

Fletcher, Gray & Jones (1988)

PHYSICAL AND CHEMICAL PROPERTIES OF AQUATIC ENVIRONMENTS

GEORGE A. JACKSON

*Institute of Marine Resources, A-018,
Scripps Institution of Oceanography,
La Jolla, CA 92093, USA*

23
file
copy

INTRODUCTION

Physical and chemical processes define the nature of planktonic systems. The transmission, absorption, and scattering of light control the availability of light energy for photosynthesis. Fluid motion controls organism location, mass transport rates, and efficiency of grazer feeding. The standard approach for analyzing processes in planktonic systems treats physical and chemical phenomena as if the included organisms were continuously distributed properties of the water rather than discrete entities separated by relatively large distances. Processes such as light absorbance, carbon production, nutrient uptake, zooplankton grazing, and nutrient regeneration are normally analyzed as continuous water properties rather than as the sum of the interactions of individuals. Process rates measured in a volume of water using uniformly added tracers have been considered to be the same as environmental rates which involve exchanges between individuals. This approach to the study of planktonic systems has generally worked well and need not be incompatible with insights derived from study of individual interactions. However, recent work has suggested that this emphasis on continuous distributions ignores important consequences of the discrete nature of organisms and of their interactions. This chapter contains an analysis of interactions between discrete organisms and a discussion of the ways in which physical and chemical processes constrain them.

The effect of particle size on fall velocity is an example of how the behavior of individual organisms can be used to provide information for the continuous distribution approach. Because organisms tend to have densities greater than the surrounding waters, they tend to sink under the pull of gravity. Their fall velocities are affected by organism size, density, shape, and motility in ways that have been discussed by Hutchinson (1957) and Smayda (1970), among

others. Results from studies of bioparticle fall velocities can be used to estimate average biomass loss rates from water parcels, regardless of whether organisms are assumed to be continuously distributed.

Munk & Riley (1952), in a study later extended by Gavis (1976), analyzed organisms, particularly microalgae, as discrete entities and provided useful insights into the process of nutrient absorption which have not been incorporated easily into the continuous distribution approach. Munk & Riley noted that the uptake of a substance can be limited by the rate of transfer by molecular diffusion from solution to the organism surface. As a result, there is a region near an organism with low substance concentration and a small concentration gradient. Water motion reduces the size of this depleted region, increases the concentration gradient, and thereby increases transport to the cell. Transport enhancement by water motion depends on water velocity, organism size, organism shape, and other factors. Vertical settling can provide the fluid motion for planktonic organisms. One conclusion of these studies is that smaller organisms are less limited by diffusion kinetics than are larger organisms. This has been an important qualitative insight into cell morphology and nutrient uptake (e.g. Malone, 1980; Sournia, 1982), but this has not been generally translated into quantitative terms which can be incorporated into other process studies. Because the analysis considered discrete particles and constant nutrient concentrations, it addressed only half of the spatial and temporal nature of organism interactions.

Undetected interactions between individual planktonic organisms was suggested by McCarthy & Goldman (1979) to explain what they perceived as a puzzling problem in nutrient exchange between animal excretion and plant uptake. They noted that nutrient regeneration is not a process that occurs uniformly though a volume of water but rather occurs at discrete points for short time periods, with locally high concentrations where animals happen to be when they excrete. They suggested that short-term, high-speed nutrient uptake by phytoplankton within a few micrometers of zooplankton excretion would not be observed in the liter-sized water samples usually collected but could, nevertheless, supply the nutrient needs for the growth they expected in oligotrophic ocean areas. Such algal nutrient uptake would be at concentrations much higher than the extremely low surrounding nutrient concentrations. Goldman (1984) also noted the difficulty of obtaining accurate measurements of nitrogen uptake rates by microalgae for short exposures but noted that short-term

uptake rates are much faster than steady state conditions would demand.

Jackson (1980) and Williams & Muir (1981) noted that the rapidity of diffusion on the small scale makes the exposure time of an alga to an animal excretion pulse extremely short, allowing only a small total amount of nutrient to be taken up during a pulse event, even if the uptake rate during the pulse time was fast. Jackson (1980) and Currie (1984*a*) calculated that the frequency of algal exposure to such a pulse was very small. Currie (1984*b*) also argued that the non-linear nature of algal nutrients uptake kinetics implies that nutrient uptake at pulse concentrations is inherently less efficient than uptake at lower average concentrations. Lastly, Jackson (1980) and Currie (1984*b*) disputed the requirement for a pulse mechanism to explain phytoplankton growth.

Lehman & Scavia (1982*a, b*) were able to show that rapid uptake of nutrients released by zooplankton does occur. They also made more elaborate diffusion-based calculations and argued that nutrient uptake within a very short distance of release was a significant part of the recycling process. Other authors continue to explore the issue (e.g. Scavia *et al.*, 1984).

The importance of pulse uptake in ecological situations remains unclear. While Lehman & Scavia (1982*a, b*) did demonstrate that enhanced uptake of nutrients from pulses can exist in laboratory conditions, they did not establish its significance in ecological situations where different species of zooplankton and phytoplankton are present in different sizes and different abundances. Diffusion calculations made to date omit important aspects of the system. Calculations by Jackson (1980) and by Williams & Muir (1981) show the importance of spatial scales in determining short exposure times but do not adequately address the nature of plume generation or nutrient uptake. Calculations by Lehman & Scavia (1982*b*) are more inclusive, but assume nutrient uptake to be uniformly distributed, as if the phytoplankton were not discrete entities widely separated. Individual algal cells may be 1–50 μm in diameter, separated by as much as 1000 μm . Because Lehman and Scavia's calculation considered decreases of pulse concentrations within 100 μm of release, such an assumption of continuous nutrient uptake is inadequate. Furthermore, the relation between nutrient concentration and algal uptake rate is confused by the possibilities that short-term rates may be higher than we now estimate or, conversely, that diffusion limitation to individual cells makes actual rates lower than those calculated

from laboratory results. There remain many unanswered questions regarding the role of short-time uptake rates. The difficulties of conducting experiments directly on the small spatial scales involved or of making theoretical calculations that address enough of the system complexity are largely to blame.

Azam & Ammerman (1984) have suggested a second type of microorganism–microorganism interaction which depends on the discrete nature of the organisms. They noted that marine bacteria live in a low organic concentration but appear to grow rapidly. Microalgae, however, are surrounded by zones of higher organic concentrations because they leak organic matter. Azam and Ammerman proposed that the chemotactic abilities of bacteria allow them to find and stay in the high organic concentration regions around the algal cells. Such behaviour would allow the bacteria to live in regions with higher nutrient concentrations than those measured in bulk water samples.

The two types of interactions proposed by McCarthy & Goldman (1979) and Azam & Ammerman (1984) emphasize the potential importance of organism–organism interactions even at the micrometer scale. Both are difficult to study experimentally because of the extremely small scale on which they would occur. Furthermore, it is unclear how to extrapolate laboratory results to environmental conditions. Both types of interaction occur at scales where our physical intuitions are not well developed, the physical process of diffusion is extremely important, the discrete nature of the organism must be considered, and concentrations are so small that substances are better considered as a few molecules rather than as fractions of moles.

My goal in this chapter is to explore how diffusion and the discrete nature of organisms constrain the systems. First, aspects of diffusion to and from bioparticles are considered, where spherical particles represent idealized microalgal or bacterial particles. This is then extended to describe bacterial chemotaxis around leaky algal cells. The results show which ecological conditions are most suitable for the different interactions to be strongest and suggest ways to extrapolate laboratory results to environmental conditions.

DIFFUSION, DISCRETE CELLS, AND THE FATE OF PULSES

At its simplest, mass transport to a cell from solution is determined only by molecular diffusion. Water motion enhances mass transport,

but with simple molecular diffusion, a pulse lasts longer, is more confined, and should have its greatest effect.

There are two standard approaches to solving molecular diffusion problems. The first is to use differential equations describing concentration changes. The same differential equations are also used to describe temperature distributions in solids, voltage fields in electrostatics, potential flow in fluids, and ground water flow in aquifers. Solutions to various simple geometries and starting conditions have been assembled (e.g. Crank, 1956; Carslaw & Jaeger, 1959). The second approach is to consider the motion of any given molecule to be a random walk. The statistics of this motion, such as the average and mean square molecule position, are calculated by analytical techniques or by computer simulations. The fraction of a large number of molecules originally at one location having a particular fate is equal to the probability that one molecule has that same fate. Studying the probabilities of the motion of one molecule can provide information about the fate of a discrete release, such as a pulse. The two different approaches, one involving a differential formulation and the other the random walk, complement each other by the ease with which they answer different aspects of the same problem.

Diffusion-determined concentrations around a sphere at steady state

The standard differential equation for diffusion to a spherical particle in the absence of fluid motion or diffuse sources or sinks is

$$\partial C / \partial t = D \nabla^2 C \quad (1)$$

where D is the diffusivity, C is the concentration, and ∇^2 equals $(\partial^2 / \partial x^2 + \partial^2 / \partial y^2 + \partial^2 / \partial z^2)$.

For the simple steady state case of a sphere of radius a with concentration C_0 far away (at infinity) and concentration C_1 at the sphere's surface, the concentration at a distance r from the sphere center is:

$$C = (C_1 - C_0)ar^{-1} + C_0 \quad (2)$$

The flow of molecules towards or away from the cell per unit time, F , is given by

$$F = -4\pi Da(C_1 - C_0) \quad (3)$$

Maximum flow inward occurs when the concentration at a is the lowest possible value, 0. Munk & Riley (1952) assumed that C_1 was 0 in their study of mass transport and flow rate. Gavis (1976) modified

their results by assuming that F was related to C_1 by a Monod relation. Either F or C_1 is sufficient to define the cellular concentration (eqn 3).

Eqn 2 can be rewritten in terms of F :

$$C = C_0 - F(4\pi D)^{-1}r^{-1} \quad (4)$$

The sphere has proven to be a useful approximation to a cellular microorganism because the spherical case is more easily solved and provides results similar to those for other more complicated but more realistic shapes. For studies of the flux into a cell absorbing some constituent, C_0 is usually assumed to be 0 because the result is the maximum inward flux.

Fate of a molecule released near a sphere

A molecule present at a distance r from a sphere of radius a has a finite probability of ever hitting the sphere as part of the random walk that is molecular diffusion. This probability (p_0) is (Berg, 1983)

$$p_0 = ar^{-1} \quad (5)$$

The probability varies with distance from the sphere, ranging from 1 at the sphere's surface to 0 when the molecule is infinitely far away. It falls to 0.5 when the molecule is a spherical radius away from the surface.

If molecules are released uniformly in space, then the probability, p_1 , that molecules released within a distance R of the sphere's center will strike the sphere is determined by integration:

$$p_1(R) = (4\pi/3)^{-1}(R^3 - a^3)^{-1} \int_a^R (a/r)4\pi r^2 dr \quad (6)$$

$$= 1.5a(R + a)(R^2 + aR + a^2)^{-1} \quad (7)$$

$$\approx 1.5a/R \text{ for } R^2 \gg a^2 \quad (8)$$

The fraction of molecules released within a given distance from a sphere that ultimately diffuse to it varies inversely with the distance.

The fate of a molecule released in a suspension of perfectly absorbing spherical particles is more complicated to calculate. If the spheres are randomly distributed, what is the probability that the molecule will be absorbed within a distance R ? The probability of the molecule being absorbed by a particular sphere at r is less than that in eqn 5, because the molecule could be absorbed by a

different particle first. To solve the problem in which particles compete for the molecule is more difficult than the problem where they do not. If the particles do not compete and if ρ is the particle abundance (number/volume), then the probability, dp_p , of a particle being within a distance ranging from r to $(r + dr)$ is

$$dp_p = 4\rho\pi r^2 dr \quad (9)$$

The probability of the molecule hitting a particle in the range of r to $(r + dr)$ distant is the probability of a particle being there, multiplied by the probability of the molecule hitting that particle:

$$dp_2 = dp_p \cdot p_0 \quad (10)$$

$$= 4\pi\rho a r dr \quad (11)$$

The total probability p_2 of a particle being taken up within a distance R of its initial position is then the sum (integral) of all the dp_2 :

$$p_2(R) = \int_0^R 4\pi\rho a r dr \quad (12)$$

$$= 2\pi\rho a R^2 \quad (13)$$

This estimate is not the true probability but an overestimate because of the assumption that the particles do not compete for the molecule.

The distance $R_{1/2}$ at which p_2 is 0.5 is given by

$$R_{1/2} = (4\pi\rho a)^{-0.5} \quad (14)$$

Diffusion, random walks, and planktonic particles

Bacteria and microalgae are neither perfectly absorbing nor are they spheres. However, using the result of calculations that assume they are so allows us to place an upper boundary on the nutrient uptake that is independent of uptake rate measurements. We can determine a minimum distance that a pulse expands before it is taken out of solution by algal uptake.

Environmental phytoplankton sizes and abundances vary widely. Selected examples from the Pacific Ocean show abundances ranging from 4×10^2 to 10^6 cells cm^{-3} and dominant algal radii ranging from 0.5 to 13.0 μm (Table 1). These situations demonstrate typical values for the fraction of nutrient input that could be consumed by the nearest microalgal cell ($p_1(S/2)$) and the distance that a spike spreads

Table 1. *Pulse fate for different environmental conditions. Values for algal abundance (ρ) and algal radius (a) are representative of reported values. Costa Rica Dome is an extremely eutrophic area. The populations from the area off Hawaii are of cyanobacteria (5) and Chrysochromulina-like cells (6). The biomass density of the latter was about 15 times greater than that of the former. The area off southern California had a *Prorocentrum micans* bloom. S is the separation distance, $\rho^{-1/3}$. $R_{1/2}$ is the distance a pulse travels before half is absorbed. $p_1(S/2)$ is the fraction of a pulse absorbed by the nearest alga, which is within $S/2$ of the pulse.*

Case	a (μm)	(cells cm^{-3})	S (μm)	$P_1(S/2)$	$R_{1/2}$ (cm)	Location	Citation
1	3.0	10^5	220	0.041	0.052	Laboratory	Lehman and Scavia, 1982a, b
2	2.0	4×10^2	1400	0.004	1.0	North Pacific Central Gyre (28°N 15°W)	Beers <i>et al.</i> , 1975
3	0.5	10^6	100	0.015	0.040	Costa Rica Dome (9°25'N 93°30'W)	Li <i>et al.</i> , 1983
4	0.5	10^4	460	0.003	0.40	Eastern tropical Pacific (9°45'N 83°45'W)	Li <i>et al.</i> , 1983
5	0.5	3×10^3	690	0.002	0.73	Off Hawaii (~21°N 158°W)	Laws <i>et al.</i> , 1984
6	2.0	10^3	1000	0.006	0.63	Off Hawaii (~21°N 158°W)	Laws <i>et al.</i> 1984
7	13.0	4×10^2	1400	0.028	0.39	Off southern California	Eppley <i>et al.</i> , 1977

before half could be consumed ($R_{1/2}$) if the algal cells were perfect sinks. Potential uptake by the nearest alga ranged from 0.2 to 2.8%; distance for half uptake ranged from 0.04 to 1.0 cm. The shortest distance occurred for the very eutrophic situation with extremely small cells at the Costa Rica Dome (Table 1, case 3). A *Prorocentrum micans* bloom off southern California (case 7) and oligotrophic situations (cases 2, 5, 6) had widths at half uptake closer to 1 cm. The Lehman & Scavia (1982a, b) laboratory experiment (case 1) was more similar to the eutrophic Costa Dome situation than to those of the other oceanic areas.

This analysis has considered a phytoplankton population to have a single, well defined size or, as in cases 5 and 6, has considered two different populations separately. Phytoplankton in most communities occur with a range of sizes. A fuller treatment that includes a distribution of microalgal sizes can easily be made by modifying eqns 9–14 to include an integration over the algal size spectrum.

The results would be more complete but would not alter the importance of algal size and abundance. A more important effect that should be accounted for is algal competition for the molecules. This would result in much larger values of $R_{1/2}$.

These arguments imply that the uptake of a nutrient pulse is more localized for greater algal abundances and larger algal cells. Both cannot be increased indefinitely. What are the optimal conditions for uptake for a given biomass density? If the biomass of an individual algal cell is proportional to the a^2 (Mullin, Sloan & Eppley, 1966), then the abundance is proportional to a^{-2} and $R_{1/2}$ is inversely proportional to the square root of a . Small cells are more effective per unit biomass with respect to localized uptake of pulses. Small is better.

The relative importance of pulses to phytoplankton also depends on the actual concentrations of the pulses and of other nutrient sources. Without information about the actual concentration field around a zooplankter and data on the background concentrations in the water, it is difficult to make exact predictions. Maximum concentrations from a pulse decrease rapidly with distance from a zooplankter (Jackson, 1980). If the initial source is a plume 100 μm thick, the maximum concentration 0.1 cm from the plume is less than 10^{-3} of the initial concentration. The concentration at 0.04 cm, the $R_{1/2}$ of the Costa Rica Dome, is not much greater. At least half of nutrient uptake takes place when the concentration of a pulse is decreased by 1000 or more. If the size of the initial plume is smaller, as it would be if microzooplankton excretion were important, then the dilution at $R_{1/2}$ is even greater. The tendency of small algae to be eaten by small grazers suggests that this will be true for situations where the small algae dominate.

The conditions most conducive to pulse uptake are those where microalgae are most abundant. Such a condition is more characteristic of eutrophic than oligotrophic conditions.

BACTERIAL CHEMOTAXIS AROUND A LEAKING MICROALGAL CELL

Chemotactic behavior

Like most planktonic organisms, bacteria are not immobile particles whose locations are subject only to fluid motions but rather have limited ability to find and move to suitable conditions. One important

need for a microorganism can be that for a better chemical environment. The ability of organisms to move, on average, towards a preferred chemical environment is known as chemotaxis. This behavior has been widely observed in aquatic bacteria and dinoflagellates (e.g. Fitt, 1985; Paerl & Gallucci, 1985; Spero, 1985) and intensively studied for those laboratory standards *Escherichia coli* (e.g. Berg & Brown, 1972; Berg & Purcell, 1977; Berg, Manson & Conley, 1982; Block, Segall & Berg, 1982, 1983) and *Salmonella typhimurium* (e.g., Koshland, 1979; Macnab & Han, 1983). As a result, much is known about the mechanism of swimming, the molecular nature of bacterial response, and bacterial response kinetics.

A bacterial cell is too small to be able to discern concentration gradients by sensing concentration differences over its length. Instead, a cell detects and responds to the temporal changes of concentrations surrounding it. A cell swimming up a concentration gradient sees an increase in concentration with time. The cell's motion translates a spatial gradient that it cannot sense to a temporal change to which it can respond.

Bacterial motion typically consists of two phases. The first is a run phase, in which a bacterium moves in a nearly straight trajectory. The forward motion of a run is interrupted by the transition to the second phase, the tumble, during which the bacterium rotates its orientation to a random new direction. After the tumble, it begins a new run. The length of a run is a random variable whose statistics are changed by increases or decreases in concentration of the sensed substance. While chemical concentrations improve, the run length, on average, lengthens; when chemical concentrations worsen, the run length, on average, shortens. The bacterial motion in the absence of chemical cues is a form of Brownian motion. In the presence of a chemical gradient, the changes in average run length give the cell a random walk with a bias which provides a net drift towards better conditions.

Brown & Berg (1974) developed a model to describe the influence of concentration history on run length. Mean bacterial run length depends on the rate of change of binding of the attractant to a protein receptor. Brown & Berg followed 'synthetic' bacteria as they swam through a 'synthetic' concentration field by using a Monte Carlo simulation to generate the random changes from run to tumble mode and to select new travel directions during tumbles. Their model results agreed with results from laboratory studies on bacteria.

Bacterial chemotaxis was invoked to explain bacterial-algal inter-

actions as early as 1894, when Engelmann observed bacteria clustering around photosynthesizing microalgae under a microscope coverslip. In this case, bacteria in anoxic water clustered around the algae when there was enough light to support photosynthesis but not otherwise. Engelmann explained this clustering as the result of chemotactic movement to the high oxygen conditions around the algae.

It has long been known that algae naturally leak organic matter. There is a range of estimates for the rate at which this occurs. Recent measurements ranged from 5 to 30%, but were typically about 10%, of net photosynthesis (Mague *et al.*, 1980). For a given specific leakage rate (expressed as fraction of algal mass leaked per day), the concentration around an alga is a function of cell size. If the specific growth rate of algal cells is typically 1.0 day^{-1} , then typical specific leakage rates could be 0.1 day^{-1} .

Combining molecular diffusion and bacterial chemotaxis

I have developed a computer model which simulates the behavior of marine bacteria around an algal cell. It uses the model of Brown & Berg (1974) to describe behavior and a molecular diffusion model to describe the concentration around a cell (G. A. Jackson, unpublished data). With this system, I have tested factors which allow chemotactic orientation as proposed by Azam & Ammerman (1984).

In the presence of a very leaky, large cell, a bacterium can dance its way closer (Fig. 1). The average movement of a large number of bacteria initially uniformly distributed around the alga is more deliberate (Fig. 2). The rate of this net movement is a convenient way of comparing the effects of different conditions. For an alga of radius $10 \mu\text{m}$, increased specific leakage rates cause increased drift rates toward the alga (Fig. 3); for an alga of radius $2.5 \mu\text{m}$, there is no drift toward the alga for specific leakage rates as high as 2 day^{-1} . This suggests that there is a size below which chemotactic behavior cannot be used to sense another cell. Additional evidence for this comes from more extensive simulations of the system (G. A. Jackson, unpublished data).

An important determinant of bacterial sensitivity is the half-saturation binding constant, K_D , of the protein which acts as the chemical detector on the bacterial surface. The results discussed thus far have used the value of 0.1 mM determined by Brown & Berg (1974) for *E. coli* movement towards aspartate. Increasing the value of K_D

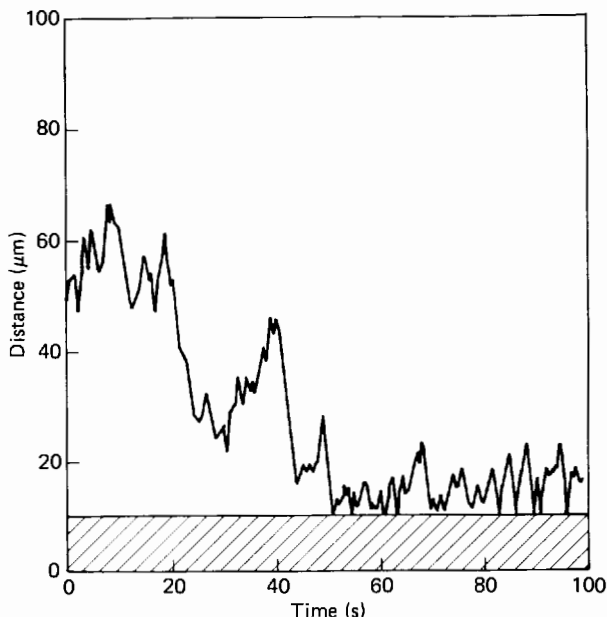


Fig. 1. Computer-simulated movement of a bacterium with a chemosensory response to a leaking alga. The alga has a radius of $10\ \mu\text{m}$ and is leaking 100% of its carbon content per day. The random nature of the bacterial movement causes its position to vary but its chemotactic response gives it a net movement toward the alga. Distance is from algal center. Shaded portion represents the alga.

by a factor of 1000, to $0.1\ \mu\text{M}$, does allow a bacterium to detect smaller sources (Fig. 4), but there is still a limit to the organism size that can be detected. Another constraint comes from the presence of a background concentration of the sensed substance (Fig. 5). Notice that the presence of a background concentration works to inhibit the effectiveness of lower values of K_D smaller than a critical value.

Importance of size and leakage rate

There are two important aspects to a chemotactic interaction: the sensing bacterium and the leaking alga. As the leaking alga becomes smaller, the chemical signal around it becomes smaller for two reasons. The first is that a smaller alga leaks less material to the water because it has less material available to leak. Because the biomass of a phytoplankton increases approximately as the square of its radius (Mullin, Sloan & Eppley, 1966), an algal cell with twice the radius of a smaller one will have approximately 4 times the biomass. If both have the same specific growth rate and the same fraction of this

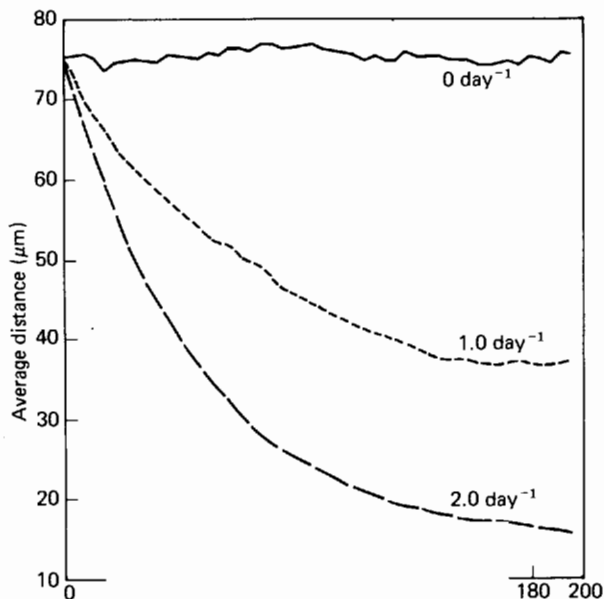


Fig. 2. Computer simulation of the average position of 800 bacteria around an algal cell with radius of $10\ \mu\text{m}$ and leakage rates of 0, 1 and $2\ \text{day}^{-1}$ as a function of time. The bacteria are initially uniformly distributed in a sphere that has a radius of $100\ \mu\text{m}$ around the algal center (10 times that of the algal cell). Distance is from algal center.

growth leaking, the larger will leak approximately 4 times as much material. There is a smaller concentration signal for a bacterium to sense around the smaller alga. The second reason is that the concentration of the leaked material decreases faster with increasing distance from a small cell than from a large one. For the case of two algal cells, one with radius A and the other with radius $2A$, the concentration at distance A from the surface is half its surface concentration for the smaller cell but two-thirds its surface concentration for the larger cell (eqn 2). Thus, the distance over which a cell projects a signal is also a function of its size. This effect has been compensated for in these results by simulating bacterial behavior between the alga and a distance 10 times its radius. Because the volumes affected differ, two ecosystems with different-sized algae have different ecological interactions.

The ability of a bacterium to find an algal source through chemotaxis is constrained. A sensory protein with a smaller half-saturation concentration can increase the bacterial sensitivity to a weak source. However, the background concentration of the sensed substance acts to mask the signal. This fact was used by Paerl & Gallucci

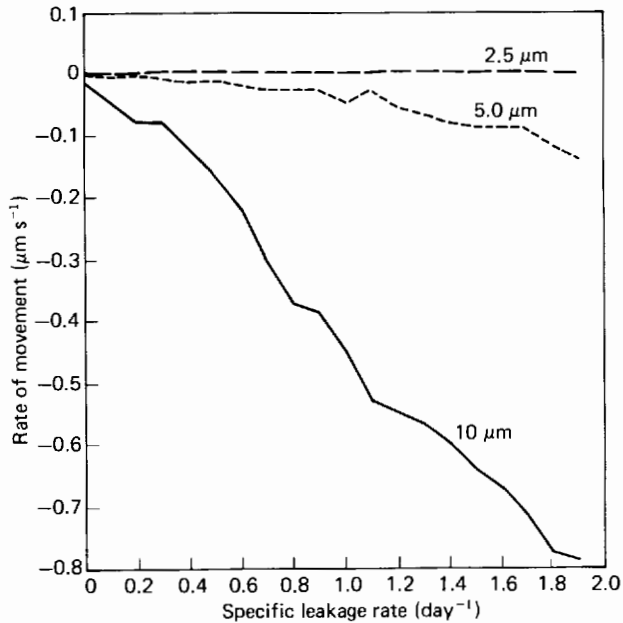


Fig. 3. The average rate at which 800 bacteria move relative to the alga as a function of leakage rate for the first 50 s of a computer simulation. This is essentially the initial slopes of the lines in Fig. 2. Negative values indicate that the average distance is decreasing as the bacteria approach the algal cell. The situations for algae of diameter 10, 5 and 2.5 μm are shown.

(1985) to demonstrate the chemotactic attraction of bacteria to nitrogen-fixing algae. The statistical nature of molecular reactions at low concentrations places the ultimate constraint on detection. Berg & Purcell (1977) have noted that the small number of molecules available to react at the bacterial surface makes the relation between number of bound sites and average concentration a statistical one. A bacterial cell can overcome the large statistical noise associated with sensing small numbers of molecules by effectively averaging any sensory signals over time, but this is achieved by slowing the response time. Slower response time makes a bacterium more susceptible to changes in position and direction caused by thermal Brownian motion and rotation. These factors place absolute constraints on the sensitivity with which bacteria can detect small sources.

The potential role of Brownian rotation suggests that large size is an important property of chemotactic bacteria. Berg (1983) has calculated that the root mean square (RMS) rotation caused by thermal Brownian rotation for *E. coli* is 30° in 1 s. This rate is similar to the angular deviation observed during *E. coli* runs, i.e. 27° in

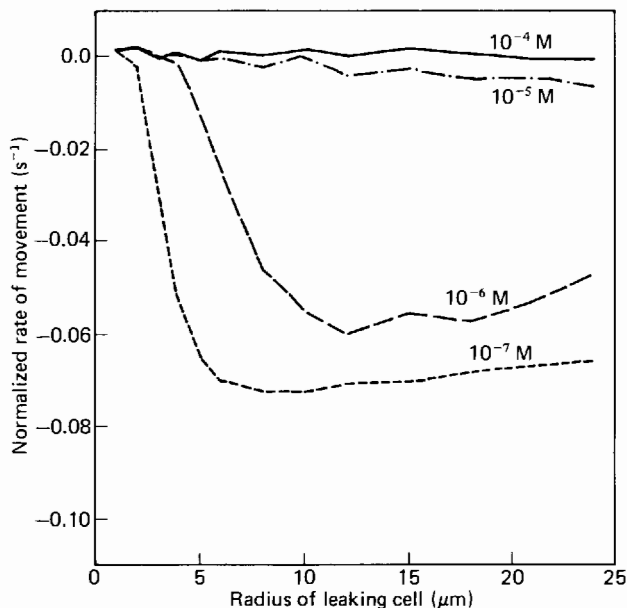


Fig. 4. Effect of algal size on bacterial sensitivity. Shown is the average normalized rate of movement for 800 bacteria as a function of leakage rate for the first 50 s of a simulation. Rates are normalized by the algal radius. The sensed molecule leakage rate is assumed to be 1.7% of the total cell carbon per day, calculated assuming that 10% of the total cell carbon is leaked per day and that half of this is in the form of a 3C molecule (such as an amino acid) detected by the bacteria. Half-saturation binding constants for these molecules are 10^{-4} , 10^{-5} , 10^{-6} and 10^{-7} M.

1 s. Because this rate is strongly dependent on size and is independent of behavioral responses, a bacterium with half the radius ($0.5 \mu\text{m}$) has the same RMS angular deviation in 0.12 s, and a bacterium with a radius of $0.25 \mu\text{m}$ has the same in 16 ms. The higher angular deviations make it more difficult for smaller organisms to maintain a direction during a run. Without a consistent heading, a cell cannot bias its runs in the direction of improving conditions. As a result, chemotaxis should be more effective with larger bacteria.

Brownian rotation could present a problem for marine bacteria because of their small size. Typical radii are on the order of $0.25 \mu\text{m}$ (e.g. Azam & Hodson, 1977; Fuhrman, 1981). Chemotactic behavior should be less of a problem for marine bacteria which are large or more elongate in shape.

The results discussed here imply that there is a minimum size of alga that bacteria can detect and around which they can maintain position. The calculations shown here suggest that this size is about $2 \mu\text{m}$.

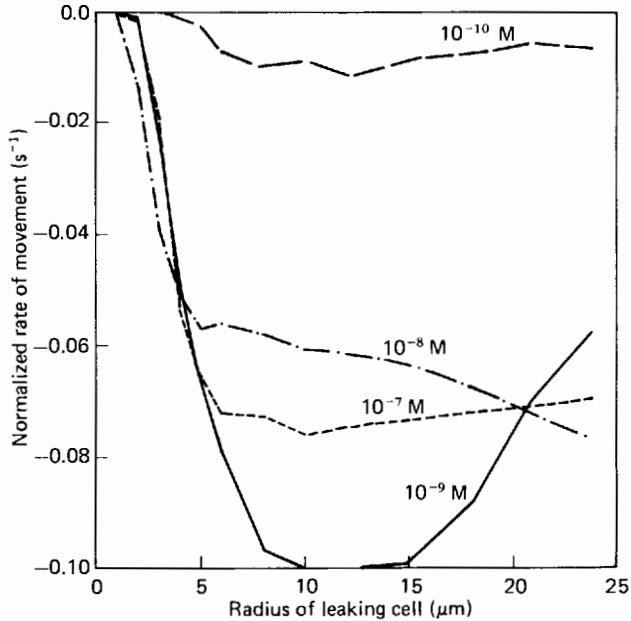


Fig. 5. Effect of algal size on bacterial sensitivity in the presence of a background concentration of the sensed substance of 10nM. Half-saturation binding constants for cases shown are 10^{-7} , 10^{-8} , 10^{-9} and 10^{-10} M. Other conditions are as in Fig. 4.

SIGNIFICANCE OF DIFFUSION AND CHEMOTAXIS IN NUTRIENT UTILIZATION

Mitchell, Okubo & Fuhrman (1985) considered the problem of bacterial chemotaxis to leaky algal cells by making several scaling arguments. They concluded that the microzone of high concentration around an algal cell with a radius of $5\ \mu\text{m}$ would be too small to be very effective. The arguments presented here show this is the cell size at which algal cells tend to become undetectable by chemotaxis. Mitchell *et al.* also noted that algal cells tend to fall at rates faster than bacteria can swim but that this fall is slowed at density gradients. They concluded that the most likely zone in which chemotaxis would be important would be at a steep density gradient. The present study has not addressed the effect of bacterial settling. Algal motion may, in fact, limit the ability of bacteria to be chemotactically attracted to them. However, the hydrodynamics of sinking particles is complicated and should be explicitly considered in a study of chemotactic behavior.

The nature of bacterial chemotaxis offers an insight into the nature of interactions between organisms. The inability to use chemical

cues to find organisms below a particular size should not be unique to bacteria but should be common to all organisms trying to sense other organisms smaller than that size. Chemotaxis is an important means allowing one organism to find another. It is important for feeding, for example, by allowing a copepod to detect edible food particles in the presence of inedible plastic spheres of the same size (Price & Paffenhöfer, 1986). It enables two zooplankters to find each other and mate (Katona, 1973). It could allow bacteria to find leaky food sources (Azam & Ammerman, 1984). It does not allow any of these if the particle to be sensed is too small.

That small particles, less than about $2\ \mu\text{m}$ radius, are not detectable from a distance through chemotactic, visual, or any other sensory means suggests certain ways in which microorganisms in this size range interact. Interactions must involve physical contact, although there may be chemical aspects to this touching. Aggregation of small microorganisms must involve physical contact or association with a larger particle/organism releasing a detectable chemical signal. Any feeding on small microorganisms should be quite mechanical.

Observed microorganism feeding patterns are in accord with these deductions. Fenchel (1984) has measured the feeding rates of various bacterivores. His analysis of the feeding processes relies on simple physical models with no active prey detection.

Similarly, bacteria of the genus *Bdellovibrio* have been observed to prey on other aquatic bacteria (Varon & Shilo, 1980). A bdellovibrio finds its prey by making a straight run which is interrupted only by its striking another organism, such as its prey. The absence of adequate chemical cues from the small prey organisms makes this an efficient way to feed. If a bdellovibrio were to use a Brownian walk to find its prey, it would not only have no chemical cues but it would also spend considerable time re-searching the same volumes of water. The uninterrupted run is the reasonable response to the lack of chemical cues from bacterial-sized prey.

McManus & Fuhrman (1986) have found that some bacterivores feed on artificial spheres at the same rates as they feed on bacteria. The implication is that bacterivores are unable to distinguish between the two particle types and certainly unable to find the bacteria with any extra skill.

Chemosensing has been established as an important part of copepod feeding behavior, from both laboratory studies (Friedman & Strickler, 1975; Price & Paffenhöfer, 1986) and mathematical simula-

tion studies (Andrews, 1983). There is a lower limit to the particle size on which copepods feed. For example, Frost (1972, 1977) reported that *Calanus pacificus* does not feed on particles smaller than about 14 μm diameter. Mullin (1980) has suggested that the lower limit on crustacean feeding is about 5 μm diameter. In contrast, salps filter food particles as small as bacteria with diameters of about 1 μm (Madin, 1974; Harbison & McAlister, 1979). Salp feeding involves the passive filtration of particle-containing water through a non-sensate mucus web. Rubenstein & Koehl (1977) have suggested that the lower limit of copepod filtration is determined by the nature of the filtration process and the low removal efficiency of particles in this size range. The inefficiency of small particle detection by chemosensing suggests another explanation, that is that copepods cannot detect bioparticles smaller than about 2.5 μm radius. While the details of chemosignal processing must be different in a larger, multicelled organism than in a bacterium, the problem of insufficient signal must occur for the copepod trying to find a small cell. The fact that these theoretical studies of bacterial chemotaxis yield an algal cell of a minimum detectable size that is similar to the minimum crustacean food size suggests that this limit is set by the inability of chemosensing to detect small organisms.

Despite pulse uptake by phytoplankton and the chemotactic orientation of bacteria, a large amount of released material is not taken up in the immediate vicinity of its release. This material must be taken up within the oceanic system if it is not to accumulate there. If there are cells which rely on localized uptake to survive, then there must also be cells which rely on the diffuse sources for their nutrient needs. The possible role of the localized uptake invoked in the pulse and chemotactic hypotheses does not eliminate the importance of more steady state uptake but rather adds a new method of survival through specialization. Localized uptake could thus provide more niches in plankton ecosystems.

CONCLUSION

The arguments in this chapter have emphasized the determination of conditions under which different types of microorganism interactions could occur in planktonic ecosystems. The difficulty of doing experiments on the very small scales involved places a premium on knowing how to relate scenarios, experiments, and environmental

situations. The results developed here imply that pulses of nutrients are most important in high densities of large algae. Optimal conditions for chemosensory interactions include large leaking cells and low background concentrations of the sensed molecule. High abundance of cells would increase the relative volume influenced by the leakers. The large and small sizes and low and high densities which yield different results are those that are found within naturally occurring conditions. As such, they should be controlled in experimental studies and their importances acknowledged when trying to extrapolate from one situation to another.

ACKNOWLEDGEMENTS

This work was done in collaboration with E. Stewart, who assisted with the computer programming. It was funded by ONR Contract N00014-85-K-0473.

REFERENCES

- ANDREWS, J. C. (1983). Deformation of the active space in the low Reynolds number feeding current of calanoid copepods. *Canadian Journal of Fisheries and Aquatic Science*, **40**, 1293–302.
- AZAM, F. & AMMERMAN, J. W. (1984). Cycling of organic matter by bacterioplankton in pelagic marine ecosystems: microenvironmental considerations. In *Flows of Energy and Material in Marine Ecosystems*, ed. M. J. R. Fasham, pp. 345–60. New York, Plenum Press.
- AZAM, F. & HODSON, R. E. (1977). Size distribution and activity of marine microheterotrophs. *Limnology and Oceanography*, **22**, 492–501.
- BEERS, J. R., REID, F. M. H. & STEWART, G. L. (1975). Microplankton of the North Pacific Central Gyre: population structure and abundance, June 1973. *Internationale Revue der Gesamten Hydrobiologie*, **60**, 607–38.
- BERG, H. C. (1983). *Random Walks in Biology*. Princeton, N.J., Princeton University Press.
- BERG, H. C. & BROWN, D. A. A. (1972). Chemotaxis in *Escherichia coli* analyzed by three-dimensional tracking. *Nature*, **239**, 500–4.
- BERG, H. C., MANSON, M. D. & CONLEY, M. P. (1982). Dynamics and energetics of flagellar rotation in bacteria. *Symposia of the Society for Experimental Biology*, **35**, 1–31.
- BERG, H. C. & PURCELL, E. M. (1977). Physics of chemoreception. *Biophysics Journal*, **20**, 193–219.
- BLOCK, S. M., SEGALL, J. E. & BERG, H. C. (1982). Impulse responses in bacterial chemotaxis. *Cell*, **31**, 2115–226.
- BLOCK, S. M., SEGALL, J. E. & BERG, H. C. (1983). Adaptation kinetics in bacterial chemotaxis. *Journal of Bacteriology*, **154**, 312–23.
- BROWN, D. A. & BERG, H. C. (1974). Temporal stimulation of chemotaxis in *Escherichia coli*. *Proceedings of the National Academy of Sciences of the United States of America*, **71**, 1388–92.

- CARSLAW, H. S. & JAEGER, J. C. (1959). *Conduction of Heat in Solids*, 2nd edn. Oxford, Oxford University Press.
- CRANK, J. (1956). *The Mathematics of Diffusion*. Oxford, Clarendon Press.
- CURRIE, D. J. (1984a). Phytoplankton growth and the microscale nutrient patch hypothesis. *Journal of Plankton Research*, **6**, 591–9.
- CURRIE, D. J. (1984b). Microscale nutrient patches: do they matter to the phytoplankton? *Limnology and Oceanography*, **29**, 211–14.
- ENGELMANN, T. W. (1894). Die Erscheinungsweise der Sauerstoff ausscheidung chromophyllhaltiger Zellen im Licht bei Anwendung der Bacterienmethode. *Pfluegers Archiv fuer die Gesamte Physiologie des Menschen und der Tiere*, **57**, 375–86.
- EPPLEY, R. W., HARRISON, W. G., CHISHOLM, S. W. & STEWART, E. F. (1977). Particulate organic matter in surface waters off Southern California and its relationship to phytoplankton. *Journal of Marine Research*, **35**, 671–96.
- FENCHEL, T. (1984). Suspended marine bacteria as a food source. In *Flows of Energy and Material in Marine Ecosystems*, ed. M. J. R. Fasham, pp. 301–15. New York, Plenum Press.
- FITT, W. K. (1985). Chemosensory responses of the symbiotic dinoflagellate *Symbiodinium microadriatica* (Dinophyceae). *Journal of Phycology*, **21**, 62–7.
- FRIEDMAN, M. M. & STRICKLER, J. R. (1975). Chemoreceptors and feeding in calanoid copepods (Arthropoda: Crustacea). *Proceedings of the National Academy of Sciences of the United States of America*, **72**, 4185–8.
- FROST, B. W. (1972). Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography*, **17**, 805–15.
- FROST, B. W. (1977). Feeding behaviour of *Calanus pacificus* in mixtures of food particles. *Limnology and Oceanography*, **22**, 472–91.
- FUHRMAN, J. A. (1981). Influence of method on the apparent size distribution of bacterioplankton cells: epifluorescence microscopy compared to scanning electron microscopy. *Marine Ecology – Progress Series*, **5**, 103–6.
- GAVIS, J. (1976). Munk and Riley revisited: nutrient diffusion transport & rates of phytoplankton growth. *Journal of Marine Research*, **34**, 161–79.
- GOLDMAN, J. C. (1984). Oceanic nutrient cycles. In *Flows of Energy and Material in Marine Ecosystems*, ed. M. J. R. Fasham, pp. 137–70. New York, Plenum Press.
- HARBISON, G. R. & MCALISTER, V. L. (1979). The filter-feeding rates and particle retention efficiencies of three species of *Cyclosalpa* (Tunicata, Thaliacea). *Limnology and Oceanography*, **24**, 875–92.
- HUTCHINSON, G. E. (1957). *A Treatise on Limnology*, 2 Vols. New York, John Wiley.
- JACKSON, G. A. (1980). Phytoplankton growth and zooplankton grazing in oligotrophic oceans. *Nature*, **284**, 439–41.
- KATONA, S. K. (1973). Evidence for sex pheromones in planktonic copepods. *Limnology and Oceanography*, **18**, 574–83.
- KOSHLAND, D. E., JR (1979). A model regulatory system: bacterial chemotaxis. *Physiological Reviews*, **59**, 811–62.
- LAWS, E. A., REDALJE, D. G., HAAS, L. W., BIENFANG, P. K., EPPLEY, R. W., HARRISON, W. G., KARL, D. M. & MARRA, J. (1984). High phytoplankton growth and production rates in oligotrophic Hawaiian coastal waters. *Limnology and Oceanography*, **29**, 1161–9.
- LEHMAN, J. T. & SCAVIA, D. (1982a). Microscale patchiness of nutrients in plankton communities. *Science*, **216**, 729–30.
- LEHMAN, J. T. & SCAVIA, D. (1982b). Microscale nutrient patches produced by

- zooplankton. *Proceedings of the National Academy of Sciences of the United States of America*, **79**, 5001-5.
- LI, W. K. W., SUBBA RAO, D. V., HARRISON, W. G., SMITH, J. C., CULLEN, J. J., IRWIN, B. & PLATT, T. (1983). Autotrophic picoplankton in the tropical ocean. *Science*, **219**, 292-5.
- MCCARTHY, J. J. & GOLDMAN, J. C. (1979). Nitrogen nutrition of marine phytoplankton in nutrient depleted waters. *Science*, **203**, 670-2.
- MACNAB, R. M. & HAN, D. P. (1983). Asynchronous switching of flagellar motors on a single bacterial cell. *Cell*, **32**, 109-17.
- MCMANUS, G. B. & FUHRMAN, J. A. (1986). Bacterivory in seawater studied with the use of inert fluorescent particles. *Limnology and Oceanography*, **31**, 420-6.
- MADIN, L. P. (1974). Field observations on the feeding behavior of salps (Tunicata: Thaliacea). *Marine Biology*, **25**, 143-7.
- MAGUE, T. H., FRIBERG, E., HUGHES, D. J. & MORRIS, I. (1980). Extracellular release of carbon by marine phytoplankton; a physiological approach. *Limnology and Oceanography*, **25**, 262-79.
- MALONE, T. C. (1980). Algal size. In *The Physiological Ecology of Phytoplankton*, ed. I. Morris, pp. 433-63. Berkeley, University of California Press.
- MITCHELL, J. G., OKUBO, A. & FUHRMAN, J. A. (1985). Microzones surrounding phytoplankton form the basis for a stratified microbial ecosystem. *Nature*, **316**, 58-9.
- MULLIN, M. M. (1980). Interactions between marine zooplankton and suspended particles. In *Particulates in Water*, ed. M. C. Kavanaugh & J. Leckie, pp. 233-41. Advances in Chemistry Series, no. 189. Washington, D.C., American Chemical Society.
- MULLIN, M. M., SLOAN, P. R. & EPPLEY, R. W. (1966). Relationship between carbon content, cell volume, and area in phytoplankton. *Limnology and Oceanography*, **11**, 307-11.
- MUNK, W. H. & RILEY, G. A. (1952). Absorption of nutrients by aquatic plants. *Journal of Marine Research*, **11**, 215-40.
- PAERL, H. W. & GALLUCCI, K. K. (1985). Role of chemotaxis in establishing a specific nitrogen-fixing cyanobacterial-bacterial association. *Science*, **277**, 647-9.
- PRICE, H. J. & PAFFENHÖFER, G.-P. (1986). Capture of small cells by the copepod *Eucalanus elongatus*. *Limnology and Oceanography*, **31**, 189-94.
- RUBENSTEIN, D. I. & KOEHL, M. A. R. (1977). The mechanism of filter feeding: some theoretical considerations. *American Naturalist*, **111**, 981-94.
- SCAVIA, D., FAHNENSTIEL, G. L., DAVIS, J. A. & KREIS, R. G. JR (1984). Small-scale nutrient patchiness: some consequences and a new encounter mechanism. *Limnology and Oceanography*, **29**, 785-93.
- SMAYDA, T. J. (1970). The suspension and sinking of phytoplankton in the sea. *Oceanography and Marine Biology Annual Review*, **8**, 353-414.
- SOURNIA, A. (1982). Form and function in marine phytoplankton. *Biological Review*, **57**, 347-94.
- SPERO, H. J. (1985). Chemosensory capabilities in the phagotrophic dinoflagellate *Gymnodinium fungiforme*. *Journal of Phycology*, **21**, 181-4.
- VARON, M. & SHILO, M. (1980). Ecology of aquatic bdellovibrios. *Advances in Aquatic Microbiology*, **2**, 1-48.
- WILLIAMS, P. J. L. & MUIR, L. R. (1981). Diffusion as a constraint on the biological importance of microzones in the sea. *Ecohydrodynamics*, ed. J. C. J. Nihoul, pp. 209-18. Amsterdam, Elsevier.