Diffusion and Ecological Problems

Modern Perspectives
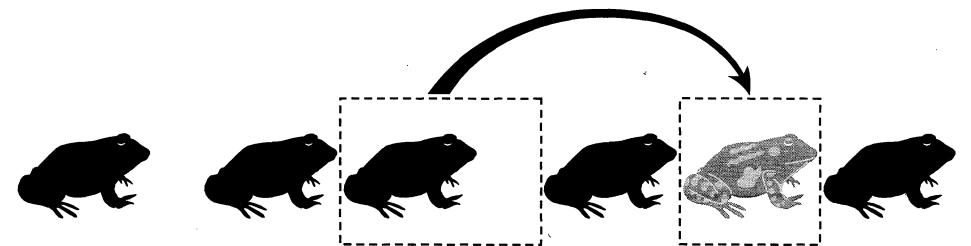
Akira Okubo

Simon A. Levin

Second Edition

Springer

provided. Any mistakes are all my own. Without Dr. Levin and Mr. Yano, this book would probably not have been born.

The fifth part of good luck is attributed to Dr. G. N. Parker, who helped me in translating the original Japanese text and later in improving my English text. He is one of the rarest American scientists; one who can speak, read, and write Japanese as fluently as the natives. This gift is due partly to his intellectual Japanese wife and partly to his own talent. Throughout the preparation of this book, Dr. and Mrs. Parker encouraged me very much; often they whipped the lazy horse to keep running. Without their push this book would have been delayed at least five years.

The sixth part of good luck is very much biological; animals must eat. In the isolated village of Stony Brook, a determined nondriver was suffering from malnutrition. Then a miracle happened. After a random walk, or rather "drunkard walk," I discovered a cozy Japanese restaurant in Port Jefferson, least expected on this "remote" island. Thanks to the kindness and warm hospitality (e.g., free warm *sake*) of the Hashimotos, the hungry mouse narrowly escaped starvation, and the fire of life kept burning. Without the Hashimotos this book would have been written in a hospital bed.

Finally, the seventh part of good luck is due to an enormous amount of help and encouragement received from many other people, including friends and colleagues.

To all of these people I am very grateful. Also, I should like to express my thanks to Eileen Quinn for her skillful and patient typing of the final manuscript, to Joanne D'Amico and Deborah Ulrich for their efficient typing of the drafts, to Deborah Bray for indexing, and to Dean Loose, Marie Eisel, and Carol Cassidy for the illustrations; last of all, to Chiyo for her companionship in the long, long agonizing period of writing.

Stony Brook, New York
November 1978   *Akira Okubo*

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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).

4
Diffusion of "Smell" and "Taste": Chemical Communication

Akira Okubo, Robert A. Armstrong, and Jeannette Yen

The natural world is filled with a vast variety of "invisible," "inaudible" smells upon which animals depend for their lives through chemical communication. For the behavior of many mammal species, in particular carnivora and nocturnal animals, the role of the olfactory sense is more important than that of the auditory sense. Animals living in underground burrows, deep-sea fish, and many species of insects make use of smell. In the deep sea, with its low turbulence and perpetual darkness, scent may perhaps be even more important for aquatic animals than for terrestrial organisms (Hamner and Hamner, 1977).

Chemical communication between animals occurs upon the completion of three essential steps: (a) the release of a chemical (olfactory or gustatory) signal; (b) the transmission of that signal through the environment; and (c) its reception by another individual.

Diffusion apparently controls process (b). However, an understanding of the entire process of olfactory or gustatory response in animals requires a knowledge of chemotaxis as well as the mechanics of diffusion of chemical signals. In essence, the environmental transmission of chemicals can be attributed to a passive diffusion process; thus, the diffusion theory presented in Chap. 2 may well be applicable. On the other hand, certain aspects peculiar to chemical communication in animals deserve special discussion in this chapter.

4.1   Diffusion of Insect Pheromones

Pheromones are "odor" chemicals released by animals and utilized for chemical communication between members of the same species. They thus contrast with allomones and kairomones used for communication between members of different species. The diffusion theory of insect pheromones was founded by Wilson (1958) and Bossert and Wilson (1963). Although their theoretical treatment was still quite elementary, significance should be attached to their pioneering role in this field.

Some important practical aspects of the diffusion problem concern the following:

i) the amount of pheromone released, in terms of initial concentration or source intensity;
ii) the rate of transmission in terms of components due to, for example, wind velocity and diffusion;
iii) the effective duration of the signal and its fade-out rate; and
iv) the most efficient mode of transmission.

The last of these items may have some significance from an evolutionary standpoint.

A discussion of a few models of pheromone diffusion under various conditions or release follows.

4.1.1   Instantaneous Emission in Still Air

Ignoring the effects of wind and turbulence and assuming an isotropic diffusion of Fickian type with a constant diffusivity D, we can write the three-dimensional diffusion equation as

$$\frac{\partial S}{\partial t} = D\left(\frac{\partial^2 S}{\partial x^2} + \frac{\partial^2 S}{\partial y^2} + \frac{\partial^2 S}{\partial z^2}\right), \tag{4.1}$$

where S is the concentration of pheromone, t is time, and x, y, and z are Cartesian spatial coordinates.

It is supposed that M molecules of pheromone are released instantaneously at the origin ($x = y = z = 0$). The solution of (4.1) in an infinite domain is (Carslaw and Jaeger, 1959)

$$S(x, y, z, t) = M/(4\pi D t)^{3/2} \exp(-r^2/4Dt), \tag{4.2}$$

where $r^2 = x^2 + y^2 + z^2$. Isoconcentration contours are thus seen to form spherical surfaces about the origin.

The ground is assumed to be a reflecting plane at $z = 0$, implying the boundary condition:

$$\partial S/\partial z = 0 \quad \text{at } z = 0. \tag{4.3}$$

Equation (4.3) states that no flux of substance occurs across the surface.

The method of images (Carslaw and Jaeger, 1959) can now be used to show that instantaneously, if the point source is located at the ground, the solution to the diffusion problem on a semiinfinite domain ($z > 0$) embodied in (4.1) and the boundary condition (4.3) is simply twice the solution in infinite space given by (4.2) (see Fig. 4.1). Thus, for a ground source,

$$S(x, y, z, t) = 2M/(4\pi D t)^{3/2} \exp(-r^2/4Dt). \tag{4.4}$$

Let C (mole/cm^3) be a minimum or threshold concentration of substance, such that the receiving animal can respond only to concentrations C and

FIGURE 4.1. Diffusion of pheromone in still air from an instantaneous source on the ground.
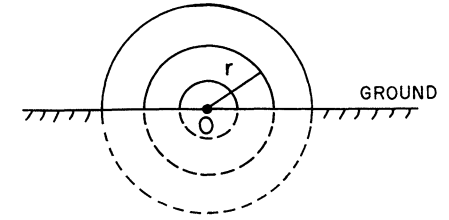
greater. Here (mole/cm^3) denotes the number of molecules per cm^3. As in Sect. 3.3.2, we shall investigate the way in which the isoconcentration surface represented by the threshold concentration changes with time. Clearly, that surface will initially remain in the vicinity of the source, gradually spread out, reach a certain maximum distance from the origin, and then shrink back to zero, i.e., the origin. The radius of the sphere representing the threshold concentration is determined from the value of r at which $S = C$ (constant) in (4.2) or (4.4): $r = R(t)$. The time variation of R is illustrated in Fig. 4.2. As can be seen, the effective radius of odor chemicals attains a maximum, R_m, at time t_m, and becomes zero at t_f, at which time chemical communication ceases.

For an infinite space:

$$R_m = 0.527(M/C)^{1/3}, \tag{4.5}$$

$$t_m = (0.0464/D)(M/C)^{2/3}, \tag{4.6}$$

$$t_f = e t_m = (0.126/D)(M/C)^{2/3}. \tag{4.7}$$

One simply replaces M in the above equations by $2M$ for ground sources. Note that R_m depends only on the ratio M/C and is independent of D.

Actually we often know little about the values of M, C, and D; however, these parameters may be estimated using the theoretical relations obtained. Thus, knowledge of R_m enables evaluation of M/C, and a combined knowledge with t_m determines D from (4.6). Wilson (1958) studied alarm commu-
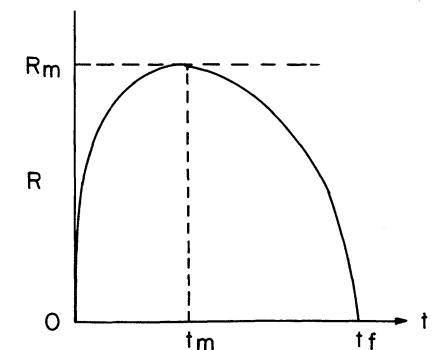
FIGURE 4.2. Time variation of the effective radius (R) representing a threshold concentration of pheromone.

nication with the harvest ant, *Pogonomyrmex badius*. The experiments were designed to determine the above parameters. It was found that the maximum alarm radius of the alarm pheromone was 6 cm, the arrival time was 32 sec, and after the arrival the signal ceased within 35 sec. From the measured volume of the mandibular glands of several minor workers, Wilson estimated an average value of M of 6.26×10^{16} moles. It was then calculated that $C = 4.5 \times 10^{13}$ (mole/cm^3) and $D = 0.43$ cm^2/s.

The short range and duration of the pheromone should be desirable for the alarm system, avoiding unnecessary persistence of the signal after the period of danger has passed. If necessary, the signal may be relayed to farther distances by a release of pheromones from one of the ants initially receiving the alarm.

4.1.2   Continuous Emission in Still Air

As in the previous case, a ground source is assumed to be located at the origin, $x = y = z = 0$. Let us suppose that a pheromone is released at the constant rate Q (mole/s). Since the solution from an instantaneous source is known, i.e., (4.4), the principle of superposition may be invoked to obtain the solution for a continuous source. This principle is often used to obtain the solution of a continuous source by integrating over time, i.e., "superposing" the solution of diffusion from an instantaneous source. It is based on the simple concept that a continuous source may be regarded as a continuous release of instantaneous sources. The principle may also be used for a spatially extended source by integrating the solution for a point source over the space in question.

The amount of release during an infinitesimal time dt is denoted as $Q dt$. Replacing M in (4.4) by $Q dt$ and integrating with respect to time, we obtain

$$S(r, t) = \int_0^t 2Q/(4\pi Dt')^{3/2} \exp(-r^2/4Dt') \, dt'$$

$$= Q/2\pi Dr[1 - \Phi\{r/(4Dt)^{1/2}\}], \quad (4.8)$$

in which Φ is the error function.*

As the release of pheromone continues for a long time ($t \to \infty$), the concentration approaches the steady-state limit,

$$S(r) = Q/2\pi Dr. \quad (4.9)$$

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*The error function is defined by

$$\Phi(a) = (2/\pi^{1/2}) \int_0^a e^{-b^2} db, \quad a \geq 0,$$

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

In other words, the concentration decreases linearly with distance from the source. The radius of the sphere containing concentrations above the threshold value C surrounding the source, R_m, can be deduced from (4.9) to be

$$R_m = Q/2\pi CD. \quad (4.10)$$

This corresponds to the maximum effective distance for chemical communication associated with long-term release from the source.

Let us return to the *P. badius* alarm system and apply the above results. Supposing that worker ants arrive at the alarm zone at a constant rate of one individual each five seconds, it is seen that $Q/C = M/C \div 5 = 1400/5 = 280$ cm^3/s. Taking $D = 0.43$ cm^2/s as before, the sphere surrounding the alarm zone, which contains concentrations above the attractive threshold of the pheromone, is found to possess a radius $R_m = 104$ cm. Thus, the maximum effective radius is about 1 m; the time required for the alarm to propagate to a distance of half this radius can be found to be 6400 s = 1 h 47 min.

4.1.3   Continuous Emission from a Moving Source

Herein the diffusion of substances associated with chemical trails is considered. Such insects as ants leave a trail of pheromone by releasing the substance as they move across the ground. It is assumed that the release of pheromone lasts for a sufficiently long time. The odor substance evaporates, and a diffuse pheromone cloud extends along the ground and into the air. The trail serves to lead other workers to food sources.

We define u to be the velocity of the ant and define the origin to coincide with the location of the insect. With reference to this coordinate system attached to the moving ant (Fig. 4.3), the steady-state distribution of substance in the pheromone trail obeys the following advection–diffusion equation:

$$u\frac{\partial S}{\partial x} = D\left(\frac{\partial^2 S}{\partial y^2} + \frac{\partial^2 S}{\partial z^2}\right), \quad (4.11)$$

where diffusion in the direction of the ant's locomotion (x-axis) is ignored (an assumption that is usually accurate).

If Q is the rate at which the ant emits its pheromone, the solution of (4.11) is given by

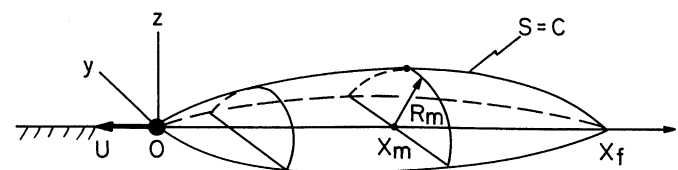$$S(x, y, z) = (Q/2\pi Dx) \exp\{-u(y^2 + z^2)/4Dx\}. \quad (4.12)$$

FIGURE 4.3. Boundary surface of a pheromone trail emitted by a moving ant (C: threshold concentration; U: ant's walking speed).

It is noted that, if we set $x/u = t$ in (4.11), the resultant equation becomes a two-dimenional diffusion equation, the solution of which, for an instantaneous source, is the two-dimensional version of (4.4). The substitutions $M \rightarrow Q/u$ and $t \rightarrow x/u$ in the solution of (4.4) thus yield (4.12).

As before, the boundary of the trail can be defined by some threshold concentration C; thus, the equation representing the boundary becomes the surface for which $S(x, y, z) = C$ in (4.12) (Fig. 4.3). The point X_f at which the surface intersects the x-axis determines the maximum length of the trail. From (4.12) we have

$$X_f = Q/2\pi CD. \tag{4.13}$$

The maximum trail radius in a plane perpendicular to the x-axis, R_m, is

$$R_m = (2Q/e\pi Cu)^{1/2}, \tag{4.14}$$

and it occurs at $x = X_m = X_f/e$.

From experiments on fire ant trails, Wilson (1962) obtained $X_f = 42$ cm, $R_m = 1$ cm. Taking the velocity of the trail-laying ant to be $u = 0.4$ cm/s, it can be seen from (4.14) that $Q/C = 1.71$ cm^2/s, and from (4.13) that $D = 0.00649$ cm^2/s. This value for D seems very small for the molecular diffusivity of the substance in air; this may be due to the fact that not all of the substance is initially in the gaseous state. Since the substance is quite volatile, however, the model is still acceptable with a value of D reduced by an appropriate factor to account for the evaporation time. The fade-out time of the trail due to diffusion is about 100 s. In other words, 100 s after the last ant returns from an exhausted food source, the trail disappears so that the use of unproductive old trails is avoided. For more details about odor trails in ants, see Wilson (1971).

4.1.4   Continuous Emission of Pheromone in a Wind

In comparison with the transmission of ant pheromones, the effective range of the sex attractants of larger insects such as moths is far greater. As may be expected from the results of Sects. 4.1.1 and 4.1.2, such long-range communication is possible only by taking advantage of the wind, i.e., the movement of the environmental medium itself.

Since the wind not only carries the pheromone molecules but also creates its own turbulence, pheromone diffusion cannot be treated by the simple methods of Sect. 4.1.3. One must enter the realm of turbulent diffusion, the characteristics of which depend on the wind structure and properties of boundary surfaces. In effect, we must use the theory of diffusion in atmospheric boundary layers described in Chap. 2.

Bossert and Wilson (1963) employed Sutton's diffusion Eq. (2.23). Analogously to Sect. 4.1.3, they were able to obtain the characteristics of sex attractant pheromone plumes. Thus, the maximum length, X, maximum width, Y, and maximum height, Z, of the pheromone plume determined by a
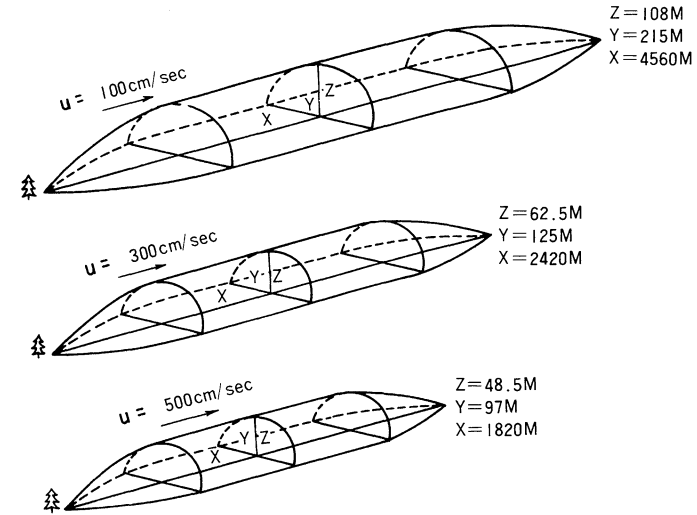
FIGURE 4.4. Threshold volume of sex attractant pheromone downwind from a single female gypsy moth at various wind velocities. The maximum values of the dimensions are given (from Bossert and Wilson, 1963).

certain threshold concentration, C, are given by

$$X = (2Q/C\pi c_y c_z u)^{1/2-n}, \tag{4.15}$$

$$Y = c_y(2Q/C\pi c_y c_z ue)^{1/2}, \quad \text{and} \tag{4.16}$$

$$Z = c_z(2Q/C\pi c_y c_z ue)^{1/2}. \tag{4.17}$$

From experiments with the gypsy moth, *Porthetria dispar*, it was found that Q/C for a single female is in the range from 1.87×10^{10} to 3.03×10^{11} cm^3/s. Taking 10^{11} cm^3/s to be a typical value for Q/C and taking the diffusion parameters as $n = 0.25$, $c_y = 0.4$ cm$^{1/8}$, $c_z = 0.2$ cm$^{1/8}$, the maximum values X, Y, and Z can be calculated from (4.15)–(4.17) for various wind speeds (Fig. 4.4).

Note that for the range of winds shown in Fig. 4.4, stronger winds reduce the effective range of attraction. This is due to the increased turbulent diffusion associated with higher wind velocities, which spreads the attractant more uniformly through space. The result is thus seen to be fundamentally different from the case of constant diffusivity in still air outlined in Sect. 4.1.3. It is seen from the calculated result (Fig. 4.4) that male moths can detect females located at a distance of as much as 1 km.

The experiments of Kaae and Shorey (1972), which demonstrated that the pheromone-releasing behavior of noctuid moth (*Trichoplusia ni*) females is greatly influenced by wind velocity, are worthy of mention. Females were found to spend more time releasing pheromones when exposed to air veloc-

ities ranging from 0.3 to 1.0 m/s than higher or lower velocities. It appears that evolution has endowed the females with the ability to recognize wind conditions that are favorable to chemical communication.

Using diffusion models similar to those given herein, Bossert (1968) analyzed the transmission of chemical information associated with time-varying pheromone release. It is found in this case as well that a moderate wind can make communication practical over a longer range.

Thus far, we have discussed the diffusion of pheromones. However, the mechanism by which insects actually follow the pheromone cloud presents an entirely different problem. It is found that the concentration gradients of pheromone as calculated directly from the diffusion theory are certainly too small to be detected by source-seeking insects.

Schwink (1954), Wright (1964), and Farkas and Shorey (1972) are among those who consider anemotaxis to play an important role in the orientation process. Thus, male moths respond to the attractant pheromone of females by initiating an upwind flight; if they by chance miss the pheromone plume, they engage in a zigzag movement until the plume is rediscovered, and then they continue to fly upwind. By repeating this chemo-anemotactic process, the male moth can finally locate the female. This kind of zigzag movement is not only used by flying insects in chemotaxis, but also by ants in following odor trails laid on the ground (Hangartner, 1967). According to Rust and Bell (1976), nonflying insects such as the cockroach also use chemo-anemotaxis in response to air that is laden with sex pheromone.

Gillies and Wilkes (1974) discovered in experiments with host-seeking mosquitoes that their search flight before the detection of host stimuli is generally in the downwind direction; upon encountering the odor plume of a host, they turn around and track back upwind toward the host. This constitutes a very efficient host-seeking strategy, as, for a given output of energy, the insect is able to cover a much larger area than if it were restricted to upwind movements.

Almost all the models of pheromone diffusion, including those of Bossert and Wilson, are based on the assumption that the substance spreads in a continuous, regular plume when released continuously, as shown in Fig. 4.5(a). Actually, the diffusion pattern of the substance consists of numerous
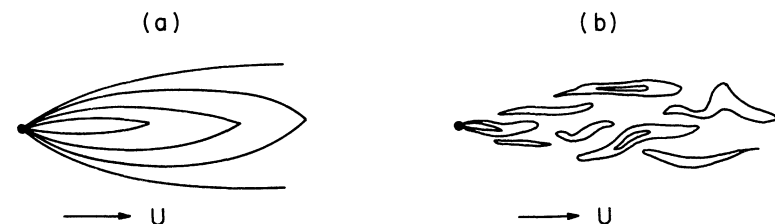
FIGURE 4.5. Diffusion plumes in the environmental fluid of velocity U. (a) idealized plume; (b) realistic plume (filamentary plume).

meandering filaments generated by turbulence in the environmental fluid (Fig. 4.5(b)). Thus, the mean concentration of pheromone does not vary regularly in space, but rather the pheromone concentration fluctuates at random and on the average tends to increase toward the source. Such a temporal and spatial pattern of concentration fluctuation might provide new information to insects which the imaginary plume shown in Fig. 4.5(a) lacks, and it is possible that this random pattern enhances the chemotactic behavior of insects. However, appropriate modeling of the pattern of Fig. 4.5(b) would be extremely difficult due to the need to know not only $\bar{S}$, but also the statistical properties of S', and furthermore, the probability density $p(S, \mathbf{x}, t)$ mentioned in Sect. 1.3. Csanady's book (Csanady, 1973) provides a discussion of the variance of concentration fluctuations in the environment. For another development, consult Meyers et al. (1978).

4.2   A Diffusion Problem Concerning the Migration of Green Turtles

Determination of the basis for animal orientation and navigation during migration has proved to be a vexedly difficult problem. The various theories that have been proposed differ from species to species (Orr, 1970). In this section, we shall examine the study by Koch et al. (1969) of the migration of the green turtle, *Chelonia mydas*, which provides an example of directional information that is intimately associated with diffusion.

A tagging experiment (Carr, 1967) showed that green turtles hatched on Ascension Island in the South Atlantic traveled over a distance of 1200 nautical miles to the Brazilian coast for feeding; females then returned to the same island, and even to the same beach of birth, to lay eggs (Fig. 4.6).

We should like to determine the mechanism of their homing migration. How is it possible for green turtles to return without fail to a solitary island only 10 km wide and removed from the South American coast by over 1200 nautical miles? Celestial navigation seems to be unacceptable. Visual and auditory cues are most unlikely because of the distance. The only remaining sensory cue is "smelling" or "tasting."

According to Sverdrup et al. (1942), the South Atlantic Equatorial Current flows approximately from east to west in the latitudes between 0° and 20° S, and it forms a prevailing current more than 1000 miles wide. It extends from the surface to a depth of several tens of meters with a mean speed of 1 kt (50 cm/s). If one rode on the current, it would take about 50 days to travel from Ascension Island to the coast of Brazil.

Koch et al. (1969) speculated that an unknown chemical substance originating at Ascension Island is carried westward by the equatorial current, and that this substance provides a chemical stimulus to the migrating green turtle. The substance would tend to mix uniformly within a surface layer,
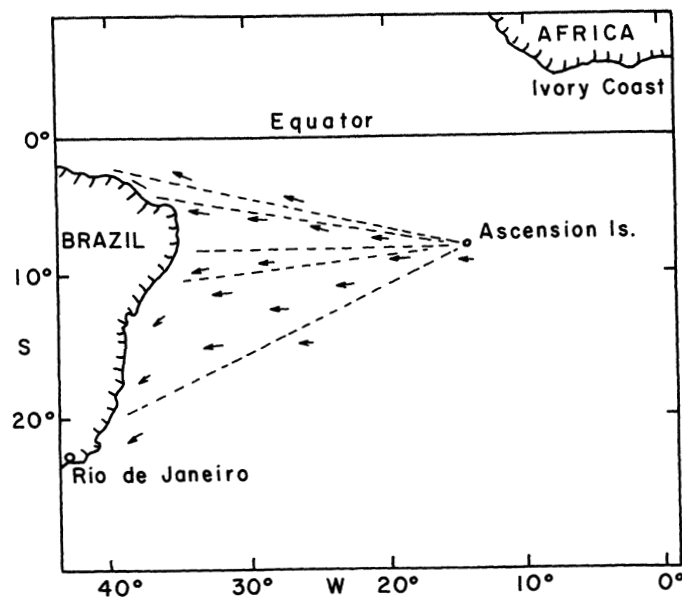
FIGURE 4.6. Ascension Island in the South Atlantic Ocean. Arrows represent surface current trends (from Koch et al., 1969).

50 m deep on the average, and flow toward the coastal region of Brazil subject to horizontal diffusion.

To facilitate calculation of the concentration distribution, we assume that the substance is chemically stable for the period of travel. The x-axis is taken to be in the east–west direction, and the y-axis, in the north–south direction; the substance is assumed to mix uniformly within a depth of h in the vertical direction.

The diffusion equation for a Fickian model reads

$$u\frac{\partial S}{\partial x} = D\frac{\partial^2 S}{\partial y^2},\qquad (4.18)$$

where u is the velocity of the current, S is the substance concentration, and D is a constant diffusivity. The diffusion in the x direction is ignored. When Q is the rate of release of the substance at the source ($x = y = 0$), the solution of (4.18) is given by

$$S(x, y) = \{Q/h(4\pi Dux)^{1/2}\}\exp\{-uy^2/4Dx\}.\qquad (4.19)$$

A model of oceanic diffusion that is more realistic than the Fickian model is provided by the solution of Joseph-Sendner (1958) as given by (2.26). However, (2.26) is the solution for an instantaneous source; to modify it for our case of continuous release, we could invoke the principle of super-

position directly. Koch et al. (1969) chose rather to use an approximate method of the superposition (Frenkiel, 1953; Gifford, 1959), corresponding to the oft-used approximation that diffusion in the direction of the mean flow may be ignored in evaluating concentration from a continuous source. In effect, the Joseph-Sendner solution (2.26) representing diffusion in the x and y directions is replaced by a one-dimensional version of its solution representing diffusion only in the y direction; that is,

$$S(x, y) = (m/2hPt)\exp(-y/Pt).\qquad (4.20)$$

The transformation $m \to Q/u$, $t \to x/u$ applied to this formula [see the similar method used in Eq. (4.12)] leads to the solution for a continuous source:

$$S(x, y) = (Q/2hPx)\exp(-uy/Px).\qquad (4.21)$$

For calculations of the concentration distribution from (4.19) and (4.21), Koch et al. assumed $Q = 1$ mol/s, $u = 24$ N.M./day (nautical miles per day), $h = 50$ m, (Fickian) $D = 5 \times 10^7$ cm^2/s (Montgomery, 1939; Montgomery and Palmén, 1940), and (Joseph-Sendner) $P = 1$ cm/s. Figures 4.7 and 4.8 illustrate the result.

Though the Joseph-Sendner model provides a more accurate description for oceanic diffusion than the Fickian model, there is little difference between the two models at large distances from Ascension Island. Koch et al. conclude that either model suggests that the dilution factor is not so great as to exclude chemical perception, by an aquatic animal in the coastal water of Brazil, of a substance released from Ascension Island.

FIGURE 4.7. Steady-state concentration based on the Fickian diffusion model; x: distance from Ascension, y: distance from stream-axis, C: concentration in moles/ℓ. It is assumed that the release rate is 1 mol/s, mean current velocity is 24 nautical miles/day, thickness of mixed layer is 50 m, and diffusivity is 5×10^7 cm^2/s (from Koch et al., 1969).

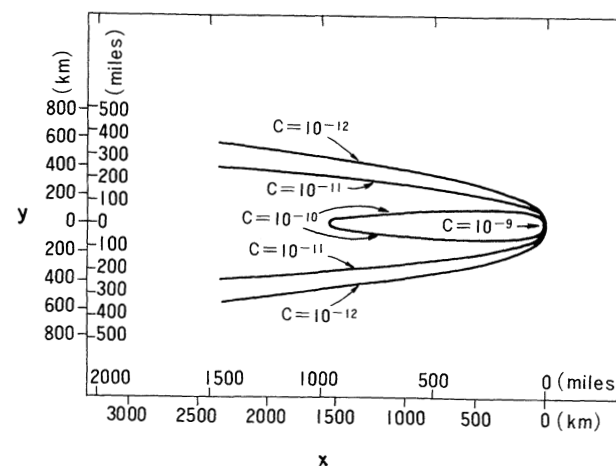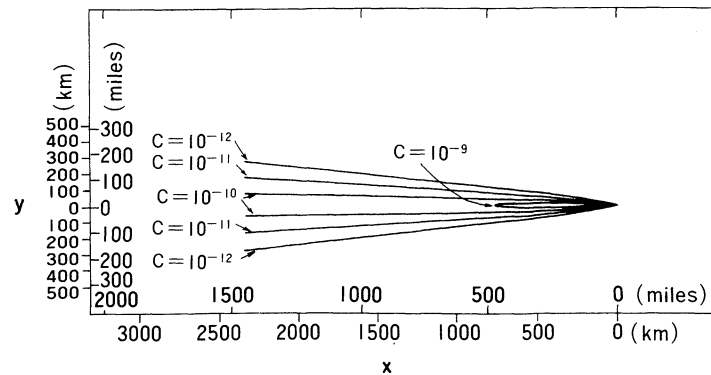FIGURE 4.8. Steady-state concentration based on the Joseph-Sendner diffusion model. Most of the parameters are used as in Fig. 4.7. The value of P (diffusion velocity) is taken to be 1 cm/s (from Koch et al., 1969).

But how could turtles be able to follow the chemical trail? The precise mechanism remains unknown. According to calculations, the concentration gradient is extremely small. Thus, at a point 1600 km west of Ascension Island, a turtle would have to swim approximately 80 km north or south to experience a tenfold change in concentration. The streamwise gradient is even smaller; in fact, much more so.

As northwest trade winds prevail over the oceanic region concerned, the direction of the current may approximately coincide with the direction of incident waves and swells. It seems conceivable that a turtle might use the waves as a directional clue to its orientation. Of course, the identity of the chemical substance, if it exists, should be investigated in the future. Moreover, a precise estimate of the amount of release will be a prerequisite for a critical evaluation as to whether or not the concentration in the water is sufficient to allow green turtles to detect the substance by smell or taste.

The migratory behavior of the green turtle in other areas should also be compared with that of the Ascension Island population. In fact, Balazs (1976) conducted tagging studies in the Hawaiian Archipelago. He found that, unlike the *Chelonia* population migrating to Ascension Island, Hawaiian green turtles migrating from the southeast to French Frigate Shoals were moving *with* prevailing currents. This would prohibit the direct use of chemical cues originating from the breeding site for possible navigational purposes, as Koch et al. hypothesize.

Finally, Carr and Coleman (1974) have proposed the hypothesis of seafloor spreading to explain open-sea migratory adaptations in the Ascension Island *Chelonia* population in an evolutionary framework; the ancestors of *Chelonia mydas* subpopulation, which now migrates 1200 nautical miles from Brazil to Ascension Island for breeding, were induced to swim oceanward for increasing distances during the gradual separation of South America

and Africa in the earliest Tertiary. Perhaps a small plume of chemicals arising from the island might have provided the turtle with a pathway to the final landfall.

4.3   Chemical Communication in Aquatic Organisms

In the example of the previous section, we used large-scale eddy diffusivity to calculate the average concentration of a chemical attractant downstream from a point source. For the case of green turtles, this assumption is probably appropriate, since the "point source," Ascension Island (area: 88 km^2), is large enough to interact with the mesoscale eddy field in the surface ocean. However, if we consider parcels of attractant (or any other chemical) as they leave a much smaller source, we see that in the short term they will expand only slowly due to molecular diffusion and small-scale eddy diffusion. The succession of such parcels describes a filament (Fig. 4.5), which may become tortuously folded by larger-scale eddy motions as it proceeds downstream. Over time, the position of the filament changes; over long enough time, the ensemble average of the filaments produces a large-scale diffusive plume.

The problem for this section is to explore the situations in which each description—diffusion plume or filamentary plume—is appropriate. For the green turtles of Section 4.2, the source is large, minimizing the filamentary nature of the plume; and the turtles themselves swim relatively slowly, so that they can get repeated whiffs of attractant as they proceed upstream, averaging over any filamentary structure that is present. For smaller sources and faster-moving receptors, however, the filamentary structure will dominate.

In this section we consider two applications. First we consider the problem of chemical communication in aquatic organisms whose body sizes span several orders of magnitude. We then discuss an "inverse" problem from chemical oceanography, where the sensor (a sediment trap) is fixed, and the problem is to relate the signal sensed by the trap to photosynthetic production in the surface layer of the ocean.

4.3.1   Temporal and Spatial Scales for Chemical Communication

Physical Scales.   The effects of the physical environment on the structure and transmission of odors in fluids differ significantly at small versus large temporal and spatial scales. Over time intervals of seconds, there is little effect of microbial decay or turbulent eddy diffusion. At these scales, flow has been attenuated by viscous forces, and the low Reynolds number of this regime creates a laminar flow field. Within this field, the major force affecting the odor structure is molecular diffusion. If, at these time scales, flow is

created biologically at small spatial scales—for example, in the feeding current or wake of a copepod—then advection would dominate over diffusion in the distribution of the odorant. Turbulent distribution of odorants into filaments forming a plume occurs at large spatial and temporal scales where currents and tides impose directionality on the distribution of the odors. Current research focuses on how such physical variation in odorant structure affects the chemosensory guidance systems of aquatic organisms.

Biological Scales.   Given these scaling differences in the physical distributions of odorants, organisms ranging in size from bacteria to lobsters show temporal and spatial variations in their response to chemical signals. Furthermore, each organism, as a consequence of individual size and speed, lives in its own biologically created Reynolds number regime that will interact with the Re regime of the physical environment. Small organisms like bacteria and protozoans live in a low Re realm where signals are transported in a predictable manner along a diffusional gradient. Copepods swim slowly and live in an intermediate (1–100) Re realm where signals are still transported in a predictable manner along a diffusional gradient or along orderly streamlines. In contrast, larger organisms like crabs and lobsters swim faster and live in a high Re realm. The flow is turbulent and is only predictable in a statistical sense. The problem with this statistical structure is that the animals respond in a near-instantaneous manner modified by specific reaction times. Recent advances in chemical ecology have focused on how aquatic organisms use chemicals for communication and the impact of physically derived turbulence.

Bacteria.   Bacteria (0.84 to 73 µm for motile genera; 0.14 to 12 µm for nonmotile genera; Dusenbery, 1997) respond to the diffusive component of the odor field and exhibit kinesis (stimulus-induced movement, without directional orientation) but not taxis (directed motion). A chemical gradient is detected by comparing differences in the chemical concentration using either spatial or temporal sampling (Dusenbery, 1998). If the bacteria seek the signal source and experience higher chemical concentrations, they continue to move in a straight line; if they do not experience increased concentration, then they tumble in a random direction. If the uptake rate is greater than the rate of diffusion to the cell, there will be a deficit in the area surrounding the cell. To improve conditions, a cell can move either by its own form of motility or by utilizing turbulence. However, at the scale of bacteria, viscous forces minimize the effectiveness of turbulence to cause relative movement between a cell and its local fluid environment (Lazier and Mann, 1989). Since physical mixing cannot enhance nutrient flux, large bacteria rely on self-generated movement (Dusenbery, 1997).

Protozoans.   Two main marine protozoan (20–200 µm) groups are flagellates and ciliates (Fenchel, 1987), swimming from 200 µm/s (flagellates) to 1000 µm/s (ciliates). Many protists show both taxis and kinesis. Some flag-

ellates exhibit helical chemotaxis to help in orientation (Crenshaw, 1996). At the scales of protists, molecular diffusion rates limit rapid signal transport to less than hundreds of micrometers. To enhance nutrient flux, protozoans in the size range of 63 to 100 µm benefit from commonly observed levels of small-scale turbulence (Karp-Boss et al., 1996). Organisms less than 200 µm are considered too small to communicate by pheromones (Dusenbery and Snell, 1995), so Wolfe (2000) proposed that protozoans could still signal cells in close proximity with a non–steady-state excretion.

Copepods.   Copepods (1–10 mm) can detect chemical molecules transported to their receptors by molecular diffusion. However, this is a slow process, so the copepod can use its feeding current to increase the rate of transport by advective flow. The feeding current generated by copepods is a low Re feature (Strickler, 1982). Hence, when the active space of an algal cell is entrained in the flow field, it is deformed in a predictable way and the particle path is predetermined by the position of entry into the flow field (Alcarez et al., 1980). When the odors activate antennulary sensors, the copepod is alerted to the approach of a cell from a specific location in the three-dimensional space of the flow field. Within the feeding current, the Peclet number is greater than 1, and advection distorts the distribution of odorant on a time scale too fast for diffusion to erase (Andrews, 1983). Here, advection enhances aquatic communication by accelerating the process of chemical transport beyond the limitations imposed by molecular diffusion.

However, many copepods (1 mm in length, 1 mm/s swimming speed, Re ≈ 1) do live at or below the Kolmogorov scale, the size of the smallest eddies formed by physical mixing where molecular diffusive forces dominate, and flow is attenuated by viscous forces and is isotropic. Within these Kolmogorov eddies, copepods exhibit a remarkable behavior of precisely following the three-dimensional trails left by their mates (Doall et al., 1998; Weissburg et al., 1998; Yen et al., 1998). Female copepods leave a pheromone in their laminar wake at a concentration and location that remain detectable by male copepods. Here, instead of limiting chemical communication, the slow rate of diffusion enhances chemical communication by allowing the trail to persist long enough for the male to find it. Observations that certain species of copepod reside in layers of high Richardson's number (Gallager et al., 1997) or low energy dissipation rate ε (Incze, 1996) also provide evidence of the importance of water stability to preserve these communication signals for successful mating and subsequent recruitment into the population. Shrimp (Hamner and Hamner, 1977) follow chemical trails by combining chemotaxis with geotaxis to travel down the scent trail to scavenge on the sinking foodfall. This can occur in the deep sea, where water is stable.

Decapods.   In contrast to bacteria and protists that rely on molecular diffusion for mass flux, crabs and lobsters (1 cm to greater than 10 cm) respond to the advective transport of the chemical (Basil and Atema, 1994; Atema,

1996; Weissburg, 1997). These decapods live in a relatively high Reynolds realm where flow has a strong effect on mixing the odorant. According to current ongoing research, signals emitted into a turbulent flow are deformed by the turbulent features that pick up the odorant from the point of emission; these deformations in the odor field appear to persist despite differences in the ambient velocity field at least under some conditions (Weissburg, 2000). These organisms respond to the immediate structure of the plume with reaction times of less than a few seconds. The combination of edge detection and the detection of odor filaments with the detection of fluid flow guides their search to the odor source. Snails and starfish that may respond at longer time scales, integrating the rate of contact and/or concentration of the individual filaments, could indeed be responding to the time-averaged structure of the odor plume (Weissburg, 2000). Analyses of the population response of crabs and lobsters also may show that, as a group, the response to a stationary source (not live, moving prey) represents the time-averaged structure.

Summary.   For bacteria and protozoans, the final collection of approaches and paths taken to reach the source most closely matches the statistically time-averaged diffusing odor. Similarly, but at the large scale, the tracks of turtles reconstruct the statistically time-averaged plume structure. In between, we see some fantastically intriguing chemosensory behavior where at intermediate Re, copepods follow a trail that is slowly expanding spatially due to molecular diffusive forces, but temporally for times less than those where turbulent eddy diffusion begins to erase the trail. The copepod's behavior matches the instantaneous structure of the signal. At higher Re, the element of chaos leads to unpredictable spatial distributions of the filaments within odor plumes. Due to this unpredictability, crabs and lobsters rely on two modalities to find the source: odor and flow. When the odor is detected, the response is to move upstream. Without flow, the crabs are not able to find the source. The paths taken to the odor source define neither the time-averaged nor the instantaneous filament structure. (See Table 4.1.)

TABLE 4.1. Scaling of the fluid physical regime with biological responses of aquatic organisms

Size	Organism	Physical Regime	Biological Response
10 μ	Bacteria	Molecular diffusional gradient	Kinesis
100 μ	Protozoans	Molecular diffusional gradient	Kinesis and taxis
1 mm	Copepods	Molecular diffusional gradient and laminar flow	Orient to trails and predictable flow
10 cm	Decapods	Turbulent flow	Orient by whiffs and directional currents
1 m	Turtles	Eddy diffusional gradient	Track gradients?

4.3.2   Models of Chemical Communication in Aquatic Organisms

Use of laser-induced fluorometry and other flow-visualization techniques (Weissburg, 2000) confirms that the structure of a turbulent odor plume is comprised of many individual filaments of odorants, as depicted in Fig. 4.5. Current research in the aquatic realm seeks to couple an instantaneous visualization of an odor plume's *physical* structure with *behavioral* observations of aquatic organisms orienting to the odor. Reactions to the filaments instead of the time-averaged edge of the plume would confirm the importance to the organism of the fine-scale structure of the odorant. The behavioral responses of moths (Vickers and Baker, 1994) to an odor plume created in a wind show that both the increment in the odorant concentration in the direction of the odor source and the temporal and spatial patterns of concentration fluctuation do provide information to guide their chemotactic behavior. In contrast, orientation in turbulent aquatic odor plumes occurs largely via simple mechanisms of edge detection (that is, by detecting spatial patterns in odorant levels: Webster et al., 2001), with a generalized up-current response. Recent research (Webster and Weissburg, 2001) suggests that the instantaneous structure is too unpredictable to provide accurate information on source location. Hence, the complexity of the internal instantaneous structure of an odor plume still limits our present ability to model odor tracking in a turbulent environment.

In contrast, the simplicity of the laminar viscosity-dominated environment of small organisms like copepods and bacteria makes them more amenable to modeling efforts. For instance, Andrews' (1983) model of the transport of phytoplankton odor entrained in a sheared feeding current of a copepod shows a separation of the leading edge of the active space of the odorant. Activated sensors along the copepod antennule would detect the odor prior to the arrival of the odor source, the algal cell. With this advance warning, the copepod could have time to redirect the streamline or reorient to the approach of the alga. This indeed was the behavior observed when *Eucalanus* perceived the algal cell 1250 μm away and 450 msec prior to ingestion (Koehl and Strickler, 1981). These dynamics of odor deformation were recently examined electrochemically at the time and space scales of copepod flow fields (Moore et al., 1999).

Likewise, we can apply equations for Fickian diffusion [Eqs. (4.18) and (4.19)] to model the use of the three-dimensional mating trails for chemical communication between copepods. If λ is the ratio of the initial concentration over the threshold concentration for detection and A is the source area, we can calculate the length of the detectable trail x^* and its fade-out time t^* for a small (600 μm) zooplankter ($A = 10^{-4}$ cm^2, $U = 10^{-1}$ cm/s; $D = 10^{-5} - 10^{-8}$ cm^2/s for small to large molecules, respectively) relying on a large molecular weight pheromone. (See Table 4.2.). For trail lengths over 10 cm, turbulent processes become increasingly effective in reducing the fade-out time.

TABLE 4.2. Length of the detectable copepod mating trail x^* and its fade-out time t^* for different values of λ, the ratio of the initial pheromone concentration over the threshold concentration for detection

λ	x^*	t^* (s)
1	0.1 mm	0.1
10	1 cm	10
100	100 cm	1000
1000	100 m	100,000

If the threshold for detection is on the order of 10% of the original concentration (= 10), then the predicted lifetime of a three-dimensional trail diffusing by molecular process is on the order of tens of seconds for lengths of 10 cm or less. And indeed, the longest documented trail followed by a mate-tracking copepod (Doall et al., 1998; Weissburg et al., 1998; Yen et al., 1998) was 13.7 cm, and the oldest trail 10.3 s old. The male also precisely follows the trail of the female, indicating that the trail structure is changing only very slowly. This confirms that eddy diffusion is minimal at these short (<10 s), small (<10 cm) scales, and zooplankton of about 1 mm would be most effective in using pheromonal trails.

4.3.3 An Inverse Problem: Estimating the "Statistical Funnel" of Sediment Traps

In the previous section, the problem was for an individual to follow a plume to its source. In the present section, we consider a case where the "organism" (here a sediment trap) is fixed, and the problem is to relate the mass of sediment particles collected to their source in the surface layer of the ocean.

In the ocean, carbon dioxide is converted by phytoplankton photosynthesis into organic carbon. Through processes of aggregation and grazing, these organic compounds are formed into larger particles. Mineral materials such as calcium carbonate and silica are also produced by some groups of phytoplankton; these materials are denser than seawater, allowing the particles to sink. This sinking flux acts as a "biological pump" for carbon from the surface ocean to the deep ocean; the strength of this pump (along with the "solubility pump" driven by temperature) determines the rate at which the oceans can take up carbon dioxide from the atmosphere.

Chemical oceanographers deploy sediment traps at various depths in the ocean to capture this flux. A major goal has been to relate the fluxes caught in traps to surface production by phytoplankton, which can be estimated using satellite imagery. A major problem with making this linkage is that particles sink rather slowly (the canonical value is 100 m/d) when compared

to currents, so that the source area for particles, even for a trap at 3-km depth, may be hundreds of km away. Around this mean flow field, there are also strong eddy motions, and in some places the flow field meanders considerably. For example, Deuser et al. (1988) noted that in the Sargasso Sea off Bermuda, the dominant pattern was seasonal and was easily captured by sediment trap collections; but off the northeast coast of South America, low-salinity filaments from the Amazon and Orinoco rivers meandered over the trap site, creating a signal in the traps that looked random despite the fact that satellite images showed coherent structures.

The statistical connection between surface productivity and sediment trap records was explored in a series of papers by Deuser et al. (1988, 1990), Siegel et al. (1990), and Siegel and Deuser (1997). Deuser et al. (1988) coined the term "statistical funnel" to describe the notion that particles collected by sediment traps originate at the surface intersection of a cone-shaped statistical structure whose apex is the sediment trap. By correlating the seasonal pattern of satellite chlorophyll observations near Bermuda to the seasonal pattern of deposition in sediment traps at 3200 m, Deuser et al. (1990) and Siegel and Deuser (1997) showed that the center of the surface opening of the statistical funnel for these traps was approximately 200 km northeast of the trap mooring, implying that sinking particles move almost horizontally, with a very small vertical vector component (Siegel and Deuser, 1997).

The size of the statistical funnel was explored in a series of simulations by Siegel and Deuser (1997). Releasing particles at the surface to see where they ended up would not work, since a vanishingly small proportion of particles would reach the trap. Instead, they released particles at the trap and allowed them to float to the surface with characteristic velocities of 50 m/d, 100 m/d, and 200 m/d. (Alternatively, they allowed the particles to sink backward in time.) As the particles rise from one depth to the next, their horizontal velocities may change slightly. The statistics of this change are described by a Lagrangian autocorrelation structure with time scale $\tau = 10$ d, which means that the correlation of velocity after 10 d with the original velocity is only $1/e$. This correlation structure is simulated using a recursion relationship; for the x direction (east), the eddy-induced velocity u_i' of particle i is given by

$$u_i'(z, t + \Delta t) = (1 - \Delta t/\tau)u_i'(z, t) + \sqrt{(2\Delta t/\tau)}\,\sigma_u(z)r,$$

where z is depth, Δt is the time interval used in the simulation, r is a random number drawn from a standard normal distribution $N(0,1)$, and $\sigma_u(z)$ is the square root of the turbulence-induced variance $\sigma_u^2(z)$ at depth z. This variance is directly proportional to the eddy kinetic energy at any depth z, which is higher near the surface; its mathematical form near Bermuda was estimated from data to be

$$\sigma_u^2(z) = 30 \exp\{3.7 \exp(-z/600)\}.$$

The simulation was run using several thousand particles released at each of several depths, and with several sinking velocities. Each particle follows a

TABLE 4.3.

		H (m)		
		500	1500	3200
	50	151	224	264
V (m/d)	100	81	130	168
	200	43	71	99

discrete trajectory that could be considered the center of a filament perhaps 100 m in diameter (Siegel and Deuser, 1997). Particles intersect the surface at time H/V, where H is the depth of the trap and V is the sinking velocity. Remarkably, even with the assumptions of autocorrelated motion and variation of σ_u with depth, the resulting statistical funnels are circular normal (Armstrong and Siegel, 2001); the sizes of the statistical funnels can therefore be characterized uniquely by their standard deviations s (km); see Table 4.3.

Table 4.3 contains values of 2.80 s (in km) from the simulations of Siegel and Deuser (1997). (Because the distributions are circular normal, 98% of particles originate at distances $\leq 2.80\ s$.) As the table shows, the area from which particles are drawn increases with trap depth H and decreases with sinking velocity V. Even in the case of very fast (200 m/d) particles sinking to a very shallow (500 m) trap, the size of the statistical funnel is still very large, with a 98% origination contour of 43 km. For slow-sinking (50 m/d) particles and deep (3200 m) traps, the 98% collection distance becomes enormous (264 km).

However, large distances do not imply that surface patterns of productivity cannot be correlated with patterns from subsurface particle collectors, at least if one is interested in averages over long time periods. For example, Deuser et al. (1990) found that the coherence between time series of trap values and of satellite chlorophyll values had a correlation coefficient $r = 0.96$ when (i) the values within each two-week period were averages over several years, (ii) the surface box studied was aligned 200 km northeast of Bermuda, and (iii) the transit time from the surface to the trap was assumed to be 1 month. So, in analogy to previous examples, a diffusion model seems to be quite useful for describing suitably averaged time series of trap data.

However, for shorter deployments, Siegel and Deuser (1997) pointed out that the "funnel" at any one time is only a filament of perhaps 100-m diameter at the surface, and that this filament can move quite a distance (due to the passage of mesoscale eddies) during the course of a short (30 d) trap deployment. At these short time scales, heterogeneity in sinking rates may also be important. At short time periods, the filament model is appropriate, and predicting the surface origin of fluxes at depth would require exquisite knowledge of fluid motions for hundreds of kilometers around the trap.

5
Mathematical Treatment of Biological Diffusion

Akira Okubo and Daniel Grünbaum

In the lifetime of most animals there occurs a time when the site of inhabitation is abandoned in favor of migration. Thus, in an environment changing through space and time, the most probable strategy for a new individual to adapt to survive and reproduce may not necessarily consist of remaining to compete with its parents or congeners, but may rather consist of migrating elsewhere to find an empty niche to inhabit (Taylor and Taylor, 1977; see also Lidicker and Caldwell, 1982). As a result the spread of population, i.e., dispersal, takes place. Such animal movement includes nomadism, whereby animals wander with no particular direction in search of sustenance, in a manner that resembles the random walk; and migration, which may be either periodic as animals move from one habitat to another in a repetitive cycle, or nonperiodic, implying a certain degree of permanence to the move. In addition, animals may display a restricted movement as they carry on their daily activities within a given domain of their habitat (home range).

The migration and dispersal of animals, while containing subjective elements that may not be totally controlled by animals, by and large constitute a ceaseless, active effort on the part of the animal to put itself in advantageous circumstances. However, the movement of two individuals placed in the same environment is not identical. It is necessary to consider animal motion as a random variable (see Sect. 2.1). Nevertheless, the random motion of animals in general cannot be considered to be that of a "simple diffuser" such as the random walker.

A degree of success has been achieved in the analysis of dispersal of animal populations by starting with a direct analogy to the random walk or physical diffusion, with an additional consideration of intra- and interspecific population interaction. The work of Skellam (1951) has provided a profound and lasting contribution to this approach. However, a more realistic model of biological diffusion must be built by properly combining the following concepts: correlated random walks; diffusion incorporating space–time variation of parameters and nonuniformities; treatment of individual inter-