthic surface (marine snow, etc.) and the rate at which the surface is increasing in elevation above a fixed datum. Neglecting time-dependent compaction of sediments, this allows the constituents of the benthic zone to be considered to be moving downward relative to the benthic surface, at a constant rate equivalent to the sedimentation velocity. At the benthic surface, in the absence of surface reactions and hydraulic gradients, the *diffusive* flux of dissolved nutrients from the boundary layer above the surface must equal the interstitial flux in the sediments relative to the surface (the sum of a diffusive and an advective term). Similarly, the *advective* flux of solid-phase nutrients (particles) in the water column is equal to the sum of a diffusive and advective flux in the sediments, where the diffusive term is typically due primarily to bioturbation (Sect. 3.5.2). A detailed treatment of the boundary conditions at the sediment-water interface is presented in Boudreau (1997), but also see Thibodeaux (1996) for detailed examples.

3.3 Diffusion of Spores

In antiquity people believed that winds carried diseases to man, animals, and crops: "when the wind is in the East 'tis good for neither man nor beast." This concept takes its modern form in terms of the problem of diffusion and transport of minute organisms in the air, which was the subject of an entire issue of the *Philosophical Transactions of the Royal Society Series B* in 1983 ("The Aerial Transmission of Disease," vol. 302, pp. 437-604). Often, these microbes are *spores* such as the endospores of bacteria, the spores of Actinomycetes, fungi, ferns, and the pollen of flowering plants. We will also include the seeds and fruits of plants in our discussion of spores. In addition to settling under the influence of gravity, spores diffuse passively in the atmosphere.

The process of spore dispersal has four principal states: (1) spore liberation; (2) dispersion in the air or in water; (3) deposition; and (4) germination. Here we are concerned primarily with stage (2) in the air. Stages (1) and (3) are important only insofar as they specify the initial and boundary conditions.

A *dispersal spore* may consist of one or more cells. Its specific gravity ranges from 0.5 to 1.5; usually it is slightly heavier than water. Its size varies approximately from 1 to 100 μm with the exception of bacteria; for fungi, the range is 3 to 30 μm , and for pollen, it is 20 to 60 μm . Seeds and fruits, collectively known as diaspores, may be considerably larger than this range. Since spores are heavier than air, they tend to fall at a constant terminal velocity in still air.

3.3.1 Settling Velocity

According to Stokes' law, a small sphere of radius a moving with velocity v in still, viscous fluid with viscosity η is subject to a resistive force F , given by

$$F = 6\pi a\eta v.$$

When this force of resistance balances the immersed weight of the sphere (absolute weight minus the force of buoyancy), the sphere falls with a constant velocity. We call this terminal velocity the *settling velocity*, v_s . Constructing a force balance, we obtain

$$\underset{\text{resistance}}{6\pi a\eta v} = \underset{\text{weight}}{4/3\pi a^3 \rho_1 g} - \underset{\text{force of buoyancy}}{4/3\pi a^3 \rho g} = 4/3\pi a^3 (\rho_1 - \rho)g, \quad (3.16)$$

where ρ_1 is the density of the sphere, ρ is the density of the fluid, and g is the acceleration of gravity. From (3.16) we have

$$v_s = 2(\rho_1 - \rho)ga^2/9\eta. \quad (3.17)$$

Since the density of spores is roughly 1 g/cm^3 and that of air is of the order of 10^{-3} g/cm^3 , the influence of the buoyancy force may be ignored for spores falling in the atmosphere. This is not true for spores in water since $\rho_1 \cong \rho$; a spore may fall slowly in water or even float on the surface.

Stokes' law holds satisfactorily for spores of radius $a = 1$ to $100 \text{ }\mu\text{m}$ falling in the atmosphere, for which the calculated settling velocity varies from 0.01 to 100 cm/s (see Fig. 3.11). In water, Stokes' law holds from microbes (plankton) of radius $a = 1$ to $250 \text{ }\mu\text{m}$, for which the calculated settling velocity varies from 10^{-6} to 0.1 cm/s . For an excellent review on the settling velocity of plankton in the sea, consult Smayda (1970). Stokes' law does not apply under more inertial conditions (i.e., $\text{Re} > 0.5$) due to turbulence, but v_s can be estimated before the onset of turbulence using the following relationship:

$$v_s = 2K_I a_0 \left(\frac{\rho_1 - \rho}{\rho} \right)^{2/3} / \nu^{1/3},$$

where K_I is a dimensional constant, and a_0 is the relative radius given by

$$a_0 = a - \zeta A,$$

where ζ is a constant (0.4 for spheres), and A is the largest radius that would satisfy Stokes' law (Dallavalle, 1948; also see Vogel, 1994). Sundby (1983) applied these models for v_s to the eggs of three pelagic fish species where $\text{Re} < 5$ and $K \approx 19$ (cgs). The terminal velocity was predicted to range from 0.2 to 2.5 mm/s corresponding to Re between 0.2 and 3 , and these were presented in composite figure relating a and the density difference, $\Delta\rho$.

The relationship between particle shape and settling velocity has been an area of considerable interest. Komar et al. (1981) derived a semiempirical equation for the settling velocity of ellipsoidal and cylindrical particles sinking in water. This model compared favorably with settling velocity data

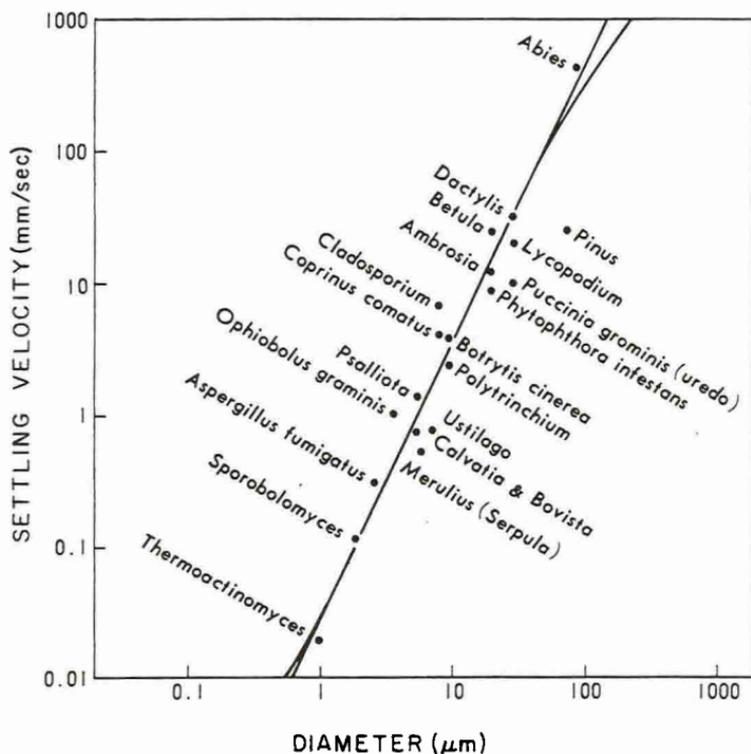


FIGURE 3.11. Observed settling velocities of spores and pollen related to diameter. The straight line represents calculated settling velocity of smooth sphere (density 1) from Stokes' law (copied with permission from Fig. 3 in Gregory, P. H.: *The Microbiology of the Atmosphere*, 2nd ed. J. Wiley & Sons, 1973).

obtained from the cylindrically shaped fecal pellets produced by copepods and euphausiids. Takahashi and Honjo (1983) measured the sinking speeds of the skeletal remains of 55 species of marine protists known as radiolarians. v_s ranged from 13 to 416 m/day, i.e., 1.5×10^{-4} to 4.8×10^{-3} m/s. These speeds are generally lower than those predicted by Stokes' law. Non-sphericity can account for only part of this departure, but other factors, such as density, may also be of importance. Interestingly, the density of settling particles has been measured only directly, rather than inferred via settling rate experiments, in a number of species (e.g., Oliver et al., 1981; Ackerman, 1989, 1997b; see below and Sect. 3.2.2). Jackson (1989) revealed the importance of $\Delta\rho$ to settling velocity by reexamining the phytoplankton reviewed by Smayda (1970) and demonstrating the nonlinearity of $\Delta\rho$ with the cell diameter ($d = 2a$; $\Delta\rho \propto d^{-0.83}$). In this case, $v_s \propto d^{1.17}$ for phytoplankton, which was confirmed by Deibel (1990) for fecal pellets ($v_s \propto d^{1.14}$). Ross and Quentin (1985) measured the sinking rates of embryos of the Antarctic krill, *Euphausia superba*, at two hydrostatic pressures (10 and 1000 dbar). No sig-

nificant differences in the sinking rates of embryos were found at any time during embryonic development. This result implies that while the water density increases at greater depths, the density of embryos also increases, thus maintaining the same density difference. Conversely, Cambalik et al. (1998) used a new motion analysis and experimental apparatus to examine the effects of salinity (i.e., density) on the ascending eggs of Atlantic menhaden. Ascending rates were found to be greatest at intermediate salinity and less at later stages of embryonic development.

When the concentration of particles is higher than a critical value, a new phenomenon occurs by which a group of particles settles as a whole to form a vertical density current. Bradley (1965, 1969) suggested the importance of this phenomenon in the natural environment. Both theoretical and experimental studies of the settling behavior of a group of particles has been examined (Adachi et al., 1978; Crowley, 1976, 1977; Thacker and Lavelle, 1978). Weiland et al. (1984) examined the sedimentation of two-component mixtures of solids and observed that (1) when the total suspension concentration is less than 10% by volume, both solid components settled at reduced rates, (2) for concentrations greater than 10%, the relative motion between particles leads to instabilities and "fingering settling" occurs. In this context, Batchelor and van Rensburg (1986) describe bulk vertical streaming motions that developed when two different species of small particles are dispersed uniformly in a fluid and are settling under gravity. They also present an instability model to explain the phenomenon.

Bienfang (1981) introduced a sinking-rate method that was suitable for the analysis of natural assemblages. Results from this method indicate (1) higher sinking rates in assemblages dominated by large cells, (2) decreased sinking rates after nutrient enrichment, and (3) buoyancy response to light levels. This would indicate that the settling velocity of phytoplankton depends largely on the conditions of the cells, with senescent cells sinking faster than the actively growing ones. The sedimentation of colonial cyanobacteria (*Microcystis aeruginosa*), which are buoyant, can be accounted for by their aggregation with colloidal precipitation (Oliver et al., 1985). Similar coagulation processes in lakes can be sufficiently rapid to significantly affect the downward flux of suspended material (Weilenmann et al., 1989). Results indicate that calcium ions act as destabilizing agents, while dissolved organic matter stabilizes particles and retard coagulation. Since the chemistry of lakes varies widely, natural coagulation rates should differ among lacustrine systems.

The coagulation of particulate matter into marine snow was discussed in Sect. 3.2.2, as was a model for the settling velocity of marine snow, which incorporated the porosity and mucous content of the aggregate. In situ settling velocities measured using stroboscopic photography have revealed size-related differences in v_s , with large aggregates settling slower than small particles (Asper, 1987). As described above, the dimensions (D) of marine aggregates are fractal between $D = 1.7$ and 2.3, which is less than 3, which

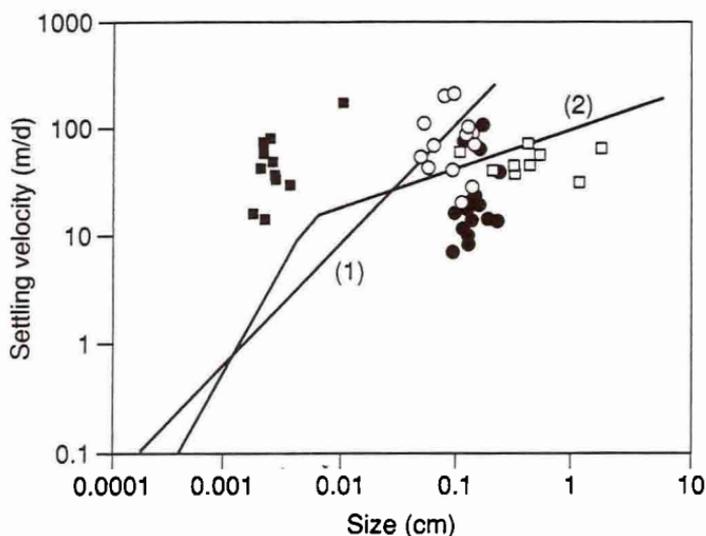


FIGURE 3.12. Size dependence of aggregates on settling velocity. Legend: \circ Bedford Basin, \bullet diatom aggregates, \square and \blacksquare in situ measurements, line (1) from Jackson (1989), line (2) from Stokes' law (after Ruiz, 1997).

would be expected for a sphere or cube (see Jackson and Burd, 1998). Johnson et al. (1996) generated fractal aggregate models in the laboratory using latex microspheres. Their analysis revealed that the settling velocity of aggregates was on average 4 to 8.3 times higher than predicted by Stokes' law or the porosity models described in Sect. 3.2.2, which assume a homogeneous distribution of particles in the aggregate. The largest deviation from theoretical predictions occurred when D was less than 2 and the porosity was overestimated. These phenomena are also evident in Ruiz's (1997) review of the relationship between settling velocity and aggregate size presented in Fig. 3.12.

The study of solid particles in turbulent flow is a very complex process. However, for spherical Stokesian particles whose size is smaller than the Kolmogorov microscale ($\lambda = 2$ to 7 mm) of turbulence, the average settling velocity equals the settling velocity in still water. Nonlinearities in the drag force may result in reduction of the average settling velocity (see Lande and Wood, 1987). Lande and Wood (1987) analyzed a physical model of particle motion utilizing information on sinking rates of particles and the rate of turbulent diffusion as a function of depth to estimate the average time that particles, starting at a given depth, remain in the surface mixed layer or the euphotic zone. The total duration of suspension at each depth before the particles leave the upper layers, whether the first time or permanently, was also estimated. They achieved this by projecting the stochastic trajectories of the individual particles instead of tracking the concentration of continuously distributed substances as the normal approach.

3.3.2 Diffusion Model

The analysis of experimental data on the dispersion of clouds of spores, pollen, and diaspores from the standpoint of atmospheric diffusion theory has provided insight into the dispersal of plants and other sessile organisms (Gregory et al., 1961; Gregory, 1973; Rombakis, 1947; Schrödter, 1960; Raynor et al., 1970, 1972, 1973; Okubo and Levin, 1989; Greene and Johnson, 1992, 1996).

It was in relation to epidemiology, i.e., the spread of disease-producing agents, that Rombakis (1947), probably for the first time, and Schrödter (1960) dealt with the theoretical aspects of spore dispersion in the atmosphere, using a simple model of turbulent diffusion. The problem is considered only in two-dimensional space, where the x -axis lies downwind along the ground and the z -axis is vertically upward. The origin of the coordinate system is placed at the source of spores (Fig. 3.13).

Assuming constant advective flow and diffusivity, the concentration of S of a steady-state distribution of spores satisfies

$$u \frac{\partial S}{\partial x} - w_s \frac{\partial S}{\partial z} = \frac{\partial}{\partial z} \left(K_z \frac{\partial S}{\partial z} \right), \quad (3.18)$$

where u is the wind velocity, w_s is the settling velocity of the spores, S is the concentration of spores in the air, and K_z is the vertical diffusivity (assumed constant here). We ignore diffusion in the x direction (see Sect. 2.6.1) as well as nonconservative terms.

Under the conditions that at $x = 0$ a cloud of N_0 spores is released and that the diffusive flux vanishes at the ground, we solve (3.18) to find

$$S = N_0 \left(\frac{u}{\pi K_z x} \right)^{1/2} \exp \left\{ - \frac{(z + w_s x/u)^2}{4 K_z x/u} \right\}. \quad (3.19)$$

Inspection of (3.19) shows that the concentration distribution of spores over height z is a Gaussian plume, with mean and variance that vary linearly with distance x . The condition at the ground means that the diffusive flux would vanish at $z = 0$ if there were no settling, i.e., $w_s = 0$. A more reasonable treatment of boundary conditions is given in further discussion in this section. The number of spores N found above height z per unit horizontal area

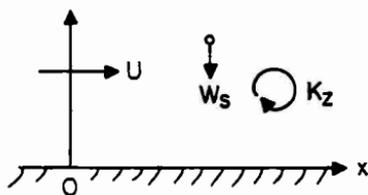


FIGURE 3.13. Model for spore diffusion in the air. U : wind velocity, w_s : settling velocity of spores, K_z : vertical diffusivity.

is given by integrating (3.19) over z :

$$N = \int_z^{\infty} Sdz' = N_0 \left[1 - \Phi \left\{ \frac{(z + w_s x/u)}{2(K_z x/u)^{1/2}} \right\} \right], \quad (3.20)$$

where Φ is the error function, which is defined by

$$\Phi(a) \equiv \frac{2}{\sqrt{\pi}} \int_0^{\bar{a}} e^{-b^2} db, \quad a \geq 0,$$

and its numerical values lie between $\Phi(0) = 0$ and $\Phi(\infty) = 1$.

We shall now discuss some characteristics of spore dispersion on the basis of (3.20). We define the probable boundary of spore dispersal to be a curve both above and below of which 50% of the total number of spores released are found. We can obtain the equation of this curve by setting $N = N_0/2$ or by equating the argument of the error function (3.20) to 0.4768 since $\Phi(0.4769) = 1/2$. It follows that

$$\frac{(z + w_s x/u)}{2(K_z x/u)^{1/2}} = 0.4769. \quad (3.21)$$

The curve representing the boundary is thus seen to be a parabola passing through the origin (Fig. 3.14). Of course, we are free to choose other boundary curves characterized by different percentages, say $N = N_0/10$, which implies that $\Phi(1.1631) = 9/10$. However, this alters only the details of the argument, e.g., the numerical coefficients of the parameters in (3.22).

From (3.21) we can calculate (a) the range of dispersal X , i.e., the point at which the curve intersects the x -axis, (b) the height of dispersal, Z_m , i.e., the highest point of the curve, and (c) the duration of dispersal $T = X/u$, i.e., the effective flight duration of a spore. The results are found to be

$$X = 0.91K_z u/w_s^2, \quad Z_m = 0.2274K_z/w_s, \quad T = 0.91K_z/w_s^2. \quad (3.22)$$

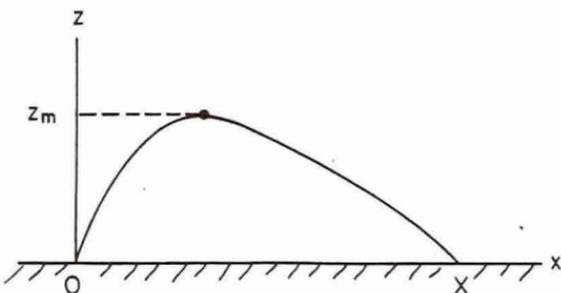


FIGURE 3.14. Curve representing the probable boundary of spore dispersal. X : range of dispersal, Z_m : height of dispersal.

TABLE 3.1 Calculated values of the range of dispersal (X), height of dispersal (Z_m), and duration of dispersal (T) for various values of diffusivity (K_z), wind speed (u), and settling velocity of spore (w_s)

(1)

K_z (m^2/s)	u (m/s)	w_s (cm/s)	X (km)	Z_m (m)	T
1	4	2	9.1	11.4	38 min
2	4	2	18.2	22.7	1 h 16 min
2	8	2	36.4	22.7	1 h 16 min
2	8	1	145.6	45.5	5 h

(2) $K_z = 1 m^2/s$, $u = 6 m/s$

size of spore (μ)	w_s (cm/s)	X (km)	Z_m (m)	T
small 5×3	0.035	44571	650	86 days
medium 14×6	0.138	2867	165	5 days 13 h
large 20×16	0.975	57.4	23.3	2.7 h
<i>Phytophthora</i>	1.3	32.3	17.5	1.5 h

(Remark) Reported range of dispersal for *Phytophthora* is between 200 m and 64 km.(3) Various values of K_z (m^2/s)

size of spore (μ)	w_s (cm/s)	$K_z = 1$		$K_z = 2$		$K_z = 5$		$K_z = 10$	
		Z_m (m)	T	Z_m (m)	T	Z_m (m)	T	Z_m (m)	T
small 5×3	0.035	650	86 d	1300	172 d	3250	430 d	6500	860 d
medium 14×16	0.138	165	5.5 d	330	11.1 d	825	27.7 d	1650	55.4 d
large 20×16	0.975	23.3	2.7 h	46.6	5.4 h	116.5	13.5 h	233	27 h
<i>Phytophthora</i>	1.3	17.5	1.5 h	35.0	3.0 h	87.5	7.5 h	175	15 h

These quantities serve as parameters indicating the extent of spore dispersal. Note that both Z_m and T do not depend on wind velocity; only the range of dispersal is influenced by this parameter. Table 3.1 shows calculated values of X , Z_m , and T for various values of diffusivity, settling velocity, and wind velocity (Schrödter, 1960). The range of dispersal is inversely related to the settling velocity. Thus, the smaller the size of the organism, spore, or diaspore, the farther it will be blown if other parameters are unchanged. However, the other parameters are not likely to remain fixed. For example, female first-instar larvae of cochineal insects (*Dactylopius austrinus*) develop long, wax filaments on their dorsal surfaces that reduce their settling velocity and thereby enhance dispersal (Moran et al., 1982). The males have fewer, shorter filaments and are not dispersed as far. Augspurger and Franson (1987) found the deposition distance of samaras (winged fruit) of the tropical tree *Tachigalia versicolor* to be proportional to the average horizontal wind

speed and inversely proportional to the square root of wing loading (weight of seed over projected cross-sectional area) over a range of sizes; they noted, however, that the effect of variation in wind speed is greater than that of variation in mass (see also Greene and Johnson, 1992).

Deviations of the flow-field parameters (velocity and diffusivity) from their steady-state values influence dispersal. Variance in deposition distance can be related to variance in wind direction, velocity, and turbulence (Matlack, 1992; Greene and Johnson, 1989, 1996). Matlack (1992) observed expected relationships between primary dispersal and seed size with *Betula lenta* seeds in a laboratory airstream, but noted only weak relationships in the field, presumably due to variations in the flow field.

Despite these caveats, the values of the parameters for spore dispersal given in Table 3.1 are not unreasonable, and Rombakis' (1947) model serves as a rough evaluation of spore dispersal. However, the fact that the model does not incorporate the structure of the atmospheric boundary layer renders it unsatisfactory. More advanced modeling relies on Sutton's equation diffusion (see Sect. 2.6.1) for atmospheric diffusion (Sutton, 1943; Schrödter, 1960).

The boundary condition at the ground creates some problems in obtaining an analytical solution. If there were no ground, the effect of spore settling could be taken into account simply by replacing the vertical coordinate z by $z + w_s t$ for an instantaneous source or by $z + w_s x/u$ for a continuous source, in the solution of atmospheric diffusion presented in Chap. 2. The settling effect becomes significant at places farther than a certain distance from the source. Spores settle by a vertical distance $w_s t$ during time t after release. At the same time vertical diffusion tends to spread spores by a vertical distance $(2K_z t)^{1/2}$. Hence, if we define a critical time t_c by $w_s t_c = (2K_z t_c)^{1/2}$ or $t_c = 2K_z/w_s^2$, the settling effect becomes important for times $t \geq t_c$. Likewise we may define a critical distance x_c as $x_c = ut_c = 2K_z u/w_s^2$, using the mean wind speed, u ; the settling effect becomes important for distances $x \geq x_c$. For instance, when $u = 5$ m/s and $K_z = 100$ cm²/s, the critical distance of settling for *Phytophthora infestans* ($w_s = 1.3$ cm/s) is $x_c = 600$ m. Microscopic spores of the order of 10 μ m in size can travel several tens of kilometers from the source before settling comes into effect. Considering the fact that x_c is rather large, we sometimes use Sutton's formula (2.23) without correction due to settling. This practice is permissible for evaluation near the source area—say, within 1 km.

Godson (1957) applied Sutton's theory to the diffusion of particles that settle at the ground. Starting with Sutton's solution (2.23) in the absence of a ground level and adding the effect of the settling velocity,

$$S = \frac{Q}{\pi u c_y c_z x^{2-n}} \exp \left[- \left\{ \frac{y^2}{c_y^2 x^{2-n}} + \frac{(z + w_s x/u)^2}{c_z^2 x^{2-n}} \right\} \right].$$

Note that the factor 2 in front of Q has been dropped. The boundary effect

has not yet been taken into account. Godson's proposal for the reflective boundary condition at the ground is to add a mirror-image line source below the ground level. Thus,

$$S = \frac{Q}{\pi u c_y c_z x^{2-n}} \exp\left\{-\frac{y^2}{c_y^2 x^{2-n}}\right\} \left[\exp\left\{-\frac{(z + w_s x/u)^2}{c_z^2 x^{2-n}}\right\} + \int_0^\infty \exp\left\{-\frac{(z + w_s x/u + \eta)^2}{c_z^2 x^{2-n}}\right\} f(\eta) d\eta \right], \quad (3.23)$$

where the function f represents a relative intensity of the image source per unit vertical length, which must be determined in such a way that at $z = 0$, $\partial S/\partial z = 0$, i.e., such that the reflection condition is satisfied at the ground. This method is applied to a ground source; Godson also treats an elevated source.

More recently, Okubo and Levin (1989) used a solution of (3.18) to estimate the deposition rate of seeds at ground level from an elevated source ($x = 0$, $z = H$), incorporating the effect of atmospheric structure by considering $u = u(z) = u_0 z^\alpha$ and $K_z = K_z(z) = k u_* z$, resulting in the crosswind-integrated surface deposition rate $Q(x)$:

$$Q(x) = \frac{M w_s}{H \bar{u} \Gamma(1 + \beta)} (f(x))^{1+\beta} \exp(-f(x)), \quad (3.24)$$

where

$$f(x) = \frac{H^2 \bar{u}}{2(1 + \alpha) \bar{K}_z x}, \quad \bar{u} = \int_0^H u(z) dz/H, \quad \bar{K}_z = \int_0^H K_z(z) dz/H,$$

where $\beta = w_s/(k u_* (1 + \alpha))$, k = von Karman's constant (= 0.41), u_* = friction velocity (see Sect. 2.6.1), and M is the rate of seeds released per unit length of a crosswind line source at height H .

Deposition rates estimated from (3.24) are similar to those resulting from a "tilted Gaussian plume" solution like (3.19) for small and large seed masses (see Fig. 3.15), but they differ somewhat at intermediate values; the modal value of the dispersal distance (i.e., the so-called seed rain) from the source is somewhat smaller than that of the Gaussian model for intermediate values of seed mass.

This seed rain is an important biological phenomenon for the ecology of plants (e.g., Harper, 1977; Willson, 1992). The aerial dispersal of diaspores has been reviewed by Van der Pijl (1972), Burrows (1975a, b, 1987), Harper (1977), Niklas (1992), and Raven et al. (1999). The small size of "dustlike" seeds of orchids allows them to be entrained into wind current, which affects their dispersal. A large number of seeds disperse ballistically, including *Impatiens* (touch-me-nots) and Mistletoes, which may disperse far from the

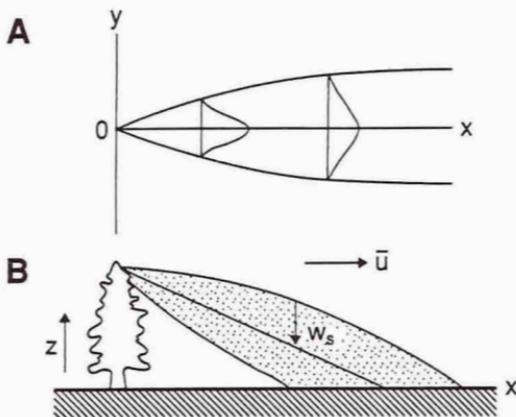


FIGURE 3.15. Gaussian plume model viewed from above in A, and tilted plume model viewed from the side in B. H : release height, \bar{u} : average wind speed, w_s : settling velocity, z : height (after Okubo and Levin, 1989).

source plant. Tumble weeds (*Salsola*) detach and are the ultimate wanderers, releasing seeds as they roll in the wind. Poplars (*Populus*) and Willows (*Salix*) have diaspores with woolly hairs that reduce settling velocities and render them as floating seeds. Plumed fruits of composites, including the dandelion (*Taraxacum*), are specialized fruits with a parachute-like pappus (plume) that affects their dispersal. These plants have evolved toward maximizing their dispersal by (1) decreasing the mass of the seed, (2) increasing the ratio of the pappus to the fruit, (3) increasing the aerodynamic drag of the pappus, and (4) elevating the height of release (Harper, 1977). Perhaps the most interesting aerial dispersers are the plane-winged and autogyroscopic-winged diaspores of conifers (seeds) and the samaras (fruit) of a wide variety of plants. These asymmetrical diaspores autogyrate once they reach terminal velocity (w_s), which is related to the square root of the wing loading (described above) and the conical section traced (area = A_D) as the diaspore autogyrates, given by

$$w_s = \sqrt{2} \left(\frac{W}{\rho A_D} \right)^{1/2},$$

where W is the weight and ρ is the density (see Ward-Smith, 1984; Niklas, 1992). Diaspore dispersal also occurs on the water surface via various modes of floatation (specialized hairs, disclike shapes) and rafting of vegetative tissues, and beneath the water surface via sedimentation (Van der Pijl, 1972; Cook, 1987; Ackerman, 1998b). The classic example of floatation involves coconuts (*Cocos*) that utilize Archimedes' principle, but many familiar plants like cattails (*Typha*) have hairs that decrease the surface tension to render themselves buoyant. Churchill et al. (1985) documented gas-bubble dispersal in the seagrass *Zostera marina*, in which gas bubbles attached to a small fraction of seeds can lead to dispersal distances orders of magnitude greater than without gas bubbles (e.g., maximum of 200 m versus 1 m). Underwater seed rains are likely to be analogous to those described above for aerial diaspores.

3.3.3 Experiments on Spore Dispersal

One of the earlier experiments on spore dispersal is credited to Stepanov (1935), who used artificial sources of spores; in one experiment he released 1.2×10^9 spores of *Tilletia caries* to study their diffusion. Gregory (1973) reexamined Stepanov's data, together with data obtained with *Lycopodium* spores, in light of Sutton's theory of atmospheric diffusion. Gregory found that the data agreed with Sutton's formula for the lateral variance

$$\sigma_y^2 = 1/2c_y^2x^{2-n}$$

if $c_y = 0.64 \text{ m}^{1/8}$ and $n = 0.25$; the data were found to be incompatible with a Fickian diffusion model with constant diffusivity, variance $\sigma_y^2 = 2K_yx/u$.

Dispersion studies conducted by the Meteorology Group at Brookhaven National Laboratory (Long Island, New York) in the 1970s with the pollen of ragweed (*Ambrosia* spp.) and timothy, *Phleum pratense*, also supported Sutton's model (Raynor et al., 1970, 1972, 1973). Ragweed pollen grains are spherical and about $10 \mu\text{m}$ in radius. Their settling velocity is approximately 1.5 cm/s. Ragweed pollen was released continuously at the height of 1.5 m above ground level, from point sources and from circular area sources of various sizes. Samples were taken at four heights (0.5 to 4.6 m) and at four or five distances from the source, to a maximum of 69 m. The sample counts were converted to average concentration in grains per 1 m^3 and to deposition in grains per 1 m^2 .

Figure 3.16 shows some horizontal distributions of pollen concentration at a height of 1.5 m and some cross-sectional distributions along the plume centerline. The mean wind speed at 1.5 m was 2.9 m/s. Figure 3.17 shows

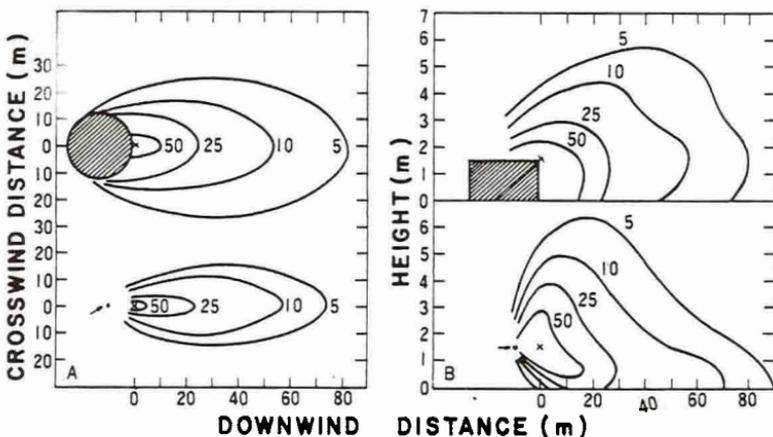


FIGURE 3.16. Diffusion of the pollen of ragweed from circular and point sources. A: Horizontal distributions at a height of 1.5 m. B: Vertical distributions along the plume centerline. The concentration at the point (x) is taken as 100 units (from Raynor et al., 1970).

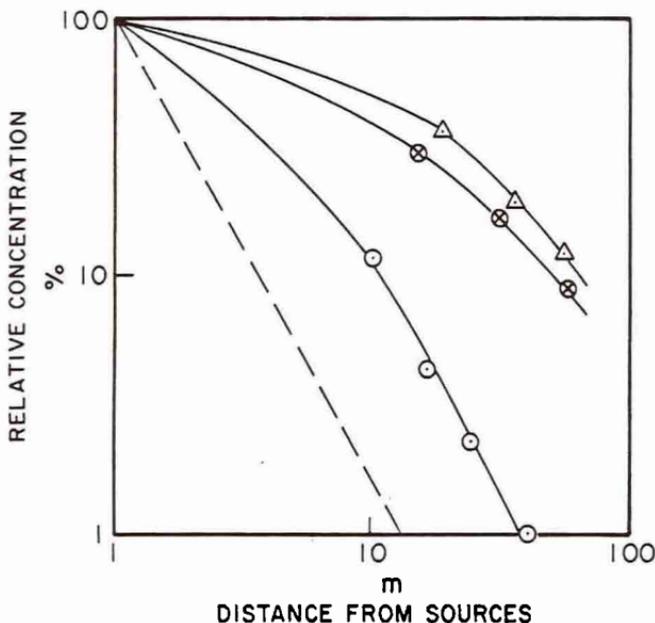


FIGURE 3.17. Variations of mean relative centerline concentration of ragweed pollen with distance. —○— data from a point source, —⊗— data from a circular source of 18.3 m in diameter, —△— data from a circular source of 27.4 m in diameter. (— — —) theoretical curve due to Sutton (from Raynor et al., 1970).

examples of the variations of mean relative centerline concentration with distance. Also shown is a point source calculated from Sutton's formula and corrected for deposition. The slope of Sutton's curve is similar to that of the experimental point source curve beyond 10 m. The area source curves also tend toward a similar slope at distances increasing with source size.

The ratio of the standard deviations of plume height and width, i.e., σ_z/σ_y , ranges from 0.10 to 0.25. These values are smaller than the value of 0.5 given by Sutton's theory (Sect. 2.6.1), indicating that lateral dispersion predominates over vertical dispersion close to the ground.

The mean velocity of deposition, calculated from the measured amounts of deposition on the ground, was found to be 5.05 cm/s, considerably larger than the computed settling velocity of 1.56 cm/s. Higher values of the velocity of deposition were found near the source.

It was estimated that about 1% of the pollen grains remain airborne at a distance of 1 km from the source. A single ragweed plant can release in excess of 10^6 grains per day during the height of the pollination season; even if only 1% of these remain airborne, the implied concentration of airborne ragweed pollen during the season is quite large. For an estimate we take an area inhabited by 10 ragweed plants per m^2 . If the airborne pollen grains were distributed uniformly from ground level up to a height of 100 m, the air would contain 1000 grains per m^3 .

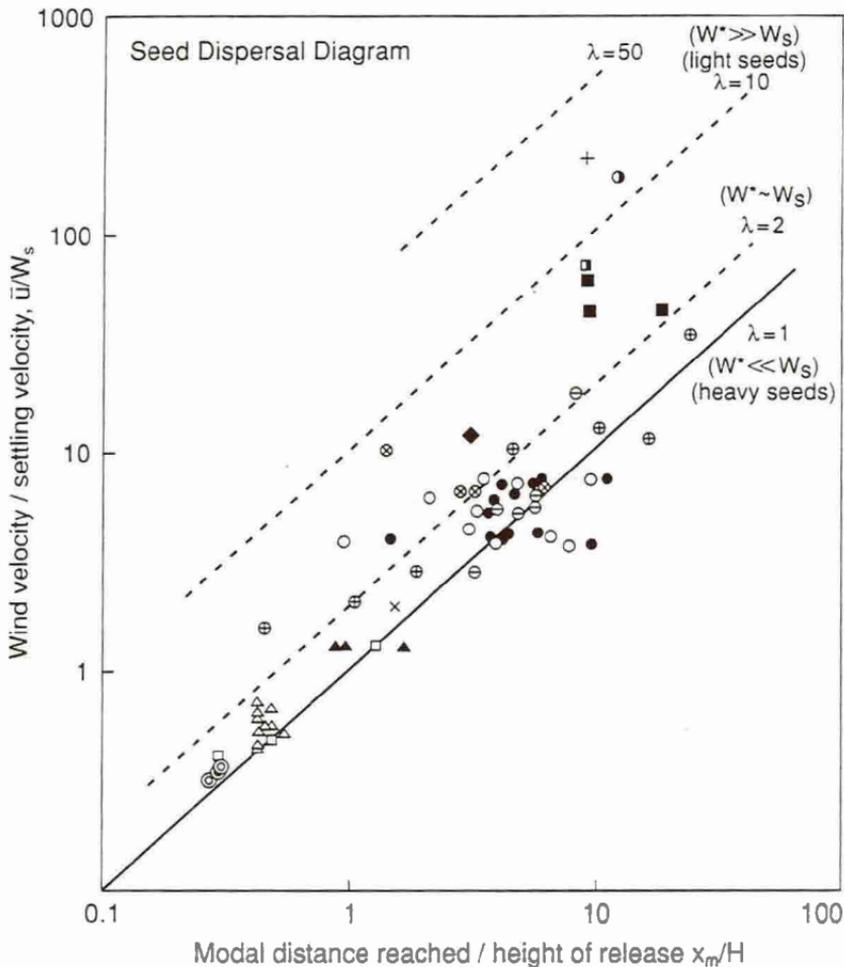


FIGURE 3.18. Seed dispersal diagram, which shows the relationship between the mode of dispersal distance and the mean wind speed (nondimensionalized form) for various values of λ ($\lambda = (\bar{u}/W_s)/(x_m/H)$). Legend: x_m : mode of seed dispersal distance, H : height of seed source, \bar{u} : mean wind speed, W_s : denotes settling velocity of seed. Here $\lambda = (\bar{u}/W_s)/(x_m/H)$. \odot Augspurger-Hogan, \triangle Augspurger-Franson, \otimes McEvoy-Cox. \blacklozenge Gross, \square Cremer, \oplus Platt-Weis, \blacktriangle Watkinson, \ominus Isaac, \bullet Morse-Schmidt, \times Colwell, \blacksquare + Srceramula-Ramalingam, \blacksquare Tonsor, \circ Raynor. (From Okubo and Levin, 1989).

Okubo and Levin (1989) collected dispersal data from 15 field studies and tabulated the dispersal parameters to compare with their dispersal equation (3.24) (see Table 1 in Okubo and Levin, 1989). The resulting dispersal diagram (Fig. 3.18) plots average wind speed normalized by seed settling velocity against modal dispersal distance normalized by the height of seed release on a log scale. Heavy seeds match the predicted behavior especially well, with the modal dispersal distance $\approx Hu/w_s$, where H is height of release, u is

average wind velocity, and w_s is settling velocity. Lighter seeds, with settling velocity smaller than the local turbulent mixing velocity w^* (speed at which the particle would "settle" via turbulence in the absence of gravity), tend toward a modal distance $\approx Hu/w^*$.

Spore distribution in higher atmospheric strata over longer distances is a very important problem from the viewpoint of epidemiology as well as of genetics and paleoecology (Moore, 1976; Mollison, 1977a; Aylor et al., 1982; Aylor, 1986). For example, the aerial transport of fungal spores has been known to be responsible for spreading plant diseases over distances of 500 km or more. A logical framework for estimating long-distance transport of viable spores involves (1) the reproduction of spores at the source area, (2) the escape of spores into the air above the canopy, (3) the transport and diffusion of spores in the atmosphere, (4) the survival of airborne spores, and (5) the deposition of spores onto a distant crop. The survival of spores and deposition or washout during rainfall are difficult to predict. On a much larger scale, the panspermia hypothesis is doubtful given Weber and Greenberg's (1985) experiments involving the inactivation of *Bacillus* by vacuum ultraviolet radiation to simulate interstellar conditions. Remarkably, the damage produced by low temperatures (e.g., 10 K) was less than the damage due to UV radiation in the range of 200 to 300 nm, but both were sufficient to kill the cells.

3.3.4 Vertical Distributions over Wide Regions

Thus far we have dealt with spore dispersion from given local sources. Now we shall discuss vertical distributions of dust, spores, and pollen grains over the globe as a whole or as a mean state over a wide area. In this case the effects of local source are smoothed out, and horizontal advection and diffusion may be ignored after averaging over a large horizontal area. We thus consider only the steady-state distribution in the vertical direction determined by

$$\frac{d}{dz} \left(K \frac{dS}{dz} \right) + \frac{d}{dz} (wS) = 0, \quad (3.25)$$

where K is a virtual diffusivity in the vertical direction, which incorporates the effect of various processes arising from the averaging, such as small-scale vertical convection. In this sense K is not identical with K_z , which is appropriate for small-scale diffusion processes. By the same token, w should be interpreted as a virtual settling velocity. Both K and w depend in general on height.

Integrating (3.25) over z from the base height z_0 (which could be the top of a crop canopy, or the ground, $z = 0$) to a height z , we obtain

$$K \frac{dS}{dz} + wS = \left(K \frac{dS}{dz} + wS \right)_{z=z_0} \equiv P, \quad (3.26)$$

where P is the upward vertical flux of S at the base. That is, under the assumption of steady state and no net horizontal flux, average vertical flux is constant ($= P$). Integrating (3.26) once more over z , we find

$$S = \left[S_0 + \int_{z_0}^{\bar{z}} P/K \exp \left\{ \int_{z_0}^{z'} w/K dz'' \right\} dz' \right] \exp \left\{ - \int_{z_0}^{\bar{z}} w/K dz' \right\}, \quad (3.27)$$

where S_0 denotes the concentration at $z = z_0$. The total number of airborne spores per unit surface area is given by

$$N = \int_{z_0}^{\infty} S dz. \quad (3.28)$$

Some special models are considered below.

Model 1. K, w : constant, $z_0 = 0, P = 0$.

From (3.27) and (3.28),

$$\begin{aligned} S &= S_0 \exp(-wz/K), \\ N &= S_0 K/w. \end{aligned} \quad (3.29)$$

Spore concentration is seen to decrease exponentially with height (Fig. 3.19).

Model 2. $K = a(z + z_1), w = \text{constant}, z_0 = 0, P = 0$ (a and z_1 are constants).

$$\begin{aligned} S &= S_0 \left(1 + \frac{z}{z_1} \right)^{-\lambda}, \quad \lambda \equiv w/a, \\ N &= \begin{cases} S_0 z_1 / (\lambda - 1), & \text{if } \lambda > 1, \\ \infty, & \text{if } \lambda \leq 1. \end{cases} \end{aligned} \quad (3.30)$$

The distribution represented by (3.30) corresponds to the vertical profile of insects due to Johnson (1969). See Sect. 6.2.

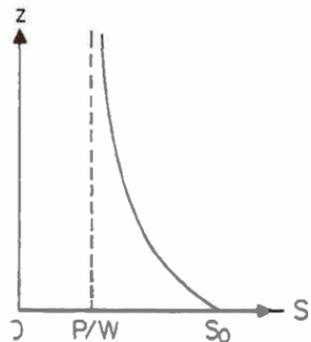


FIGURE 3.19. Theoretical distribution of spore concentration (S) in the vertical direction (z) ("normal" type).

Model 3. $K = az(1 - z/d)$, $w = \text{constant}$, $z_0 > 0$ (a and d are constants).

$$S = \frac{P}{w} + \left(S_0 - \frac{P}{w}\right) \left(\frac{d - z_0}{d - z} \frac{z}{z_0}\right)^{-\lambda}, \quad \lambda \equiv w/a, \quad (3.31)$$

$$N = \infty.$$

This distribution results from a parabolic profile of K that occurs at near-neutral conditions (Clarke, 1970; Foda, 1983). If $P = 0$, then $S = 0$ at $z = d$, corresponding to a diffusion ceiling or "inversion lid," above which the concentration is assumed to be negligible. In this case, N depends on λ . Foda (1983) discusses (3.31) with $P = 0$ in the context of dust transport from the desert to the sea, where the surface boundary condition changes from $S = S_0 > 0$ to $S = 0$ (a perfect sink).

Model 4. K , w : constant, $P \neq 0$, $z_0 = 0$.

$$S = P/w + (S_0 - P/w)\exp(-w/Kz), \quad (3.32)$$

$$N = \infty.$$

If $wS_0 > P > 0$, i.e., the flux at the ground is smaller than that of settling, S decreases with height and approaches a constant value, P/w (Fig. 3.19). If $P > wS_0 > 0$, i.e., the flux at the ground is larger than that of settling, S increases with height and approaches P/w (Fig. 3.20). In other words, depending on the value of the flux at the ground, the concentration does not necessarily decrease with height. Craigie (1945) observed vertical distributions of *Puccinia graminis* uredospores over Manitoba, Canada, which look similar to Fig. 3.20. However, spore distributions that exhibit decreasing concentration with height are more commonly observed.

If we consider the case $P = 0$ and choose $K = 10 \text{ m}^2/\text{s}$ and $w = 3 \text{ cm/s}$ as typical values, the concentrations at heights of 1 km and 10 km are calculated from (3.29) to be, respectively, e^{-3} and e^{-30} of the concentration at the ground S_0 . On the other hand, microscopic spores for which, say $w = 0.03 \text{ cm/s}$, are expected to diffuse into the stratosphere, above 10 km.

Data from the Krakatao eruption of August 1882 (Flohn and Penndoff, 1950; Deirmendijan, 1973; Lamb, 1970), from the Mount St. Helens erup-

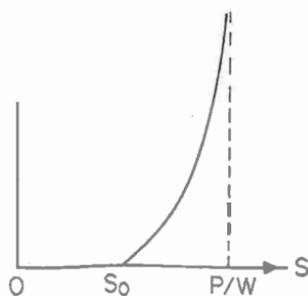


FIGURE 3.20. Theoretical distribution of spore concentration (S) in the vertical direction (z) ("abnormal" type).

tions of May and June 1980 (Danielsen, 1981; Pollack, 1981), from the El Chichón eruption of April 1982 (Robock and Matson, 1983), and from thermonuclear bomb tests (Machta, 1959) have shown that fine dust particles, once carried to heights above 10 km, are transported by the prevailing winds and spread over global dimensions on a time scale of weeks. Dust has been shown to be carried from terrestrial sources in Northern Africa to the Atlantic and from Asia to the Northern Pacific (Prospero, 1981, 1990; Parrington et al., 1983; Chen, 1985; Zhang et al., 1992). Smaller dust plumes originate in North America and Europe. This worldwide dispersion of dust is relevant to the problem of mineral nutrient fertilization of the open ocean (Martin et al., 1991; Duce et al., 1991; Prospero et al., 1996) and to long-distance dispersal of microbes (Close et al., 1978). As long as distantly dispersed microbes remain viable, they can reproduce after deposition and represent a potential threat to crops, livestock, and natural populations, as well as to humans.

An obvious limitation of the one-dimensional, steady-state equations described above is that they do not incorporate the details of known patterns of atmospheric circulation, scavenging and other atmospheric processes, and the distribution of sources that sophisticated numerical models include, e.g., GESAMP (Duce et al., 1991), the GFDL Global Chemical Transport Model (Levy et al., 1982), and others (Prospero et al., 1996). Variations in the surface cover within a region (e.g., open water, vegetative canopy, bare soil) affect the surface boundary condition as well as the average profiles of wind velocity and eddy diffusivity, so (3.26) is most appropriate over large regions of uniform cover. However, it can also be considered as a side-boundary condition for horizontal transport at the interface of two regions of different cover (cf. Foda, 1983).

3.3.5 *Wind and Water Pollination*

The last section on spore dispersal will focus on the transport and capture of pollen by receptive surfaces (e.g., pollination droplets and flowers), i.e., pollination, in aerial and aquatic environments. In these cases, pollination occurs via the fluid media, not an animal vector, and is therefore referred to as *abiotic*. While some early concepts considered abiotic pollination to be largely a stochastic event (e.g., Faegri and Van der Pijl, 1979), there is sufficient evidence to indicate that wind pollination (i.e., anemophily) and water pollination (i.e., hydrophily) represent sophisticated fluid mechanical solutions to the problem of pollen release, dispersal, and capture (see below and the recent review by Ackerman, 2000).

Anemophily is much more common than hydrophily, in that about 98% of the plants that pollinate abiotically are pollinated by wind (Faegri and Van der Pijl, 1979). Indeed, some of the earliest seed plants were pollinated by wind (Niklas, 1992), as are present-day gymnosperms (e.g., conifers), catkin-bearing trees (e.g., birches, oaks), and herbaceous plants, including

many important cereals (e.g., grasses, sedges) (see reviews in Faegri and Van der Pijl, 1979; Regal, 1982; Whitehead, 1983; Niklas, 1985, 1992; Proctor et al., 1996; Ackerman, 2000). As mentioned, traditional views held that anemophily was a wasteful and inefficient process because pollen-to-ovule ratios can be as high as $10^6 : 1$ and the aerodynamics of pollination were not understood (Faegri and Van der Pijl, 1979). The large pollen-to-ovule ratios are not unique or representative of all anemophilous plants, and some researchers have interpreted the large production of pollen to be related to the differences in metabolic costs relative to biotically pollinated plants (e.g., Niklas, 1992) and intramale competition (e.g., Midgley and Bond, 1991). Pollen are small relative to biotically pollinated plants (i.e., 20–60 μm versus $\leq 200 \mu\text{m}$; Harder, 1998) and are unornamented without surface oils, etc. (the so-called pollenkitt), to eliminate the possibility of clumping (Crane, 1986). Experiments have shown that clumped pollen have higher settling rates than unclumped pollen (Niklas and Buchmann, 1988; see Sect. 3.3.1).

The receptive reproductive structures of wind-pollinated plants include strobili (cones), catkins (flexible tassel-like inflorescences), and spikelets of grass flowers, which in the latter two cases have brush or featherlike stigmas to aid in pollen capture (Proctor et al., 1996). These reproductive structures are neither showy or colorful, nor do they contain the nectaries, odors, and other rewards that biotically pollinated plants use to attract pollinators. These generalizations, however, are not necessarily valid for the large numbers of families with species that are secondarily abiotically pollinated (cf. Renner and Ricklefs, 1995; Ackerman, 2000).

Ecologically, anemophily is associated with the spatial or temporal separation of male and female reproductive structures (i.e., monoecy and phenological allochry, respectively), which may encourage outcrossing (Charlesworth, 1993; Renner and Ricklefs, 1995). Atmospheric conditions influence pollen release, which usually occurs under dry conditions and before leafing, which favor dispersal (Whitehead, 1983). There are important geographic associations of anemophilous plants with “stressful” environments, where species diversity is low, which leads to higher proportions of conspecifics, and conditions may be dry (e.g., high latitudes versus tropical rainforests; Regal, 1982; Whitehead, 1983). However, the interpretation of the reasons behind these associations has been called into question (Midgley and Bond, 1991).

The majority of the data related to the mechanisms of wind pollination in plants can be attributed to Niklas and co-workers (see reviews in Niklas, 1985, 1992), who used techniques to visualize the flow patterns (e.g., helium bubbles) and transport of pollen (stroboscopic photograph) around female reproductive structures in wind tunnels. Essentially, they showed that female organs and associated vegetative structures (e.g., bracts) modify the airflow in ways that favor pollination, as can be seen in Fig. 3.21. These modifications include changing flow patterns, flow patterns directed to receptive structures, downstream eddies that generate circulation, and alternating

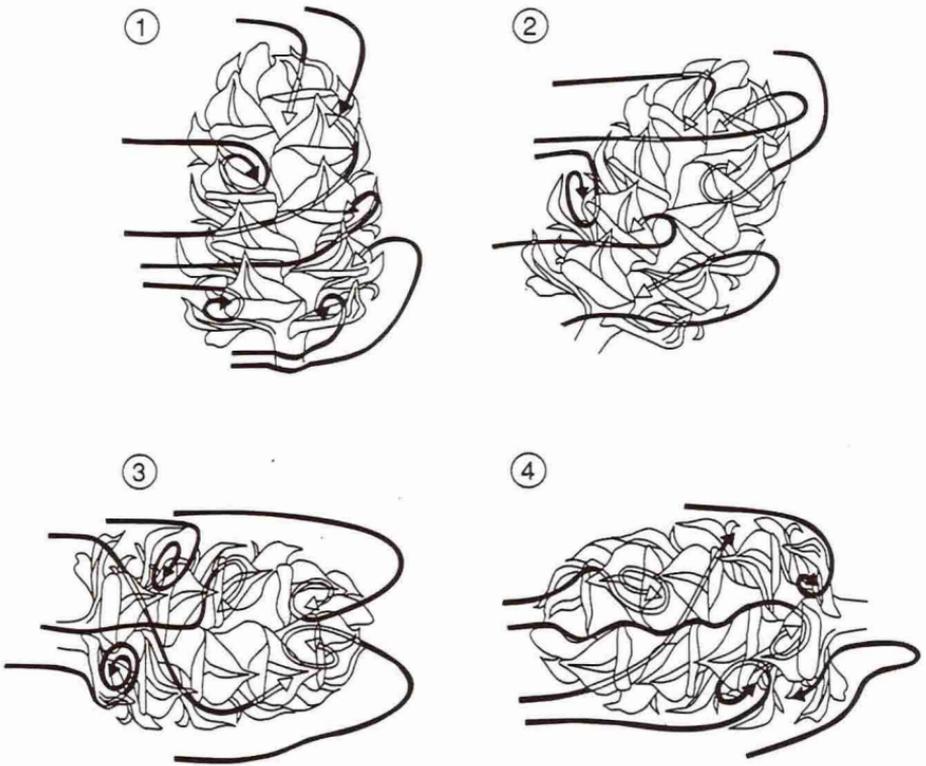


FIGURE 3.21. Characteristic airflow patterns around *Pinus* female cone obtained from statistical surveys at 5 m/s flow from left. Note the different orientations of the cone with respect to the direction of flow (from Niklas and Paw U, 1983).

Reynolds numbers (Niklas, 1985). Pollen capture, which is essentially an aerosol process, is favored in these fluid dynamic environments. The strongest support for anemophily as a highly canalized process comes from data that indicate there is aerodynamic segregation among species in the environment. For example, Niklas and Paw U (1983) demonstrated that pollination by the same pine species occurred at higher frequencies than pollination by congenics in laboratory experiments. Niklas and Buchmann (1987) demonstrated striking pollen discrimination between pollen and ovules of two species of *Ephedra* in the laboratory, which were supported, in part, by field observations reported by Buchmann et al. (1989). More recently, Linden and Midgley (1996) demonstrated pollen discrimination among four species of anemophilous plants from four different families (!) in South Africa. Their field survey revealed that while stigmatic surfaces included alien pollen, a minimum of 40% of conspecific pollen was found on stigmas (>80% in one case), which was always greater than the background frequencies obtained on gel-coated slides. These observations confirm that

wind pollination is a highly canalized process involving the interaction of aerodynamics and biology.

Although well known (see reviews in Faegri and Van der Pijl, 1979; Proctor et al., 1996), water pollination is also proving to be a highly canalized process although data are scant and only recently available (Ackerman, 1995, 1998b, 2000). Pollination in most aquatic vascular plants occurs in the air through either biotic pollination or anemophily. The apparently high proportion of anemophilous aquatic plants is due to systematic rather than functional affiliation (Cook, 1988). Hydrophily occurs in a limited number of aquatic plants and is categorized by the location of pollen transport. Ephydrophily is characterized by pollination on the water surface, in which surface and wind currents cause pollen and/or anthers "raft" to emergent or slightly submerged (i.e., meniscus) female flowers and inflorescences. Cox (review in 1988) has expended considerable effort in applying random search theory, which considers Brownian recurrence in two and three dimensions and predicts that the probability (P) of a surface ship moving along a path (L) in a given area (A) finding a submerged target is given by

$$P = 1 - e^{-(WL)/A},$$

where W is the width of the sonar beam (Koopman, 1956). Unfortunately, while the theory is valid, the application to pollination is flawed because, among other things, it assumes pollen transport to be random and therefore recurrent, which is not the case as wind-generated and other surface movements are directional (Ackerman, 1995, 1998b). Hyphydrophily, or underwater pollination, occurs in less than 20 genera of freshwater and marine plants (i.e., seagrasses; Ackerman, 2000). The most common mechanism of hyphydrophily in freshwater plants, which do not experience regular water currents, is for pollen, which is released higher in the water column, to "shower" down to enlarged stigmatic surfaces (Guo et al., 1990). Interestingly, a form of self-pollination can occur on the surfaces of air bubbles that may form underwater around flowers and inflorescences (Philbrick, 1988).

True hydrophily, i.e., submarine pollination that occurs through the action of water currents, occurs in the seagrasses, which are the only "higher plants" in the marine environment (den Hartog, 1970). Intertidal seagrasses may pollinate on the surface when they are exposed at low tides, but this is not the case when they or subtidal populations exist at considerable depths (see Ackerman, 1998b). Although this functional group of about 50 species is comprised of 12 or 13 genera in five families within three clades (Les et al., 1997), a number of consistent features are associated with hydrophily (Ackerman, 1995, 2000). For example, seagrass pollen has evolved convergently to filamentous shapes, either directly as pollen, as in the case of the Potamogetonales, or functionally, as in the case of the Hydrocharitales (Ackerman, 1995). In the case of the former, the genus *Amphibolus* is reported to have pollen that is 6 mm long, while in the latter, the genus *Thalassia* has spherical pollen that is released in monofilamentous aggregates

or germinate precociously, and the genus *Halophila* releases monofilaments composed of linear tetrads of pollen. The strong association of filamentous pollen shapes and hydrophily is discussed below (also see Pettitt, 1984).

The female flowers of seagrasses are generally elongated stigmatic surfaces of highly reduced green-colored flowers, which, as in the case of anemophilous flowers, lack petals, nectaries, or other features characteristic of biotically pollinated plants (see drawings in den Hartog, 1970). As in the case of anemophily, flowers can be monoecious, can be dioecious, or have phenological separation between pollen release and pollen reception (Pettitt et al., 1981; Les et al., 1997). Pollen-to-ovule ratios have been estimated in only one species, and these were on the order of $10^4 : 1$ (Ackerman, 1993). The seagrasses are found in coastal areas throughout the world, including Hudson's Bay (den Hartog, 1970).

Field and laboratory observations have been made of the pollination mechanisms of seagrasses in a number of species; these are reviewed in Pettitt (1984). Unfortunately, these observations are limited taxonomically, and this is even more acute with respect to the documentation of the mechanics of submarine pollination mechanisms, which exists only for the north temperate seagrass, *Zostera marina*. Pollination in this species was examined in the laboratory using stroboscopic photography and in the field using pollen models and gel-coated surfaces (Ackerman 1989, 1997a, b). Hydrophily appears to be governed more by smooth and more viscous conditions (i.e., lower Re) than the turbulent eddies described for anemophily. The phenological emergence of female flowers from within the inflorescence results in an increase in the shear stress (τ) in the local flow (Ackerman, 1997a). When the filamentous pollen ($2.7 \text{ mm} \times 7.5 \text{ }\mu\text{m}$) encounter this environment, they rotate and cross streamlines toward female flowers on account of τ and thereby increase the opportunity for pollination (Fig. 3.22; Ackerman, 1997b). Given two-dimensional flow, the axial force (F_A) that causes these movements is given by

$$F_A = \frac{\pi\mu L^2\gamma}{8(\ln 2r - 1.75)} \cos 2\phi,$$

where μ is the viscosity, γ is the shear rate, L and r are the length and aspect ratio, respectively, of the pollen, and ϕ is the angle to the normal (Forgacs and Mason, 1958). Unlike spherical pollen, filamentous and functionally filamentous pollen need only be in the vicinity of female flowers to pollinate by (1) direct interception on stigmas, (2) rotating within half a pollen length of stigmas, and (3) by being redirected through streamlines toward flowers. Field observation confirmed the flow conditions necessary for these laboratory-based observations (Ackerman and Okubo, 1993), as did the differential recovery of filamentous versus spherical pollen models (Ackerman, 1989). Recent observations of the submarine pollination of *Amphibolis* in the field were consistent with these findings (Verduin et al., 1996). These obser-

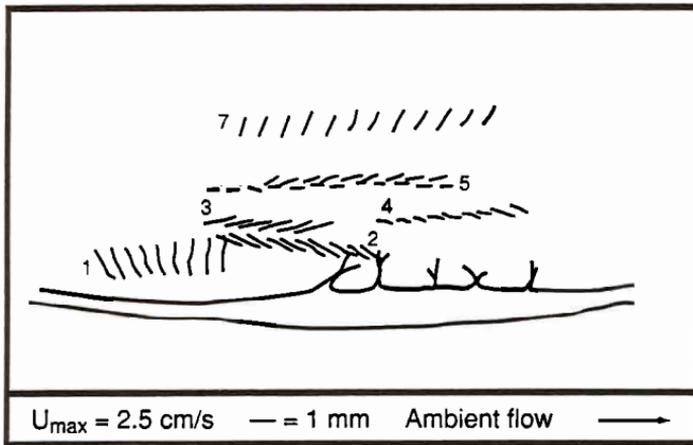


FIGURE 3.22. A composite tracing of seven selected pollen pathlines around a *Zostera marina* inflorescence in side view. Pollen rotate and cross through fluid streamlines (pathlines 1, 3, and 4) as they travel through the water with a maximum instantaneous pollen velocity (U_{\max}) presented. This motion increases the potential for pollination. (From Ackerman, 1997b.)

vations and the strong convergence of filiform pollen in seagrasses indicate that filiform pollen is a functional adaptation for submarine pollination.

While data on the fluid dynamic segregation of pollen by sympatric species do not exist, genetic studies reveal that submarine pollination is successful in maintaining relatively high outcrossing rates in several species (Ruckleshaus, 1995; Waycott and Sampson, 1997). There are a large number of similarities between wind and water pollination; however, observations and characterization of the mechanics are lacking for a large number of taxa (Ackerman, 2000). This is an area rich in possibilities.

3.4 Dispersal of Gametes and Organisms

The evolution of reproductive mechanisms in animals originated with the dispersal of gametes and the results of their union in the external media, i.e., water. Subsequent time and evolution have led to the myriad of internal reproductive mechanisms that are more common to the reader. In this section, we concentrate on the relatively recent developments involving organisms that broadcast their gametes into the water column, where they are fertilized externally. Readers are directed below and to a review by Okubo (1994) for additional information on the diffusion of gamete dispersal.

While external fertilization can be found in most major taxonomic groups, much of our current understanding stems from a few well-researched model organisms such as echinoderms (e.g., starfish and sea urchins, especially the

TABLE 3.2 Factors influencing the fertilization of broadcast spawning invertebrates (adapted from Levitan, 1995)

A. Gamete	B. Individual	C. Population	D. Environmental
(1) <i>Sperm</i> Morphology Behavior Swimming speed Longevity	(1) <i>Spawning Behavior</i> Aggregation Synchrony Posture Spawning rate	(1) <i>Size & Spatial Aspects</i> Population size Population density Nearest-neighbor distance	(1) <i>Fluid Dynamics</i> Turbulence Mixing Water column discontinuities Fronts
(2) <i>Egg</i> Size Jelly coat Surface chemistry	(2) <i>Morphology</i> Size Fecundity	(2) <i>Demography</i> Sex ratio Age structure Size structure	(2) <i>Topography</i> Complexity Water depth Shelter
(3) <i>Condition</i> Age Compatibility	(3) <i>Condition</i> Age Energy reserves	(3) <i>Inter-Population</i> Other spawning species Predation	(3) <i>Water Quality</i> Temperature Salinity pH

genus *Strongylocentrotus*), corals (scleractinian and gorgonians), worms, and fish. The process of gamete dispersal has four principal states: (1) gamete release; (2) gamete dispersion in water; (3) gamete recognition; and (4) fertilization. We will examine aspects of each of these stages with the exception of (3), which is beyond the scope of this work (see Epel, 1991).

3.4.1 Broadcast Spawners and External Fertilization

One of the most essential aspects of reproduction is finding a mate, and this is of no less importance for broadcast spawners whose gametes (sperm and eggs) must be able to contact one another in the water column. Several patterns can be observed in nature in which mass spawners congregate and/or participate in synchronous mass spawning events. In addition, a number of factors affect gametes, individuals, populations, and environments that influence reproductive success in broadcast spawners (see Table 3.2).

Denny and Shibata (1989) used Gaussian plume models (see Sect. 2.6) to examine the physical conditions that favored successful reproduction in broadcast spawners under turbulent conditions. Their models predicted that the best opportunities for reproduction occur (1) when organisms aggregate in large numbers, (2) when they spawn synchronously, and (3) when there is weak to moderate energy in the environment. There is considerable empirical support for these predictions. Pennington (1985) provided empirical support for each of these predictions in experiments involving sea urchins in which fertilization success was examined in the field. Importantly, gamete concentrations are diluted rapidly, and fertilization success decreased with distance from the sperm source, which is similar to what was reported in

Sect. 3.3.3 for spore dispersal (Pennington, 1985; Levitan, 1991; Babcock et al., 1994; Benzie et al., 1994). Mead and Denny (1995) confirmed the last prediction by examining the fertilization success of sea urchin gametes exposed to different shear stress in a Couette cell. They found that while moderate shear led to increased rates of fertilization, high rates of shear led to lower fertilization success and developmental problems for embryos.

The size, motility, and viscosity of gametes may also influence reproductive success. Sperm are much smaller than eggs and are the motile of the two gametes. Vogel et al. (1982) modeled the fertilization success (ϕ) resulting in contact between sperm (S) and eggs (E) in the water using a Poisson distribution

$$\phi = 1 - \exp\left(-\frac{\beta S}{\beta_0 E}(1 - e^{-\beta_0 E \tau})\right),$$

where β is the rate of fertilization, β_0 is the rate of collision ($\beta_0 = v\sigma$, where v is the sperm swimming velocity and σ is the cross-sectional area of the egg), and τ is the half-life of the sperm. It is evident from the model that egg size and aspects of sperm performance are important for fertilization success. Levitan (1993) noted that an increase in egg size (i.e., σ) among broadcast spawners was a mechanism by which females compete for sperm, as sperm limitation is considered to be common among broadcast spawners (Levitan, 1995; Lasker et al., 1996). Experiments with sea urchins confirmed this prediction in that the largest eggs required the least number of sperm for successful fertilization (Levitan, 1996). The one important stabilizing force is the fact that increased egg size also increases the probability of polyspermy (fertilization by more than one sperm), which results in reproductive failure (Styan, 1998).

Lifestyle can have a profound influence on broadcast spawners. Sessile broadcast spawners can be found at high densities, can be hermaphrodites, and can also reproduce asexually. Conversely, mobile organisms must meet at the correct time and place to ensure successful reproduction. We will examine these phenomena in sessile and mobile broadcast spawners.

Reef-building or scleractinian corals reproduce sexually either as broadcast spawners or as brooders (Fadlallah, 1983). Spawning can be synchronous over a period of several days or a period of a month, or seasonal with continuous spawning or monthly cycles (Richmond and Hunter, 1990). There are spectacular mass spawning events (i.e., 90% of species) that occur during the week following the full moon in the austral spring in the Great Barrier Reef of Australia (Babcock et al., 1986). Individual species appear to spawn at distinct times of the night, which may be a way to maximize fertilization success and limit hybridization (Harrison et al., 1984). The spawning species release sperm and eggs, which are both buoyant and float to the surface where they form large slicks (Harrison et al., 1984). The dispersal of these slicks and the interaction of island wakes and winds were reviewed by Pattiaratchi (1994). At least three different modes of gamete release occur in

different species of corals: (1) extruded buoyant egg bundles that break at the surface; (2) streams of buoyant egg-sperm bundles; and (3) sperm release followed by sticky eggs (Harrison et al., 1984). Analogous variations in gamete release (i.e., plume versus strings versus clumps) have been observed in other invertebrates. The non-Newtonian nature of the gamete "packages" can lead to "shear thinning," where the form of gamete release is a function of the rate of shear (e.g., viscous packages under low shear; Thomas, 1994). This may account for some of the variation observed within species.

Sea urchins are important grazers in the benthic environments, which also participate in mass spawning events. In this case, there would need to be some type of environmental cue to lead the urchins to aggregate. Lamare and Stewart (1998) report such a mass spawning event in which *Evechinus* urchins aggregated along a 100-m-long line at densities up to 30 individuals per m^2 at a depth of 5 m to spawn (they are normally found at densities of 1.5 individuals per m^2 between 3 and 15 m depth). The buoyant eggs and sperm formed a 0.5-m-high cloud that was restricted by a halocline at 3-m depth. The low-salinity interface is believed to have increased the contact between sperm and eggs because it acts as a barrier to gamete dispersal.

The image of spawning salmon should be a familiar one to many readers. Salmon are anadromous, returning to their natal stream to spawn. Resident male and females excavate a redd in the gravel bottom of the stream and then release eggs and sperm in a cloudlike mass (Groot and Margolis, 1991). The fertilization of many marine fish can be more complex, involving stereotyped behaviors and territoriality in some cases. Such is the case in the tropical angelfish, *Pygoplites diacanthus*, in which the male and female courtship swim leads to the female's external release of eggs in the water column. The male flips his tail and swims downward, causing the egg mass to form a 50-cm-diameter vortex ring, which ascends upward at 27 cm/s (Gronell and Colin, 1985). The vortex confines the eggs and sperms and thereby increases gamete contact and fertilization. Okubo (1988) modeled this system by considering the impulse (I) of the force required to generate the vortex ring

$$I = \pi\rho R^2 X,$$

where ρ is the density, R is the radius of the vortex ring, and X is the circulation around the ring given by

$$X = 2\pi \int_0^a \xi \omega(\xi) d\xi,$$

where ξ is the radial coordinate in the vortex, and ω is the vorticity given by

$$\frac{\partial \omega}{\partial t} = v \left(\frac{\partial^2 \omega}{\partial \xi^2} + \frac{1}{\xi} \frac{\partial \omega}{\partial \xi} \right),$$

where ν is the kinematic viscosity. The predicted ascent speed and maximum height obtained by the vortex agreed with observation. A diffusion model of this system confirmed that a higher fertilization would be expected through the concentration of gametes confined within the vortex ring.

3.4.2 *The Dispersal of Fish Eggs and Larvae in the Sea*

Marine scientists have long recognized that currents and turbulence in the sea may transport and disperse fish eggs and larvae over distances that are very important from the standpoint of regional ecology and gene flow (e.g., Scheltema, 1971c, 1975, 1986; Levin, 1983; Rothlisberg et al., 1983; Scheltema and Carlton, 1984; Norcross and Shaw, 1984; Emler, 1986; McGurk, 1987; Roughgarden et al., 1987; Boicourt, 1988; Frank et al., 1993; Okubo, 1994). Eggs are considered to diffuse more or less passively. Larvae in the early stages of development may still be carried by water, although in the later stages they can perform their own motion, in particular vertical migration. Aggregation effects (i.e., patches) may be observed in the distribution of fish eggs and larvae for the same reasons they are observed in other plankton. As outlined by Okubo (1984), these include (1) behavioral reactions of the larvae to environmental factors (Sinclair, 1988; Houde, 1997), (2) food-chain associations in predator-prey interactions (McGurk, 1987; Sinclair and Iles, 1989), (3) aggregative feeding behaviors of larvae, and (4) mechanical retention in "structures" of the flow field (e.g., convective cells, gyres, and fronts between different water masses (Okubo, 1994; Bailey et al., 1997; Dickey-Collas et al., 1997; Munk et al., 1999).

Well-controlled diffusion experiments using eggs or larvae are difficult to perform. Ordinarily the distributions of eggs and larvae in the sea are measured and interpreted in the light of oceanic diffusion theory (Strathmann, 1974; Talbot, 1974, 1977; McGurk, 1988; Kim and Bang, 1990; Hill, 1990, 1991; Possingham and Roughgarden, 1990). Often the available data of larval distribution are not sufficiently detailed to permit a direct and accurate comparison with the theory. Despite these problems, estimates of the dispersal of eggs and larvae have been made using dye tracers, such as Rhodamine B (Hirano and Fujimoto, 1970; Talbot, 1977; Becker, 1978), fluorescein (Koehl et al., 1993; Koehl and Powell, 1994), and small particles (Koehl and Powell, 1994). At larger scales, satellite-tracked drifters, drogued to match the depths of larval concentrations, have been used for several years to estimate larval dispersal patterns (Hinckley et al., 1991; Bailey et al., 1997).

The mortality of eggs or larvae must be taken into account in a discussion of their dispersal patterns; however, the variance of the spatial distribution from an instantaneous source would not be altered by mortality, provided the process is density-independent, i.e., behaves according to first-order kinetics. This can be seen easily; the effect of the density-independent mortality process on the spatial distribution is simply to bring in a multiplicative factor $e^{-\nu t}$, with ν the death rate and t the time after release, to the distribution

without mortality, i.e., the distribution of a conservative quantity (Hill, 1990, 1991). Since the factor does not depend on spatial location, the variance—which is the second moment of the radial coordinate from the center of mass of a patch—is invariant. The variance will doubtlessly be influenced by mortality if it is density-dependent or if the source is continuous (McGurk, 1988).

Whether or not the mortality of an egg or larva is density-dependent, it is likely to be organism size-dependent because of both the effect of size on its average residence time in the water column and its desirability as food (McGurk, 1986). Mackenzie et al. (1994) suggested a dome-shaped relationship between the level of turbulence of the flow and ingestion rates of larval fish.

Some studies of larval dispersal conducted in estuaries in conjunction with dye tracer experiments suggest that larvae cannot diffuse as rapidly as might have been expected on purely physical grounds (Talbot, 1974). It seems probable that the larvae tend to aggregate near the bottom and thus do not partake in the full movement and mixing of the water. If the shear effect in the vertical direction is responsible for longitudinal dispersion (see Sect. 2.6.2), a strong tendency for larvae to concentrate near the bottom gives rise to a large decrease in the effective thickness on which the shear can operate, thus suppressing the horizontal dispersion. If this conclusion is correct, it is important to know the vertical distribution of larvae in order to evaluate their horizontal dispersal (Strathmann, 1974). Talbot (1977) described an extensive program of investigation of the distribution of plaice eggs and larvae in the North Sea. In this area the vertical shear effect was much more important than horizontal dispersion characterized by a constant diffusivity (Bowden, 1965). The effects of the vertical distribution and migration of larvae on their horizontal transport remain an active area of research (Hill, 1995).

As a means of genetic exchange and transportation, the advection of eggs and larvae by tides and prevailing currents plays a crucial role, as recognized over a century ago by Wallace (1876). Several studies have since suggested that major oceanic currents, such as the Kuroshio, are much more important in the movement of fish eggs and larvae than diffusion (Fig. 3.23), although large-scale eddies may play an equally important role in the dispersal (Hirano and Fujimoto, 1970; Fujimoto and Hirano, 1972; Hill, 1991; Scheltema, 1995; Bailey et al., 1997; Dickey-Collas et al., 1997). Sinclair (1988) examined how currents can break up and redistribute marine larval populations. Possingham and Roughgarden (1990) used one- and two-dimensional advection-diffusion models to examine the relative importance of eddy diffusion, long-shore currents, and available habitat in organisms with a coastal adult phase and a pelagic larval phase.

An interesting example of dispersal on the ocean surface is provided by Ikawa et al. (1998), who examined the dispersal of ocean skaters (*Halobates*). This genus includes the only species (five) of truly oceanic insects, which live

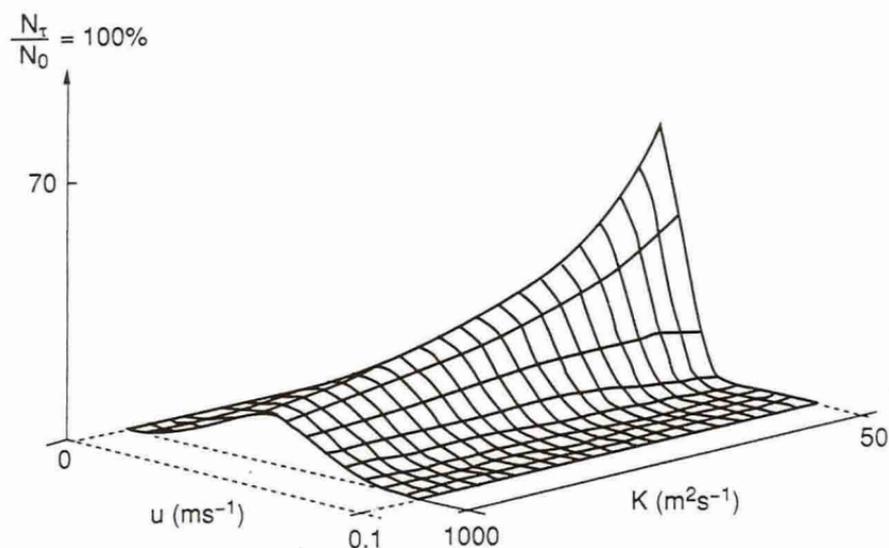


FIGURE 3.23. Relative contribution of advection (u) and diffusion (K) in larval survival at recruitment site 300 km downstream from the center of release (from Hill, 1991).

on the surface film of the major oceans between $\pm 40^\circ$ N. Their dispersal is governed by oceanic diffusion (i.e., turbulence), which is greater than the Kolmogorov scale (see Sect. 2.6.2). In this case, information from Okubo diagrams (e.g., Okubo, 1971) was used to determine that (1) dispersal could be as great as 1250 km in 60 days, (2) encounter rates between males and females could be on the order of 11 per day, and (3) slow growth rates could be offset by the relatively long life span of the insects. Importantly, the estimated encounter rates between the sexes was more than an order of magnitude greater than what was predicted by random encounters.

On the basis of extensive surveys of larvae throughout the North and Equatorial Atlantic Ocean, Scheltema (1971a, b; 1995) summarized the evidence for long-distance larval dispersal. According to Scheltema (1971a), the probability of successful transoceanic larval dispersal, p , is equal to the product of the drifting coefficient, p_d , and survival coefficient, p_s :

$$p = p_d p_s. \quad (3.33)$$

An approximate value for the drifting coefficient may be derived from a knowledge of drift-bottle and drift-card recoveries. Based on 156,276 bottles released along the North American coast, Dean F. Bumpus of the Woods Hole Oceanographic Institution evaluated the percentage of recovery in the Eastern Atlantic Ocean to be 0.2%. Also, Stander et al. (1969), using 1800 drift-cards released along the Northwest African Coast and subsequently recovered in the Western Atlantic Ocean, evaluated the recovery to be 0.18%. The percent recovery in both directions is remarkably similar. Con-

sequently, an average value of 1.9×10^{-3} may be assigned to p_d . As probably not all bottles or drift-cards that actually made the crossing were recovered, the value of p_d is considered conservative.

The value of the survival coefficient, on the other hand, is much more difficult to estimate. Scheltema assumed

$$p_s = 2/N_f,$$

where N_f is the fecundity or total number of eggs produced per female. The numerical factor 2 is derived on the basis of an equal number of males and females. For the studied species of gastropod veligers, a reasonable estimate of N_f is 5×10^6 eggs. Then the probability that a particular larva from an egg mass will survive and ultimately reach the opposite coast of the Atlantic Ocean is estimated from (3.33) to be

$$p = 1.9 \times 10^{-3} \times 2/5 \times 10^6 = 7.6 \times 10^{-10},$$

or approximately one in eight billion. This probability is extremely small, but if we estimate the number of successful larvae, N_s , by multiplying this p by the number of larvae produced by a population, we obtain approximately $N_s = 2, 2 \times 10^3, 2 \times 10^6$, and 2×10^9 , respectively, for populations of $10^3, 10^6, 10^9$, and 10^{12} individuals.

Strathmann (1974) examined short-term advantages of dispersing the sibling larvae of sedentary marine invertebrates. Although the rate of diffusion in the sea increases with time, the advantage in adding an extra day to the pelagic life of larvae probably decreases as the duration of the pelagic phase increases, because the added increment of spread, i.e., $\Delta\sigma_r^2(t)$, is smaller relative to the spread already achieved, i.e., $\sigma_r^2(t)$, the horizontal variance.

One difficulty with the above estimates of dispersal probability is the assumption that p_d and p_s are independent. In fact, Bailey et al. (1995, 1997) suggested that the conditions associated with high larval transport rates (e.g., high wind and currents and depressed primary production) are likely to be associated with depressed larval feeding rates and elevated larval mortality. Nevertheless, the significance of large-scale passive larval transport to the global distribution of even sedentary marine organisms is indisputable (Scheltema, 1995).

3.5 Transport Across the Solid Interface

As discussed above, the interface between a fluid medium (air or water) and a saturated porous medium (the soil or benthic sediments) represents an abrupt transition in flow properties, but for simple physical situations (e.g., one-dimensional flows at a "flat" interface, assumed to be at depth $z = 0$), continuity of solute fluxes and concentrations are assumed at the boundary. If the flux is considered to be the sum of advective and (Fickian) diffusive

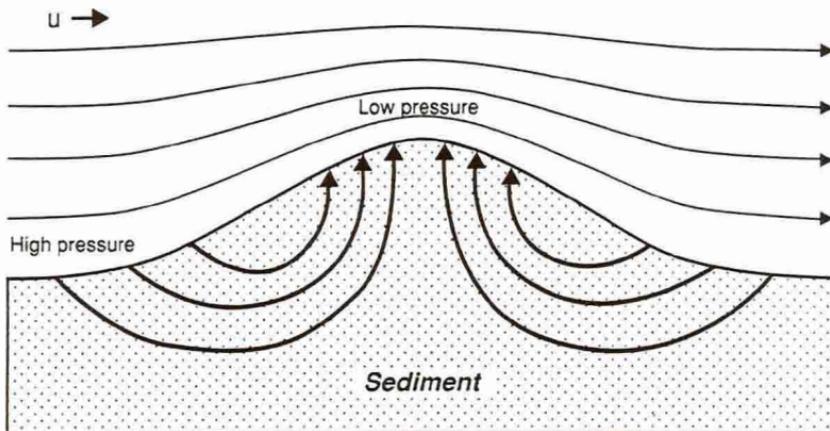


FIGURE 3.24. Effect of “wavy” topography on the interstitial flow within sediments. u : velocity. (After Boudreau, 1997.)

flux, then this is equivalent to the conditions $C_f = C_p|_{z=0}$ and $dC_p/dz = D_f/(\phi D_p) dC_f/dz|_{z=0}$, where the subscripts f and p refer to the fluid and porous media, respectively, D is the coefficient of diffusion or dispersion for the media, and ϕ is the porosity of the soil or sediment.

In the case of solid-phase material falling to the sediment surface (e.g., marine snow) and accumulating, the interfacial boundary moves upward at a rate equal to the sediment accumulation rate. From the frame of reference of the interfacial boundary, this is equivalent to an advective flux downward for both dissolved and solid-phase materials. Boudreau (1997) provides a comprehensive summary of these and other issues of the benthic interface.

For more complex geometries, such as boundaries of variable (“wavy”) elevation (e.g., a field furrowed by plowing, or a seafloor rippled by wave action) in which flow occurs in the fluid medium along the interface, Bernoulli’s principle dictates that differences in pressure will exist between high and low points on the boundary (Vogel, 1994). Assuming that the solid medium is permeable, the result will be pressure-induced advection in the porous medium (Shum, 1992, 1993; Boudreau, 1997) (Fig. 3.24). This “ventilation” may be beneficial to resident organisms in the sediment or soil (see next section). Organisms living at the interface may also directly modify its exchange properties. This is discussed in greater detail in Sect. 3.5.2.

3.5.1 Fluid Exchange in Animal Burrows

We end this chapter with the investigation of a fluid-mechanical problem relating to diffusion and ventilation in animal bores and burrows. Our discussion begins with terrestrial organisms, principally small mammals, and then we examine analogous systems involving invertebrates in aquatic envi-

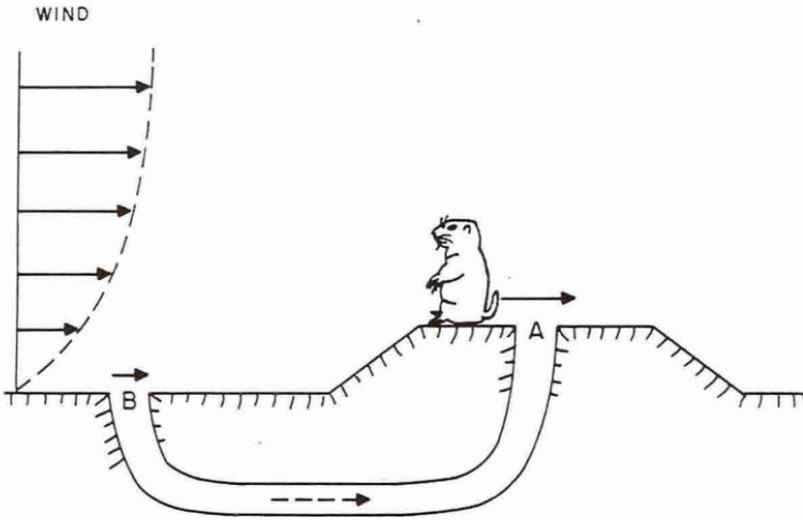


FIGURE 3.25. Schematic picture of a prairie-dog burrow, with wind profile and burrow ventilation.

ronments. Readers are also referred to an excellent symposium volume edited by Meadows and Meadows (1991), which examines the environmental impacts of burrowing animals in terrestrial and aquatic environments.

Figure 3.25 is a schematic of a prairie-dog (*Cynomys ludovicianus*) burrow. The main burrow opening A is located at a mound, while the other opening B, which presumably serves as an emergency exit, is located at the ground level. Vogel and Bretz (1972) suggested that such a structure in burrows may play an important role in ventilation and thus in determining habitat suitability (see review in Vogel, 1994). Importantly, burrowing activities may lead to significant environmental effects such as changes in plant abundance and distribution, and alteration in soil stability (see Meadows and Meadows, 1991).

At least two physical mechanisms may create wind-induced unidirectional bulk flow or "passive ventilation" (Vogel et al., 1973; Vogel, 1977a). The first is due to pressure differences generated by variations in velocity along a streamline, i.e., Bernoulli's principle. The second, "viscous sucking" or "viscous entrainment," depends on the viscosity of the fluid, and as a result stagnant fluid in a burrow may be pulled out of an aperture by adjacent rapidly moving fluid.

Either mechanism for inducing flow in a burrow requires that the openings to the burrow must be dissimilar. Differences may be in height above the ground, location on unlevel ground, or merely variations in the shape or form.

Let us study this problem more quantitatively from a fluid-mechanical standpoint. We apply Bernoulli's theorem (Tani, 1951; Batchelor, 1967) to a

stream filament along the ground (Fig. 3.25):

$$(1/2u^2 + p/\rho + gz)_{\text{at A}} = (1/2u^2 + p/\rho + gz)_{\text{at B}}, \quad (3.34)$$

where u , p , ρ , g , and z , are, respectively, the wind speed, (total) pressure, density, acceleration of gravity, and height of the point considered above a fixed horizontal plane. In (3.34) we assume a steady flow of an incompressible inviscid fluid of uniform density; the atmosphere approximately satisfies these conditions.

The total pressure is the sum of the static pressure, p_0 , and the dynamic pressure, p_1 . Since the static pressure balances the force of gravity, we have

$$(p_0/\rho + gz)_{\text{at A}} = (p_0/\rho + gz)_{\text{at B}}. \quad (3.35)$$

Subtracting (3.35) from (3.34), we obtain

$$(1/2u^2 + p_1/\rho)_{\text{at A}} = (1/2u^2 + p_1/\rho)_{\text{at B}}.$$

Hence,

$$(p_1/\rho)_{\text{at B}} - (p_1/\rho)_{\text{at A}} = 1/2(u_A^2 - u_B^2). \quad (3.36)$$

Ordinarily, the vertical profile of the wind near the ground looks like that illustrated in Fig. 3.25. Thus, the wind speed at A is greater than at B, and the right-hand side of (3.36) becomes positive. Accordingly, the dynamic pressure at B is higher than that at A. The pressure difference sets the air in the burrow in motion, in the direction of the *dashed line* shown in Fig. 3.25. In other words, the principle is the same as that of the Venturi tube; the dynamic pressure at a point where the fluid moves swiftly is lower than the dynamic pressure at a point where the fluid moves slowly, and the burrow corresponds to a U-tube manometer attached to the Venturi tube.

We shall now make some rough calculations of the flow in the burrow. We may regard the burrow as a cylindrical tube of radius a and assume that the air flow inside is laminar. The pressure gradient between A and B is $(P_B - P_A)/\ell$, where ℓ is the distance between A and B along the burrow. Applying Poiseuille's law (Tani, 1951; Prandtl and Tietjens, 1957; Batchelor, 1967) leads to the result that the flux of fluid in the burrow, Q , due to the pressure gradient is given by

$$Q = \pi a^4 (P_B - P_A) / 8\nu\ell$$

$$Q = \pi a^4 (u_A^2 - u_B^2) / 16\nu\ell, \quad (3.37)$$

where ν is the kinematic viscosity of air and (3.36) is used. If V denotes the mean velocity of ventilation in the burrow, $Q = \pi a^2 V$. Hence, from (3.37),

$$V = \pi a^2 (u_A^2 - u_B^2) / 16\nu\ell. \quad (3.38)$$

Furthermore, the time of ventilation, i.e., the time required for the air inside

the burrow to be refreshed, T , is given by

$$T = \pi a^2 \ell / Q = \ell / V$$

or

$$T = 16v\ell^2/a^2(u_A^2 - u_B^2). \quad (3.39)$$

As an example characterizing prairie-dog burrows, we take $\ell = 20$ m, $a = 6$ cm (Sheets et al., 1971), $U_A = 20$ cm/s, $U_B = 10$ cm/s (Vogel and Bretz, 1972), and $\nu = 0.15$ cm²/s. Thus, from (3.38) and (3.39), we calculate

$$V = 2.25 \text{ cm/s} \quad \text{and} \quad T = 14.8 \text{ min.}$$

The effectiveness of this ventilation is noteworthy. However, the actual burrows often do not meet all the conditions that Bernoulli's principle requires.

The Reynolds number (the ratio of inertial to viscous forces) for this flow is calculated to be $Re = 2aV/\nu = 180$, confirming the assumption of laminar flow. Turbulence can occur in a circular tube at a Reynolds number $Re \cong 2000$ or larger.

The second mechanism, however, viscous sucking, produces in general the same directional flow in a burrow as the previous mechanism, that is, fluid will leave an aperture exposed to higher external velocities and enter an aperture at the other end that is exposed to lower external flow. Viscous sucking, however, results in some additional complications of practical importance. For example, a large hole generally provides a better exit than a small hole; thus, fluid will enter a small aperture and leave through a larger one even if there is no difference in external velocity between the ends of the burrow. Also, location near the upwind edge or atop a sharp-edged crater improves the performance of an aperture as an exit for fluid.

Because of the considerable complexity of the mechanism of viscous entrainment as well as of the dual mechanisms that may operate simultaneously, Vogel (1977a) attempted to develop a semiempirical approach for predicting the internal velocity. The driving force, F , for the induced flow can be represented by

$$F = 0.15\rho Au^2, \quad (3.40)$$

where A is the cross-sectional area of the apertures, u is the free-stream velocity, and the numerical coefficient has been determined using experimental models of burrows. Equation (3.40) may be understood in terms of an analogy to the frictional law for plants (see Sect. 3.1). Combining this expression for the driving force with Poiseuille's law, we obtain

$$V = 6 \times 10^{-3} Au^2/\nu\ell, \quad (3.41)$$

which states that for a given fluid and a given aperture geometry, the internal flow velocity is proportional to the square of the external flow velocity.

However, this relationship must break down as u is increased, insofar as internal flow relieves the induced pressure. The breakdown point depends on

the burrow system. For example, measurements on models of prairie-dog burrows (Vogel et al., 1973) show that relation (3.41) holds up to a V/u ratio of about 0.1; above this value the measured curve indicates a linear relation,

$$V = ku + C$$

where k and C are constants.

Animal burrows are generally curved rather than straight. Secondary burrow flow may occur due to the curvature of the burrows. Perhaps more importantly, burrows are usually highly branched and thus differ greatly from a simple straight tube. This was demonstrated by Izumi (1973), who excavated occupied rat dens and revealed a complex network structure in his study of Norway rats in a natural environment. Davies and Jarvis (1986) confirmed this complexity and noted temporal variation in burrow construction and maintenance in two mole rat species in South Africa. They reported an average burrow length of 132 m, or 3.9 g/m in terms of biomass per unit length, in their review of more than 20 burrowing mammal species. Burrow length appears to vary indirectly with food supply, while burrow diameter appears to match closely the diameter of the animal. In terms of metabolic output, the rate of oxygen consumption while burrowing bears a linear relationship with the rate of burrowing. For example, the total energetic cost of constructing the burrow of a mole rat amounts to 79% of the estimated digestible energy available from its food source (geophyte corms) in the area (Du Toit et al., 1985).

Vogel et al. (1973) estimated that a prairie dog in a burrow has an oxygen supply sufficient for about 10 hours. Without the bulk movement of air (passive ventilation) and without diffusion through the soil, molecular diffusion through the burrow alone would require time $T \sim \ell^2/2D \sim (2000)^2/2 \times 0.2 = 10^7$ s to refresh the prairie-dog burrow; in other words, the air inside the burrow would stagnate over several months.

In fact, many animals live in burrows where they are often completely separated from the free atmosphere by a medium that does not allow bulk gas transfer; yet ultimately they must exchange carbon dioxide and oxygen with the free atmosphere. How do they manage to survive?

Wilson and Kilgore (1978) examined the exchange of respiratory gases in these animal burrows with the free atmosphere and concluded that molecular diffusion through the soil is of paramount importance. Wilson and Kilgore base their discussion on simple mathematical models for the steady-state diffusion of respiratory gases in sterile burrow-soil systems (Fig. 3.26).

The flux of respiratory gases between an element of the burrow and the free atmosphere through the soil atmosphere, F , is given by

$$F = -2/3\kappa\epsilon D(S_a - S), \quad (3.42)$$

where S_a and S are, respectively, the concentrations of gas in the free atmosphere and in the burrow element, D is molecular diffusivity in the free atmosphere, ϵ is soil porosity, and κ is a shape factor describing the geometry

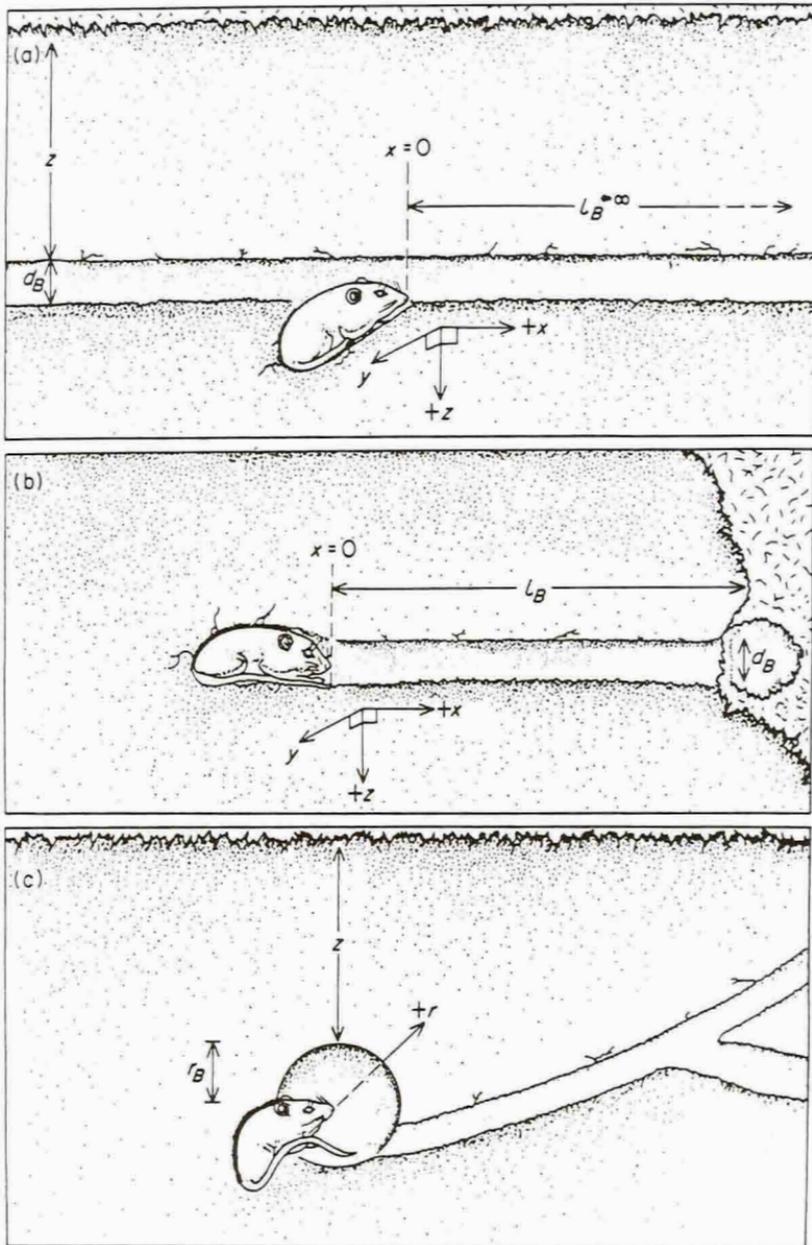


FIGURE 3.26. Diffusion models of respiratory gases in mammal burrows. (a) Model 1 (infinitely long burrow); (b) Model 1 (finite burrow open to the ground); (c) Model 2 (spherical chamber). (From Wilson and Kilgore, 1978; this figure was provided by K. J. Wilson and D. L. Kilgore.)

of the flux for a particular spatial configuration of the burrow element and the groundfree atmosphere interface; thus, κ depends on the burrow depth and the burrow diameter. Expression (3.42) is, in fact, Fick's law of diffusion, stating that the flux of gas between these two surfaces is proportional to the difference of the concentrations at the surfaces.

Two different mathematical models are constructed.

Model 1. The mammal rests in a long, cylindrical burrow. Assuming that the concentration of gases across the burrow (y - z direction) is uniform, we consider the flux balance of respiratory gas in an element of burrow with length Δx at distance x from the origin (Fig. 3.26). In the case of steady-state diffusion, the flux of gas in the burrow at x equals the sum of the flux at the distance $x + \Delta x$ and of the flux between the element and the free air through soil surrounding the burrow element. Thus, we have

$$-DA(dS/dx)_x = -DA(dS/dx)_{x+\Delta x} - 2/3\kappa\epsilon D\ell\Delta x(S_\alpha - S)_x, \quad (3.43)$$

where A is the cross-sectional area of the burrow and ℓ is the burrow circumference. Expanding, i.e., $(dS/dx)_{x+\Delta x} = (dS/dx)_x + \Delta x(d^2S/dx^2)_x + \dots$, substituting this into (3.43), and taking the limit as Δx vanishes, we obtain

$$\frac{d^2S}{dx^2} + \frac{2\kappa\epsilon\ell}{3A}(S_\alpha - S) = 0. \quad (3.44)$$

Equation (3.44) has the general solution

$$S(x) = S_\alpha + C_1e^{\beta x} + C_2e^{-\beta x}, \quad (3.45)$$

where C_1 and C_2 are constants determined from the appropriate boundary conditions, and $\beta = (2\kappa\epsilon\ell/3A)^{1/2}$.

- i. For an infinitely long burrow (Fig. 3.26a), the boundary conditions are $-DA(dS/dx)_x = \pm q/2$ at $x = 0$, i.e., animal location, and $S \neq \infty$ at $x \pm \infty$, where q denotes the source (or sink) strength of respiratory gases. The plus sign in front of q is applied to the right of the point $x = 0$, and the minus sign is applied to the left of this point.

The solution for this case is then given by

$$S(x) = S_\alpha + q/2AD\beta e^{-\beta x}, \quad x \geq 0, \quad (3.46)$$

$$S(x) = S_\alpha + q/2AD\beta e^{\beta x}, \quad x \leq 0. \quad (3.47)$$

We thus find the concentration of respiratory gases at the location of the animal ($x = 0$), S^* , to be

$$S^* = S(0) = S_\alpha + q/2AD\beta. \quad (3.48)$$

- ii. For a finite burrow with one end that opens to the ground (Fig. 3.26b), the boundary conditions are $-DA(dS/dx)_x = q$ at $x = 0$, and $S = S_\alpha$ at $x = \ell_B$. The solution for this case is then given by

$$S(x) = S_\alpha + \frac{q}{AD\beta} \frac{\sinh \beta(\ell_B - x)}{\cosh \beta\ell_B} \quad (3.49)$$

and

$$S^* = S(0) = S_x + \frac{q}{AD\beta} \tanh \beta \ell_B. \quad (3.50)$$

Model 2. The mammal rests in a spherical chamber remote from the ground surface (Fig. 3.26c).

Assuming that the mammal's body interferes negligibly with gas transfer and that the concentration of gases in the burrow chamber is spherically symmetric, we obtain the steady-state diffusion equation in a sphere (Carslaw and Jaeger, 1959):

$$\frac{d}{dr} \left(r^2 \frac{dS}{dr} \right) = 0, \quad (3.51)$$

where r is the radial coordinate. Equation (3.51) has the general solution

$$S(r) = C_1 + C_2/r,$$

where the constants C_1 and C_2 are determined from the following boundary conditions:

$$-4\pi r^2 D dS/dr = q \quad (\text{source strength}) \text{ at any } r$$

and

$$D dS/dr = 2/3\kappa\epsilon D(S_x - S) \quad \text{at } r = r_B.$$

We then obtain the solution

$$S(r) = S_x + \frac{q}{4\pi D r} - \frac{q}{4\pi D} \left(\frac{1}{r_B} - \frac{3}{2\kappa\epsilon r_B^2} \right), \quad (3.52)$$

and the concentration of respiratory gases at the location of the animal ($r = r_s$) is

$$S^* = S(r_s) = S_x + \frac{q}{4\pi D} \left(\frac{1}{r_s} - \frac{1}{r_B} + \frac{3}{2\kappa\epsilon r_B^2} \right). \quad (3.53)$$

If the gas exchange is to be adequate for a mammal, the following inequalities must be satisfied:

$$(S_\ell - S^*)_{O_2} < 0 < (S_\ell - S^*)_{CO_2} \quad (3.54)$$

where S_ℓ denotes the lethal concentration of a respiratory gas.

Based on these mathematical models, Wilson and Kilgore (1978) calculated the concentration gradient of respiratory gases along long, narrow burrows for standard mammals of various masses at different soil porosity. It was found that the distance from the mammal at which gas concentrations are negligibly different from the free atmosphere does not exceed 7.5 body lengths; for soils of high porosity, the distance is less than about 3 body lengths. On the other hand, even in highly porous soils, the greatest mass

permissible by the inequalities of (3.54) is about 0.4 kg, which is noticeably toward the lower end of the range of mammalian mass.

Wilson and Kilgore (1978) also calculated the source concentration of CO_2 , S^* , in a burrow chamber under various conditions. It was found that (i) soil porosity has a strong effect on the respiratory environment, (ii) the depth of the chamber, Z , has only a weak effect, and (iii) soil temperature within the *thermoneutral zone* of the resident mammal has a weak effect on this transfer. However, below the thermoneutral zone, where temperature modifies the rate of production or consumption of respiratory gas, the effect is strong. Large mammals are more restricted in the design and setting of burrows than small mammals. The mathematical models indicate that normothermic eutherian mammals with masses much in excess of 0.5 kg are precluded from an indefinite occupation of deep burrows in most field conditions.

Gupta and Deheri (1990) extended Wilson and Kilgore's (1978) inequality (3.54) for fluxes of gas in spherical burrows (i.e., Model 2). They show that (3.53) can be simplified to provide the following result:

$$S^* \approx S_a + 2\beta r_B^{3/2} r_s \left[\frac{1}{r_s r_B^3 - 1} + \frac{1}{r_B (r_s - r_B^3)} \right].$$

Given that $\beta = (2\kappa\ell/3A)^{1/2}$, this implies that soil porosity (κ) and the geometry of the burrow (ℓ and A) have a strong effect on the ventilation of the burrow.

Weir (1973) measured air flow through the mounds of termites, *Macrotermes subhyalinus* (Rambur), and showed that air passed into the mound at certain openings. The number of such openings varied: Small mounds 0.5 to 1.0 m high might have two or three openings, and larger mounds 2.0 to 3.0 m high might have ten or more openings.

For small mounds, air was found to enter from basal and peripheral openings and to escape from central openings on top of the mound. This is consistent with the Venturi effect. For large mounds, the circulation pattern was less clearly defined. Some peripheral and basal openings did not always function as well-defined entrances for air but could function as exits under some wind conditions. Weir (1973) suggested that vortices caused by the mound structure probably reverse the air flow. Central openings consistently function as air exits, however.

Airflow measurements made with a small-scale mound subject to environmental air speed of 2.5 to 2.7 m/s result in a mean volume of air passing through the mound of 18.5 l/s (i.e., $>1 \text{ m}^3/\text{min}$). If we assume a mean radius of the tubes of 10 cm, the above flux corresponds to a quite swift mean speed of ventilation of 59 cm/s. The air circulation in these mounds provides the colony of termites with a degree of homeostatic regulation.

Vogel (1977b) measured flow velocities through and immediately adjacent to the excurrent openings (oscula) of living sponges in their natural environment and found that the flow through the oscula was positively corre-

lated to the ambient flow. The result indicates that the passage of water through sponges is, at least in part, induced by ambient currents.

Diffusion models similar to those of Wilson and Kilgore (1978) have been considered by Withers (1978), who examined both subaquatic and subterranean animal burrows. It was concluded that due to very small molecular diffusivity in water only the smallest aquatic burrowing animals, such as boring sponges and burrowing barnacles, might rely on diffusion to sustain their metabolic demands, but also see below. On the other hand, subterranean ectotherms may be able to rely on gaseous diffusion, except when they aggregate together in large numbers, and subterranean endotherms, because of their high metabolic rates, are likely to encounter low concentrations of O_2 and high concentrations of CO_2 in their burrows.

An interesting example of ventilation was reported by Korhonen (1980), who provided information on the winter burrows of voles, which are constructed in snow. Temperature differences within the burrows led to an outflow of air provided that the external temperature was not too low. In that case, there was an inflow of air that cooled the burrows. Measured CO_2 levels were never too low to be of concern metabolically, and this is likely due to exchange within the burrow systems, through the snow, and with the water in the snow.

Burrows constructed by infaunal animals are a conspicuous feature of marine sediments. Of particular interest in the study of burrowing organisms are the population dynamics of the species, the bioturbation activity of the animal, the bioturbation effect on the sediments, and the alterations of the pore water chemistry.

Dworschak (1983) investigated the burrow structures of the thalassinid shrimp, *Upogebia pusilla*, on a tidal flat using resin casts, which revealed burrow structures that ranged from simple U-shaped tubes to U-shaped tubes with branches. One of the external openings is raised above the surface, forming a conelike mound. Allanson et al. (1992) investigated the flow in burrow structures of a related species (*Upogebia africana*) using flow chamber and field study. The induced flow through the burrow was analogous to the flow induced through the prairie-dog burrow, the mean circulation velocity of which is given by (3.38); note the need to include π in the relationship. They estimated that the mean discharge velocity would range between 1.2 and 1.7 cm/s for various cone heights, bed roughness, and boundary layers, for a free surface velocity of 15 cm/s. The induced flow was found to be proportional to the Reynolds number and the aspect ratio of the burrow.

Animals in the field showed a significant orientation toward the induced current, but there was no preferred orientation of the burrow openings, i.e., the flow induction mechanisms work in all directions as long as there is a height difference between burrow openings. Importantly, animals showed reduced pumping activity via their pleopods during tidal exchanges compared to periods of no flow. Recent investigations of the morphology and

pumping activities of another thalassinid shrimp (*Callinassa*) indicate that the active burrow flow is dominated by a coordinated series of metachronally oscillating motions of the pleopods, which can be energetically expensive (Stamhuis and Videler 1998a, b, c). These results suggest that the induced flow in burrows may play an important role in the feeding and respiratory behavior of these animals.

A number of fish species are also known to burrow and undertake a number of important functions within burrows (Atkinson and Taylor, 1991). For example, tilefish seek shelter and construct burrows at depths of 100 to 300 m on the continental shelf. Grimes et al. (1986) reported that vertical burrows are the primary habitat of these fish, and these burrows occur between depths of 80 and 305 m. It is believed that these burrows are formed by a combination of oral excavation by tilefish, secondary bioerosion by associated fauna, and the swimming motion of the tilefish. The mean depth of the burrows is 1.7 m, while the upper cone has an average diameter of 1.6 m. By injecting a dye marker from the *Johnson-Sea-Link* submersible, Grimes et al. (1986) found that the larger secondary burrows located at the burrow margin were interconnected to the main burrow shaft. The interconnected burrow structures provide a means of passive ventilation of the tilefish burrow systems at velocities approaching 50 cm/s! However, active burrow ventilation by the fish swimming motion may be equally or more important than passive ventilation.

Passive ventilation of burrows and other biological structures (e.g., tubes) also takes place in the absence of animals. Ray and Aller (1985) suggested that this phenomenon would have important implications for the chemistry of sediments. Essentially, the induced flow out of the biological structure generates a downward flux in the sediments surrounding the tube that then supplies the induced flow (see Fig. 3.27). Meyers et al. (1988) demonstrated that the spatial distribution of meiofauna responds quickly to subtle changes in sediment chemistry, principally oxygen and sulfide levels, caused by adding or removing model tubes of infaunal organisms. The cycling of water via a passive ventilation of relict biological structures such as the proteinaceous or parchmentlike tubes of polychaete worms was examined by Libelo et al. (1994). They provided a theoretical model for the induced outward and sediment flow, which was then examined using computational techniques. Results indicate that the water flux in the sediments varies with the boundary layer velocity, the hydraulic conductivity of the sediments, and the spatial distribution of tubes. They showed that the water flux rate through sediments is on the order of 10^{-3} cm/s, which is comparable to the pumping rates due to the active pumping of animals.

The exchange of water in swamps is different from that of the systems discussed above, principally due to the high clay content of the sediments and the surface-water slopes. Few animals in these systems create mounds around their burrows. Water exchange in animal burrows appears to be driven by pressure differences rather than induced flows due to Bernoulli's

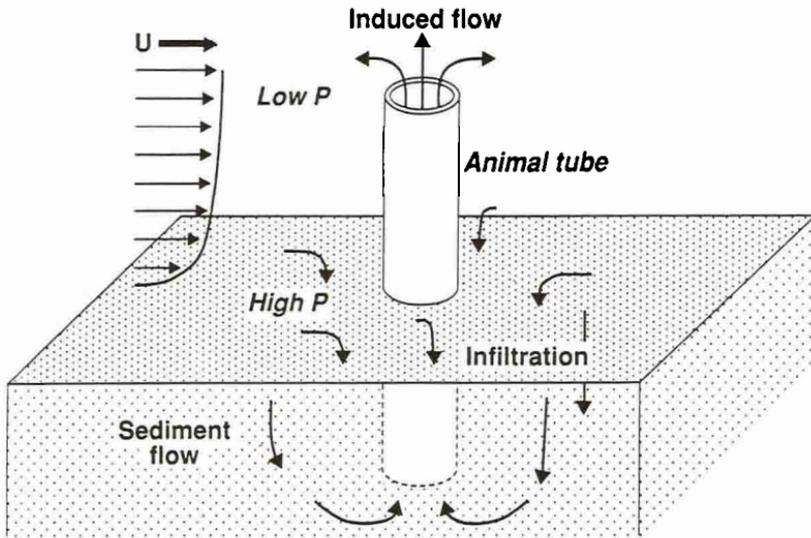


FIGURE 3.27. Cycling of water through the sediments created by passive ventilation of relict biological structures (after Libelo et al., 1994).

principle (Ridd, 1996). A surface-water slope of 1/1000 is predicted to create a pressure head of 0.5 mm for openings separated by 0.5 m, which would lead to a significant burrow flow. Ridd (1996) used the fact that burrow flow is dominated by friction, the Darcy–Wiesbach equation,

$$\frac{\Delta p}{L} = \frac{f\rho V^2}{2D},$$

where f is the friction factor, Δp is the pressure difference, L and D are the length and diameter of the burrow, and ρ and V are the density and velocity of the water, and the oscillation of water level, to predict theoretically the flow in the burrow. A rate of 0.1 to 1 cm/s was predicted for a 1-m-long burrow with a 1-cm diameter. Field measurements of burrow velocity were less than 3 cm/s, which corresponds well with the theoretical estimate. Given the density of burrows and these flow estimates, 10^3 to 10^4 m³ of water (i.e., 0.3% to 3% of the swamp water volume) is estimated to flow through the burrows per km² of mangrove swamp per tidal cycle.

While many burrowing organisms benefit from passive ventilation of their burrows, a number of air-breathing organisms (e.g., crustaceans, insects, spiders) also live within burrows in marine sediments (Wyatt and Foster, 1991). Unlike the situations discussed above, these organisms must avoid flooding their burrows, which are typically less than 3 mm in diameter. Interestingly, air bubbles trapped in the neck of a staphylinid beetle burrow act as a temporary plug, which enables the beetles to plaster over the burrow

neck to prevent flooding. Maitland and Maitland (1994) developed a theoretical model to explain these observations by considering the surface tension forces between the trapped air bubble, the burrow sediments, and the advancing tide. Their theoretical prediction of 3 mm for the maximum burrow diameter that can trap a bubble is consistent with observations from nature.

3.5.2 *Bioturbation and Related Effects*

The mixing of sediments by organism activities is called *bioturbation*. It also takes place in soil on land by burrowing creatures. In fact, Darwin (1881) examined the stirring of soils by the burrowing earthworms, and his detailed observation of these organisms and the way that they affect ecological and geological processes still deserves careful attention (cf. Cook and Linden, 1996; Bouche and Al-Addan, 1997).

Bioturbation occurs widely in aquatic sediments—lakes, estuaries, coastal waters, and the deep sea. The benthic organisms responsible for bioturbation include clams, worms, and crustacea, among others (Aller and Aller, 1992; McCall and Soster, 1990; Madsen et al., 1997). Many burrows formed by marine animals are lined with thin layers of organic material. The permeability of these linings to solute diffusion plays an important role in determining the chemical composition of surrounding sediment and the burrow habitat (Aller, 1980, 1988; Fenchel, 1996a, b). In addition, the activities of these organisms constitute mixing processes in their own right (e.g., “burrow and fill mixing”; Gardner et al., 1987; Wang and Matisoff, 1997; Boudreau, 1997, 2000).

In addition to the mixing of sediments, biogenic “nonlocal” transport of nutrients (i.e., not dependent on local concentration gradients) may result from the movement of organisms between different sediment layers during the period between feeding and defecation (Boudreau and Imboden, 1987; Boudreau, 1997) by “conveyor-belt” transport through the digestive tract of the organism (e.g., the deposit feeding behavior of some benthic worms; Boudreau, 1986b, 2000; Soster et al., 1992; Blair et al., 1996) or by pore-water irrigation (exchange of water in benthic burrows for water at the sediment surface by organismal pumping activity; Emerson et al., 1984; Christensen et al., 1987; Martin and Banta, 1992; Boudreau and Marinelli, 1994).

Recently, Boudreau (1998) proposed a general model for the depth variability of bioturbation in the benthic mixed layer limited by the availability of labile organic matter consumed by bioturbating organisms. The effective bioturbation coefficient, $D_b(z)$, is found to drop from its value at the surface ($z = 0$) to zero at the mixed layer depth ($z = L$) (approximately 10 cm) as $(1 - z/L)^2$. The corresponding steady-state concentration profiles of substances that obey an advection–diffusion–reaction equation subject to this depth-variable mixing can be expressed in terms of modified Bessel functions (Swaney, 1999).

3.5.3 Notes on Solute Transport in Soils and Sediments

As in the sea, nutrients within terrestrial ecosystems may limit the activity of primary producers, but in this case the milieu is soil, often considered an ecosystem in its own right. In recent decades, our understanding of the physical transport of nutrients and contaminants (e.g., pesticides) in soil and bedrock has grown enormously. Transport processes in soils are radically different from those of the sea or the air. Flows are characterized by low Reynolds numbers instead of the turbulent conditions frequently found in marine and terrestrial systems and constrained to occur in the interstices between soil particles (de Marsily, 1986; Marshall and Holmes, 1988). The flow of water through unsaturated porous media can itself be described as a diffusive process in which the diffusion coefficient (diffusivity) is a nonlinear function of moisture content (Childs and Collis-George, 1950). The complexities of such processes are beyond the scope of this volume. In saturated soils and sediments (e.g., in aquifers or at the bottom of the sea), the flux of water is proportional to the gradient of hydraulic head or pressure (Darcy's law) and frequently can be considered to be in steady state (de Marsily, 1986). In such cases, nutrients and other dissolved chemicals (solutes) follow a solute-transport mass-balance equation similar to (2.16) (written here for the one-dimensional case):

$$\varphi \frac{\partial S}{\partial t} = \frac{\partial}{\partial z} \left(\varphi D_z \frac{\partial S}{\partial z} \right) - \frac{\partial (\varphi w_z S)}{\partial z} + R,$$

where φ = porosity of the medium, D_z = the hydrodynamic dispersion of the medium (mixing due to microscale motions through the porous medium), w_z = the steady-state flow velocity of water through the medium, S is solute concentration, and R is the local net gain or loss of material due to chemical transformations. In aquatic sediments, this equation is often referred to as the diagenetic equation. Boudreau (1997, 2000) provides an excellent discussion of this equation and its variations.

Complications can arise from several factors, including variable water content in the vadose (unsaturated) zone of soils (Hayashi et al., 1998), which affects both transport and biogeochemical transformations; degree of adsorption of the solute to sediment and other particles (Charbeneau and Daniel, 1993; Wu et al., 1997; Bengtsson et al., 1993); gas-phase transport (Washington, 1996, and in the case of pollutant spills, transport in other liquid phases); and time-varying boundary conditions (e.g., the water table variation in response to evapotranspiration or tides). Charbeneau and Daniel (1993) and Mercer and Waddell (1993) reviewed some of these issues. Spatiotemporal patterns can result from spatial variability of physical characteristics of soils and bedrock (Wierenga et al., 1991; Arocena and Ackerman, 1998) such as soil layers and macropores and fractures of both biogenic and physical origin (cf. Stone, 1993; Li and Ghodrati, 1994, 1995; Boll et al., 1997), as well as inherent instabilities of the flows (Glass et al., 1989a, b; Liu

et al., 1994). However, as in the sea and atmosphere, relatively simple analytical solutions to advection–diffusion–reaction equations (e.g., Ogata and Banks, 1961; Lindstrom et al., 1967; Aller, 1980; Enfield et al., 1982; van Genuchten and Alves, 1982; Boudreau, 1986a, b, 1987; Jury et al., 1987; Toride et al., 1993; Angelakis et al., 1993) have been used in some cases to estimate the steady-state and transient distributions of nutrients and contaminants in soils, benthic sediments, and groundwater.

Largely in response to concerns about environmental pollution, a variety of numerical advection–diffusion–reaction models now exist with the goal of assessing groundwater quality and the spread and distribution of contaminant plumes (e.g., Carsel et al., 1984; Pacenka and Steenhuis, 1984; van der Heijde et al., 1985; Wagenet and Hutson, 1989; Wagenet and Rao, 1990; Pennell et al., 1990; Follet et al., 1991). In the last decade, a more general class of models, called *transfer-function* models, have extended the idea of the advection–diffusion model beyond simple Fickian diffusion by considering the probability distributions of the travel times of solutes moving through soils of various configurations (cf. Jury et al., 1986, 1990; Jury and Roth, 1990).

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